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Journal of Biogeography   WILEY

Plant height and lifespan predict range size in southern African grasses

Aluoneswi C. Mashau[1,2] | Gareth P. Hempson[2] | Caroline E. R. Lehmann[2,3,4] |
Maria S. Vorontsova[5] | Vernon Visser[6,7] | Sally Archibald[2]

[1]National Herbarium, South African National Biodiversity Institute (SANBI), Pretoria, South Africa

[2]Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[3]Tropical Diversity, Royal Botanic Garden Edinburgh, Edinburgh, UK

[4]School of GeoSciences, University of Edinburgh, Edinburgh, UK

[5]Comparative Plant and Fungal Biology, Royal Botanic Gardens Kew, Richmond, UK

[6]SEEC – Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Rondebosch, South Africa

[7]African Climate and Development Initiative, University of Cape Town, Rondebosch, South Africa

Correspondence
Aluoneswi C. Mashau, National Herbarium, South African National Biodiversity Institute (SANBI), Private Bag X101, Pretoria, 0184, South Africa.
Email: c.mashau@sanbi.org.za

Abstract

Aim: To understand the geographical distribution of grasses in sub-Saharan Africa with reference to key plant traits thought to affect range size in this family (Poaceae). Specifically, to test hypotheses on the importance of plant height and lifespan in determining range size and invasion potential in the context of their evolutionary history.

Location: Sub-Saharan Africa.

Taxon: Poaceae.

Methods: The range sizes of 757 grass species native to southern Africa were estimated for the sub-Saharan African region from geo-referenced herbarium records using the alpha hull function. Phylogenetic generalised least squares models and linear mixed effects models were fitted to test whether grass range size was related to plant height and lifespan. Tribe-level relationships between range size and plant height were assessed with linear models. For species introduced to other continents, generalised linear mixed effects models were fitted to test whether invasiveness was related to native range size, plant height and lifespan. Differences in native range size among species in four invasion-related categories were assessed with linear mixed effects models.

Results: Grass range sizes are larger for taller species and for species with shorter lifespans. The relationship between plant height and range size varies widely among tribes, with some range-restricted tribes having a non-significant effect on plant height. Grasses with larger native range sizes and shorter lifespans are more likely to become invasive after being introduced to other continents. Grass species introduced to other continents have larger native range sizes than those that have not, and native range size increases along the introduced-naturalised-invasive continuum.

Main conclusions: The increased dispersal opportunities of annual-biannual grasses appear to have a greater positive effect on range size than do the longer generation times of perennial grasses. Grass height has and continues to be an important driver of grass biogeography, with implications for understanding the spread of certain grass tribes over the Miocene. Factors that promote large native range sizes are also likely to increase the probability of a species becoming invasive.

1 | INTRODUCTION

The geographical area a species occupies is a complex product of environmental, competitive, geographic and biological factors (Brown et al., 1996; Gaston, 2003; Morueta-Holme et al., 2013; Sheth et al., 2020). Within even a single genus, species can vary in their range size from narrow endemics to almost cosmopolitan distributions (Fish et al., 2015). Exploring the determinants and ecological consequences of variation in range size has been the subject of research for decades (Brown et al., 1996) to gain insight into the evolutionary origins and ecological characters of species and has also been used to explain species richness (Dexter & Chave, 2016). Moreover, human activities impact all parts of the Earth, and range size is important for assessing extinction risk and adaptation capacity (Manne et al., 1999; Staude et al., 2020) and, conversely, the potential for species to become naturalised and invasive when introduced to new areas (Hui et al., 2011; Procheş et al., 2012; Pyšek et al., 2009).

In plants, range size is the outcome of multiple underlying factors including intrinsic ecological limits such as propagule dispersal potential and propagule establishment success, and relatedly, the degree of genetic isolation of different populations (Estrada et al., 2015; Sonkoly et al., 2017). While the ability to disperse over long distances is one mechanism that can generate large range sizes, species with wide distributions may also have broader niche breadths, allowing them to be competitive across a diverse range of habitats and environments (Slatyer et al., 2013). Moreover, large range sizes can also be a consequence of low speciation rates (Gaston, 1998). Each of these processes such as dispersal potential, establishment success, and speciation rates are the result of multiple organismal traits, with range size an emergent property of these interacting processes (Figure 1). Interestingly, many of the characters used to explain species range sizes are often explored as explanations for invasive species success (Blackburn et al., 2011), as species invasions necessitate an increase in the organisms' existing range size. Studies have indicated that, once introduced, factors shaping plant reproduction and dispersal characteristics are likely as important as habitat suitability and establishment success in determining whether a species will become invasive (Pyšek et al., 2009). Supporting these ideas, Hui et al. (2011) demonstrated that invasive Acacias are more likely to have larger native range sizes in Australia than non-invasive species.

There is much interest in how habitat suitability determines range size, and this is also important for predicting how range sizes will vary into the future as a product of environmental change. For example, the frequently observed relationship between latitude and range size (Rapoport's rule; Stevens, 1989) has been explained with reference to the larger seasonal variation experienced at higher latitudes that enable organisms to succeed in a wider range of environments (Morin & Lechowicz, 2011; Morueta-Holme et al., 2013). Other studies have found that biome area, or the extent of suitable habitat, is
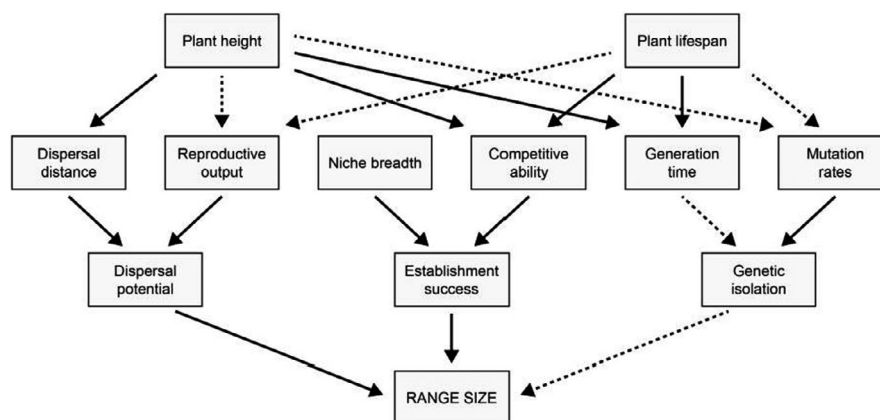
FIGURE 1 Conceptual diagram showing the various mechanisms by which grass height and lifespan could affect range size. Solid lines represent positive relationships and dashed lines represent negative relationships. Plant height can increase range size by increasing dispersal potential, but decrease it through reduced relative reproductive output and thus reduced dispersal opportunities. Likewise, plant height increases competitive ability, which increases establishment success and can lead to larger range sizes, but long generation times and slow mutation rates will increase genetic isolation and promote speciation, which results in smaller range sizes. Moreover, short-lived plants are expected to have larger range sizes because they have higher reproductive output and dispersal potential, but they also have low competitive ability and short generation times, which might decrease establishment success and increase genetic isolation and speciation respectively, resulting in overall lower range size. Therefore, the slope of the relationship between plant height, lifespan and range size helps to determine which of these processes is more important for explaining patterns in the grass family. These are not the only traits or mechanisms affecting range size; for a comprehensive discussion, please see Sheth et al. (2020)

an important determinant of range size (Gallagher, 2016; Sheth et al., 2020). However, Baselga et al. (2012) found that while the environment was particularly important for determining range size in widespread species, dispersal limitation was a more important control on range size in narrowly distributed species. Wind-pollination is also thought to increase plant range sizes, because long-distance pollen transport enables new populations on the edge of the species range to remain in genetic contact with range centres, while also diminishing dependence on specific animal pollinators (Gallagher, 2016). Relatedly, self-pollination is a further mechanism shown to promote range size in plants, likely due to the higher establishment success in new environments when freed from the constraint of mate limitation (Grossenbacher et al., 2015). A recent meta-analysis by Sheth et al. (2020) of the factors predicting geographic range size in plants showed niche breadth to be consistently important, and although evidence for the role of other proposed drivers such as dispersal ability was more varied, concluded that both intrinsic and extrinsic factors will inevitably shape the edge of species distribution ranges.

