Range size and dispersal of grasses (Poaceae) in Africa

Aluoneswi Caroline Mashau

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Faculty of Science, Department of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

DECLARATION

I, Aluoneswi Caroline Mashau, declare that the thesis that I hereby submit for the degree Doctor of Philosophy at the University of the Witwatersrand, Johannesburg, is my own work and has not previously been submitted by me for a degree at this or any other university.

Supervisor:
Prof. Sally Archibald
Dr Caroline E. R. Lehmann
Dr Maria S. Vorontsova
Dr Gareth P. Hempson

University of the Witwatersrand, Johannesburg, South Africa

Aluoneswi Caroline Mashau

Date 29.05.2023

ABSTRACT

Geographic range size is the outcome of both evolutionary and ecological processes. Therefore both historical contingencies, and the ecological characteristics (traits) of particular species, interact to result in observed distribution patterns. These distribution patterns are also changing – expanding as species invade into new ecosystems, and shrinking as species are filtered from ecosystems due to climate change or changing land management. Understanding current distributions and range sizes is therefore important for helping explain biogeographic patterns and processes, for informing conservation action, the management of invasive plants, and interventions to adapt to climate change. The grass family (Poaceae) covers approximately 31–43% of the land surface globally, and started to spread during the Miocene period (approximately 8–20 Million years ago) to achieve its current dominance. This would have occurred through rapid range expansion as well as speciation and has resulted in some species with almost cosmopolitan (global) distributions, as well as rare grass species found in only a few localities. This study aims to understand the drivers of range size and dispersal traits of grasses in Africa with the purpose of quantifying differences between clades and functional types, and determine the floral traits that likely influence dispersal modes.

In Chapter 1 I compiled general introduction of the whole thesis including background, rationale, aims and objectives. **In Chapter 2** I aimed 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. 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. Geographic range sizes were larger for taller grass species and for species with shorter lifespans. The relationship between plant height and range size varies widely among tribes, with some environmentally-restricted tribes not showing significant responses to 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. The increased dispersal opportunities of annual-biannual grasses appears 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.

Grass floral structures vary greatly but we have very little understanding of their functional significance. Due to the varied dispersal mechanisms shown by grasses, certain syndromes of floral traits would likely be associated with particular strategies for dispersal, and consequently, different environments. In particular, effective seed maturation and dispersal in fire-prone tall grasslands would require different floral trait syndromes than in short, frequently grazed ecosystems. In **Chapter 3** I quantified floral traits of nearly 200 Poaceae species from savanna and grassland ecosystems in southern Africa and explored how their floral structures co-vary and correlate with other functional characteristics such as grass height. Using field information on the dominance disturbance regime of 163 of these grass species it was tested whether certain floral traits are more associated with fire vs grazing. Non-metric multi-dimensional scaling (NMDS) was used to illustrate how floral traits covaried among grass species, and to group them into syndromes based on these traits. Analysis of variance (ANOVA) was used to test whether certain floral trait syndromes were more associated with fire vs grazing. I identified four clear floral trait syndromes separated largely by awn length and the presence of hooks/prickles or bristles. Long-awned species were more likely to be found in frequently burned environments and were also usually taller than species without awns. Grazer-dominated systems appear to select for two different floral trait syndromes. The study has improved our ecological and taxonomic understanding of how floral traits differ among the range of tribes in one family across African countries. It can help in understanding dispersal limitations in grasses and predicting which species are likely to flourish in particular grassland habitats.

The grass family (Poaceae), despite having only emerged and spread in the last 50 million years, is cosmopolitan, and many species have large, almost cosmopolitan distributions. Lineage age and dispersal ability are two factors thought to explain the variation of range size and grasses show a wide range of floral structures and heights associated with different dispersal strategies. In **Chapter 4** I aimed to assess how dispersal syndrome (inferred from floral structures and other functional traits) and evolutionary history affect range size in the grass subtribe Eleusininae – a tropical grass clade with variation in floral structures. Global location records for 97 grass species of 29 Eleusininae genera were used to quantify range size, and linear models were used to test the relationship between range size and interaction between plant height, and lemma awn state (absent/present), caryopsis length (mm) and genus age. Taller grass species with awned lemmas were found to have a larger range size, and this supports my hypothesis (developed in **Chapter 2**) that the importance of grass height in driving range size depends on the dispersal syndrome. It was found that there is no relationship between genus age versus floral and functional traits used in this analysis. The study can help to explain some of the differences in biogeographic history between different lineages and also determine dispersal syndromes.

In Chapter 5 I compiled general discuss or overview of the study, including geographical distribution of the southern African grasses, grass clades co-vary according to their floral traits, conservation and management implications, limitations of this study and needs for future research and conclusion.

DEDICATION

I dedicate this thesis to my husband, Fulufhelo Mashau and my children Tsiko, Huwelelani and Rovhidzwa Mashau

Thank you for support and words of encouragement.

ACKNOWLEDGEMENTS

The research project expenses were covered by the South African National Biodiversity Institute (SANBI) for paid University tuition fees, and other funds were from Newton Advanced Fellowship (NA17095) and a Royal Society International Collaboration Award (IC170015). The University of Witwatersrand and South African National Biodiversity Institute (SANBI) are thanked for their support and all funders for making this research possible.

I would like to say a big thanks to my supervisor Prof. Sally Archibald and co-supervisors Dr Caroline E. R. Lehmann, Dr Maria S. Vorontsova and Dr Gareth P. Hempson for making my dream come true, giving me support and encouragement and believing in me. A special word of thanks to all co-authors Dr Vernon Visser, Dr Abraham Dabengwa, Dr Cedrique L. Solofondranohatra and Dr Watchara Arthan for contributing to three valued papers of this research study. Thank you Ms Thando Caroline Twala (University of Witwatersrand) for assistance in the R-studio programme, Dr Jan Hackel (RGB Kew) for merging a recent grass phylogenetic tree with the list of grass genera found in southern Africa.

Thank you to South African National Biodiversity Institute (SANBI) colleagues for supporting and listening to my problems now and then, especially the late Dr Elizabeth Retief. Former SANBI supervisor, Dr Jacques van Rooy, thanks for consistent mentoring, guidance and support. A special word of thanks to Mrs Nicole L. Meyer for editing this thesis and Ms Sandra Turck for designing the illustrations plate.

Lyn Fish (former Poaceae specialist) who showed me love and support that cannot be overstated, and acted like a mother, teacher, mentor, adviser and finally a granny to my children. Special thanks to my husband Mr Fulufhelo Mashau for being an understanding person and my children, Tsiko, Huwelelani and Rovhidzwa Mashau for such support, and even being an inspiration to me. Finally thanks to my wonderful mother Aifheli Sarah and my late dad Ntsundeni Jack Mudau for bringing me onto this earth.

TABLE OF CONTENTS

Chapter 3 | Floral trait syndromes in tropical grasses and their environmental associations…………………………………………………………………………….………..48

Chapter 4 | Do dispersal syndromes and evolutionary history determine the range size of the subtribe Eleusininae (Poaceae: Chloridoideae: Cynodonteae) worldwide?……………………………………………………………………………………72

LIST OF FIGURES

Genus nested within tribe was fitted as a random intercept term in the model to partially account for evolutionary constraints.

Figure 2.5. Tribe-level relationships between range size (km^2, 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 is shown in brackets after the tribe name.

Figure 2.6. 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 2.7. 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 ($p < 0.05$).

Figure 3.1. Conceptual diagram based on the information from the literature about which floral traits are associated with each dispersal syndrome. Also shown are leaf and growth form functional traits that would be expected also to be associated with particular dispersal syndromes. Plant height and floral traits can function together to influence dispersal mode (either wind, epizoochory or endozoochory) and also to change the ecosystem community in a different environment.

Figure 3.2. Dendrogram plot of hierarchical clustering of 163 grass species grouped based on similar floral trait syndromes, group A (in red colour), group B (in blue colour), group C (in green colour) and group D (in black colour).

Figure 3.3. Non-metric multi-dimensional scaling (NMDS) ordination of grass species in two-dimensional space based on six floral traits (lemma awn action, callus sharpness, lemma awn length and fertile spikelet length, dispersal unit and hooks/prickles). Orthogonal axes of trait variation are indicated by arrows representing directions of increase in trait values. Also shown is the hierarchical clustering of the four main groups projected onto the NMDS. *Note: Species abbreviations are used – full names can be found in Appendix B, Figure S3.6. The species abbreviations are formed by the first three letters of the genus name and plus the first three letters of the specific epithet. Some species are not represented in biplot to reduce overlap and increase clarity.

Figure 3.4. Different grass flowering structures according to the clustering groups, A) long active lemma awn and sharp callus (Fish et al., 2015; Artists: S. B. Chiliza, M. Franks, W. Roux, C. Smith); B) passive lemma awns and a blunt callus (Fish et al., 2015; Artists: S. B. Chiliza, W. Roux, M. Ueckermann); C) no lemma awns, blunt or no callus sharpness (Fish et al., 2015; Artists: S. B. Chiliza, C. Letty, W. Roux); and D) hooks/prickles or bristles and no callus sharpness (Fish et al., 2015; Artists: S. B. Chiliza, B. Connell, M. E. Connell, G.E. Lawrence, C. Smith). Overall species per Group A = 34, Group B = 24, Group C = 94 and Group D = 11.

Figure 3.5. Boxplots show the relationship between floral traits among four clustering groups, A) lemma awn length, B) fertile spikelet length, C) callus sharpness, D) awn action and E) hooks/ prickles vs clustering groups were significant ($p < 0.001$); F) dispersal unit vs

clustering groups was not significant (p =0.322). Four clustering groups are: Group A: long active lemma awn and sharp callus, Group B: passive lemma awns and a blunt callus, Group C: no lemma awns, blunt or no callus sharpness, and Group D: hooks/prickles and no callus sharpness.

Figure 3.6. The associations between dominance disturbance regime of 163 species (fire, intermediate or grazing environment) and clustering groups. Four clustering groups are: Group A: long active lemma awn and sharp callus, Group B: passive lemma awns and a blunt callus, Group C: no lemma awns, blunt or no callus sharpness, and Group D: hooks/prickles and no callus sharpness. The clustering Group A and B are dominated by fire grasses, whereas Group C and D are dominated by grazing grasses.

Figure 3.7. Boxplots showing how (A) lemma awn length and (B) fertile spikelet length varies in relation to the environment the grasses are generally found in. Grazing grasses have significantly (AOV P = 0.001) shorter awns than fire grasses. However, there is no difference in their spikelet lengths (AOV P = 0.193).

Figure 3.8. Graph showing the associations between 163 grass species in 14 tribes and clustering of groups. The clustering Group A is dominated by Andropogoneae Group B is dominated by Cynodonteae and Group C and D are dominated by the Paniceae tribe.

Figure 3.9. Tribe random effect intercept estimates from the linear mixed effect model, which assessed lemma awn length in response to plant height. The model was fitted to data for 67 long lemma awn grass species representing 10 tribes in African countries. Tribe Andropogoneae, Aristideae and Tristachydeae had an intercept > 0.0, whereas Arundineae, Eragrostideae and Paniceae, Poeae and Triraphideae had an intercept < 0.0, while intercept estimates for Brachypodieae and Cynodonteae overlapped zero.

Figure 3.10. The tribes fitted as a random effect, which assessed log lemma awn length (mm) in response to log of seed mass (g). The model was fitted to data for 38 grass species representing 6 tribes in African countries. Three tribes Andropogoneae, Aristideae and Tristachydeae had longer lemma awns and large seeds, whereas Cynodonteae, Eragrostideae and Paniceae tribes had short lemma awns and small seeds.

Figure 4.1. The phylogeny by Hackel et al. (2018) merged with the 97 grass species from 29 genera in the subtribe Eleusininae. There was only DNA data for 33 species in 19 genera; the other species were given the genus age. The phylogenetic tree indicates that the current species have a range of ages, that awns are ancestral characters in the Eleusininae, and that species without awns have evolved several times. Therefore, this is an appropriate subtribe to test the hypotheses about the importance of dispersal mode and genus age on range size.

Figure 4.2. Boxplots show the relationship between lemma awn state (absent= 0 and present=1) among three functional and floral traits, A) grass species with awned lemmas tended to have a large caryopsis/grain (these floral traits show a significant positive relationship with lemma awn state where $p < 0.001$); B) there was no relationship with height($p = 0.655$); C) genus age shows a slight difference in the species with lemma awn present/absent ($p< 0.001$).

