Botanical Journal of the Linnean Society, 2026, **00**, 1–13
https://doi.org/10.1093/botlinnean/boaf106

Original Article

Biogeographical patterns and compositional turnover of African vascular plants

Thinabakho R.L. Ncube[1,2], Jon C. Lovett[3,4,*], Helen M. De Klerk[2,5], Cang Hui[1,6]

[1]Biodiversity Informatics Unit, Department of Mathematical Sciences, Stellenbosch University, Stellenbosch 7602, South Africa
[2]Department of Geography and Environmental Studies, Stellenbosch University, Stellenbosch 7602, South Africa
[3]Herbarium Royal Botanic Gardens, Kew, Richmond TW9 3AE, United Kingdom
[4]School of Geography, University of Leeds, Leeds LS2 9JT, United Kingdom
[5]Centre for Geospatial and Computing Studies, School of Landscape Architecture, Lincoln University, Lincoln, Christchurch 7647, New Zealand
[6]National Institute for Theoretical and Computational Sciences, African Institute for Mathematical Sciences, Cape Town 7945, South Africa

[*]Corresponding author. Herbarium Royal Botanic Gardens, Kew, Richmond TW9 3AE, United Kingdom. E-mail: j.lovett@leeds.ac.uk

ABSTRACT

Exploring biogeographical patterns of species richness and compositional turnover, and their responses to environmental factors is essential for predicting biodiversity responses to future global change. However, our understanding at continental scales remains limited, especially in Africa, due to data gaps and uneven sampling. Using a model-based distribution dataset of >23000 vascular plant species in sub-Saharan Africa, we mapped species richness, estimated as species counts at site-level and explained using generalised additive modelling (GAM). Compositional turnover was mapped according to the nonmetric multidimensional scaling of between-site Jaccard dissimilarity and explained using multi-site generalised dissimilarity modelling (MS-GDM) of zeta diversity. We used deviance partitioning to identify potential underlying mechanisms of these biogeographical patterns. The results revealed species-rich pockets and compositional clusters of vascular plants across sub-Saharan Africa. The GAM fits the richness variation well (89.7% deviance explained) and identified mean annual precipitation (contributing 8.52% alone), mean annual temperature, fire frequency, human footprint, soil clay content, and topographic roughness as significant predictors. The MS-GDM explained 63% and 38.49% of the deviance in compositional turnover of narrow-range and widespread species, respectively. Geographical distance between sites contributed the most to the turnover of narrow-range species (9% deviance explained), whereas turnover of widespread species was affected by between-site differences in soil pH (7.55% deviance explained). Turnover of narrow-range and increasingly widespread species was driven mostly by environmental heterogeneity (14% and 10% deviance explained, respectively). These insights enhance our understanding of the processes shaping African plant biogeography and provide a foundation for predicting continental-scale biodiversity responses to future environmental change.

Keywords: African conservation; biogeographical patterns; biodiversity hotspots; compositional turnover; multi-site generalised dissimilarity; zeta diversity

INTRODUCTION

Exploring biogeographical patterns of species richness and compositional turnover, and how they differentially respond to environmental factors, is essential for predicting biodiversity responses to future global change amid accelerating land-use transformation and climate shifts. Although considerable progress has been made over the years to explain these patterns, no consensus has been reached. Most research has focused on richness variation in environmental, geographical, and trait spaces, describing site-level alpha diversity (Whittaker 1960, 1972, Nilsson *et al.* 1989, Nekola and White 1999, Vellend 2001, Qian and Ricklefs 2007, Kreft and Jetz 2007, Violle *et al.* 2011, Linder *et al.* 2012, Baker *et al.* 2025). Climatic, topographic, edaphic, and disturbance factors are often cited as major determinants of plant species richness (Cowling *et al.* 1996, Meentemeyer *et al.* 2001, O'Brien *et al.* 2003, Linder *et al.* 2012, Moura *et al.* 2016, Guitet *et al.* 2018, Mateo *et al.* 2022, Wedegärtner *et al.* 2022, Berihun Tenaw *et al.* 2024).

In particular, the effect of water–energy dynamics has been positively correlated with patterns of species richness, underscoring the pivotal role of water and energy availability in shaping plant diversity and distribution (O'Brien 1998, Hawkins *et al.* 2003, Kreft and Jetz 2007, Cramer and Verboom 2024, Bhattarai *et al.* 2025). However, these patterns are often contextual, complex, and nonlinear. For instance, at certain montane sites along a broad elevational gradient, species richness follows a unimodal trend, peaking at mid-elevations (Bruun *et al.* 2006, Gebrehiwot *et al.* 2019, Cirimwami *et al.* 2019).

Received: 4 March 2025; revised 16 October 2025; accepted 22 October 2025

In contrast, at other montane sites, tree species richness remains unchanged across a 2-km elevational range in plot samples (Lovett 1996, Lovett *et al.* 2006). An explanation for the unimodal pattern is that montane species are constrained by climatic and edaphic variations at higher elevations (Rahbek 1995, Körner 2007), though disturbance is also considered to play an important role (Lovett 1999). Physicochemical soil properties corresponding to nutrient availability and water-holding capacity reinforce species richness (Kammer *et al.* 2013), through plant growth and development, and consequently plant distributions (Zellweger *et al.* 2015). The effect of disturbance on richness involves an interplay between disturbance agents (biotic and abiotic) and species adaptive strategies (Mackey and Currie 2001, Miller *et al.* 2011, Veldman *et al.* 2015, Bond and Zaloumis 2016, Courtenay *et al.* 2024). Generally, species richness peaks at intermediate levels of disturbance (Grime 1973, Dornelas 2010, Weeks *et al.* 2023). On either end of the gradient, plant diversity is limited by competitive exclusion and species-specific regenerative constraints (Dornelas 2010).

In contrast to richness, the component of compositional turnover in biogeographical patterns describes assemblage differences between site-pairs, known as beta diversity (Whittaker 1960, 1972, Legendre *et al.* 2005). Biodiversity partitioning into alpha and beta diversity often contains missing unspecified information that prescribes overall assembly processes (stochastic versus deterministic processes) and differentiates the contributions to compositional turnover of narrow-range species and species that are more widespread (McGeoch *et al.* 2019, Deane *et al.* 2023). To provide a full set of biodiversity partition metrics, zeta diversity was proposed for quantifying multi-site compositional turnover (Hui and McGeoch 2014).

Beta compositional turnover of plants has mostly been associated with environmental heterogeneity (Palmer 2007, Stein *et al.* 2014, Bakker *et al.* 2023) and spatial connectivity (Wiens and Donoghue 2004, Harrison and Cornell 2008). Under heterogeneous environments, compositional turnover may be expected to reflect resource partitioning between species and geographical distance decay of compositional similarity (Ricklefs 1977, Dufour *et al.* 2006, Stein *et al.* 2014). Exploring multi-site zeta diversity can further tease apart potential drivers of compositional turnover for narrow-range species from increasingly widespread species (Latombe *et al.* 2018). Such analyses at continental scales particularly for African vascular plants are lacking, due largely to data discrepancies that include uneven geographical coverage and inconsistent sampling intensity, all of which constrain our understanding of biogeographical patterns at broad spatial scales.