Plant height, through impacting both ecological (Diaz et al., 2016; Westoby, 1998) and evolutionary processes (Boucher et al., 2017; Lanfear et al., 2013) is likely key in determining a species' geographic range size. For example, taller plant species have a larger dispersal potential (Thomson et al., 2011) and are therefore more likely to expand their range by encountering new suitable habitats (e.g. Murray et al., 2002; Kristiansen et al., 2009). Height can also increase competitive ability (Falster & Westoby, 2003) and therefore establishment success. From an evolutionary perspective height in plants is positively associated with generation times due to slower mutation rates and therefore lower rates of speciation that can also facilitate larger range sizes (i.e., it is more likely that geographically isolated individuals will remain within the same species due to both high dispersal capacity and low mutation rates; Lanfear et al., 2013). Conversely, small plants invest proportionally more into reproduction (Niklas, 2004), which may increase dispersal potential (Sonkoly et al., 2017), although their smaller seeds tend to have lower survival and establishment rates (Moles & Westoby, 2006).

Plant lifespan is likely to independently affect range size through impacts on reproduction and establishment (Figure 1). Annual plants with their large investment in reproduction (Wilson & Thompson, 1989) may increase both the likelihood of dispersal and establishment success and thereby act to increase range size (Estrada et al., 2015). However, the short generation times of annual plants might increase diversification rates and reduce range size, as has been shown in some animals (Boucher et al., 2017). Therefore, both lifespan and plant height have the potential to influence range size via multiple, sometimes contradictory pathways (Figure 1). The most important factor, and the mechanism by which it works, is likely to be context-dependent both in terms of the ecosystem and the organism (Sheth et al., 2020).

The grass family represents a unique opportunity for exploring the role of plant height and lifespan in driving range size. Ecosystems dominated by Poaceae cover approximately 31%–43% of the land surface globally (Archibald et al., 2019; Gibson, 2009; Linder et al.,

2018), and they spread to achieve their current dominance from the start of the Miocene, 10–20 million years ago (Strömberg, 2011). Grass species range sizes vary from narrow endemics found on just single hillsides (e.g. *Pentameris trifida* (Galley) Galley & H.P. Linder and *Trisetopsis barbata* (Nees) Röser & Wölk) to species with wide pantropical distributions (e.g. in *Hyparrhenia hirta* (L.) Stapf and *Themeda triandra* Forssk.). Grasses show a wide range of life forms and lifespan strategies—plant height ranges from <10 cm to >4 m (Clayton et al., 2015; Fish et al., 2015). Grasses are largely wind-pollinated, but display a bewildering variety of dispersal syndromes (Clayton, 1990; Kellogg, 2015). These dispersal syndromes tend to be associated with particular grass clades, as the floral attributes of the grasses are strongly linked to their evolutionary history and are therefore phylogenetically constrained and are also key in morphological taxonomy (Doust et al., 2014; Kellogg, 2015). Grasses show both C3 and C4 photosynthetic pathways that are also phylogenetically constrained: different grass clades dominate in different environmental conditions (Edwards & Smith, 2010; Visser et al., 2012) and evolved at different times (Hackel et al., 2018). Therefore, understanding relationships between plant height, lifespan and range size within and among grass clades could help assess the relative importance of these factors in understanding the distribution of grasses globally. Finally, grasses are some of the most consequential invaders globally and understanding how functional traits constrain range size in this family could help predict invasiveness (Canavan et al., 2019; Hui et al., 2011). Tall annual grasses have high probabilities of establishment outside their native ranges and tend to be naturalised in warm climates (Monnet et al., 2020). However, it has not been determined whether height and lifespan are associated with larger native range sizes.

We quantified range size in 757 grass species indigenous to southern Africa, representing 12 tribes and 144 genera. We aimed to assess the importance of height and lifespan in determining range size and whether these characters help to explain the likelihood of grass species becoming invasive. We focus on plant height and lifespan as characters readily available for all 757 species as determinants of range size. In Figure 1, we highlight how plant height and lifespan have the potential to influence range size via multiple mechanisms. Moreover, it should be possible to elaborate on other range size constraints within grasses by comparing these relationships among tribes. For example, the area suitable for C3 grass photosynthesis in sub-Saharan Africa is limited to montane and winter rainfall regions, principally the southernmost part of the continent (Scott, 2002; Vogel et al., 1978). Habitat suitability would therefore be expected to be the major constraint on the range size of C3 grasses, and in most C3 grass tribes the relationship with height or lifespan would then be less apparent than in tribes primarily comprised of C4 species. Likewise, if strong relationships were found between plant height and range size in tribes with particular floral structures and dispersal syndromes, this would be evidence that the effect of height on dispersal is the dominant mechanism driving this relationship (rather than generation time). Overall, we expected a general positive relationship between range size and plant height across

the region. With respect to lifespan, it is unclear whether annual-biannual or perennial grasses should *a priori* be expected to have larger range sizes: (1) perennial grasses have longer generation times that should reduce speciation rates and thus promote range sizes, while (2) annual-biannual grasses produce more seeds that are also smaller which would likely enhance dispersal opportunities and distances, and hence their range sizes. We expected that species that have been introduced to other continents are likely to have larger native range sizes than non-introduced species, because widespread species are more likely to be encountered and intentionally or accidentally introduced to new areas. Following the introduction, we expect that factors that promote larger native range sizes will likely also enhance the probability of a species becoming invasive.

2 | MATERIALS AND METHODS

2.1 | Species occurrence data and mapping

We limited our study to native species occurring in five southern African countries (Namibia, Botswana, Lesotho, Eswatini and South Africa), to make use of the unique and well-curated species occurrence and trait dataset prepared by Fish et al. (2015). We extracted and analysed all occurrence records of native southern African Poaceae from herbarium specimens housed in the National Herbarium (PRE), Pretoria; Compton Herbarium (NBG and SAM), Cape Town; KwaZulu-Natal Herbarium (NH), Durban; herbarium acronyms following Index Herbariorum (Thiers, 2020). All the above-mentioned herbaria are managed by the South African National Biodiversity Institute (SANBI), held in the Botanical Database of southern Africa (BODATSA, 2019), including the species identifications recently

confirmed in preparation of Fish et al. (2015). However, the range sizes of these southern African species were then calculated across the whole sub-Saharan African region, making use of a total of 138,953 locality records, to get a realistic indication of the ranges of widespread species. Species occurrences outside Africa were not included in this study.

To improve range size estimations for the whole of sub-Saharan Africa, the geo-referenced data from the BODATSA/BRAHMS database were augmented with location data from the Global Biodiversity Information Facility (GBIF.org, 2019). The occurrence data for indigenous species identified to species-level were extracted from BODATSA and GBIF. The 'CoordinateCleaner' package (Zizka et al., 2019) was used to clean the occurrence data by removing all records with the following issues: no geographical coordinates, duplicates, localities in the sea or other water bodies, country centroids and localities of biodiversity institutions. Intraspecific taxa including varieties and subspecies were merged to species-level. The distribution map of species occurrences in our study (Figure 2) represents sampling intensity (records) prepared using R (R Core Team, 2021). The occurrence data for Africa are too sparse to be confident about quantifying the environmental requirements (or niche breath) of all species in this analysis. Therefore, we were unable to explicitly test the role of niche breath in controlling range size (but see Section 4).