Figure 4.3. Correlation relationships between range size (km^2, log-scale) and plant height (mm, log-scale) for 97 grass species in the subtribe Eleusininae globally with lemma awn state, awn present (solid symbols and line) or awn absent (light symbols and dash line). The shaded areas represent the 95% confidence interval for plant height and lemma awn state coefficient estimates.

Figure 4.4. Correlation relationships between range size (km^2, log-scale) and plant height (mm, log-scale) for 97 grass species in the subtribe Eleusininae globally: the linear model was run on continuous caryopsis (mm, log scale) data, but for visualisation I plotted the response to the mean size, as well as the mean+-1 standard deviation. The relationship with height does not vary with caryopsis size. The shaded areas represent the 95% confidence interval for plant height and log caryopsis coefficient estimates.

Figure 4.5. Correlation relationships between range size (km^2, log-scale) and log genus age (million years ago) of the 97 grass species of 29 genera, shows that there is no significant relationship between these two variables. The shaded areas represent the 95% confidence interval for the range size and log genus age coefficient estimates (coefficient = -0.817, p-value = 0.199). Many species have the same age because they could only be assigned a genus age. This might limit the strength and power of the analysis.

Figure 5.1 From Visser *et al*. (2012); Figure 2. Predicted distribution of species richness for the four major C4 grass clades. Darker colours represent a high number of species for a particular clade in South Africa.

LIST OF TABLES

Chapter 1 | General introduction

Background, rationale, aims and objectives

1 | General Introduction

1.1 Background

The Poaceae or Gramineae grass family is the fifth largest plant family worldwide, ranking behind only Asteraceae, Fabaceae, Orchidaceae and Rubiaceae in number of species. There are about 700 genera worldwide and approximately 11 000 grass species (Clayton *et al.*, 2015), but southern Africa is represented by ± 978 species in ± 200 genera (Fish *et al*., 2015). Grasses started evolving at least in the late Cretaceous or Paleocene and occurred at or after 55–70 million years ago and achieved their worldwide distribution due to long-distance dispersal mechanisms (Christin *et al.*, 2014), and through harnessing fire and grazing to create appropriate habitat (Linder *et al*., 2018). Poaceae is the dominant vegetation in the tropics, Arctic and Antarctic areas and occurs in all habitats including swamps, deserts, forests, mountain tops and seashores. Ecosystems dominated by Poaceae cover almost 31–43% of the land surface (Gibson, 2009; Linder *et al*., 2018; Archibald *et al*., 2019). It is therefore an important family, both ecologically and economically. Grasses are cultivated especially as food for humans and animals. In fact, they are the major source of all our food (grains and fodder for livestock) (Strömberg, 2005; Fish *et al*., 2015; Linder *et al.*, 2018). Grasses are also cultivated for lawns and erosion control, as well as garden ornamentals (Van Oudtshoorn, 2014; Fish *et al*., 2015).

1.1.1 The value and potential of using taxonomic resources to explore ecological questions

Increasingly, researchers are realizing the potential of using taxonomic data for asking ecological questions. Some of the main herbaria house several hundreds of thousands of plant vouchers from across the globe, and these are increasingly being digitized and converted into formats that are accessible for researchers from other disciplines to use. The geolocation data and detailed information on plant characters that are provided by classic taxonomic vouchering approaches provide information at large spatial scales; and linking these functional traits with data on the evolutionary history and phylogenetics of different plant groups enables important biogeographic and ecological questions to be asked.

South African National Biodiversity Institute (SANBI, https://www.sanbi.org/) conducts nationwide biodiversity conservation assessments of various plants and animals, which involve field trips for the collection data. Data on the identified and occurrence of South African grasses have been compiled at the SANBI herbarium by G.E. Gibbs Russell, L. Watson, M. Koekemoer, N.P. Barker, H.M. Anderson, M.J. Dallwitz, L. Fish (Smook), A.C. Mashau, M.J. Moeaha and M.T. Nembudani between 1980's–2015 (Gibbs Russell *et al*. 1990; Fish *et al*., 2015). A biodiversity knowledge and information management system by SANBI integrated with the existing information resources of database such as Botanical Database of southern Africa (BODATSA/BRAHMS) (BODATSA, 2019) and Global Biodiversity Information Facility (GBIF.org, 2019) which can be access by both internal and external users. Kew Royal Botanic Garden, UK integrated their biodiversity information to Plants of the World Online (POWO, 2019) and GrassBase (Clayton *et al*., 2015) which are freely accessible.

1.1.2 Range size or spatial distribution

Range size is a measure of the size of the geographical area (Brown *et al.*, 1996; Gaston, 2003; Morueta-Holme *et al.*, 2013, Sheth *et al.*, 2020) where the species occurs. Geographic range size can change through time due to the evolutionary and ecological characteristics of a species (Gaston & Fuller, 2009). Due to human impact, organismal range sizes are changing, and assessing current range size, and its drivers, is important for assessing extinction risk and adaptation capacity (Manne *et al.*, 1999; Staude *et al.*, 2020). Moreover, invasion is the process of increasing range size and understanding and managing invasions requires understanding the factors constraining range size. Once a species is 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).

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 (Murray *et al.*, 2002; Kristiansen *et al.*, 2009). However, there is evidence that the importance of plant height in driving dispersal also depends on the dispersal mode employed (Thomson *et al.*, 2011). As well as affecting dispersal, plant height also increases competitive ability, which increases establishment success and can lead to larger range sizes, as can long generation times, but can slower mutation rates associated with tall plants (Lanfear *et al*., 2013) will increase genetic isolation and promote speciation, and will result in smaller range sizes (Sheth *et al*. 2020).

Understanding the emergent effects of these sometimes counter-acting processes is key to explaining the drivers of range size. Finally, a recent meta-analysis by Sheth *et al.* (2020) of the factors predicting geographic range size in plants showed niche breadth (habitat suitability) to be consistently important. A plant can have a large range size but still not be dominant in any of the environments that it occurs in. Whether plants with large ranges are also the dominant species in their environments is therefore an interesting question – and would imply a correlation between the ecological factors promoting large range size and competitive ability.

Plant lifespan is an independent factor that affects range size through impacts on reproduction and establishment. Annual-biannual grass species have higher reproductive allocation than perennial grasses (Wilson & Thompson, 1989; Vico *et al*., 2016), and this has been shown to correlate with dispersal distance and hence range size (Sonkoly *et al*., 2017). Therefore, 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 an overall lower range size (Sheth *et al*., 2020).

1.1.3 Grass dispersal modes

The dispersal of plant seeds is likely to influence the range size of certain species because long-distance dispersal (Thomson *et al*. 2018) is the major mechanism for range expansion and invasion of a species into new suitable environments (Murray *et al*., 2002; Kristiansen *et al*., 2009). Environmental factors such as fire and herbivory are likely to influence grass reproduction and also dispersal (Forrestel *et al*., 2015; Archibald & Hempson, 2016; Linder *et al*., 2018). Grasses are mainly wind pollinated, although bees and other insects feed on grass pollen, thereby contributing to the pollination process (Clayton & Renvoize, 1986; Kellogg, 2015). In wind-pollinated plants, height is important for gene-flow (Gallagher, 2016; Boucher *et al*., 2017), and in plants with larger inflorescences outcrossing is likely to appear frequently because large inflorescences produce many seeds (Kellogg, 2015). Grass species are shown to vary morphologically between clades and due to that, certain dispersal syndromes of floral traits would likely be associated with particular strategies for dispersal (Kellogg, 2015).

Epizoochory and endozoochory are dispersal modes that may play an important role in the evolution and life history of grass species (Rosas *et al*., 2008). Both epizoochory and endozoochory can be effective mechanisms for dispersing seeds over long distances (Rosas *et al.*, 2008; Anderson *et al.*, 2014). More studies are still needed on why endozoochory species become dominant in certain environments where there is a high population of herbivores (Anderson *et al*., 2014). Based on the literature one would expect that animal-dispersed seeds would have larger range sizes than wind-dispersed seeds (Rosas *et al.*, 2008; Anderson *et al.*, 2014), and that the importance of grass height in driving dispersal distance (and therefore, potentially range size) would be higher for wind-dispersed seeds (Thomson *et al*., 2018). The positive relationship between seed mass and dispersal structure mass is thought to be useful to help larger seeds to disperse further (Edwards *et al*., 2006).

1.2 Rationale

The first comprehensive account of the geographical distribution and plant characters of the ± 978 southern African grass species in ± 200 genera was by Fish *et al.* (2015). This, together with geographic location data from GBIF, provided an opportunity to study the drivers of range size and dispersal of the southern African native grass species in sub-Saharan Africa, and to test theories around the relative importance of dispersal potential, niche breadth, environmental variability and age as drivers of range size (Sheth *et al.*, 2020). Grass floral structures vary greatly but we have very little understanding of their functional significance. Therefore it was first necessary to determine what floral structures and syndromes exist in African grass species, how these are correlated with key drivers of grasslands such as fire and grazing, and which dispersal syndromes these floral structures are associated with. Quantifying this floral trait diversity and its ecological correlated will enable better understanding of how floral traits link with specific dispersal syndromes in this important plant family, and importantly, the degree to which they are associated with other key plant characters and the broader life history strategy schemes shown in tropical grasslands.

1.3 Aims and objectives

The study aims to understand the drivers of range size and dispersal traits of grasses in Africa with the purpose of quantify differences between clades and functional types, and to determine the floral traits that likely influence dispersal modes.

The thesis is written as three separate data chapters, each intended to be submitted as a stand-alone manuscript. **Chapter 2** has already been published in the Journal of Biogeography. In this chapter I aimed 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. The objectives are: to quantify the range size of the full data set of 757 native grass species in 144 genera and 12 tribes to southern Africa and were estimated for the sub-Saharan African region and I analysed the range size as a predictor of invasiveness of the 250 grass species that are native to South Africa and that have been introduced to Australia, Chile, Europe and/or the USA.

Chapter 3 has been written to be submitted to the Journal Biotropica. In this chapter I aimed to describe the range of floral structures in a range of tropical grasses from African countries and assess how they covary and whether one can identify particular floral trait syndromes. I quantified floral traits of nearly 200 Poaceae species from savanna and grassland ecosystems in southern Africa and explored how their floral structures co-vary and correlate with other functional characteristics such as grass height. Using field information on the dominance disturbance regime of 163 of these grass species I tested whether certain floral traits are more associated with fire vs grazing.

Chapter 4 has been written to be submitted to the Journal of Vegetation Science: Here I expanded my analysis to a global scale, but focused on just one grass clade which varied in its floral structures. The aim was to assess how dispersal syndrome (inferred from floral structures and other functional traits) and evolutionary history affect range size in the grass subtribe Eleusininae – a tropical grass clade with variation in floral structures. i.e. I integrated information from both **Chapters 2** and **Chapters 3** to test some of the hypotheses that arose from that work. I systematically sampled 97 grass species from 29 genera of the subtribe

Eleusininae across the globe. The objectives were to quantify key dispersal traits, age, and range size and test the relationship between range size and interaction between plant height and lemma awn state (absent/present), caryopsis and genus age.

Chapter 2 | Plant height and lifespan predict range size in southern African grasses

This chapter has been published in the Journal of Biogeography

Mashau, A. C., Hempson, G. P., Lehmann, C. E. R., Vorontsova, M. S, Visser, V. & Archibald, S. (2021). Plant height and lifespan predict range size in southern African grasses. *Journal of Biogeography*. 48(12): 3047–3059. https://doi.org/10.1111/jbi.14261

AUTHORS' 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.

2.1 | 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 appears 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.

Keywords: alpha hull, biogeography, distribution, extent of occurrence (EOO), invasive, phylogeny, Poaceae, range size

2.2 | 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 (Pyšek *et al*., 2009; Hui *et al*., 2011; Procheş *et al*., 2012).

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 2.1). 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.