Global plant diversity records are highly uneven, with African plant distributions poorly represented by herbarium botanical collections that form the basis of global data compilations (Küper *et al.* 2006, Ahrends *et al.* 2011). Consequently, we use a model-based distribution dataset (https://bien.nceas.ucsb.edu/) and map the biogeographical patterns displayed by more than 23,000 vascular plant species in sub-Saharan Africa. Specifically, we map in parallel the biogeographical patterns of species richness and compositional turnover at 20-km resolution and explore the influence of factors associated with climate, disturbance, and environmental heterogeneity for potentially explaining these patterns. Compositional turnover reflecting the gain and loss of largely narrow-range species to increasingly widespread species is differentiated using zeta diversity of different orders.

MATERIALS AND METHODS

Study area

The study was confined to mainland sub-Saharan Africa (Stuart *et al.* 1990, De Klerk *et al.* 2002, Ncube *et al.* 2025) encompassing approximately 24 million km^2 of land (Fenta *et al.* 2020), south of 20°N latitude, and between 20°W and 55°E longitude. Proximate islands were excluded as their ecological dynamics are expected to differ from those of the mainland (Whittaker *et al.* 2008). The continent is topographically complex, including a series of rift valleys (Lamptey 2021), with prominent peaks in the eastern (Kilimanjaro–5895 m), southern (Thabana-Ntlenyana–3482 m) (Maxted *et al.* 2004), and western and central (Cameroon–4040 m) regions (Cheek *et al.* 2021). The climate is highly variable, influenced by its broad latitudinal span across both the northern and southern hemispheres. This geographical range results in diverse climatic zones, ranging from arid, tropical, and temperate, contributing to the significant regional climatic variation (Hulme *et al.* 2001, Collins 2011). Approximately one-third of the region's soils are highly acidic (pH <5.5) (Pauw 1994) and suffer from infertility due to an interplay of socioeconomic, climatic, topographic, and geological factors (Tully *et al.* 2015). These soils tend to be rich in clay and silt but lack sufficient organic matter (Zingore *et al.* 2015, Bado and Bationo 2018). The high plant diversity (Klopper *et al.* 2007, Linder 2014, Catarino and Romeiras 2020) has been classified into major bioregions (Dinerstein *et al.* 2017, Ncube *et al.* 2025). Some of these bioregions are ecologically dynamic; for instance, large areas of the tropical and subtropical grasslands, savannas, and shrublands are flammable (Goldammer & De Ronde, 2004, Bond and Zaloumis 2016) and burn frequently (Archibald *et al.* 2010).

The plant dataset

A dataset of model-based species distributions for 23,189 native African vascular plant species was used in this study. We relied on predicted distributions due to data deficiencies in occurrence records of vascular plants in Africa (Küper *et al.* 2006). This dataset was generated as part of the Spatial Planning for Area Conservation in Response to Climate Change (SPARC) global project and compiled by the Botanical Information and Ecology Network (BIEN) group, together with external partners (https://bien.nceas.ucsb.edu/). It was obtained from online resources maintained by Conservation International. The predicted distributions were based on the MaxEnt model, which implemented spatially thinned and taxonomically verified occurrences, with climate and soil data (Merow *et al.* 2019). Each model prediction was converted into a binary raster of presence/absence using the 5th percentile threshold (Merow *et al.* 2019).

We converted the predicted distribution dataset into a site-by-species matrix for mapping and analysing the biogeographical patterns of the African vascular plants. We achieved this by mapping the binary raster of a species' distribution onto a 'fishnet' grid of 20 × 20-km cells, using Albers equal area conic projection (WGS1984) in ArcGIS v.10.8.1 with two standard parallels of 20°N and 23°S (ESRI 2020), which was then pruned to cover the entire spatial extent of mainland sub-Saharan Africa. The final matrix generated using the 'raster' R package (Hijmans 2020, R Core Team 2020) comprised 23,189 species and 55,815 sites. These species represent a substantial portion of the estimate of 47,714 native vascular plant species in sub-Saharan Africa (Qian *et al.* 2021).

Environmental predictors

We selected a range of environmental predictors to explain the patterns of species richness and compositional turnover. The overall choice of selection was informed by their relative importance and partial contributions in explaining species diversity for vascular plants (Gentry 1988, Lee and Chun 2016). These were categorised according to three key potential explanations: climate, disturbance, and environmental heterogeneity (Supporting Information Table S1).

We used four bioclimatic predictors (Fick and Hijmans 2017): mean annual temperature (bio1), maximum temperature of warmest month (bio5), mean temperature of warmest quarter (bio10), and mean annual precipitation (bio12) (worldclim.org). Fire frequency and human footprint were used in this study as proxies for fire and human disturbance, which are known to regulate African rangeland ecology. In the absence of herbivory data, we were not able to include a herbivory layer. However, fire can exert effects considered to be analogous to herbivory (e.g. African megafauna) on such systems (Bond and Keeley 2005, Mndela *et al.* 2025), so we selected fire to explore the intermediate disturbance trend in shaping plant diversity. The human footprint, which characterises the cumulative human pressure placed on the environment (Venter *et al.* 2018), was obtained from sedac.ciesin.columbia.edu. We used the fire data (Andela *et al.* 2019) and calculated fire frequency as the number of times a pixel burnt for the period 2003-2016. Specifically, fire layers on days of burn per year were resampled using the 'aggregate' tool in ArcGIS 10.8.1 (ESRI 2020) and then converted into binary maps; the number of times a pixel burned during the said period was counted. Fire frequency of a pixel is thus the number of counted fires in the pixel during the 14-year period. Environmental heterogeneity was represented by soil and topographic roughness. The soil data from SoilGrids (soilgrids.org) include physical and chemical properties of topsoil (<5 cm in depth), namely soil clay content, soil sand content, bulk density, soil pH, and soil organic carbon. Only topsoil properties were included as they can strongly affect plant growth and thus plant diversity (Rivera *et al.* 2014), while deep soil structures often are strongly correlated with properties of topsoil. For topographic roughness, the standard deviation of elevation within a grid cell (Irl *et al.* 2015) was computed from the digital elevation model (DEM) (srtm.csi.cgiar.org), using the 'terra' R package (Hijmans 2021).

Prior to the statistical analyses, all 12 predictors (Supporting Information Table S1) were screened for collinearity with a variance inflation factor (VIF), using the 'car' R package (Fox and Weisberg 2019). The criterion of VIF < 10 was used for removing predictors in a sequential fashion (Dormann *et al.* 2013), and this procedure retained 10 predictors for subsequent analyses: mean annual precipitation (MAP), mean annual temperature (MAT), soil clay content (SCC), soil sand content (SSC), bulk density (BD), soil pH (pH), soil organic carbon (SOC), topographic roughness (TR), human footprint (HFP), and fire frequency (FF) (Table S2). All environmental predictors were resampled according to a 'fishnet' grid of 20-km cells, using Albers equal area conic projection (WGS1984) in ArcGIS v.10.8.1 with two standard parallels of 20°N and 23°S (ESRI 2020), which were pruned to cover the entire mainland of sub-Saharan Africa.