2.2 | Species trait data

Maximum average plant height in millimetres was obtained from herbarium specimens collected in southern Africa, by measuring from the base of the culm to the tip of inflorescence during data collection toward Fish et al. (2015). Lifespan is the length of the
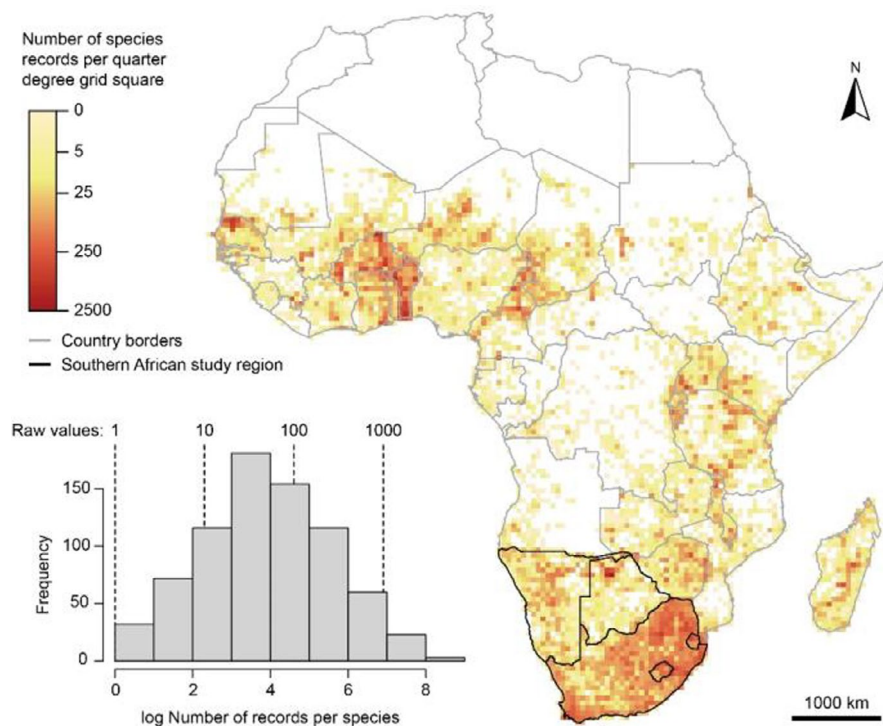
FIGURE 2 Map of the study area showing the number of herbarium records for Poaceae per quarter degree grid square, which provides an indication of the variation in sampling effort across the continent. The 757 species assessed in this study are all native to the region occupied by the five southern African countries outlined in black, however, their range sizes were calculated for the entire sub-Saharan Africa region including Madagascar

living cycle of a plant, and all species were scored as either annual-biannual (i.e. annual or biannual) or perennial following Fish et al. (2015). Photosynthetic type (i.e. C3 or C4) was obtained for each grass species from Osborne et al. (2014). As photosynthetic type is strongly linked with evolutionary history in grasses, we did not include it in our analyses, but we did use it to help interpret the results.

2.3 | Range size calculations

Methods used to calculate range size vary from underestimates, such as area of occupancy (AOO; only grid cells where the species was physically observed), to overestimates, such as estimating the extent of occurrence (EOO) by fitting a convex hull that encompasses all recorded occurrence data points (Gaston & Fuller, 2009). Burgman and Fox (2003) propose that it is more appropriate to use an alpha hull method (Edelsbrunner et al., 1983), as this avoids some of the more egregious overestimates of the convex hull method, but still makes some assumptions about presence between scattered occurrence records. The alpha hull method removes all edges from the convex hull that exceed the value of the mean edge length (L) multiplied by alpha (α; i.e. $L_i > L \times \alpha$). Thereafter, the total area of all remaining triangles is taken to be the range size (Burgman & Fox, 2003). As the value of alpha increases, it eventually causes the alpha hull to become equivalent to the convex hull, while small alpha values make the alpha hull become scattered points (Burgman & Fox, 2003; Hui et al., 2011).

We estimated range size using the 'EOO.computing' function (extent of occurrence) in a development version of the ConR package kindly provided by Gilles Dauby (Dauby, 2020; Dauby et al., 2017). This version incorporates a planar mode that allows range size to be estimated using the alpha hull method and projected coordinates, thus partially accounting for the effect of Earth's curvature on range size estimates; we used the Africa Albers Equal Area Conic projection for our range size estimates. We visually assessed the estimated distribution ranges for well-known species produced by the use of different alpha values (see Figure S1 for examples), with expert opinion (A. C. Mashau) recommending the selection of alpha = 200 km (with 10 km buffer) for our analyses. This choice was felt to provide an appropriate compromise between overestimating ranges in well-sampled regions, and underestimating ranges in poorly sampled regions (Figure S1). We found that using alpha = 100 km (5 km buffer), 200 or 300 km (15 km buffer) did not change the overall results and conclusions of the analyses described below, because although estimated range sizes are highly sensitive to alpha values, the relative differences in range size between species remain approximately the same and produce the same relationships with height and lifespan (see Tables S1–S4 and S6–S8). Alpha hulls cannot be computed for species with fewer than three occurrence records. In these cases, we used the 'AOO.computing' function (area of occurrence) with raster grid sizes of 10, 20 and 30 km to provide range size estimates to complete the data sets with alpha values of 100, 200 and 300 km, respectively. We used 20 random raster grid starting positions; the analysis determines how many raster grid cells the species records are likely to occupy and then sums the area of these grid cells.

2.4 | Grass phylogeny

The checklist of southern African native grass species in Fish et al. (2015) was used to select the relevant branches from the grass phylogenetic tree by Spriggs et al. (2014) and match them. The *keep. tip* function from the R package 'ape' (Paradis et al., 2004) was used to keep only the genus-level branch tips. This resulted in a genus-level phylogenetic tree which contained 120 of the 144 genera, covering 350 of the 757 native grass species from southern Africa in the dataset (Figure S2).

2.5 | Statistical analyses

Phylogenetically controlled analysis of range size

Phylogenetic generalised least squares (PGLS; pgls function in 'caper' R package; Orme et al., 2018) models were fitted to test whether species range size was influenced by plant height and lifespan. The analysis was restricted to the 350 species included in the grass phylogeny estimated by Spriggs et al. (2014), which was used to account for potential non-independence among species arising from relatedness. Branch lengths were optimised for the full additive model via maximum likelihood estimation of Pagel's lambda (λ), with this λ estimate subsequently used in all candidate models (Pagel, 1997, 1999; Orme et al., 2018). Range size (km^2) was log-transformed prior to analyses, with the full set of candidate models comprising height (mm; log-transformed) and lifespan (two-level factor: 'annual-biannual' or 'perennial') as predictors fitted independently, additively and as an interaction. In this and all subsequent analyses, model selection was performed based on Akaike's information criterion (AIC), with the simplest model with ΔAIC <4 relative to the lowest model AIC value adopted as the best model (Burnham et al., 2011).

Range size analysis for the full species dataset

Linear mixed effect models (LMMs) were fitted to test the relationship between range size and plant height and lifespan, which were fitted as fixed effects. The analysis included all tribes with more than five species, resulting in a dataset of 757 species in 144 genera and 12 tribes. The model selection was performed based on AIC, with the simplest model with ΔAIC <4 relative to the lowest model AIC value adopted as the best model (Burnham et al., 2011). The random effects component of the models accounted for differences in intercepts among grass genera nested within the tribe. Range size (km^2) was log-transformed to conform to a normal distribution prior to analyses, with the full set of candidate models comprising height (mm; log-transformed) and lifespan (two-level factor:

'annual-biannual' or 'perennial') as predictors fitted independently, additively and as an interaction. Maximum likelihood and t-tests using Satterthwaite's method (lmerModLmerTest; Kuznetsova et al., 2017) were used to fit and calculate approximate p-values for these models.

Tribe-level range size versus plant height relationships

Linear regression models were fitted to assess the relationship between range size and plant height and plant lifespan for each of the 12 tribes. Range size (km^2) and height (mm) were both log-transformed prior to fitting the models. Lifespan was omitted from models for Arundineae, Oryzeae and Tristachydeae due to low representation of annual species (≤2 species).

Range size as a predictor of invasiveness

The degree of invasiveness of 250 grass species that are native to South Africa and that have been introduced to Australia, Chile, Europe and/or the USA was assessed. Due to the lack of data on invasive status for most countries and the difficulty in acquiring these, we used the determinations for the four regions selected by Visser et al. (2016). Species were classified into three categories following Visser et al. (2016), based on how far along the 'introduction-naturalisation-invasion' (INI) continuum they had progressed (Blackburn et al., 2011): (1) introduced (but not [yet] naturalised or invasive), (2) naturalised (i.e. introduced and now naturalised but not [yet] invasive) and (3) invasive (i.e. introduced, naturalised and now invasive). Generalised linear mixed effect models (GLMMs) were fitted to test if native range size (i.e. in sub-Saharan Africa), plant height or lifespan predict whether species have become invasive or not when introduced to other continents. Binomial models with a logit link function were fitted with species classified as invasive scored as 1 and introduced or naturalised scored as 0. Range size (km^2) and

height (mm) were both log-transformed prior to analyses. Tribe was fitted as a random effect, with genus omitted due to model convergence issues arising from the particular subset of introduced species. Candidate models included the full set of combinations of these variables. In a separate analysis, an LMM was fitted to test for differences in range size (the response) among each of the three INI invasion categories, with the addition of another category for those species that were not introduced to other continents (the only fixed effect). Genus nested within the tribe was fitted as a random effect. The model selection was performed based on AIC, with the simplest model with ΔAIC <4 relative to the lowest model AIC value adopted as the best model (Burnham et al., 2011). All analyses were done in the R environment (R version 3.5.1; R Development Core Team, 2021).