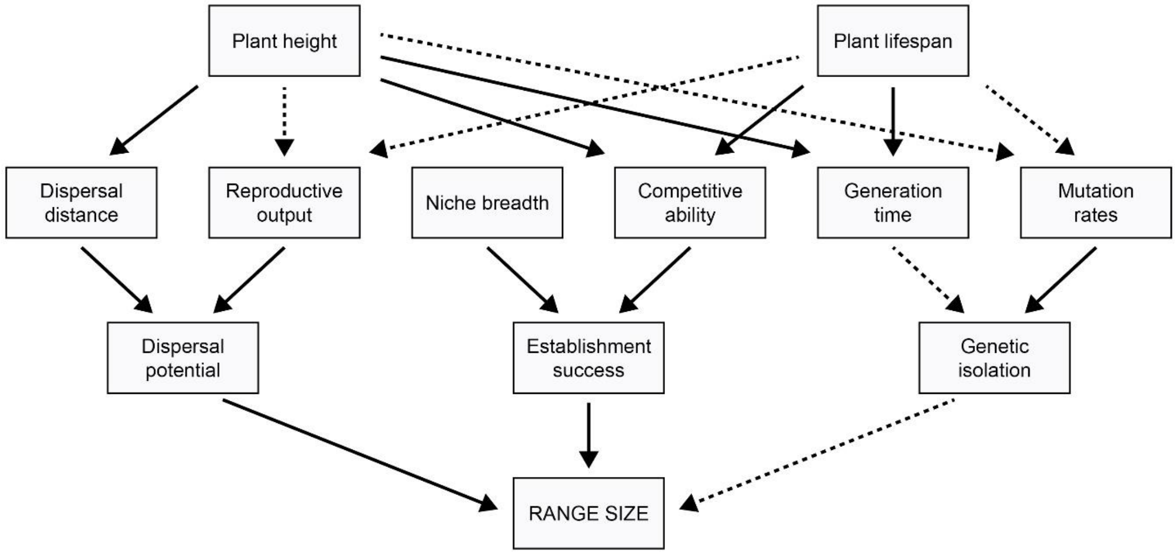

Figure 2.1 Conceptual diagram showing the various mechanisms by which grass height and lifespan could affect range size. Solid lines represent positive relationships and dashed lines represent negative relationships. Plant height can increase range size by increasing dispersal potential, but decrease 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 an 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).

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 enables 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, are important determinants of range size (Gallagher, 2016; Sheth *et al*., 2020). However, Baselga *et al*. (2012) found that while 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 (Westoby, 1998; Diaz *et al*., 2016) and evolutionary processes (Lanfear *et al*., 2013; Boucher *et al*., 2017) 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 2.1). 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 2.1). 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 (Gibson, 2009; Linder *et al*., 2018; Archibald *et al*., 2019), 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 C_3 and C_4 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 (Hui *et al*., 2011; Canavan *et al*., 2019). 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 2.1, 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 C_3 grass photosynthesis in sub-Saharan Africa is limited to montane and winter rainfall regions, principally the southernmost part of the continent (Vogel *et al*., 1978; Scott, 2002). Habitat suitability would therefore be expected to be the major constraint on the range size of C_3 grasses, and in most C_3 grass tribes the relationship with height or lifespan would then be less apparent than in tribes primarily comprised of C_4 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 introduction, we expect that factors that promote larger native range sizes will likely also enhance the probability of a species becoming invasive.

2.3 | Materials and Methods

2.3.1 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 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 waterbodies, 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 2.2) represents sampling intensity (records) prepared using R (R Development 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 discussion below).

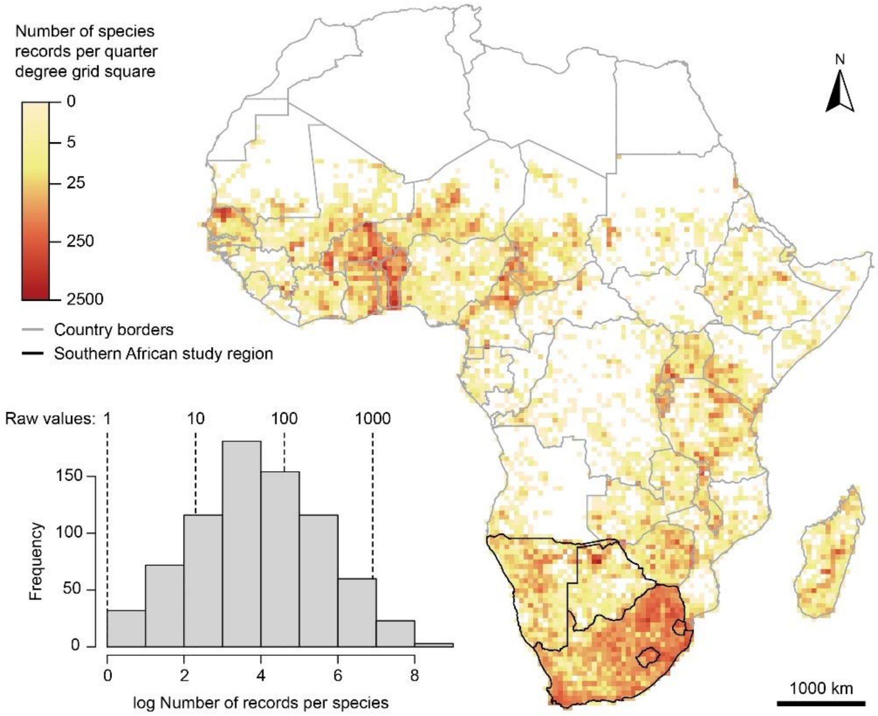

Figure 2.2 Map of the study area showing the number of GBIF records for Poaceae per quarter degree grid square, which provides an indication of the variation in sampling effort across the continent. The 757 species assessed in this study are all native to the region occupied by the five southern African countries outlined in black, however, their range sizes were calculated for the entire sub-Saharan Africa region including Madagascar.

2.3.2 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 towards Fish *et al*. (2015). Lifespan is the length of the 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. C_3 or C_4), 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.

2.3.3 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 & 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 *et al*., 2017; Dauby, 2020). 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 Appendix A: Figure S2.1 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 (Appendix A: Figure S2.1). We found that using alpha = 100 km (5 km buffer), 200 km 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 Appendix A: Tables S2.1-S2.4 and S2.6-S2.8). 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 km, 20 km and 30 km to provide range size estimates to complete the data sets with alpha values of 100 km, 200 km 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.

2.3.4 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 (Appendix A: Figure S2.2).

2.3.5 Statistical analyses

2.3.5.1 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).

2.3.5.2 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 Akaike's Information Criterion (AIC), with the simplest model with $\Delta AIC < 4$ 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 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.

2.3.5.3 Tribe level range size vs 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 low representation of annual species (<= 2 species).

2.3.5.4 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, a 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 tribe was fitted as a random effect. The 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). All analyses were done in the R environment (R version 3.5.1; R Development Core Team, 2021).

2.4 | Results

The median range size of southern African Poaceae was c. 120 000 km^2, with an interquartile range of c. 25 000 km^2 to 520 000 km^2 (Figure 2.3). However, 7 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).

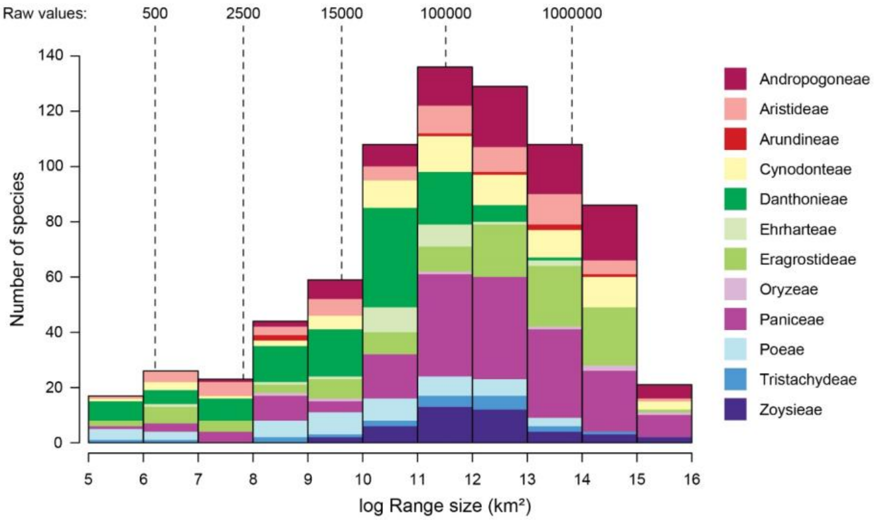

Figure 2.3 Histogram of the range sizes (km^2, log-scale) of southern African grasses, estimated using the alpha hull method with alpha = 200 km. Tribe-level range size distributions are indicated by stacked colour bands.

2.4.1 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 (Appendix A: Table S2.1 & S2.2; Figure S2.3; $r^2 = 0.14$), with no clear evidence for an interaction between these predictors ($p = 0.828$; $\Delta AIC = 1.952$). 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 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 km^2 to 455 000 km^2, and for a perennial grass from c. 77 000 km^2 to 152 000 km^2. 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.

2.4.2 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 2.4). The best model included height and lifespan as additive effects (Appendix A: Table S2.3 & S2.4; Figure S2.4; marginal $r^2 = 0.08$, conditional $r^2 = 0.25$), with no clear evidence for an interaction between these predictors ($p = 0.662$; $\Delta AIC = 1.808$). Consistent with the phylogenetic analyses, height had a positive effect on range size ($\beta \pm SE = 0.872 \pm 0.127$, $p < 0.001$), and range sizes for perennial grasses were significantly smaller than for annual-biannual grasses ($\beta \pm SE = -0.870 \pm 0.170$, $p < 0.001$). 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 (Appendix A: Figure S2.5).

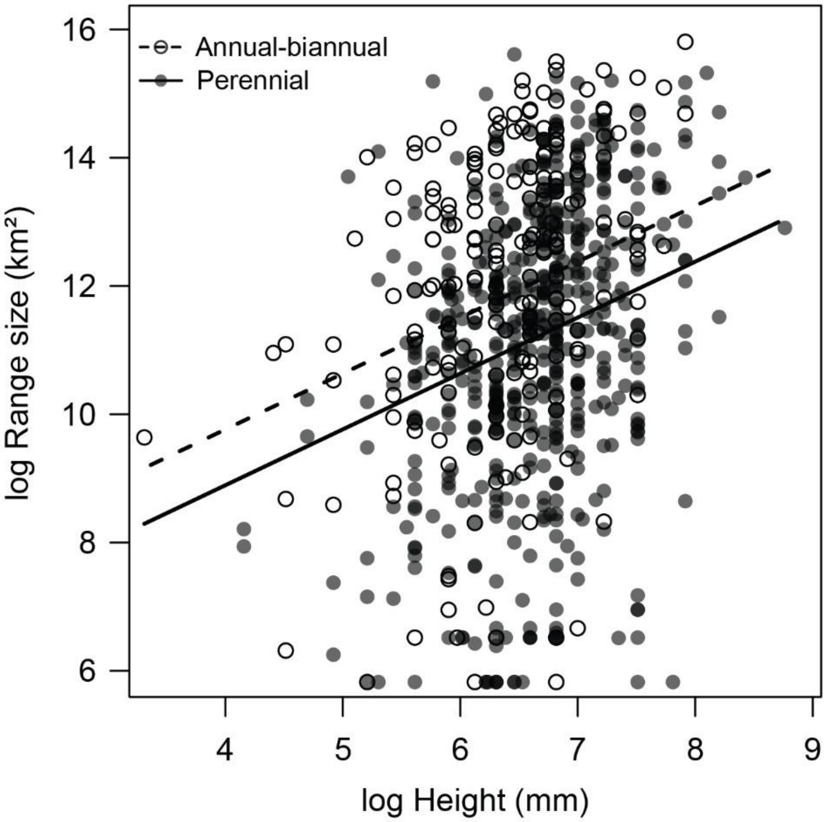

Figure 2.4 Relationships between range size (km^2, log-scale) and plant height (mm, log-scale) for 757 southern African grasses with annual-biannual (open symbols and dashed line) or perennial (solid symbols and line) lifespans, as estimated by a linear mixed effects model. Genus nested within tribe was fitted as a random intercept term in the model to partially account for evolutionary constraints.

2.4.3 Tribe level range size vs plant height relationships

The linear models showed that most C_4-dominated tribes (Andropogoneae, Aristideae, Eragrostideae, Paniceae and Zoysieae) had positive significant relationships with plant height (Figure 2.5; Appendix A: Table S2.5), with the exceptions being the Cynodonteae and Tristachydeae, where height had a non-significant effect on range size. Among the C_3 tribes, the Arundineae, Oryzeae and Poeae had significant and positive height vs. range size relationships, but this relationship was non-significant for the Danthonieae and Ehrharteae.