Mapping richness and compositional turnover

Sub-Saharan vascular plant species richness was mapped as species counts at site level confined in a 20-km grid cell, using the 'vegan' R package (Oksanen *et al.* 2020). Compositional turnover was mapped using the nonmetric multidimensional scaling (nMDS) of the Jaccard dissimilarities (Jaccard 1900, Dexter *et al.* 2018), in the 'vegan' R package (Oksanen *et al.* 2020). The dissimilarity matrix of the turnover between site-pairs was decomposed into three dimensions ($k = 3$) to achieve an acceptable stress level <0.10 (Clarke 1993, Oksanen *et al.* 2020).

Normalised scores from the ordination axes were used to map the species composition in an RGB colour space, assigning red to axis 1, green to axis 2, and blue to axis 3, using the 'raster' R package (Hijmans 2020). The final maps were generated in ArcGIS v.10.8.1 (ESRI 2020).

Generalised additive modelling

To explain the variation of species richness, we used generalised additive modelling (GAM) (Hastie and Tibshirani 1990, Wood 2011) with the 10 environmental predictors. Concurvity was also calculated to detect generalized collinearity in GAMs (Wood 2017). The GAM was fitted with the restricted maximum likelihood (REML) method using the 'mgcv' R package (Wood 2017), with a negative binomial family distribution, to account for error overdispersion, and a log link function. Spatial autocorrelation in the model residuals was assessed both visually by directly inspecting the spatial distribution of model residuals and quantitively by calculating the Moran *I* metric using the 'ape' R package (Paradis and Schliep 2019). Both methods identified apparent spatial autocorrelation (Supporting Information Fig. S1) with Moran's $I = 0.09$ ($P < .001$). To account for this trend of spatial autocorrelation in the data, a longitude–latitude interaction was included in the GAM.

Upon addressing concurvity and spatial autocorrelation, the final GAM comprised fire frequency, human footprint, mean annual precipitation, mean annual temperature, soil clay content, and topographic roughness. Soil predictors, namely bulk density, soil pH, soil sand content, and soil organic carbon, were excluded because of high concurvity. Furthermore, the contribution of each predictor was estimated by comparing the relative drop in deviance explained between the full model and a reduced model with the focal predictor removed, with the smooth terms in the GAM fixed (Wood 2017). The contributions of joint effects from a set of predictors, representing climate, disturbance, and environmental heterogeneity, were also evaluated following the same procedure.

Multi-site generalised dissimilarity modelling

To explain compositional turnover of different orders, we used multi-site generalised dissimilarity modelling (MS-GDM) of zeta diversity (Hui and McGeoch 2014, Latombe *et al.* 2017). Zeta diversity of order *N* represents compositional similarity among *N* sites. Using a site-by-species matrix with dimensions 53,795 × 23,189, we computed zeta diversity for orders 1-15 with each order utilising 10,000 randomly selected site combinations. We produced zeta decline curves, illustrating zeta diversity estimates with increasing orders (Hui and McGeoch 2014, McGeoch *et al.* 2019). The same set of environmental predictors (Supporting Information Table S2) were used in the MS-GDM.

Due to the excessively large dimension of the site-by-species matrix, we ran MS-GDM with 1000 and 10,000 site combinations, to ensure the robustness of the response, as captured by the *I*-splines. We used the Simpson-equivalent normalised zeta diversity metric (ranging between 0 and 1) for zeta orders 2 and 5, to capture true turnover among sites (Latombe *et al.* 2018). The contribution of each predictor was estimated using the same method as above, by assessing the relative decrement of deviance explained between the full model and a reduced model for zeta orders 2 and 5 with 1000 site combinations. These analyses were all run using the 'zetadiv' R package (Latombe *et al.* 2017). All analyses performed in this study were conducted in R programming language v.3.6.3 (R Core Team 2020).

RESULTS

Biogeographical patterns of African vascular plants

The biogeographical patterns displayed by African vascular plants, represented by species richness and compositional turnover, were mapped across the study extent (Fig. 1). The counted species richness ranged from two to 5033 species in the 20-km grid cells (Fig. 1A). Species richness resulting in as low as two vascular plants, particularly in drylands, may be attributed to prolonged drought events and variable precipitation trends (Berg and McColl 2021, Smit *et al.* 2024), leading to the sparse vegetation cover of the present-day (Maestre *et al.* 2021). In contrast, higher levels of species richness were almost exclusively concentrated in eastern, central, western, and southern regions of Africa (Fig. 1A).

In eastern Africa, we found that species richness was notably high in the eastern Afromontane region, but only in the Democratic Republic of Congo, Rwanda, Burundi, Tanzania, and Malawi, with Ethiopia revealing lower richness levels in comparison. Although the Coastal Forests in eastern Africa are generally recognised for their high species richness, we observed relatively lower levels of species richness (<2941) along the entire extent (Fig. 1A). This discrepancy could potentially be influenced by the plant dataset used. Species richness was notably high in Gabon, Equatorial Guinea, and Cameroon in central Africa.

Similarly, regions in West Africa corresponding to the Guinean forests also exhibited high levels of richness. High species richness in southern Africa was shown to occur in regions that coincide with the locations of Maputaland-Pondoland-Albany and Cape Floristic Region (CFR) centres of diversity. A similar richness patterning has been shown in sub-Saharan Africa for plants (Barthlott *et al.* 1996, Myers *et al.* 2000, Linder 2001, La Ferla *et al.* 2002) and other taxa (Jenkins *et al.* 2013), but these are not necessarily congruent.

The spatial variation in the species composition is shown in Fig 1B (stress = 0.057). This turnover map configured sub-Saharan Africa into different compositional communities in which regions with similar species compositions were depicted by similar colour gradients. Compositional structures differed considerably