3 | RESULTS

The median range size of southern African Poaceae was c. 120,000 km^2, with an interquartile range of c. 25,000 to 520,000 km^2 (Figure 3). However, seven grass species have range sizes >5 million km^2—i.e. they cover over half of the total area of sub-Saharan Africa (land area c. 9,200,000 km^2).

3.1 | Phylogenetically controlled analysis of range size

Grass species range sizes were strongly related to both plant height and lifespan. The best PGLS model included height and lifespan as additive effects (Tables S1 and S2; Figure S3; $r^2 = 0.14$), with no clear evidence for an interaction between these predictors ($p = 0.828$; ΔAIC = 1.952). Plant height had a positive effect on range size ($\beta \pm SE = 0.876 \pm 0.154$, $p < 0.001$), and perennial grasses had significantly smaller range sizes than annual-biannual grasses ($\beta \pm SE = -1.098 \pm 0.185$, $p < 0.001$). When range size and height
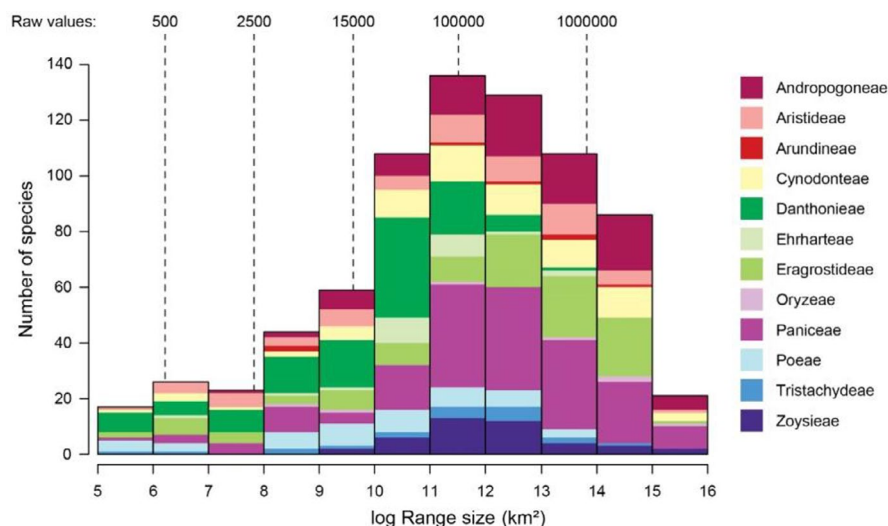

FIGURE 3 Histogram of the range sizes (km^2, log-scale) of southern African grasses, estimated using the alpha hull method with alpha = 200 km. Tribe-level range size distributions are indicated by stacked colour bands

are back-transformed to their original measurement scales, the model suggests that the range size of an annual-biannual grass will increase over the interquartile range of observed grass heights (550 to 1200 mm) from c. 230,000 to 455,000 km², and for a perennial grass from c. 77,000 to 152,000 km². The λ estimate of 0.681 suggests that the range size of grasses is structured to some extent by phylogenetic relationships and grass evolutionary history.

3.2 | Range size analysis for the full species dataset

The LMMs fitted to data for all southern African grass species confirmed that range size was significantly related to both plant height and lifespan (Figure 4). The best model included height and lifespan as additive effects (Tables S3 and S4; Figure S4; marginal $r^2 = 0.08$, conditional $r^2 = 0.25$), with no clear evidence for an interaction between these predictors ($p = 0.662$; ΔAIC = 1.808). Consistent with the phylogenetic analyses, height had a positive effect on range size ($\beta \pm$ SE = 0.872 ± 0.127, $p < 0.001$), and range sizes for perennial grasses were significantly smaller than for annual-biannual grasses ($\beta \pm$ SE = −0.870 ± 0.170, $p < 0.001$). Examination of the tribe-level intercept in the random effects suggests that there are unaccounted for effects that result in both the Danthonieae and Poeae having smaller range sizes than the other tribes and the Andropogoneae having unexpectedly large ranges (Figure S5).
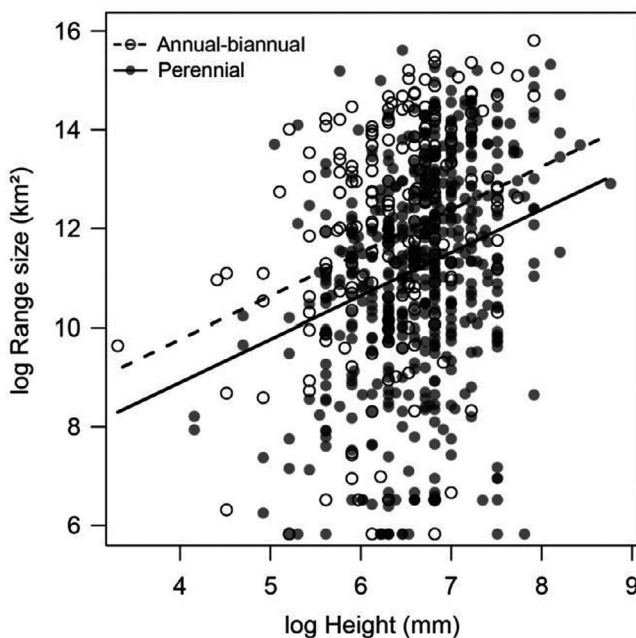

FIGURE 4 Relationships between range size (km², log-scale) and plant height (mm, log-scale) for 757 southern African grasses with annual-biannual (open symbols and dashed line) or perennial (solid symbols and line) lifespans, as estimated by a linear mixed effects model. Genus nested within tribe was fitted as a random intercept term in the model to partially account for evolutionary constraints

3.3 | Tribe-level range size versus plant height relationships

The linear models showed that most C4-dominated tribes (Andropogoneae, Aristideae, Eragrostideae, Paniceae and Zoysieae) had positive significant relationships with plant height (Figure 5; Table S5), with the exceptions being the Cynodonteae and Tristachydeae, where height had a non-significant effect on range size. Among the C3 tribes, the Arundineae, Oryzeae and Poeae had significant and positive height versus range size relationships, but this relationship was non-significant for the Danthonieae and Ehrharteae.

3.4 | Range size as a predictor of invasiveness

The invasiveness data revealed that the probability of a South African grass becoming invasive after being introduced to other continents was related to both its native range size and lifespan (Figure 6). The best GLMM model included range size and lifespan as additive effects, and tribe as a random effect (Tables S6 and S7; marginal $r^2 = 0.12$, conditional $r^2 = 0.14$). Invasiveness was positively related to range size ($\beta \pm$ SE = 0.576 ± 0.167, $p < 0.001$), and perennial grasses had marginally significant lower probability of becoming invasive than annual-biannual grasses ($\beta \pm$ SE = −0.670 ± 0.349, $p = 0.055$).

The LMM using all grass species confirmed that range size differences existed between invasion categories (Table S8; Figure 7; Figure S6). Species that had not been introduced to other continents had significantly smaller range sizes than all other categories (54 567 km²; $p < 0.001$). Native range size increased steadily along the INI continuum: introduced (377,566 km²), naturalised (496,481 km²) and invasive (1,026,022 km²), although the difference in range size between introduced and naturalised species was not significant ($p > 0.05$).

4 | DISCUSSION

We found that grass height has a positive correlation with range size, where taller grasses have larger range sizes (Figure 4). The strength of the plant height-range size relationship, which persists when controlling for phylogeny, was expected based on well-documented relationships between plant height and increased dispersal ability (Thomson et al., 2011) and decreased diversification (Boucher et al., 2017), and mutation rates (Lanfear et al., 2013). However, there is also potentially an ecological factor related to competitive abilities: tall grasses tend to outcompete small grasses and remain dominant in an occupied area (Falster & Westoby, 2003).