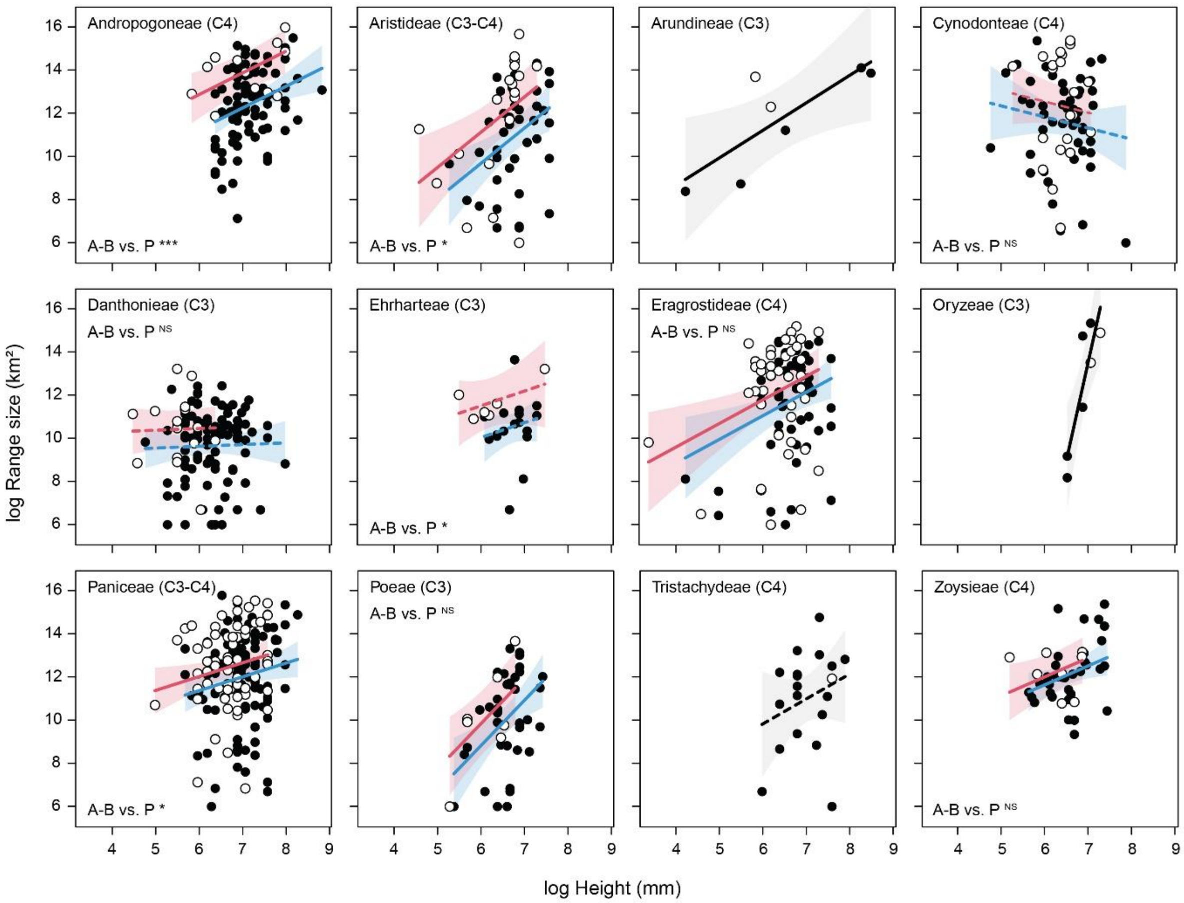

Figure 2.5 Tribe-level relationships between range size (km^2, log-scale) and plant height (mm, log-scale) and plant lifespan (annual-biannual vs. perennial) for 757 species in 144 genera and 12 tribes of southern African grasses. Linear models were fitted to species range size data for each tribe separately, 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. C_3 and/or C_4) occurring in each tribe is shown in brackets after the tribe name.

2.4.4 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 2.6). The best GLMM model included range size and lifespan as additive effects, and tribe as a random effect (Appendix A: Table S2.6 & S2.7; marginal $r^2 = 0.12$, conditional $r^2 =$

0.14). Invasiveness was positively related to range size (β ± SE = 0.576 ± 0.167, $p < 0.001$), and perennial grasses had marginally significant lower probability of becoming invasive than annual-biannual grasses (β ± SE = -0.670 ± 0.349, p = 0.055).

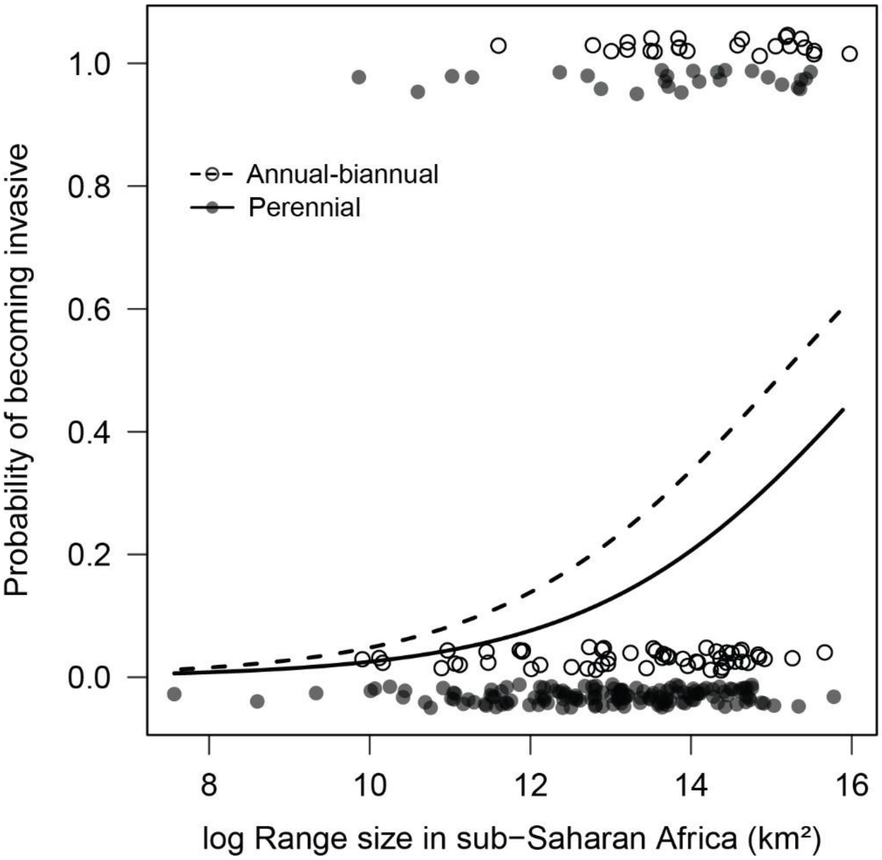

Figure 2.6 Probability of South African grasses becoming invasive following introduction to other continents as a function of their native range size in sub-Saharan Africa (km^2, log-scale) and lifespan (annual-biannual: open symbols and dashed line, or perennial: solid symbols and line). Probabilities 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.

The LMM using all grass species confirmed that range size differences existed between invasion categories (Appendix A: Table S2.8; Figure 2.7 & S2.6). Species that had not been introduced to other continents had significantly smaller range sizes than all other categories (54 567 km^2; $p < 0.001$). Native range size increased steadily along the INI continuum: introduced (377 566 km^2), naturalised (496 481 km^2) and invasive (1 026 022 km^2), although the difference in range size between introduced and naturalised species was not significant ($p > 0.05$).

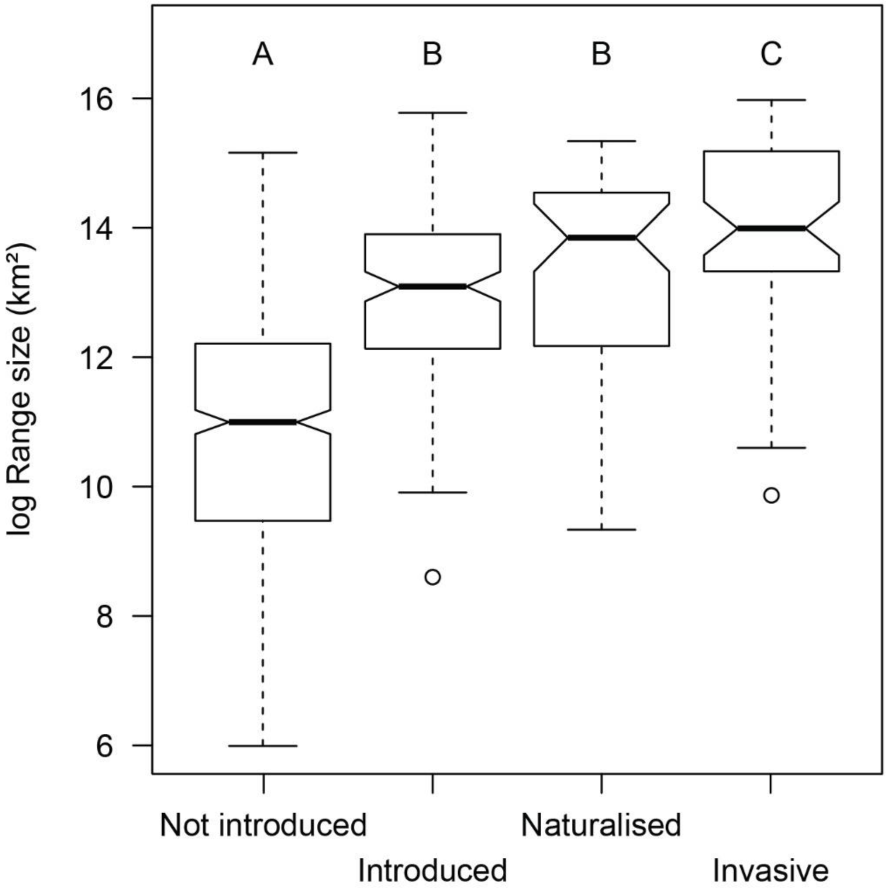

Figure 2.7 Boxplot showing variation in native range sizes among 757 southern African grasses after classification into four invasion status categories: 1) not introduced to other continents, 2) introduced (but not [yet] naturalised or invasive), 3) naturalised (i.e. introduced and now naturalised but 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 ($p < 0.05$).

2.5 | Discussion

We found that grass height has a positive correlation with range size, where taller grasses have larger range sizes (Figure 2.4). 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 2.4). 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 than perennial grasses (Wilson & Thompson, 1989; Vico *et al*., 2016), and often also smaller seeds (Moles *et a1*., 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 (Taylor *et al*., 2010; Ripley *et al*., 2015) at the expense of reproductive effort. Finally, while annual grasses always flower within the first year, many perennial tropical grasses can also produce seed 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 C_3 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 C_4 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 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 C_3 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 C_3 and C_4 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 (Thomson *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 2.5. 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 (Appendix A: Figure S2.5). 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 (Schmidt *et al*., 2011; Fish *et al*., 2015) 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 2.7), and annual-biannual grasses had a significantly higher probability of being invasive than perennial grasses (Figure 2.6). 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 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 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 (Pyšek *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 S2.6). 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 considered a predictor of species extinction risk (IUCN, 2001; Gaston & Fuller, 2009). Grass species with 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 further identify grass species in need of particular protection, especially those with small range sizes.

2.6 | 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.

Chapter 3 | Floral trait syndromes in tropical grasses and their environmental associations

This chapter has been prepared for submission to the Journal Biotropica

3.1 | Abstract

Grass floral structures vary greatly but we have very little understanding of their functional significance. Due to the varied dispersal mechanisms shown by grasses, certain syndromes of floral traits would likely be associated with particular strategies for dispersal, and consequently, different environments. In particular, effective seed maturation and dispersal in fire-prone tall grasslands would require different floral trait syndromes than in short, frequently grazed ecosystems. Here I quantify floral traits of nearly 200 Poaceae species from savanna and grassland ecosystems in southern Africa and explore how their floral structures co-vary and correlate with other functional characteristics such as grass height. Using field information on the dominance disturbance regime of 163 of these grass species it was tested whether certain floral traits are more associated with fire vs grazing and the mean rainfall arranged from 323–1256 mm.yr^{-1} in the study areas. Non-metric multi-dimensional scaling (NMDS) was used to illustrate how floral traits covaried among grass species, and to group them into syndromes based on these traits. Analysis of variance (ANOVA) was used to test whether certain floral trait syndromes were more associated with fire vs grazing. I identified four clear floral trait syndromes separated largely by awn length and the presence of hooks/prickles or bristles. Long-awned species were more likely to be found in frequently burned environments and were also usually taller than species without awns. Grazer-dominated systems appear to select for two different floral trait syndromes which are no lemma awns, blunt or no callus sharpness. The study has improved our ecological and taxonomic understanding of how floral traits differ among the range of tribes in one family across African countries. It can help in understanding dispersal limitations in grasses and predicting which species are likely to flourish in particular grassland habitats.