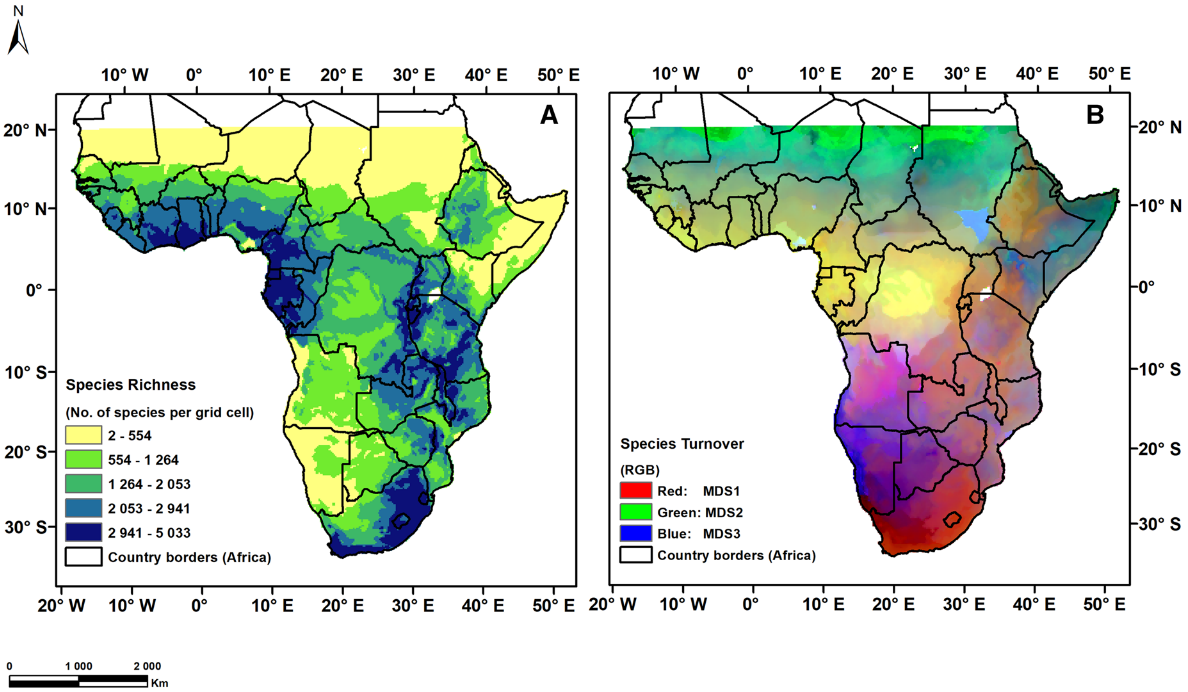

Figure 1. Biogeographical patterns of African vascular plants species diversity partitioned as A) species richness and B) species compositional turnover. Species richness was estimated as the number of plant species within a 20 km grid cell. Turnover in species composition, derived from the Jaccard dissimilarity measure, is represented by the normalised scores from the first three nMDS axes and visualised through the Red (R), Green (G), and Blue (B) colour channels. Sites dominated by a single colour indicate regions characterised by geographically distinct plant communities.

between northern and southern parts of the sub-continent. Plant assemblages appear similar throughout the central and western African ranges, coinciding with the African rainforest (Küper *et al.* 2004). In southern Africa (~25°S), the central interior and south-east regions exhibit relatively similar compositions with subtle transitions, whereas the southwest is more clearly differentiated, suggesting sharper transitions between these neighbouring plant communities.

Explanations of species richness

The final GAM, with spatial autocorrelation accounted for, explained 89.7% of the richness variation with fire frequency, human footprint, mean annual precipitation, mean annual temperature, soil clay content, and topographic roughness, all significant predictors ($P < .001$, potentially due to the high number of sites; Table 1). Consequently, the shape of the response and the contribution of each predictor are more informative ways to describe a predictor's potential role in explaining richness variation.

Table 1. Summary statistics of the final generalised additive model, explaining the variation in species richness and the individual effects of predictors associated with climate, disturbance, and environmental heterogeneity, respectively, partitioned as percentage of deviance explained by the GAM models.

Predictor	**edf**	**Deviance explained (%)**
s(FF)	5.17***	7.23
s(HFP)	6.934***	7.26
s(MAP)	13.783***	**8.52**
s(MAT)	10.679***	7.54
s(SCC)	9.829***	7.15
s(TR)	10.865***	7.36

Bold value represents the highest contribution. See Supporting Information Table S1 for acronyms of the predictors. The estimated degrees of freedom (edf) indicate the nonlinearity of the smoothed response, with greater values (>1) reflecting more nonlinear relationships.

$^{***}P < .001$.

Nonlinear local responses of species richness were identified with varied trends as the values of the six studied environmental gradients increased. Specifically, we found that increasing fire frequency was associated with a positive relationship with richness, peaking at sites that burned 14 times between 2003 and 2016 (Fig. 2A). This result suggests fire frequency likely contributes to the floristic variability in sub-Saharan Africa and is associated with species-rich floras adapted to burning, such as the CFR in the southern African Cape (He *et al.* 2016). At sites with low and high levels of human footprint on the environment, species richness was at its lowest, while it was higher at moderately disturbed sites (Fig. 2B). This trend is consistent with the intermediate disturbance hypothesis, which states that species richness is maximised at intermediate levels (Grime 1973).

There was a steeper positive response of species richness with mean annual precipitation up to 1100 mm (Fig. 2C), indicating the importance of water availability for recruitment opportunities in open patches of the drylands, leading to increased diversity. Beyond this threshold, we observed a fluctuating trend along higher levels of the gradient, reaching its highest in wetter sites receiving about 3000 mm of precipitation. Richness is maximised at this threshold due likely to the establishment and maintenance of broader refugia for the plant assemblages. Species richness gradually responded with increasing mean

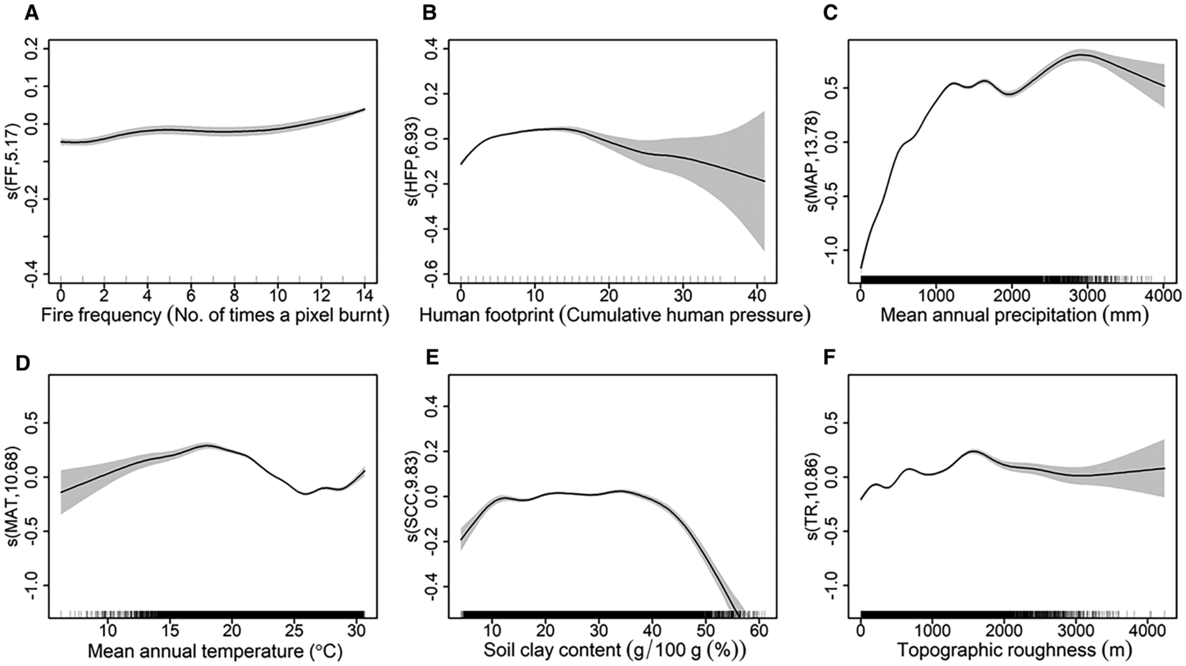

Figure 2. The generalised additive model response curves of the African vascular plant species richness to A, fire frequency; B, human footprint; C, mean annual precipitation; D, mean annual temperature; E, soil clay content; and F, topographic roughness. The y-axis represents the partial effect of each predictor, and values in parentheses represent the degrees of freedom per spline function. Tick marks above the x-axis indicate the data distribution of the observations for each predictor. The shaded error bands are the standard-error confidence intervals.

annual temperature, reaching its highest at approximately 18°C (Fig. 2D), suggesting plant diversity peaks at this moderate temperature. Beyond this temperature, there was a gradual negative trend in richness, which saw a slight positive effect at the higher end of the gradient between 25°C and 30°C. A low soil clay content exerted a steep positive effect on species richness up to 12 g/100 g (%), with a relative stabilisation above this point, which then became increasingly negative at a higher soil clay content (Fig. 2E). Along the topographic roughness gradient (Fig. 2F), richness exhibited a varied response, maximising at about 1800 m, after which it gradually and negatively affected at sites with a rougher topography >2000 m.