Range sizes of annual-biannual grasses were larger than for perennial grasses in sub-Saharan Africa (Figure 4). There are several reasons why within the grass family, annual-biannual grasses might be expected to have larger range sizes. One reason may be because annual-biannual grass species have higher reproductive allocation
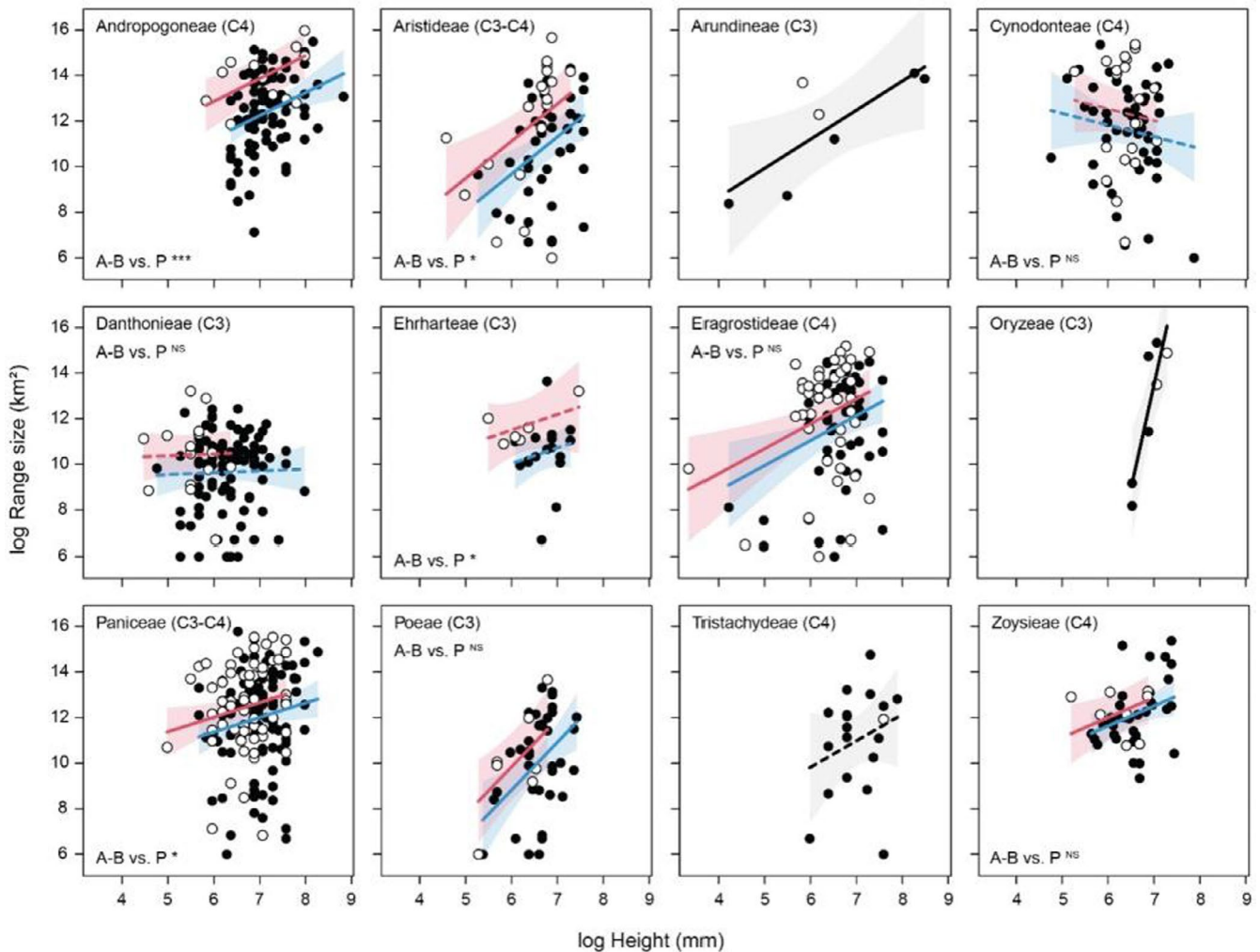
FIGURE 5 Tribe-level relationships between range size (km², log-scale) and plant height (mm, log-scale) and plant lifespan (annual-biannual vs. perennial) for 757 species in 144 genera and 12 tribes of southern African grasses. Linear models were fitted to species range size data for each tribe separately, with height fitted as a predictor in all models, and lifespan fitted where annual-biannual and perennial categories were represented by five or more species each. Solid lines represent a significant effect of plant height, and dashed lines represent a non-significant effect of plant height; shaded areas represent the 95% confidence interval for height parameter estimates. Red lines and shading represent annual-biannual species, blue represents perennial species, and black lines with grey shading represent all lifespans. The significance of lifespan effects on range sizes are indicated in each panel ('A-B vs. P' = annual-biannual vs. perennial), where *** = $p < 0.001$, * = $p < 0.05$ and NS = $p > 0.05$. The photosynthetic pathways (i.e. C3 and/or C4) occurring in each tribe are shown in brackets after the tribe name

than perennial grasses (Vico et al., 2016; Wilson & Thompson, 1989), and often also smaller seeds (Moles et al., 2004), and this has been shown to correlate with dispersal distance and hence range size (Sonkoly et al., 2017). Perennial grasses such as *Hyperthelia dissoluta* (Nees ex Steud.) Clayton allocate resources to above-ground biomass, clonal reproduction, and rapid height gain (Ripley et al., 2015; Taylor et al., 2010) at the expense of reproductive effort. Finally, while annual grasses always flower within the first year, many perennial tropical grasses can also produce seeds within months of germinating (unpublished data S. Archibald and C. Lehmann). Therefore, although annual species have short generation times, they are not necessarily always shorter than those of co-occurring perennial grasses. Overall, our results show that grasses with shorter lifespans have larger range sizes, suggesting that, for annual-biannual grasses,

the positive effect on range size of increased dispersal opportunities and dispersal distance is greater than the negative effect of short generation times and hence faster speciation rates (Boucher et al., 2017).

Contrary to our expectations, the strongest positive relationships with height were found in three C3 tribes, Oryzeae, Arundineae and Poeae (although note that the Oryzeae showed little variation in range size); however, for the C3 Danthonieae and Ehrharteae, the relationship was not significant. The C4 clades generally had strong positive relationships with plant height, but the Cynodonteae is an exception. These results can in part be explained with reference to habitat suitability and dispersal syndromes. In particular, Oryzeae and Arundineae are largely wetland species (Fish et al., 2015), and, by promoting the ability to disperse easily from one isolated wetland
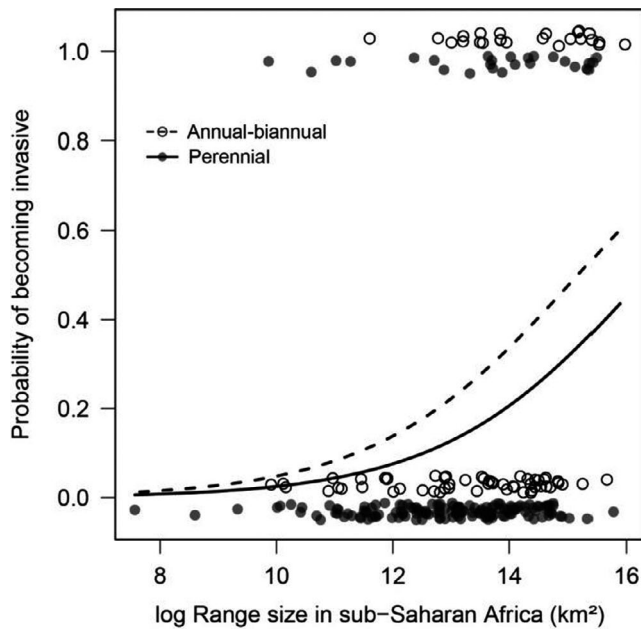
FIGURE 6 Probability of South African grasses becoming invasive following introduction to other continents as a function of their native range size in sub-Saharan Africa (km^2, log-scale) and lifespan (annual-biannual: open symbols and dashed line, or perennial: solid symbols and line). Probabilities were estimated by fitting a binomial generalised linear mixed effects model fitted to data for 250 grasses categorised as invasive (1) or introduced or naturalised (0) following Visser et al. (2016). Tribe was fitted as a random intercept in the model