Keywords: Floral traits, fire, grazing, lemma awn, spikelet

3.2 | Introduction

Grasses (Poaceae) started evolving at least in the late Cretaceous or Paleocene, occurring at or after 55–70 million years ago (Christin *et al*., 2014). The distribution of the grass lineages started to spread from their Gondwanan center of origin after the breaking up of the southern supercontinent (McLoughlin, 2001; Bremer, 2002; Bremer & Janssen, 2006; Bouchenak-Khelladi *et al*., 2010; Christin *et al*., 2014). Members of the subfamily Pooideae have greatly diversified in the northern hemisphere, while the other remaining subfamilies have their greatest diversity in the tropics and on the continents that originated from the break-up of Gondwana (McLoughlin, 2001; Bremer, 2002; Bremer & Janssen, 2006; Bouchenak-Khelladi *et al*., 2010; Christin *et al*., 2014; Kellogg, 2015). The grass lineages achieved their world-wide distribution due to long-distance dispersal mechanisms (Christin *et al*., 2014).

There is a wide diversity of floral structures in grasses, and they are often the main morphological characters distinguishing different grass clades (Kellogg, 2000, 2015). The whole grass flower is called a spikelet (diaspore) (Kellogg, 2015). The spikelet comprises the axis or rachilla with two glumes (bracts) at the base and one or more florets (lemma) borne alternately up the rachilla (Fish *et al*., 2015; Kellogg, 2015). There are fertile and sterile spikelets. Fertile grass spikelets function as a female reproductive organ. The grass reproduction occurs inside the spikelet. Floral structures are fairly phylogenetically conserved, and there are strong links among grass lineages, growth forms and environmental drivers, particularly grazing and fire (Kellogg, 2000; Kellogg, 2015). Accordingly, it is likely that floral trait syndromes, which are linked to both lineages and environmental conditions, will encompass traits that allow effective use of the dispersal opportunities in these different environments.

While grass pollination is mostly (but not exclusively) by wind, dispersal agents are more diverse and include epizoochory and endozoochory (Soderstrom & Calderón, 1971; Huang *et al*., 2002; Sajo *et al*., 2009; Ruiz-Sanchez *et al*., 2017). The dispersal of grass seed is closely associated with the structure and composition of spikelets (Schrager-Lavelle *et al*., 2017) (Figure 3.1).

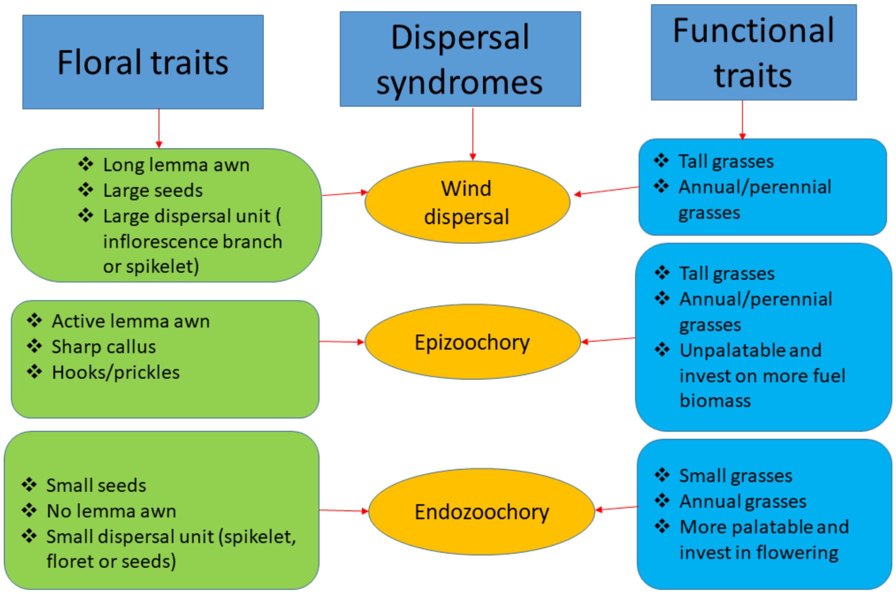

Figure 3.1 Conceptual diagram based on the information from the literature about which floral traits are associated with each dispersal syndrome. Also shown are leaf and growth form functional traits that would be expected also to be associated with particular dispersal syndromes. Plant height and floral traits can function together to influence dispersal mode (either wind, epizoochory or endozoochory) and also to change the ecosystem community in a different environment.

The major adaptive structures that have facilitated a rich diversity of dispersal modes in grasses are the hygroscopic awn – which may or may not be a present, sharp point on the callus, and a range of hooks or bristle structures (Peart, 1979; Clayton & Renvoize, 1986; Davidse, 1987; Peart & Clifford, 1987; Kellogg, 2015). Rosas *et al*. (2008) found that the majority of small seeds were found undamaged in bison dung and therefore the endozoochory by bison proved to be a long-distance dispersal mechanism for small seeds. Others have also found that small, smooth, hard seeds or diaspores are associated with endozoochory (Shiponeni & Milton, 2006; Rosas *et al*., 2008) protecting it from the molar mill and during the passage through the gut. Moreover, the dispersal unit of endozoochorous plants needs to be sufficiently attractive to encourage animals to eat it, so hairs, awns and prickles are likely not to be characteristics of endozoochorous grasses. In contrast, hooks and prickles on the spikelet and lemma awns facilitate epizoochoric dispersal (Davidse, 1987; Kellogg, 2015). The lemma awn is a variable structure among grasses and has been proposed to affect seed dispersal, as well as germination and seedling establishment (Peart, 1979, 1981; Peart & Clifford, 1987; Garnier & Dajoz, 2001;

Elbaum *et al*., 2007). Grass species with active lemma awns, which produces a twisting motion, can help to bury the seeds deeper in the soil and this has been proposed to increase seed survival during fires (Roux, 1969; Schrager-Lavelle *et al*., 2017). Although it has been reported that long lemma awns increase short-distance dispersal of about less than 1 m (Diacon-Bolli *et al*., 2013) there are also references indicating that long awns can be an impediment to dispersal by bury awns into animal fur (Van der Pijl, 1982; Fischer *et al*., 1996; Rosas *et al*., 2008; Clayton *et al*., 2015; Fish *et al*., 2015; Kellogg, 2015; Schrager-Lavelle *et al*., 2017). The size of the dispersal unit can also range widely in grasses – with some species (e.g. *Cymbopogon caesius* (Hook. & Arn.) Stapf, *Hyparrhenia hirta* (L.) Stapf and *Themeda triandra* Forssk.) disarticulating their entire inflorescence, and others only individual florets. Grass species with large dispersal units (inflorescence branch) would enable better wind or water dispersal (Doust *et al*., 2014). However, generally small seeds are also better wind dispersed than large seeds (Thomson *et al*., 2011). For more information about the functions of grass flowering structures see Table 3.1 and Figure 3.1.

The degree to which plant height affects dispersal depends on the dispersal mechanism (Thomson *et al*., 2011; Mashau *et al*., 2021). Thomson *et al*. (2011) documented the response between plant height and dispersal distance, but this was more important for wind-dispersed seeds and those with adaptations for ectozoochory. Plants dispersed by animals through endozoochory are often short, with flowers at the same level as the grass (Janzen, 1984; Anderson *et al*., 2014). Mashau *et al*. (2021) showed that the range size of some grass clades was more strongly related to grass height than others, and hypothesised that this might be related to the common dispersal modes in those clades.

The evolution and maintenance of tropical savanna grasslands are associated with fire and herbivory, as well as rainfall (Forrestel *et al*., 2015; Archibald & Hempson, 2016; Linder *et al*., 2018). Both fire and herbivore pressures are thought to have increased with the spread of grasslands during the Miocene (Forrestel *et al*., 2015; Archibald & Hempson, 2016; Linder *et al*., 2018). In Africa, fire is the dominant consumer in wetter grasslands, and grazing dominates in more arid ecosystems (Archibald & Hempson, 2016), but both fire-maintained and grazer-maintained grassland habitats are common across a wide environmental range and associated with particular grass species and functional types (Hempson *et al*., 2015; Solofondranohatra *et al*., 2020). Because fire-prone grasslands are generally associated with lower herbivore numbers (Staver & Bond, 2014) and taller grass species (Archibald *et al*., 2019), one would expect dispersal modes would also vary across these grasslands. In particular, traits associated with endo- and ectozoochory would be more common under heavy grazing, and traits associated with wind dispersal more common in frequently burned grasslands (Anderson *et al*., 2014). Endozoochorous grass species in particular need to attract grazing herbivores (Janzen, 1984; Rosas *et al*., 2008) and require palatable leaves, which promote consumption by herbivores and subsequent seed dispersal.

Fire and grazing are environmental factors that are related to abiotic and biotic factors such as rainfall and patterns of modern land use (Solofondranohatra *et al*., 2020). Donaldson *et al*. (2018) showed that when grazing increases in a tall-grass fire-prone ecosystem, the grass species are replaced by shorter, more palatable species, but did not investigate how the floral structure changed. Solofondranohatra *et al*. (2020) also found that fire and grazing promote differentiation in community composition with divergent growth forms in Madagascar. If these changes also result in a turn-over in floral traits and dispersal modes it would have implications for biogeographic and evolutionary processes (e.g. population genetics and range size – Boucher *et al*., 2017; Mashau *et al*., 2021). It would also alter food availability for seed-eating birds and rodents (Pakeman, *et al*., 2002; Cousens, *et al*., 2010; Godó, 2022). It is well known that fire and grazing are important environmental factors that determine the evolution and ecology of plant diversity (Donaldson *et al*., 2018; Hempson *et al*., 2019; Solofondranohatra *et al*., 2020).

Finally, Visser *et al*. (2012) demonstrated associations between environmental factors and evolutionary history, with turnover in the dominance of particular clades across gradients of grazing, fire and rainfall. This was confirmed by Solofondranohatra *et al*. (2020), and there is growing evidence that functional attributes are phylogenetically conserved in tropical grasslands (Ripley *et al*., 2015, Griffith *et al*., 2020). Considering that floral characters are key attributes differentiating different grass clades (Kellogg, 2015; Fish *et al*., 2015) it would also be expected that dispersal mode would be strongly correlated with evolutionary history.

In this study, the aim is to describe the range of floral structures in a range of tropical grasses from African countries and assess how they covary and whether one can identify particular floral trait syndromes. I test the hypothesis that, floral trait syndromes are associated with particular environmental factors – fire vs grazing, and how they link to the phylogeny. A predominance of wind dispersal traits in grasses associated with frequent fire, and traits associated with both ecto- and endozoochory in grazing-adapted grasses (Figure 3.1) is expected. A positive relationship between plant height and wind dispersal traits is anticipated. The correlations between floral traits and other functional traits that might interact with floral traits to affect dispersal abilities is assessed.

3.3 | Materials and Methods

3.3.1 | *Classifying species as fire, grazing or intermediate environment*

Species composition data was collected from five sites in Tanzania (Serengeti National Park), 17 sites in Madagascar and 30 sites in southern Africa (including Zambia) and was used to identify 163 common grass species from selected African countries including Madagascar (Donaldson *et al*., 2018; Solofondranohatra *et al*., 2020; Hempson *et al*., 2022). The species composition data were collected according to the GGG protocol (https://globalgrassygroup.github.io/). Mean annual rainfall (mm) ranges from 323–1256 mm of the collected 30 sites (see Appendix B: Table S3.5). Therefore, the dataset covered a large range of the African grassy biome environmental space (Lehmann *et al*., 2011) but did not extend into very arid regions, so we likely missed adaptations associated with extreme aridity. In this environmental space, fire and grazing are two important environmental drivers which are known to filter grass communities and produce very different grassland habitats. The field sites had been classified into “frequently grazed” (grazed continuously for at least 10 years), and “frequently burned” (signs of recent fire and no evidence of heavy grazing). Species were then classified as “grazing”, and “fire” species respectively, based on their dominance at burned vs grazed sites and “intermediate” if a species is common in both burned and grazed sites. In situations where species were classified differently by the three different datasets I took the majority classification as correct. This was rare, however (2 out of 163 cases): generally species classification into fire or grazing species was consistent between datasets.