The deviance explained by each predictor is roughly even, ranging from 7.15% (soil clay content) to 8.52% (mean annual precipitation) (Table 1). The three categories of predictors also contributed relatively equally to the variation of species richness, with climate, explaining 9.39% of the deviance, being the top predictor cluster rather than disturbance and environmental heterogeneity (Table 2).

Table 2. Percentage of deviance explained by the GAMs and the MS-GDMs, partitioned according to predictors associated with climate, disturbance, and environmental heterogeneity, respectively.

	Category		
Model	**Climate**	**Disturbance**	**Environmental heterogeneity**
GAM	**9.39**[a]	7.35[b]	7.49[c]
MS-GDM (zeta order-2)	4.48[d]	2.53[e]	**13.7**[f]
MS-GDM (zeta order-5)	1.92[g]	1.42[h]	**10.16**[i]

Bold value represents the highest contribution. [a]Predictors in the model: mean annual precipitation, mean annual temperature. [b]Predictors in the model: fire frequency, human footprint. [c]Predictors in the model: soil clay content, topographic roughness. [d]Predictors in the model: mean annual precipitation, mean annual temperature. [e]Predictors in the model: fire frequency, human footprint. [f]Predictors in the model: bulk density soil pH, soil clay content, soil organic carbon, soil sand content, and topographic roughness. [g]Predictors in the model: mean annual precipitation, mean annual temperature. [h]Predictors in the model: fire frequency, human footprint. [i]Predictors in the model: bulk density soil pH, soil clay content, soil organic carbon, soil sand content, and topographic roughness.

Explanations of compositional turnover

The relationship between zeta diversity (average number of shared species) and zeta orders is captured by the zeta diversity decline curve (Fig. 3A). Zeta diversity declined according to an exponential form [Akaike's information criterion (AIC) = 1.207] (Fig. 3B) rather than power law (6.236), suggesting the lack of consistent non-stochastic processes that explain compositional community structures over the continent. There was a rapid decline in zeta diversity with increasing orders from 1 to 5, beyond the order of which the rate of zeta decline slowed to close to zero, suggesting hardly any species can be common in five or more randomly selected sites.

The MS-GDM, fitted for 10,000 site combinations, explained 63.3% of order-2 zeta diversity variation and 38.49% of order-5 zeta diversity variation, respectively. For both zeta orders, of the 11 environmental predictors including geographical distance we found that between-site differences in soil pH and geographical distance had the strongest effect on compositional turnover (Fig. 4). The between-site difference in mean annual temperature ranked third according to the magnitudes of corresponding *I*-spline response curves and also exerted an influential effect (Fig. 4B), though weaker for zeta order 5 (representing turnover by more widespread species). In considering the contribution of these three predictors to turnover across the low, medium, and high ranges (Tables 3 and 4), we found that changes in pH at lower and higher ends of the gradient significantly affected the compositional turnover at zeta order-2. By contrast, at order-5, the turnover was more sensitive to the entire pH gradient corresponding to acidic-neutral-alkaline soils. Compositional turnover was also strongly affected but the geographical distance at low to high ranges for zeta order-2, and low and high distances at order-5. Moderate mean annual temperature ranges had a significant impact on the turnover for both orders. All other predictors for both orders of zeta had little to no influence on compositional turnover. Using 1000 site combinations revealed similar trends (Supporting Information Fig. S2).

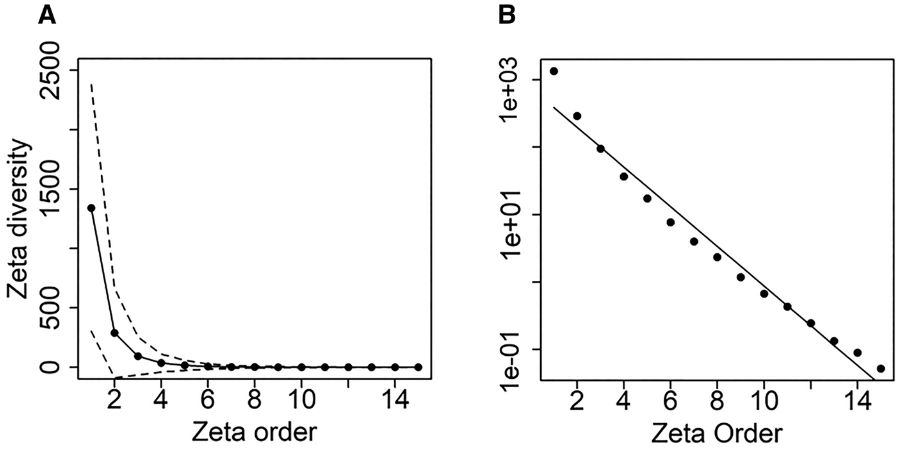

Figure 3. Zeta diversity decline of African vascular plants fitted using 23,189 species with 10,000 random site combinations for orders 1–15. A, the solid line reflects the quantified relationship between the zeta diversity and the different orders of zeta, bounded by the zeta values of the standard deviation. B, the form of the decline, corresponding to the exponential fit.

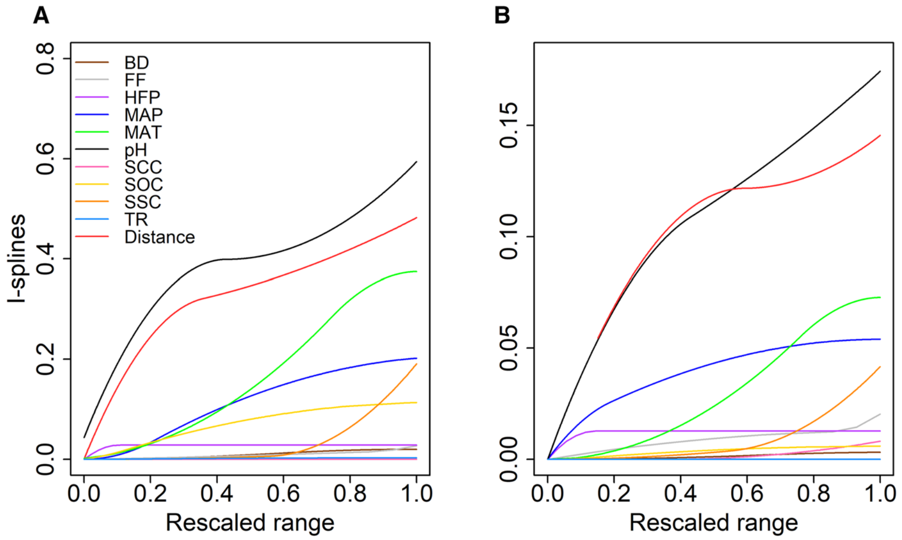

Figure 4. *I*-splines generated by MS-GDM computed for 10,000 site combinations, reflecting the relative importance of 10 environmental predictors and geographical distance in driving compositional turnover for zeta orders-2 (A) and -5 (B). Note, all predictors are rescaled to between 0 (minimum) and 1 (maximum) for illustration. The minimum value for Distance was set to zero to indicate the minimum average distance between site pairs in the random combinations. The *y*-axis indicates partial ecological dissimilarity, with the slope of a predictor at a particular horizontal value representing the local sensitivity of compositional turnover to the change in this predictor at this particular value; the right-end height represents the magnitude of contribution of a predictor. The key in A also corresponds to B, reflecting the 10 predictors and geographical distance.