FIGURE 7 Boxplot showing variation in native range sizes among 757 southern African grasses after classification into four invasion status categories: (1) not introduced to other continents, (2) introduced (but not [yet] naturalised or invasive), (3) naturalised (i.e. introduced and now naturalised but not [yet] invasive), and (4) invasive (i.e. introduced, naturalised and now invasive). Differences in range size among invasion categories were assessed using a linear mixed effects model, with genus nested within tribe fitted as a random effect. Categories with different letters are significantly different ($p < 0.05$)

fragment to another, height should strongly drive their range size. Likewise, cool environments are found scattered throughout the high-altitude mountains of Africa (Meadows & Linder, 1993), and it would be expected that grass species from the Poeae tribe, which includes Afromontane specialists, such as *Festuca* L. and *Trisetopsis* Röser & Wölk (South African species previous classified under *Helictotrichon* Besser ex Schult. & Schult. f.) would show a significant relationship with grass height. In contrast, the C3 tribe Danthonieae is predominantly limited to cooler environments in the southern Cape in Africa (Humphreys & Linder, 2013), so height (and dispersal ability) should not affect their ranges which are constrained by habitat availability (Gallagher, 2016). Linder et al. (2018) argue that frost tolerance allowed subfamilies Pooideae and Danthonioideae to invade vast areas during glacial periods. However, the Pooideae evolved earlier than the Danthonioideae and this, together with the truncated cold environments available in the Southern Hemisphere, has probably prevented the Danthonioideae from expanding their ranges as much as Pooideae (Humphreys & Linder, 2013).

Tribe Paniceae is very large and includes both C3 and C4 species and a wide variety of dispersal syndromes. It is not surprising therefore that the relationship with height is less apparent in this clade. Likewise, tribe Cynodonteae also contains species with dispersal syndromes ranging from the epizoochoric *Tragus berteronianus* Schult. to endozoochoric *Cynodon dactylon* (L.) Pers., and includes species like *Dactyloctenium giganteum* Fisher & Schweick. which is
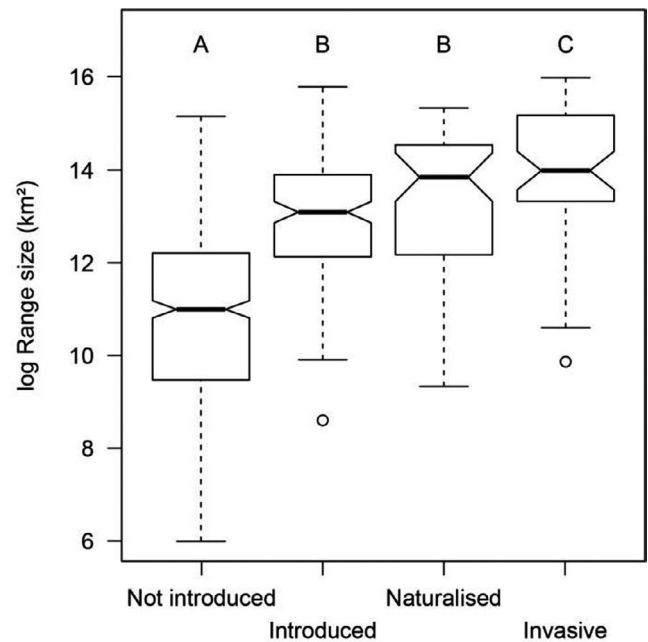
thought to be dispersed on the feet of waterbirds (personal communication I. P. J. Smit). Although the response of dispersal distance to plant height is very well-documented for wind-dispersed species (Thompson et al., 2011), it is less clear how height might facilitate dispersal with endozoochory—in fact, it is possible that there is a negative relationship here, as smaller plants are more likely to have their seeds ingested by grazing animals (Anderson et al., 2014). Perhaps as a result, Cynodonteae species are generally shorter than other clades as can be seen in Figure 5. Clearly further research linking dispersal syndromes to height and range size is urgently needed. We do not yet have clarity on which propagule traits are associated with endozoochory, epizoochory, and wind dispersal in grasses, but from data presented here, it seems this might be key to explaining biogeographic patterns in this plant family.

The tribes Danthonieae and Poeae had smaller range sizes than the other tribes once grass height and lifespan had been accounted for, while the Andropogoneae had unexpectedly large range sizes (Figure S5). Visser et al. (2012) argued that Andropogoneae are uniquely adapted to fire, and Schmidt et al. (2011) found species in this clade to be good competitors across a wide environmental range. Perhaps these two factors, together with the fact that they are generally tall and include multiple annual species (Fish et al., 2015; Schmidt et al., 2011) may account for this group's large range sizes. Interestingly, the Andropogoneae are one of the youngest grass

clades to have evolved (Welker et al., 2020), and their extremely large ranges contradict the age-and-area hypothesis that has been observed in several other plant groups (Sheth et al., 2020). Yet again, this highlights the potentially important and under-recognised role of dispersal and competition traits in driving range size.

Invasive grasses had larger native range sizes than introduced species (Figure 7), and annual-biannual grasses had a significantly higher probability of being invasive than perennial grasses (Figure 6). This is the first time this has been demonstrated for the grass family and corresponds with findings for Australian *Acacia* (Hui et al., 2011) and the flora of the Czech Republic (Pyšek et al., 2009), where species with large native range sizes are more likely to become invasive. The simplest explanation for this is that species with large range sizes are likely to be encountered by more people so have increased likelihood and hence the frequency of being chosen for introduction elsewhere (Duncan et al., 2001). Species with larger native ranges may also display greater morphological and genetic variation leading to plasticity and a capacity to more rapidly adapt and thrive in a novel environment (Buswell et al., 2011). Over the past century, African grasses have been sought after for pasture introduction and have been extensively introduced around the world (Visser et al., 2016). However, while introduced species have larger native range sizes than non-introduced ones, the introduced species that become invasive have larger native range sizes still, indicating that some ecological attributes of these species promote their invasion success. We found that lifespan, and probably also height, helped to explain the relationship between range size and invasiveness. This is not unexpected as dispersal is an important factor affecting the propensity of a species to invade (Pysěk et al., 2009). Although height was not included in the best model, it nonetheless was an important factor in two of the three models with ΔAIC <4 (Table S6). Canavan et al. (2019) argue that tall stature provides numerous ecological advantages to grasses making them much more likely to become invasive. Our finding that invasive grasses have large native range sizes could help to identify potentially invasive species and manage the risk of introducing them to new environments, but it would be worth investigating the mechanisms more closely.

Range size is included in the conservation status of IUCN red listing processes and is considered a predictor of species extinction risk (IUCN, 2001; Gaston & Fuller, 2009). Grass species with a small range size include *Ehrharta microlaena* Nees ex Trin., which is endemic to the Western Cape, South Africa. The fact that we have identified some strong life history and architectural characteristics that are associated with range size might also be helpful in efforts to identify further grass species in need of particular protection, especially those with small range sizes.

5 | CONCLUSION

Our analyses suggest that plant height has been, and continues to be, an important driver of grass biogeography with implications for understanding the spread of certain grass clades both over the Miocene and today. Our study has improved our ecological understanding of how grass range size varies across sub-Saharan Africa, and challenges the idea that dispersal potential is less important than niche breadth or environmental variability as the main driver of range size (Sheth et al., 2020). Our results also suggest that in grasses the increased dispersal opportunities and distances of annual-biannual grasses have a greater effect on promoting range size in grasses than the effect of short generation times on speciation rates. Furthermore, there is also a need to understand how floral attributes and dispersal mode relate to range size in grasses, which requires further research. Measuring range size helps to understand the evolutionary origins and ecological characteristics of a species and is important for assessing invasion and extinction risk.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The traits dataset and range size information are now available via SANBI opus data portal (http://hdl.handle.net/20.500.12143/7649).