3.3.2 │ Quantifying floral traits

Grass floral traits thought to be associated with particular forms of dispersal were identified from the literature and are summarised in Table 3.1. Continuous variables used were fertile spikelet length (mm), and lemma awn length (mm), with ordinal variables lemma awn action, callus sharpness, dispersal unit, and hooks/prickles (Table 3.1). These traits were obtained from the Plants of the World Online (POWO, 2019) (http://plantsoftheworldonline.org/, accessed 28 August 2020), GrassBase (Clayton *et al*., 2015) (https://www.kew.org/data/grasses-db.html., accessed 13 June 2020) and also herbarium specimens housed in the National Herbarium (PRE), Pretoria; Compton Herbarium (NBG and SAM), Cape Town; KwaZulu-Natal Herbarium (NH), Durban; and also at Kew Herbarium (K), UK; herbarium acronyms following Index Herbariorum (Thiers, 2020), including species descriptions from the "Identification guide to southern African grasses" (Fish *et al*., 2015). Seed mass was sourced from the Seed Information Database (https://data.kew.org/sid/, accessed 15 September 2020), but was not included in the ordination due to uncertainty in the accuracy of the estimates (some records included other structures besides the seed in the seed mass).

Table 3.1 Indication of how grass floral traits were measured and their ecological functions (especially in relation to dispersal in a fire versus grazing environment).

Floral traits	**Type of data (range of values)**	**Measurement**	**Dispersal in fire vs grazing environment (function)**	**References**
Fertile spikelet length	Continuous (0, X)	Measured (in mm) from the tip of the callus to the longest apex of the glumes or lemmas (awn excluded).	Long or short fertile spikelet (diaspore) functions as the dispersal unit and spikelet consists of lemma and awn that facilitates a wide range of dispersal syndromes.	Davidse, 1987 ; Clayton *et al*., 2015 ; Fish *et al*., 2015 ; Kellogg, 2015 ; Plants of the world online (accessed 20 September 2020)
Lemma awn length	Continuous (0, X)	Lemma principal awn measured (in mm) from where it joins to the lemma.	Long lemma awns thought to aid dispersal by wind and by sticking on animal's fur (epizoochory).	Van der Pijl, 1982 ; Fischer *et al*., 1996 ; Rosas *et al*., 2008 ; Clayton *et al*., 2015 ; Fish *et al*., 2015 ; Kellogg, 2015 ;Schrager-Lavelle *et al*., 2017 ; Plants of the world online (accessed 20 September 2020)

			Long lemma awns reduce dispersal distance (less than 1 m) more than grass with short or without lemma awns.	Diacon-Bolli *et al*., 2013 ; Schrager-Lavelle *et al*., 2017
Lemma awn action	Ordinal: 0 = none (no awn) 1 = passive 2 = active	Awns may consist of a twisted/coiled column (hygroscopic) and a flat, straight part (passive) sometimes referred to as the bristle or limb. Three types were identified: none, passive and active (hygroscopic).	When moist the hygroscopic awn drills the floret or spikelet into the soil and can survive high fire intensity.	Roux, 1969 ; Peart, 1979 ; Elbaum *et al*., 2007 ; Molano-Flores, 2012 ; Schrager-Lavelle *et al*., 2017.
			Hygroscopic (active) lemma awn is an adaptation to penetrate dead plant matter and access the soil in systems where there has been no fire and the grass is moribund.	Roux, 1969 ; Anderson *et al*., 2014 ; Clayton *et al*., 2015 ; Fish *et al*., 2015 ; Kellogg, 2015
			Hygroscopic (active) and passive awn assists floret to disperse by wind because during wind floret structure blows away from the spikelet.	Davidse, 1987
Callus sharpness	Ordinal: 0 = none (no callus) 1 = blunt 2 = sharp	The hard projection can be pungent, obtuse, acute and bifid or 2-toothed. All shapes were categorised into three types: sharp, blunt and none.	The sharp callus helps to penetrate in animals' and humans' skin (drives long-distance dispersal), whereas the use of a blunt callus has not been described yet.	Van der Pijl, 1982 ; Fischer *et al*., 1996 ; Clayton *et al*., 2015 ; Fish *et al*., 2015 ; Kellogg, 2015
Hooks and prickles	Ordinal: 0 = absent 1 = present	Hooks/prickles are spine-like outgrowths found on the lowest bracts (glumes) of the spikelet (e.g. *Tragus* spp.). They were either absent or present.	Hooks/prickles enable attachment to animals' fur, skin, feathers or people's clothes and also assist the spikelet to disperse by blowing away from the main inflorescence by the wind.	Davidse, 1987 ; Van der Pijl, 1982 ; Fischer *et al*., 1996 ; Clayton *et al*., 2015 ; Anderson *et al*., 2014 ; Fish *et al*., 2015 ; Kellogg, 2015
			Hooks/prickles make spikelets unpalatable to insects.	Not described/mentioned yet.
Seed mass	Continuous (0, X)	Seeds measurements were extracted from the Seed Information Database. Seed mass may or may not contain some error values due to minor covering structure.	Seeds contribute to the widespread dispersal of grasses. Small seeds can survive in animal guts and disperse longer distances through endozoochorous mechanisms.	Janzen, 1984 ; Anderson e*t al*., 2014 ; Kellogg, 2015 ; Seed Information Database (accessed 15 September 2020)
			Large seeds may possibly be palatable and attractive to herbivores as forage.	Not described/mentioned yet.
Dispersal unit	Ordinal: 0 = seed 1 = floret 2 = spikelet 3 = inflorescence branch	Parts of the grass inflorescence have been modified for dispersal. The dispersal unit varies based on the point where it disarticulates from the main plant: Disarticulation parts are: seed, floret, spikelet and inflorescence branch.	Grasses can disarticulate in a different part of the inflorescence during dispersal. Dispersal units can influence different dispersal modes depending on the inflorescence structure.	Doust *et al*., 2014 ; Clayton *et al*., 2015 ; Kellogg, 2015

3.3.3 | Statistical analysis

3.3.3.1 │ Clusters of grass species into floral trait syndromes

Hierarchical clustering analysis was performed in R Development Core Team (2021). Because many of the traits were categorical, the Ward D method and Gower's distance similarity index (Gower, 1971) was used to determine the similarity distance between different grass species based on the grass floral traits. The hierarchical clustering analysis of 163 grass species were used to create clusters/groups based on Gower distance similarities on the floral trait syndromes.

3.3.3.2 │ Dimensions of variation in floral traits

Non-metric multi-dimensional scaling (NMDS; Nielsen, 2000) was used to display variation in six grass floral traits (lemma awn action, callus sharpness, lemma awn length and fertile spikelet length, dispersal unit and hooks/prickles) of 163 grass species based on the Gower similarity matrix (Gower, 1971). NMDS stress values were used to evaluate the number of suitable ordination dimensions (*k*) using the metaMDS function in the "vegan" package in R Statistical software (Oksanen, 2015; R Development Core Team, 2021)

3.3.3.3 │ Associations between floral trait syndromes, dominance disturbance regime and phylogenetic relationships

For a full dataset of the data for which I had habitat-preference information (163 species), I used a chi-square test to assess whether the floral trait syndromes were evenly spread across these habitats or whether certain floral trait syndromes dominated in particular environments. I used the same chi-square analysis to test whether floral syndromes were evenly spread across different grass tribes.

Analysis of variance (ANOVA) was used to test whether the continuous variables of fertile spikelet length (mm) and lemma awn length (mm) were associated with environment (fire vs grazing). The Chi-square test was used to test the relationship between ordinal variables and category (three-level factor: fire, intermediate and grazing), with pairwise differences assessed based on Tukey's Honest Significant Difference (Tukey's HSD) tests. Again the ANOVA performed on the clustered groups vs floral traits (fertile spikelet length (mm), lemma awn length (mm)), callus sharpness, awn action, hooks/ prickles and dispersal unit). This analysis was done in the R environment (R version 3.5.1; R Development Core Team, 2021). The continuous variables were log-transformed to conform with the assumptions of the ANOVA test.

Linear mixed effect models (LMMs) were fitted to test the relationship between the presence of a lemma awn (binomial variable) and plant height using the full data set of 163 grass species in 14 tribes. So, the LMMs were fitted to test the relationship between lemma awn length and plant height in a reduced dataset of 67 lemma-awned species in 10 tribes. The random-effects component of the models accounted for differences in intercepts among grass tribes. Lemma awn length (mm) was log-transformed. Binomial models with a logit link function were fitted with species classified as lemma awn present scored as 1, and lemma awn absent scored as 0 in relation with plant height and tribes as a random effect. 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. LMMs were also used to test for associations between seed mass (g) and lemma awn length for 38 species in 6 tribes, for which I had reliable seed mass data.

3.4. │ Results

3.4.1 │ Groups of grasses with similar "floral trait syndromes" (clustering)

A cluster analysis (Figure 3.2) identified four floral trait syndromes, which are indicated by convex hulls in Figure 3.3. These four groups are listed in a Table format showing tribe allocations and combinations of floral traits association within each group (Figure 3.2).

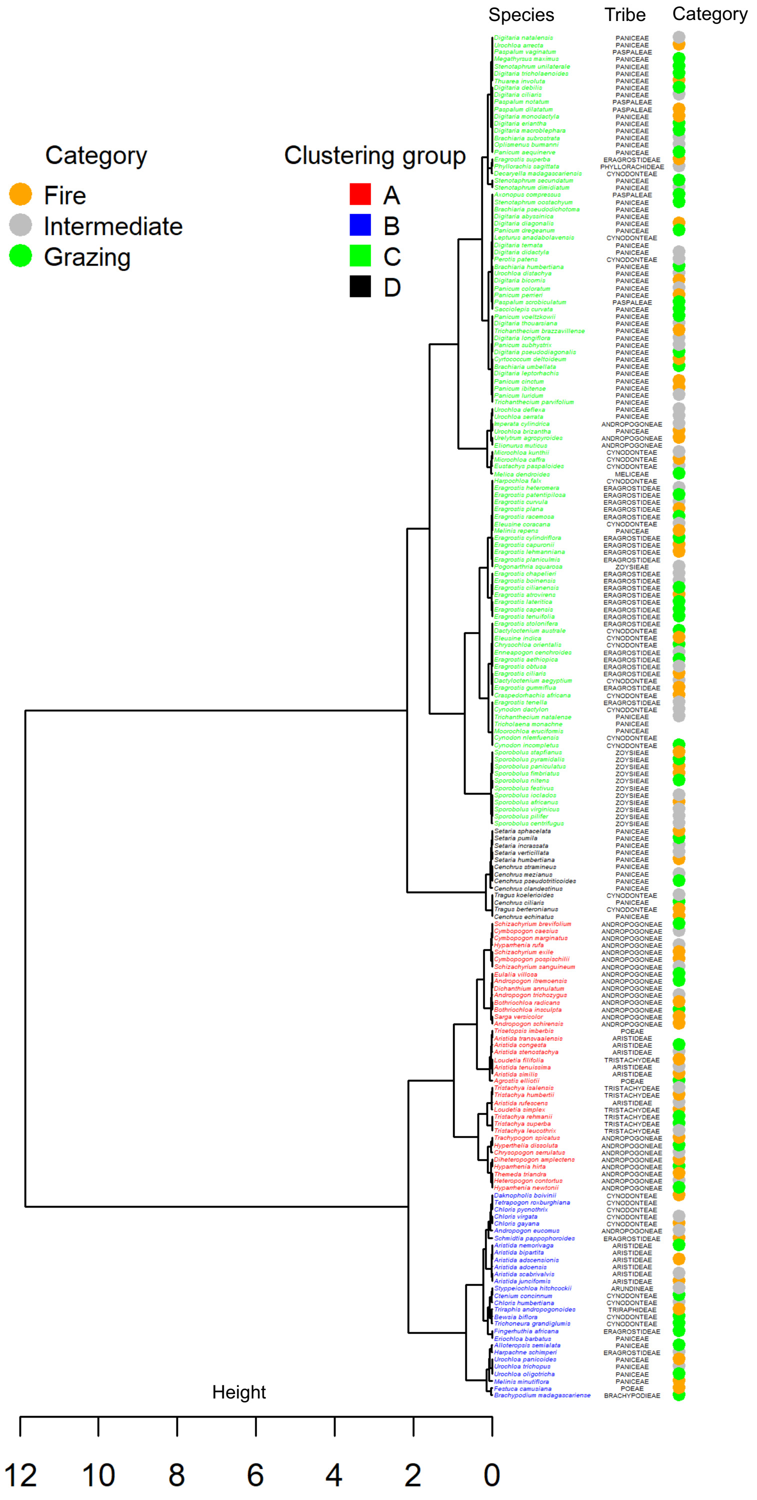

Figure 3.2 Dendrogram plot of hierarchical clustering of 163 grass species grouped based on similar floral trait syndromes, group A (in red colour), group B (in blue colour), group C (in green colour) and group D (in black colour).