Table 3. MS-GDM summary statistics for zeta order-2 reporting on the *I*-splines estimates and individual effects of predictors associated with climate, disturbance, and environmental heterogeneity, respectively; these effects were partitioned as the percentage deviance explained by the multi-site generalised dissimilarity models for zeta orders-2 reflecting compositional turnover predominately driven by the gain and loss of narrow-range species.

Predictor	**Estimates**			**Deviance explained (%)**
	Low	**Mid**	**High**	
BD	0.0000	0.0201	0.0000	0.08
FF	0.0056	0.011	0.0108$^{\#}$	0.02
HFP	0.0288***	0.0000	0.0000	0.01
MAP	0.0000	0.2060***	0.0000	0.90
MAT	0.0005	0.3743***	0.0000	3.61
pH	0.3989***	0.0000	0.2503***	6.36
SCC	0.0000	0.0000	0.0000	0.003
SOC	0.0055	0.1083***	0.0000	0.02
SSC	0.0000	0.011	0.2045***	0.82
TR	0.0000	0.0031	0.0000	0.00
Distance	0.2930***	0.0782***	0.1111***	**9.00**

Bold value represents the highest contribution.
$^{***}P < .001$; $^{\#}P < .1$.

Table 4. MS-GDM summary statistics for zeta order-5 reporting on the *I*-splines estimates and individual effects of predictors associated with climate, disturbance, and environmental heterogeneity, respectively are captured by the deviance explained; these effects were partitioned as the percentage deviance explained by the multi-site generalised dissimilarity models for zeta order-5 reflecting compositional turnover of increasingly widespread species.

Predictor	**Estimates**			**Deviance explained (%)**
	Low	**Mid**	**High**	
BD	0.0000	0.0032	0.0000	0.05
FF	0.0106*	0.0021	0.0077*	0.86
HFP	0.0127***	0.0000	0.0000	0.63
MAP	0.0191***	0.0349***	0.0000	0.23
MAT	0.0000	0.0728***	0.0000	1.67
pH	0.0884***	0.0498***	0.0425***	**7.55**
SCC	0.0000	0.0000	0.0089	0.00
SOC	0.0000	0.006	0.0000	0.05
SSC	0.0000	0.0069	0.0384***	1.78
TR	0.0000	0.0000	0.0000	0.00
Distance	0.1217***	0.0000	0.0238**	0.90

Bold value represents the highest contribution.
$^{***}P < .001$; $^{**}P < .01$; $^{*}P < .05$.

For computational efficiency we presented the relative difference in deviance explained between the full and the reduced models for 1000 site combinations. Specifically, the contributions of each predictor of order-2 zeta diversity ranked geographical distance at the top (9%), followed by soil pH (6.36%) and mean annual temperature (3.61%) (Table 3). This suggests that compositional turnover due to the gain and loss of largely narrow-range species is constrained by spatial limiting processes in plant communities. In contrast, compositional turnover reflecting increasingly widespread species (zeta order-5) identified between-site differences in soil pH as the top driver (7.55%), followed by between-site differences in soil sand content (1.78%) and mean annual temperature (1.67%) (Table 4). Regarding joint effects, environmental heterogeneity was identified as the underlying mechanism of compositional turnover for both zeta orders-2 and -5, explaining 13.7% and 10.16% of the deviance, respectively (Table 2).

DISCUSSION

Our study has shown that the biogeographical patterns of African plants exhibit spatial variation in species richness and species compositional turnover. In common with other ecological studies, we found that species richness is driven primarily by climate, with local responses varying according to fire frequency, human footprint, mean annual precipitation, mean annual temperature, soil clay content, and topographic roughness gradients. The turnover in species composition for both narrow-range and increasingly widespread species was due largely to environmental heterogeneity, with between-site differences in soil pH, geographical distance and mean annual temperature emerging as important gradients. These findings underscore the need to consider both climatic and edaphic heterogeneity in conservation planning, as they shape not only the limits of species packing but also local species composition. Identifying regions with high species diversity and strong compositional turnover can help prioritise areas for designing resilient conservation networks capable of sustaining biodiversity under accelerating climate and land-use change.

Patterns of richness and turnover

High species richness was concentrated in four major regions that coincided with recognised centres of plant biodiversity within the eastern Afromontane region in the east of Africa, Guinean forests in west and central Africa, and Maputaland-Pondoland-Albany and CFR in southern Africa. However, these patterns may alter under future global environmental change, with rising temperatures, increasing weather extremes, and variable precipitation trends. The current plant species richness particularly in eastern and southern montane regions of sub-Saharan Africa is predicted to decline by the end of the century (Vidal Junior *et al.* 2025).

Spatial incongruencies in the pattern of species richness in some regions based on existing demarcation (Barthlott *et al.* 1996, Myers *et al.* 2000, Linder 2001, La Ferla *et al.* 2002) are likely due to data deficiency (Küper *et al.* 2006, Ahrends *et al.* 2011). For instance, Linder (2001) identified central Angola as a region with high richness, while Myers *et al.* (2000) in their hotspots analysis did not recognise the east coast of southern Africa as a species-rich region.

The spatial depiction of the pattern of species turnover at 20-km resolution (through the first three nMDS axes of the normalised scores) revealed in greater detail a geographically distinct composition across the study extent (Fig. 1B). Pronounced dissimilarity between sites can be observed, indicated by spatial discontinuities in the species composition that broadly align with existing major African bioregions (Supporting Information Fig. S3), across the tropical and temperate latitudes. This configured pattern supports the existing view of the African vegetation on a continental scale as a spatially heterogeneous ecological entity (White 1983).

Explanations of species richness

Local climatic gradients of mean annual precipitation and mean annual temperature explained a greater proportion of the variation in model species richness than disturbance and environmental heterogeneity. The role of climate in driving patterns of species richness is well established (Wright 1983, Currie 1991, O'Brien 1998, Hawkins *et al.* 2003, Becerra 2016). Specifically, water-energy dynamics (e.g. mean annual precipitation) are thought to support a greater number of plant species (Pausas and Austin 2001, Fei *et al.* 2018), while climate and anthropogenic factors, together with co-limitation factors from biotic interactions and feedbacks, have been identified as dominant drivers of tree species diversity (Liang *et al.* 2022). In view of the differential responses of species richness to various environmental gradients, our results highlight the importance of fire frequency, human impact, mean annual precipitation, mean annual temperature, soil clay content, and topographic roughness in shaping plant diversity.