ORCID

Aluoneswi C. Mashau https://orcid.org/0000-0001-6028-7064
Gareth P. Hempson https://orcid.org/0000-0001-8055-4895
Caroline E. R. Lehmann https://orcid.org/0000-0002-6825-124X
Maria S. Vorontsova https://orcid.org/0000-0003-0899-1120
Vernon Visser https://orcid.org/0000-0003-2444-5015
Sally Archibald https://orcid.org/0000-0003-2786-3976

REFERENCES

Anderson, T. M., Schutz, M., & Risch, A. C. (2014). Endozoochorous seed dispersal and germination strategies of Serengeti plants. *Journal of Vegetation Science*, *25*, 636–647. https://doi.org/10.1111/jvs.12110

Archibald, S., Bond, W. J., Hoffmann, W., Lehmann, C., Staver, C., & Stevens, N. (2019). Distribution and determinants of savannas. *Savanna woody plants and large herbivores* (pp. 1–24). https://doi.org/10.1002/9781119081111.ch1

Baselga, A., Lobo, J. M., Svenning, J. C., & Araújo, M. B. (2012). Global patterns in the shape of species geographical ranges reveal range determinants. *Journal of Biogeography*, 39, 760–771. https://doi.org/10.1111/j.1365-2699.2011.02612.x

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26, 333–339. https://doi.org/10.1016/j.tree.2011.03.023

BODATSA (2019). Botanical Database of Southern Africa. Available online at South African National Biodiversity Institute. https://newposa.sanbi.org/?

Boucher, F. C., Verboom, G. A., Musker, S., & Ellis, A. G. (2017). Plant size: A key determinant of diversification? *New Phytologist*, 216, 24–31. https://doi.org/10.1111/nph.14697

Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27, 597–623. https://doi.org/10.1146/annurev.ecolsys.27.1.597

Burgman, M. A., & Fox, C. W. (2003). Bias in species range estimates from minimum convex polygons: Implications for conservation and options for improved planning. *Animal Conservation*, 6, 19–28. https://doi.org/10.1017/S1367943003003044

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multi-model inference in behavioral ecology: Some background, observations and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Buswell, J. M., Moles, A. T., & Hartley, S. (2011). Is rapid evolution common in introduced plant species? *Journal of Ecology*, 99, 214–224. https://doi.org/10.1111/j.1365-2745.2010.01759.x

Canavan, S., Meyerson, L. A., Packer, J. G., Pyšek, P., Maurel, N., Lozano, V., Richardson, D. M., Brundu, G., Canavan, K., Cicatelli, A., Čuda, J., Dawson, W., Essl, F., Guarino, F., Guo, W.-Y., van Kleunen, M., Kreft, H., Lambertini, C., Pergl, J., … Wilson, J. R. U. (2019). Tall-statured grasses: A useful functional group for invasion science. *Biological Invasions*, 21, 37–58. https://doi.org/10.1007/s10530-018-1815-z

Clayton, W. D. (1990). The spikelet. In G. P. Chapman (Ed.), *Reproductive versatility in the grasses*. Cambridge University Press.

Clayton, W. D., Vorontsova, M. S., Harman, K. T., & Williamson, H. (2015). *GrassBase – The online world grass flora*. Royal Botanic Gardens Kew. https://www.kew.org/data/grasses-db.html

Dauby, G. (2020). ConR: Computation of parameters used in preliminary assessment of conservation status. *R Package Version*, 1(3). https://cran.r-project.org/web/packages/ConR/ConR.pdf

Dauby, G., Stévart, T., Droissart, V., Cosiaux, A., Deblauwe, V., Simo-Droissart, M., Sosef, M. S. M., Lowry, P. P. 2nd, Schatz, G. E., Gereau, R. E., & Couvreur, T. L. P. (2017). ConR: An R package to assist large-scale multispecies preliminary conservation assessments using distribution data. *Ecology and Evolution*, 7, 11292–11303. https://doi.org/10.1002/ece3.3704

Dexter, K., & Chave, J. (2016). Evolutionary patterns of range size, abundance and species richness in Amazonian angiosperm trees. *PeerJ*, 4, e2402. https://doi.org/10.7717/peerj.2402

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. https://doi.org/10.1038/nature16489

Doust, A. N., Mauro-Herrera, M., Francis, A. D., & Shand, L. C. (2014). Morphological diversity and genetic regulation of inflorescence abscission zones in grasses. *American Journal of Botany*, 101, 1759–1769. https://doi.org/10.3732/ajb.1400186

Duncan, R. P., Bomford, M., Forsyth, D. M., & Conibear, L. (2001). High predictability in introduction outcomes and the geographical range size of introduced Australian birds: A role for climate. *Journal of Animal Ecology*, 70, 621–632. https://doi.org/10.1046/j.1365-2656.2001.00517.x

Edelsbrunner, H., Kirkpatrick, D. G., & Seidel, R. (1983). On the shape of a set of points in the plane. *IEEE Transactions on Information Theory*, 29, 551–559. https://doi.org/10.1109/TIT.1983.1056714

Edwards, E., & Smith, S. (2010). Phylogenetic analyses reveal the shady history of C4 grasses. *Proceedings of the National Academy of Sciences of Sciences of the United States of America*, 107, 2532–2537. https://doi.org/10.1073/pnas.0909672107

Estrada, A., Meireles, C., Morales-Castilla, I., Poschlod, P., Vieites, D., Araújo, M. B., & Early, R. (2015). Species' intrinsic traits inform their range limitations and vulnerability under environmental change. *Global Ecology and Biogeography*, 24, 849–858. https://doi.org/10.1111/geb.12306

Falster, D. S., & Westoby, M. (2003). Plant height and evolutionary games. *Trends in Ecology & Evolution*, 18, 337–343. https://doi.org/10.1016/S0169-5347(03)00061-2

Fish, L., Mashau, A. C., Moeaha, M. J., & Nembudani, M. T. (2015). *Identification guide to southern African grasses. An identification manual with keys, descriptions and distributions.* Strelitzia, (Vol. 36, pp. vi–749). South African National Biodiversity Institute.

Gallagher, R. V. (2016). Correlates of range size variation in the Australian seed-plant flora. *Journal of Biogeography*, 43, 1287–1298. https://doi.org/10.1111/jbi.12711

Gaston, K. J. (1998). Species-range size distributions: Products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353, 219–230.

Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford University Press.

Gaston, K. J., & Fuller, R. A. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology*, 46, 1–9. https://doi.org/10.1111/j.1365-2664.2008.01596

GBIF.org. (2019). GBIF Occurrence Download. https://doi.org/10.15468/dl

Gibson, D. J. (2009). *Grasses and grassland ecology*. Oxford University Press.

Grossenbacher, D., Briscoe Runquist, R., Goldberg, E. E., & Brandvain, Y. (2015). Geographic range size is predicted by plant mating system. *Ecology Letters*, 18, 706–713. https://doi.org/10.1111/ele.12449

Hackel, J., Vorontsova, M. S., Nanjarisoa, O. P., Hall, R. C., Razanatsoa, J., Malakasi, P., & Besnard, G. (2018). Grass diversification in Madagascar: In situ radiation of two large C$_3$ shade clades and support for a Miocene to Pliocene origin of C$_4$ grassy biomes. *Journal of Biogeography*, 45, 750–761.

Hui, C., Richardson, D. M., Robertson, M. P., Yates, C. J., & Wilson, J. R. U. (2011). Macroecology meets invasion ecology: Linking native distribution of Australian acacias to invasiveness. *Diversity and Distributions*, 17, 872–883.

Humphreys, A. M., & Linder, H. P. (2013). Evidence for recent evolution of cold tolerance in grasses suggests current distribution is not limited by (low) temperature. *New Phytologist*, 198, 1261–1273. https://doi.org/10.1111/nph.12244

IUCN. (2001). *IUCN. Red List categories and criteria: Version 3.1. IUCN. Species Survival Commission*. IUCN.