3.4.2 | Dimensions of variation in floral traits

A stable NMDS ordination for the two-dimensional solution using Gower distances for similarities was found after 20 iterations and had a final stress value of 0.077 (Figure 3.3). The primary axis (NMDS1) was associated with awn traits and callus sharpness, whereas the secondary axis (NMDS2) was linked with fertile spikelet length, hooks/prickles, and dispersal units. Grass species formed four groups corresponding with the previous cluster analysis (Figure 3.2). Groups were organised according to gradients of the key traits, i.e., Group A (34 species) typically had sharp calluses and long active lemma awns (active awns are significantly longer than passive awn), whereas Group B (24 species) had passive lemma awns and blunt calluses, Group C (94 species) had no lemma awns, blunt or no callus sharpness – Group D (11 species) had hooks/prickles and no callus sharpness. All linear regressions of traits in the NMDS orthogonal axes of variation were significant (Appendix B: Table S3.1).

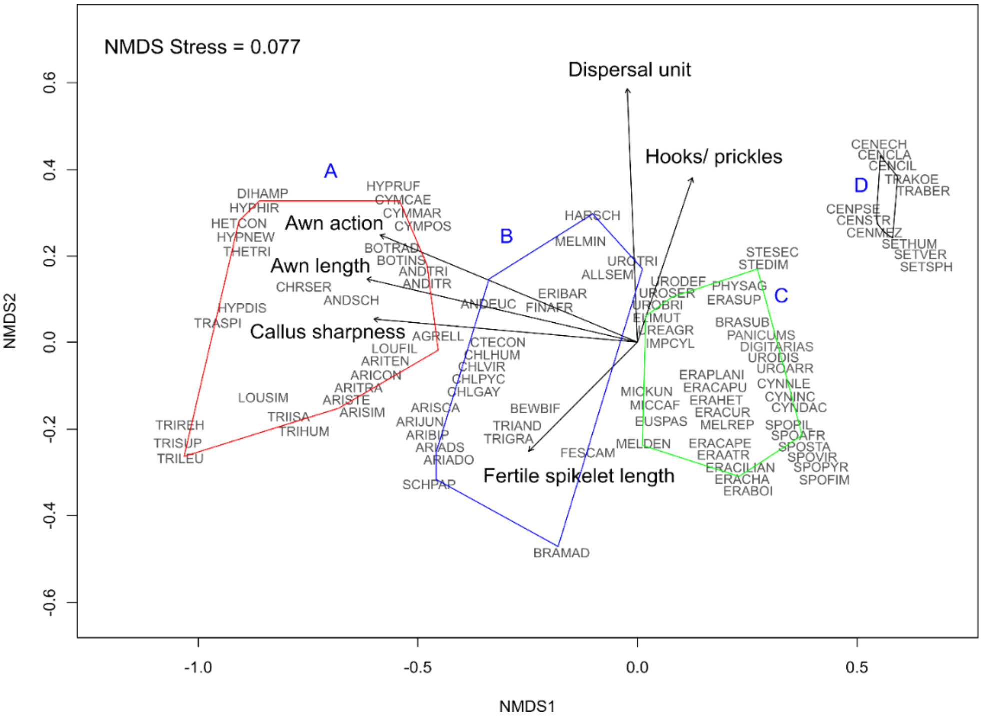

Figure 3.3 Non-metric multi-dimensional scaling (NMDS) ordination of grass species in two-dimensional space based on six floral traits (lemma awn action, callus sharpness, lemma awn length and fertile spikelet length, dispersal unit and hooks/prickles). Orthogonal axes of trait variation are indicated by arrows representing directions of increase in trait values. Also shown is the hierarchical clustering of the four main groups projected onto the NMDS. *Note: Species abbreviations are used – full names can be found in Appendix B, Figure S3.6. The species abbreviations are formed by the first three letters of the genus name and plus the first three letters of the specific epithet. Some species are not represented in biplot to reduce overlap and increase clarity.

Grass flowering structures vary widely and are often the main morphological characters distinguishing different grass clades. Different grasses with different floral structures clustered into groups that shared their functional traits (Figure 3.4).

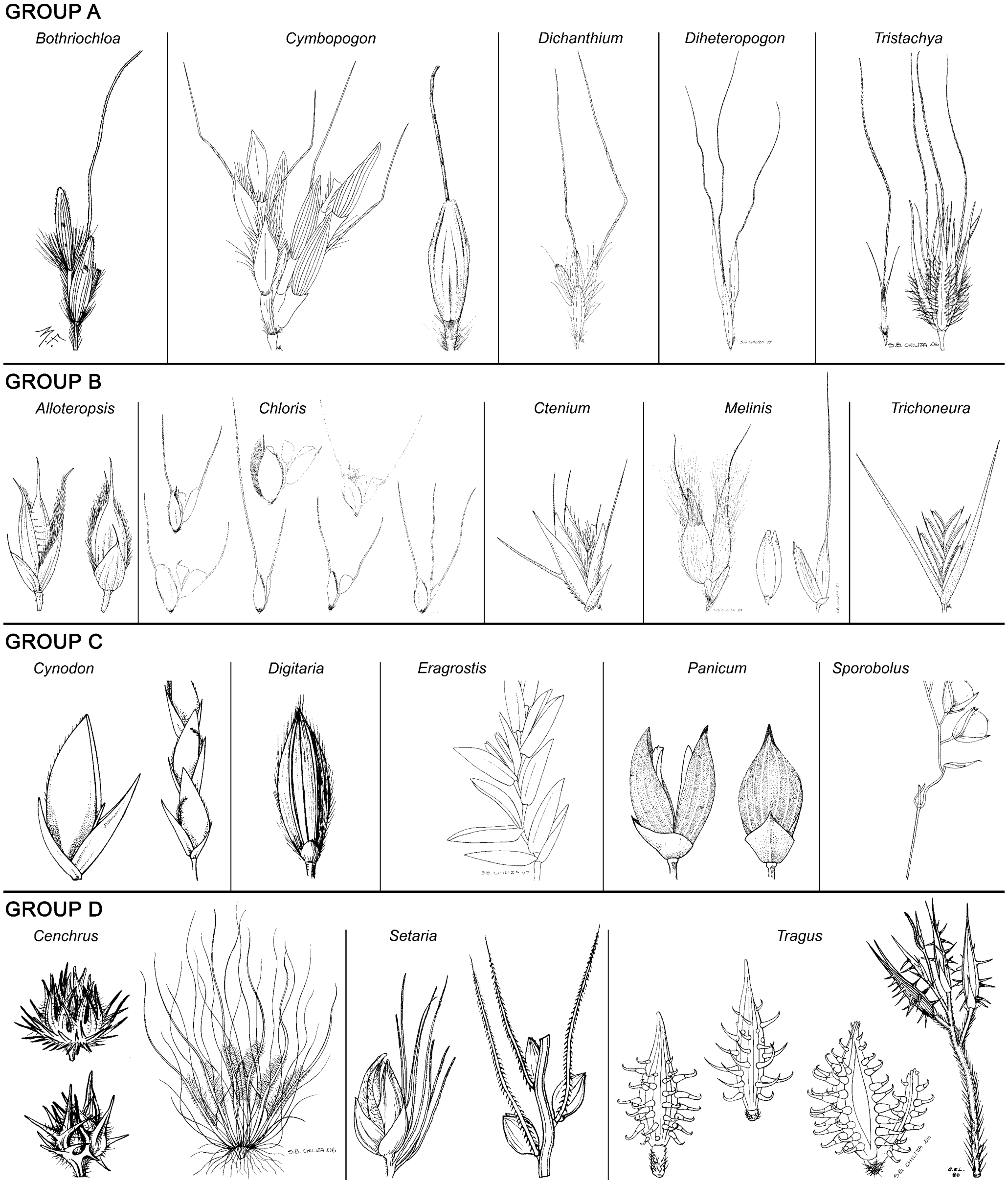

Figure 3.4 Different grass flowering structures according to the clustering groups, A) long active lemma awn and sharp callus (Fish *et al.*, 2015; Artists: S. B. Chiliza, M. Franks, W. Roux, C. Smith); B) passive lemma awns and a blunt callus (Fish *et al.*, 2015; Artists: S. B. Chiliza, W. Roux, M. Ueckermann); C) no lemma awns, blunt or no callus sharpness (Fish *et al.*, 2015; Artists: S. B. Chiliza, C. Letty, W. Roux); and D) hooks/prickles and no callus sharpness (Fish *et al.*, 2015; Artists: S. B. Chiliza, B. Connell, M. E. Connell, G.E. Lawrence, C. Smith). Overall species per Group A = 34, Group B = 24, Group C = 94 and Group D = 11.

The ANOVA in Figure 3.5 reveals that: ‘A’) lemma awn length was significantly higher in Groups A and B ($F_{1,189} = 1022$, $p < 0.001$); ‘B’) fertile spikelet length was significantly affected by clustering Group C ($F_{1,189} = 34.13$, $p < 0.001$); ‘C’) callus sharpness was significantly higher in Group A and B ($F_{1,189} = 335.3$, $p < 0.001$); ‘D’) All species with active awns were classified into Group A (active awn) and all species with passive awns were classified into Group B (passive awn) ($F_{1,189} = 2229$, $p < 0.001$); ‘E’) All species with hooks/prickles were classified into Group D ($F_{1,189} = 48.61$, $p < 0.001$); ‘F’) dispersal unit is not significantly ($F_{1,189} = 0.986$, $p = 0.322$) associated with clustering groups. All ordinal variables were score based on a range of their values, see Table 3.1.

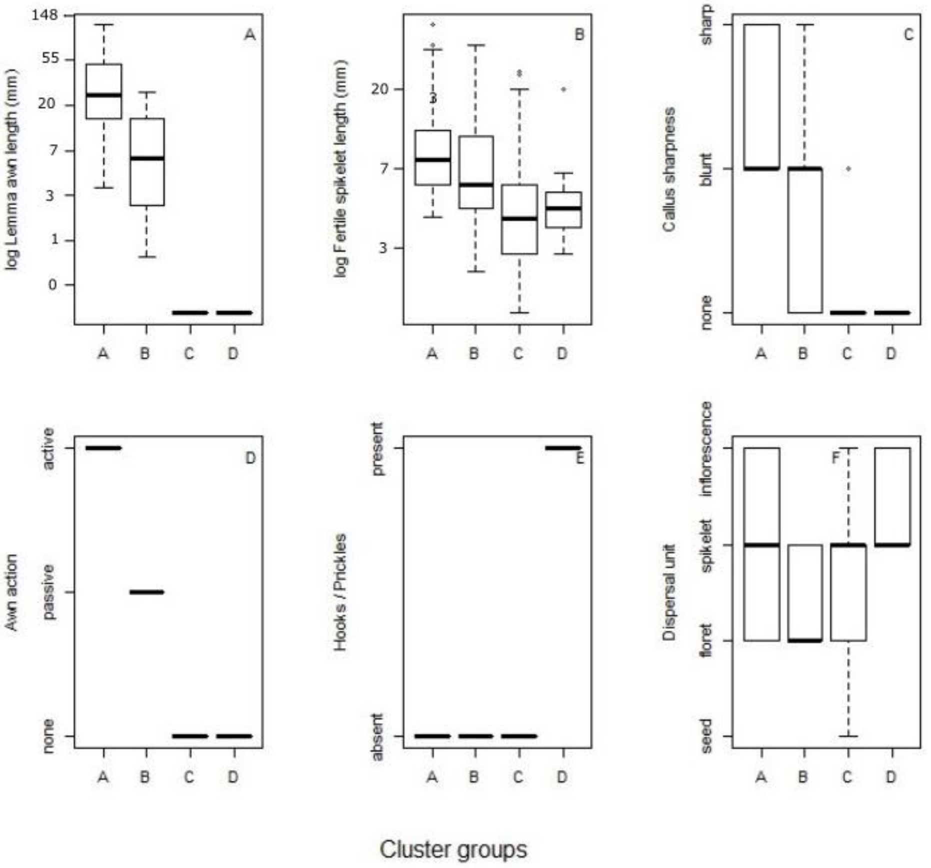

Figure 3.5 Boxplots show the relationship between floral traits among four clustering groups, A) lemma awn length, B) fertile spikelet length, C) callus sharpness, D) awn action and E) hooks/ prickles vs clustering groups were significant ($p < 0.001$); F) dispersal unit vs clustering groups was not significant ($p = 0.322$). Four clustering groups are: Group A: long active lemma awn and sharp callus, Group B: passive lemma awns and a blunt callus, Group C: no lemma awns, blunt or no callus sharpness, and Group D: hooks/prickles and no callus sharpness.