We found a positive relationship between fire frequency and plant species richness. This suggests that the highly flammable vegetation of sub-Saharan Africa, which coincides with its largest bioregion (Ncube *et al.* 2025), the tropical and subtropical grasslands, savannas, and shrublands (Supporting Information Fig. S3), is shaped and mediated by frequent fire events. This aligns with established ecological understanding that fire promotes plant diversity in fire-prone environments by maintaining open canopies, reducing above-ground biomass, and increasing microhabitat variability (Bond and van Wilgen 1996, Bond and Midgley 2012, Bond and Keane 2017, Ncube 2019). These processes facilitate niche partitioning among ground-layer species, including herbs and grasses that coevolved with frequent burning over evolutionary timescales (Bond and Zaloumis 2016). For instance, in a miombo ecosystem in Zambia, Wieczorkowski *et al.* (2024) found that fire-maintained regimes, defined by both frequency and seasonality, support higher species richness compared to fire exclusion treatments. Their long-term experimental study demonstrated that regular burning, particularly during the late dry season, promotes the coexistence of grass species characterised by distinct functional types, such as C4 grasses, sedges, and geoxyles.

Our anticipation that richness variation is maximised at intermediate disturbance was fulfilled by the effect of the human footprint. Comparable results have been found previously (Mayor *et al.* 2012, Yuan *et al.* 2016). This trend further indicates that disturbed sites subjected to either minimal or intense cumulative human pressure may limit plant diversity, which in turn jeopardises the diversity of other taxa including birds and invertebrates that depend on plant communities for habitat and resources. This aligns with the findings from previous studies which have particularly shown declining trends in bird (Tripathi *et al.* 2019, Mariano-Neto and Santos 2023) and invertebrate (Jew *et al.* 2015) diversity due to habitat fragmentation and loss.

Along the mean annual precipitation gradient, our result suggests that sites with higher precipitation tend to support a greater number of species, likely those of woody life forms. In that, increased water availability tends to facilitate the growth and survival of trees and shrubs species by reducing water stress and enhancing photosynthetic activity. As a result, wetter conditions lead to a greater woody biomass and overall ecosystem productivity. This trend is consistent with earlier research, reinforcing the importance of water-energy dynamics in promoting plant diversity (O'Brien 1993, Linder 2001, Davies *et al.* 2023, Cramer and Verboom 2024). For example, O'Brien (1993) showed that species richness of southern Africa's woody species increases significantly with precipitation.

The unimodal effect observed in the richness-temperature relationship suggests that temperature exerts a non-linear influence on plant diversity, with peak richness occurring at intermediate temperatures. This trend supports the notion that moderate temperatures may provide optimal conditions for the coexistence of diverse plant species, likely due to a balance between enhanced metabolic activity and efficient water use, which in tandem foster higher growth rates, resource availability, and niche differentiation. Temperatures exceeding 18°C reflect thermal tolerances in plants (García-Palacios *et al.* 2018). Specifically, increased heat stress and evapotranspiration rates may act as physiological limiting factors for water-dependent species. Interestingly, when temperatures depart from 25°C, we found that a higher temperature gradient can also promote species richness. This probably represents drought-adapted species that thrive under higher temperature regimes. This pattern underscores the importance of energy availability in regulating plant diversity, and is in line with previous studies (O'Brien 1998, Gaston 2000, Zhang *et al.* 2021).

The relationship between soil texture and richness variation is typically nuanced and interlinked with other environmental gradients such as climate-driven soil moisture variability and species-specific root traits, which influence root growth and subsequently distributions (Keiluweit *et al.* 2018). The observed trend between species richness and soil clay content reported here suggests that multiple plant species can coexist in soils with lower clay content, which are typically sandier and better drained. These conditions generally support herbaceous and stress-tolerant species that are well-adapted to resource-limited environments such as those of arid and semi-arid climates (Lal 1987, Wang *et al.* 2025). In such settings niche partitioning is more likely to occur, as species differentiate by optimising water use and available nutrients, promoting species richness. In contrast, a higher clay content characteristically resource-rich ∼>40 g/100 g (%), likely imposes a limitation on the richness variation due to competitive exclusion (Fig. 2E) (Medinski *et al.* 2010).

The relationship between the topographic roughness and the richness variation suggests montane regions characterised by rugged terrain ∼1800 m in altitude may promote higher plant diversity by increasing the availability of niche space. In that, a rugged terrain at moderate elevation reinforces heterogeneous environments coinciding with climatic and edaphic variations. Similar trends have been reported in various mountainous and topographically diverse ecosystems (Hortal *et al.* 2009, Irl *et al.* 2015).

Explanations of compositional turnover

Compositional turnover, measured through both lower (zeta order-2) and higher (zeta order-5) orders, was largely explained by environmental heterogeneity. This result is in line with the growing body of research linking species turnover with environmental variations (Nekola and White 1999, Dias *et al.* 2021). Further, the observed pattern in compositional turnover can be attributed in part to Africa's vast geographical extent, which is characteristically diverse in a biogeographical sense. These broad-scale environmental variations give rise to geographically distinct compositions that encompass the unique African plant assemblages.

Specifically, we found that the turnover of narrow-range species composition was strongly affected by the increasing geographical distance. A possible explanation of this trend can be attributed to the distance decay of similarity phenomenon, which postulates that the similarity of plant communities decreases with geographical distance (Soininen *et al.* 2007, La Sorte *et al.* 2008, Hui and McGeoch 2014). Turnover for increasingly widespread species was sensitive to the variation in soil pH. This is because highly acidic or alkaline soils can restrict plant growth and subsequently distributions, through nutrient deficiencies (Kidd and Proctor 2001) and a reduced water supply to the roots (Lopes *et al.* 2021). Soil pH-driven compositional turnover has been reported (Marage and Gégout 2009, Eibes *et al.* 2021). In addition, we showed that turnover of both narrow-range and increasingly widespread species was also affected by variation in mean annual temperatures in regions with moderate climates, possibly due to physiological tolerances, corresponding to species' climatic niche affinity (Harrison *et al.* 2020, Smithers *et al.* 2020).

CONCLUSION

At the scale of mainland sub-Saharan Africa, the spatial configurations of the biogeographical patterns provided a continental overview of plant diversity, characterising species richness at each site and compositional dissimilarity among sites. Our richness pattern supported the existing delimitation of key biodiversity hotspots while also identifying previously unrecognised areas of high species richness. The observed spatial incongruencies with existing richness patterns suggest discrepancies among underlying datasets and underscore the need to integrate multiple data sources to improve reliability and capture more nuanced variation in plant diversity. By applying zeta diversity to quantify species compositional turnover, we were able to disentangle possible mechanisms underlying well-configured turnover patterns driven by narrow-range versus increasingly widespread species.

Overall, the biogeographical variations in species richness and compositional turnover were best explained by the climate and environmental heterogeneity, respectively. Local responses of species richness were largely nonlinear, exhibiting varied positive and unimodal relationships with fire frequency, human footprint, mean annual precipitation, mean annual temperature, soil clay content, and topographic roughness. In contrast, turnover in species composition was most sensitive to the geographical distance and soil pH gradients for zeta orders-2 and -5, respectively. When combined with existing spatial data, these findings offer valuable insights for biodiversity conservation across Africa by informing regional assessments of species-rich areas, zones of high compositional turnover, and the mechanisms underlying these patterns –an increasingly important task in the face of global environmental change.