Kellogg, E. A. (2015). Flowering plants. Monocots: Poaceae. In K. Kubitzki (Ed.), *The families and genera of vascular plants*. Springer. https://doi.org/10.1007/978-3-319-15332-2

Kristiansen, T., Svenning, J. C., Grández, C., Salo, J., & Balslev, H. (2009). Commonness of Amazonian palm (Arecaceae) species: Cross-scale links and potential determinants. *Acta Oecologica*, 35, 554–562. https://doi.org/10.1016/j.actao.2009.05.001

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13). https://doi.org/10.18637/jss.v082.i13

Lanfear, R., Ho, S. Y. W., Davies, T. J., Moles, A. T., Aarssen, L., Swenson, N. G., Warman, L., Zanne, A. E., & Allen, A. P. (2013). Taller plants

have lower rates of molecular evolution. *Nature Communications*, 4, 1879. https://doi.org/10.1038/ncomms2836

Linder, H. P., Lehmann, C. E. R., Archibald, S., Osborne, C. P., & Richardson, D. M. (2018). Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews*, 93, 1125–1144. https://doi.org/10.1111/brv.12388

Manne, L. L., Brooks, T. M., & Pimm, S. L. (1999). Relative risk of extinction of passerine birds on continents and islands. *Nature*, 399, 258–261. https://doi.org/10.1038/20436

Meadows, M. E., & Linder, H. P. (1993). A palaeoecological perspective on the origin of Afromontane grasslands. *Journal of Biogeography*, 20, 345–355. https://doi.org/10.2307/2845584

Moles, A. T., Falster, D. S., Leishman, M. R., & Westoby, M. (2004). Small seeded species produce more seeds per square metre of canopy per year, but not per individual per life time. *Journal of Ecology*, 92, 384–396. https://doi.org/10.1111/j.0022-0477.2004.00880.x

Moles, A. T., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, 113, 91–105. https://doi.org/10.1111/j.0030-1299.2006.14194.x

Monnet, A. C., Vorontsova, M. S., Govaerts, R. H. A., Svenning, J. C., & Sandel, B. (2020). Historical legacies and ecological determinants of grass naturalizations worldwide. *Ecography*, 43, 1373–1385. https://doi.org/10.1111/ecog.04609

Morin, X., & Lechowicz, M. J. (2011). Geographical and ecological patterns of range size in North American trees. *Ecography*, 34, 738–750. https://doi.org/10.1111/j.1600-0587.2010.06854.x

Morueta-Holme, N., Enquist, B. J., McGill, B. J., Boyle, B., Jørgensen, P. M., Ott, J. E., Peet, R. K., Šímová, I., Sloat, L. L., Thiers, B., Violle, C., Wiser, S. K., Dolins, S., Donoghue, J. C., Kraft, N. J. B., Regetz, J., Schildhauer, M., Spencer, N., & Svenning, J.-C. (2013). Habitat area and climate stability determine geographical variation in plant species range sizes. *Ecology Letters*, 16, 1446–1454. https://doi.org/10.1111/ele.12184

Murray, B. R., Thrall, P. H., Gill, A. M., & Nicotra, A. B. (2002). How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology*, 27, 291–310. https://doi.org/10.1046/j.1442-9993.2002.01181.x

Niklas, K. J. (2004). Plant allometry: Is there a grand unifying theory? *Biological Reviews*, 79, 871–889. https://doi.org/10.1017/S1464793104006499

Orme, C. D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018). *caper: Comparative analyses of phylogenetics and evolution in R*. version 1.0.1. https://CRAN.R-project.org/package=caper

Osborne, C. P., Salomaa, A., Kluyver, T. A., Visser, V., Kellogg, E. A., Morrone, O., Vorontsova, M. S., Clayton, W. D., & Simpson, D. A. (2014). A global database of C_4 photosynthesis in grasses. *New Phytologist*, 204, 441–446. https://doi.org/10.1111/nph.12942

Pagel, M. (1997). Inferring evolutionary processes from phylogenies. *Zoologica Scripta*, 26, 331–348. https://doi.org/10.1111/j.1463-6409.1997.tb00423.x

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. https://doi.org/10.1038/44766

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analysis of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Procheş, Ş., Wilson, J. R., Richardson, D. M., & Rejmánek, M. (2012). Native and naturalized range size in Pinus: Relative importance of biogeography, introduction effort and species traits. *Global Ecology and Biogeography*, 21, 513–523. https://doi.org/10.1111/j.1466-8238.2011.00703.x

Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., Tichý, L., Danihelka, J., Chrtek jun, J., & Sádlo, J. (2009). The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions*, 15, 891–903. https://doi.org/10.1111/j.1472-4642.2009.00602.x

R Development Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Ripley, B., Visser, V., Christin, P. A., Archibald, S., Martin, T., & Osborne, C. (2015). Fire ecology of C_3 and C_4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology*, 96, 2679–2691.

Schmidt, M., Thiombiano, A., Zizka, A., Konig, K., Brunken, U., & Zizka, G. (2011). Patterns of plant functional traits in the biogeography of West African grasses (Poaceae). *African Journal of Ecology*, 49, 490–500. https://doi.org/10.1111/j.1365-2028.2011.01283.x

Scott, L. (2002). Grassland development under glacial and interglacial conditions in southern Africa: Review of pollen, phytolith and isotope evidence. *Palaeogeography Palaeoclimatology Palaeoecology*, 177, 47–57. https://doi.org/10.1016/S0031-0182(01)00351-0

Sheth, S. N., Morueta-Holme, N., & Angert, A. L. (2020). Determinants of geographic range size in plants. *New Phytologist*, 226, 650–665. https://doi.org/10.1111/nph.16406

Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, 16, 1104–1114. https://doi.org/10.1111/ele.12140

Sonkoly, J., Deák, B., Valkó, O., Molnár, V. A., Tóthmérész, B., & Török, P. (2017). Do large-seeded herbs have a small range size? The seed mass–distribution range trade-off hypothesis. *Ecology and Evolution*, 7, 11204–11212. https://doi.org/10.1002/ece3.3568

Spriggs, E. L., Christin, P. A., & Edwards, E. J. (2014). C_4 photosynthesis promoted species diversification during the Miocene grassland expansion. *PLoS ONE*, 9, e97722. https://doi.org/10.1371/journal.pone.0097722

Staude, I. R., Navarro, L. M., & Pereira, H. M. (2020). Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography*, 29, 16–25. https://doi.org/10.1111/geb.13003

Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, 133, 240–256. https://doi.org/10.1086/284913

Strömberg, C. A. E. (2011). Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences*, 39, 517–544. https://doi.org/10.1146/annurev-earth-040809-152402

Taylor, S. H., Hulme, S. P., Rees, M., Ripley, B. S., Woodward, F. I., & Osborne, C. P. (2010). Ecophysiological traits in C_3 and C_4 grasses: A phylogenetically controlled screening experiment. *New Phytologist*, 185, 780–791. https://doi.org/10.1111/j.1469-8137.2009.03102

Thiers, B. (2020). *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/

Thomson, F. J., Moles, A. T., Auld, T. D., & Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, 99, 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

Vico, G., Manzoni, S., Nkurunziza, L., Murphy, K., & Weih, M. (2016). Trade-offs between seed output and life span—A quantitative comparison of traits between annual and perennial congeneric species. *New Phytologist*, 209, 104–114. https://doi.org/10.1111/nph.13574

Visser, V., Wilson, J. R. U., Fish, L., Brown, C., Cook, G. D., & Richardson, D. M. (2016). Much more give than take: South Africa as a major donor but infrequent recipient of invasive non-native grasses. *Global Ecology and Biogeography*, 25, 679–692. https://doi.org/10.1111/geb.12445

Visser, V., Woodward, F. I., Freckleton, R. P., & Osborne, C. P. (2012). Environmental factors determining the phylogenetic structure of C_4 grass communities. *Journal of Biogeography*, 39, 232–246. https://doi.org/10.1111/j.1365-2699.2011.02602.x

Vogel, J. C., Fuls, A., & Ellis, R. P. (1978). The geographical distribution of Kranz grasses in South Africa. *South African Journal of Science*, 74, 209–215.

Welker, C. A., McKain, M. R., Estep, M. C., Pasquet, R. S., Chipabika, G., Pallangyo, B., & Kellogg, E. A. (2020). Phylogenomics enables biogeographic analysis and a new subtribal classification of Andropogoneae (Poaceae—Panicoideae). *Journal of Systematics and Evolution*, 58, 1003–1030. https://doi.org/10.1111/jse.12691

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213–227.

Wilson, A. M., & Thompson, K. (1989). A comparative study of reproductive allocation in 40 British grasses. *Functional Ecology*, *3*, 297–302. https://doi.org/10.2307/2389369

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., & Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, *10*, 744–751. https://doi.org/10.1111/2041-210X.13152

BIOSKETCH

Aluoneswi C. Mashau is a researcher at South African National Biodiversity Institute (SANBI) with an interest in grass taxonomy, biogeography and ecology. She is a PhD candidate at the University of Witwatersrand.

Author Contributions: S.A., C.E.R.L., G.P.H. and M.S.V. conceived the idea; A.C.M. and V.V. collected the data; A.C.M., G.P.H. and S.A. analysed the data; V.V. advised on the analyses; A.C.M., S.A. and C.E.R.L. led the writing, G.P.H. prepared the figures, and all authors provided comments and feedback on drafts of the manuscript.

SUPPORTING INFORMATION

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