ACKNOWLEDGEMENTS

The views and opinions expressed are those of the authors only and do not necessarily reflect those of the European Union or the European Commission. Neither the EU nor the EC can be held responsible for them. We are grateful to the Global Environment Facility SPARC project grant GEF-5810 for compiling the plant distribution dataset used in this analysis, and to the herbaria that contributed plant distribution data to the SPARC project. Without the invaluable long-term and painstaking work of herbaria carefully curating and identifying collections this type of analysis would not be possible: A, AAH, AAS, AAU, ABH, ACOR, AD, AFS, AJOU, AK, AKPM, ALCB, ALU, AMES, AMNH, AMO, ANA, ANSM, AQP, ARAN, ARM, AS, ASDM, ASU, AUT, AV, AWH, B, BA, BAA, BAB, BABY, BACP, BAF, BAFC, BAI, BAL, BARC, BBB, BBS, BC, BCMEX, BCN, BCRU, BEREA, BESA, BG, BH, BHCB, BIO, BISH, BKF, BLA, BM, BO, BOL, BOLV, BONN, BOON, BOTU, BOUM, BPI, BR, BREM, BRI, BRIT, BRLU, BSB, BUT, C, CAMU, CAN, CANB, CANU, CAS, CATA, CATIE, CAY, CBG, CBM, CDA, CDBI, CEN, CEPEC, CESJ, CGE, CGMS, CHAM, CHAS, CHR, CHRB, CHSC, CIB, CICY, CIIDIR, CIMI, CLEMS, CLF, CMM, CNH, CNS, COA, COAH, COCA, COFC, COI, COL, COLO, CONC, CORD, CP, CPAP, CPUN, CR, CRAI, CRP, CS, CSU, CSUSB, CTES, CTESN, CU, CUVC, CUZ, CVRD, DAO, DAV, DBG, DLF, DNA, DS, DUKE, DUSS, E, EA, EAC, EAN, ECON, ECU, EIF, EIU, EKY, EMMA, ENCB, ER, ERA, ESA, ETH, F, FAA, FAU, FAUC, FCO, FCQ, FEN, FHO, FI, FLAS, FLOR, FM, FR, FSU, FTG, FUEL, FULD, FURB, G, GAT, GB, GDA, GENT, GEO, GH, GI, GLM, GMDRC, GMNHJ, GOET, GRA, GUA, GZU, H, HA, HAL, HAM, HAMAB, HAS, HAST, HASU, HB, HBG, HBR, HCIB, HGI, HGM, HIB, HIP, HO, HPL, HRCB, HRP, HSC, HSS, HU, HUA, HUAA, HUAL, HUAZ, HUCP, HUEFS, HUEM, HUJ, HUSA, HUT, HYO, IAA, IAC, IAN, IB, IBGE, IBK, IBSC, IBUG, ICEL, ICESI, ICN, IEA, IEB, ILL, ILLS, INB, INEGI, INM, INPA, IPA, IPRN, IRVC, ISC, ISKW, ISU, IZAC, IZTA, JBAG, JBGP, JCT, JE, JEPS, JOTR, JROH, JUA, JYV, K, KIEL, KMN, KMNH, KOR, KPM, KSTC, KTU, KU, KUN, KYO, L, LA, LAE, LAF, LAGU, LBG, LCR, LD, LE, LEB, LI, LIL, LINC, LINN, LISC, LISI, LISU, LL, LMS, LOJA, LOMA, LP, LPAG, LPB, LPD, LPS, LSU, LSUM, LTB, LTR, LYJB, M, MA, MACF, MAF, MAK, MARS, MARY, MASS, MB, MBK, MBM, MBML, MCNS, MEL, MELU, MEN, MERL, MEXU, MFU, MG, MGC, MHA, MICH, MIN, MISS, MJG, MNHM, MNHN, MO, MOL, MPN, MPU, MSB, MSC, MSUN, MU, MUB, MVFA, MVFQ, MVJB, MVM, MW, MY, N, NA, NAC, NAS, NCSC, NCU, ND, NE, NH, NHM, NHMC, NHT, NLH, NMNL, NMR, NMSU, NSW, NU, NUM, NWOSU, NY, NZFRI, O, OBI, OCLA, ODU, OKL, OKLA, OS, OSA, OSC, OSH, OULU, OXF, P, PACA, PAMP, PAR, PASA, PDD, PE, PEL, PERTH, PEUFR, PGM, PH, PKDC, PMA, POM, PORT, PR, PRC, PRE, PSU, PY, QCA, QCNE, QMEX, QRS, R, RB, REG, RELC, RFA, RIOC, RM, RNG, RSA, RYU, S, SACT, SALA, SAN, SANT, SAPS, SASK, SAV, SBBG, SBT, SCFS, SD, SDSU, SEL, SEV, SF, SFV, SGO, SI, SING, SIU, SJRP, SJSU, SLPM, SMDB, SNM, SOM, SP, SPF, SRFA, STL, STU, SUU, SUVA, SVG, SZU, TAES, TAI, TAIF, TALL, TAM, TAMU, TAN, TEF, TENN, TEPB, TEX, TI, TKPM, TNS, TO, TOYA, TRA, TRH, TROM, TRT, TU, TUB, TULS, U, UADY, UAM, UAS, UB, UBT, UC, UCR, UCS, UCSB, UCSC, UEC, UESC, UFG, UFMA, UFMT, UFP, UFRJ, UFRN, UFS, UGDA, UH, UI, UJAT, ULM, ULS, UME, UMO, UNA, UNCC, UNEX, UNITEC, UNL, UNM, UNR, UNSL, UPCB, UPNA, UPS, US, USAS, USF, USJ, USM, USNC, USP, USZ, UT, UTC, UTEP, UU, UV, UVIC, VAL, VDB, VEN, VIT, VMSL, VT, W, WAG, WELT, WII, WIS, WMNH, WOLL, WS, WTU, WU, XAL, YAMA, Z, ZMT, ZSS, and ZT.

SUPPLEMENTARY DATA

Supplementary data are available at *Botanical Journal of the Linnean Society* online.

CONFLICT OF INTEREST

The authors have no competing interests.

FUNDING

T.R.L.N. is grateful to the National Research Foundation of South Africa (NRF) for the PhD scholarship; C.H. is supported by the NRF (grant 89967) and the European Union's Horizon Europe Research and Innovation Programme (B3—Biodiversity Building Blocks for policy, ID 101059592); J.C.L. was supported by the Global Environment Facility SPARC project grant GEF-5810.

DATA AVAILABILITY

The plant dataset was obtained from (https://bien.nceas.ucsb.edu/). Environmental data is available from various open sources, including (https://worldclim.org/) for climate surface layers and soil properties (https://soilgrids.org/). The topographic roughness was derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) (srtm.csi.cgiar.org). Fire data was obtained from the Global Fire Atlas: Andela N, Morton DC, Giglio l, et al., Global fire atlas with characteristics of individual fires, 2003 –2016. ORNL DAAC, Oak Ridge, Tennessee, USA, 2019.

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