3.4.3 │ Associations between floral trait syndromes, dominance disturbance regime *and phylogenetic relationships*

There were strong associations between floral trait syndromes and dominance disturbance regime. Many more species from Groups A and B were found in fire environments, than grazing and intermediate environments, and conversely, Groups C and D are dominated by grasses found in heavily grazed environments (Figure 3.6). These differences were significant according to a Pearson's Chi-squared test (X-squared = 26.907, df = 6, p-value = 0.001).

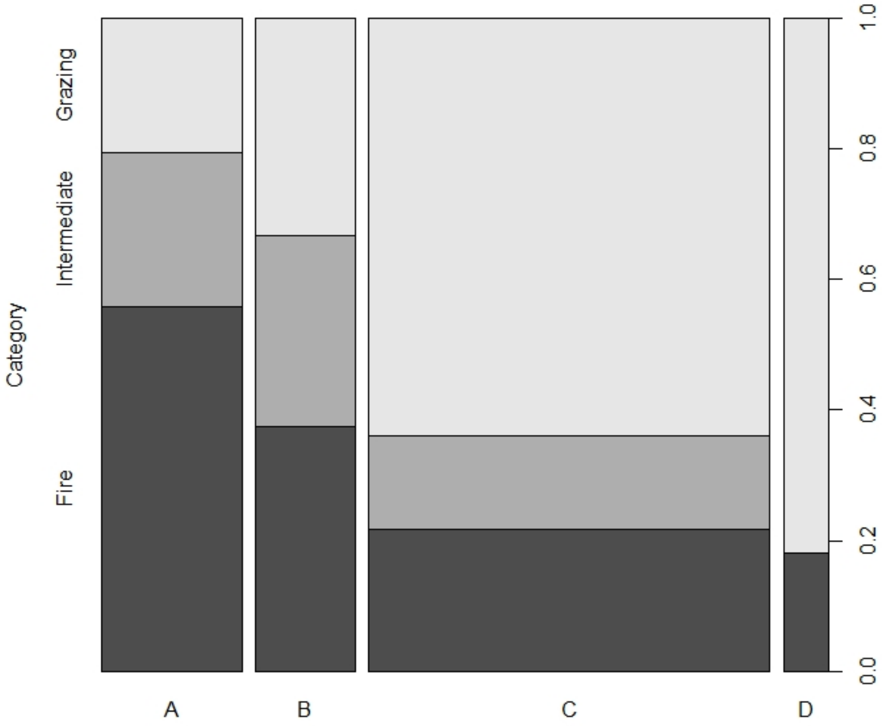

Figure 3.6 The associations between dominance disturbance regime of 163 species (fire, intermediate or grazing environment) and clustering groups. Four clustering groups are: Group A: long active lemma awn and sharp callus, Group B: passive lemma awns and a blunt callus, Group C: no lemma awns, blunt or no callus sharpness, and Group D: hooks/prickles and no callus sharpness. The clustering Group A and B are dominated by fire grasses, whereas Group C and D are dominated by grazing grasses.

Likewise, at an individual trait level, there were strong differences between environments. Lemma awn length was significantly affected by grassland habitat ($F_{2,160} = 13.59$, $p < 0.001$), but there were no differences in fertile spikelet length ($F_{2,160}$ = 1.705, p = 0.185) (Figure 3.7). Tukey's HSD tests showed that significant differences in lemma awn length among categories were restricted to the fire vs. grazing categories (difference = -1.724, p < 0.001). For categorical traits, callus sharpness and awn action were both significantly (p< 0.001) associated with fire grasses, whereas hooks/prickles (p = 0.084) and dispersal unit (p = 0.321) are not significantly associated with particular fire and grazing environments (Appendix B: Table S3.2).

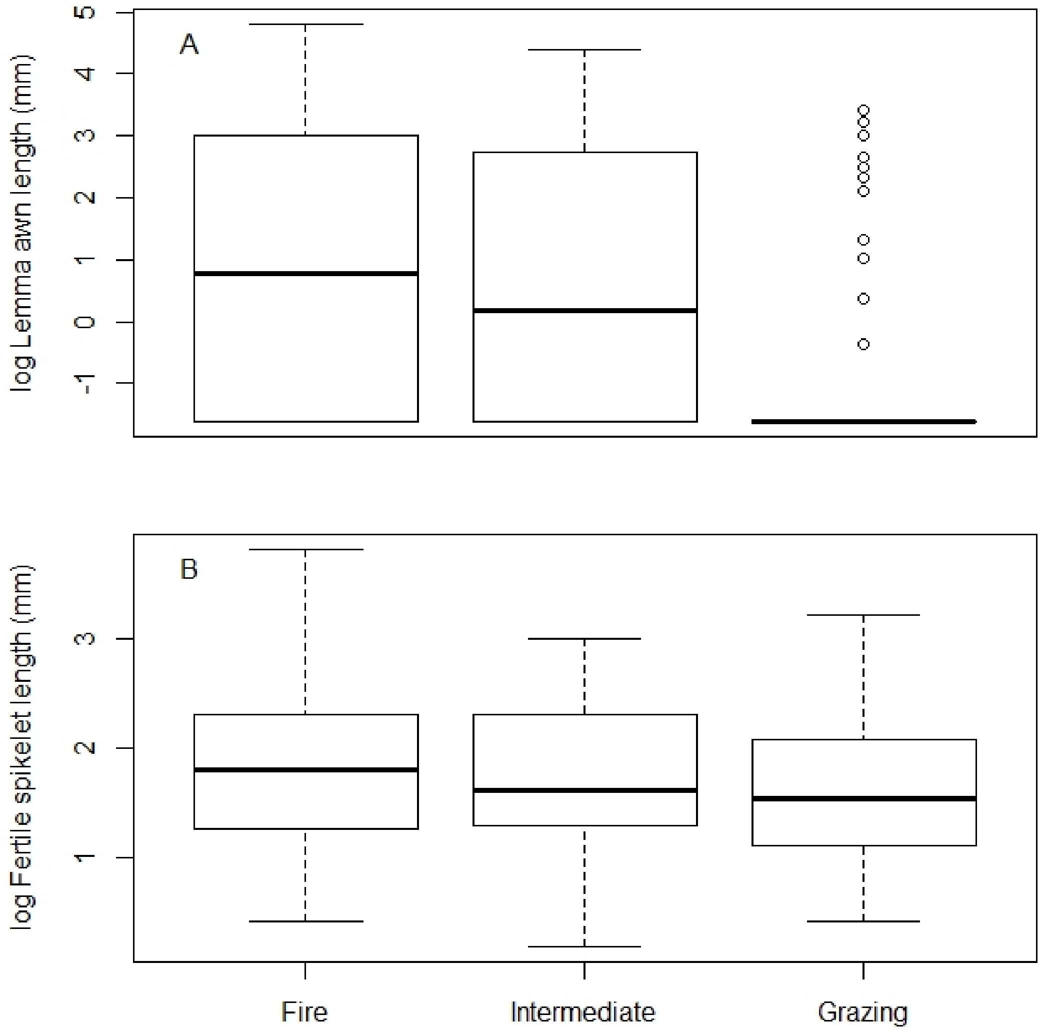

Figure 3.7 Boxplots showing how (A) lemma awn length and (B) fertile spikelet length varies in relation to the environment the grasses are generally found in. Grazing grasses have significantly (AOV P = 0.001) shorter awns than fire grasses. However, there is no difference in their spikelet lengths (AOV P = 0.193).

The proportion of Andropogoneae decreases, and the proportion of Paniceae increases as one moves from group A to group D (Figure 3.8) (Pearson's Chi-squared test = 209.95, df = 39, p-value = 0.001). Most of the species in Group A are in the Andropogoneae (23 species), with members of Aristideae (6 species), Poeae (2 species) and Tristachydeae (7 species) also present (Figure 3.8), Group B are dominated by tribes Aristideae (6 species), Cynodonteae (9 species), Eragrostideae (3 species), and Paniceae (6 species). Tribes found in Group C are Andropogoneae (3 species), Cynodonteae (16 species), Eragrostideae (24 species), Paniceae (49 species), Paspaleae (5 species) and Zoysieae (12 species), whereas Group D is dominated by tribes Cynodonteae (2 species) and Paniceae (9 species).

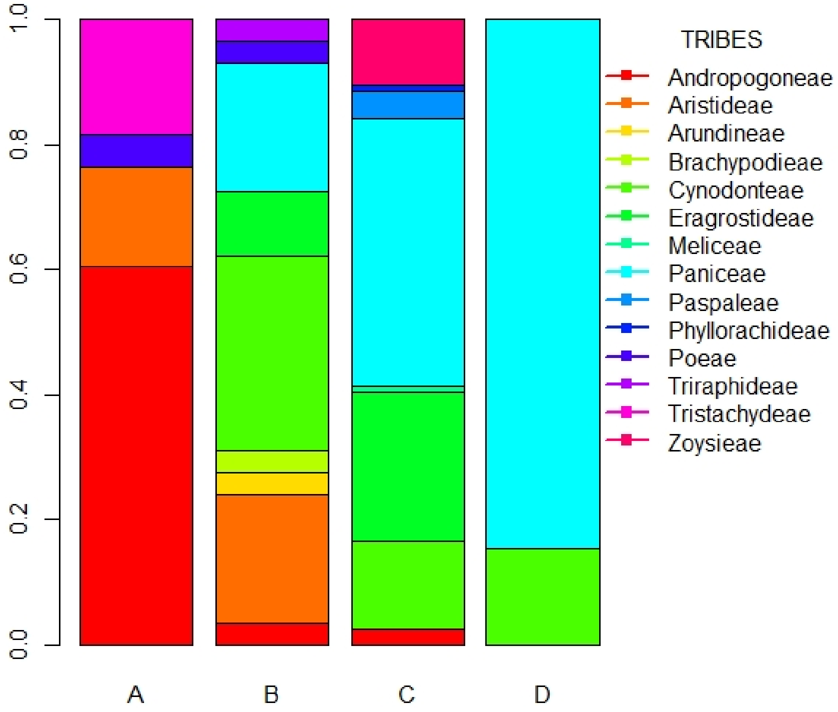

Figure 3.8 Graph showing the associations between 163 grass species in 14 tribes and clustering of groups. The clustering Group A is dominated by Andropogoneae, Group B is dominated by Cynodonteae, and Group C and D are dominated by the Paniceae tribe.

The LMMs fitted to data for 67 African grass species in 10 tribes confirmed that grass species with long lemma awns have a positive and significant relationship with plant height (β ± SE = 0.555 ± 0.226, $p < 0.05$). However, there was no evidence that the presence of awns was associated with plant height (β ± SE = 0.728 ± 0.449, $p = 0.105$). The model included lemma awn length and height with tribe as a random effect (Appendix B: Table S3.3; marginal $r^2 = 0.05$, conditional $r^2 = 0.63$). Examination of the tribe-level intercept (Appendix B: Table S3.3) in the random effects suggests that the Andropogoneae, Aristideae and Tristachydeae had longer lemma awns, whereas Arundineae, Eragrostideae, Paniceae, Poeae and Triraphideae had shorter lemma awns than other tribes, while the tribes Brachypodieae and Cynodonteae had species with both long and short lemma awns (Figure 3.9).

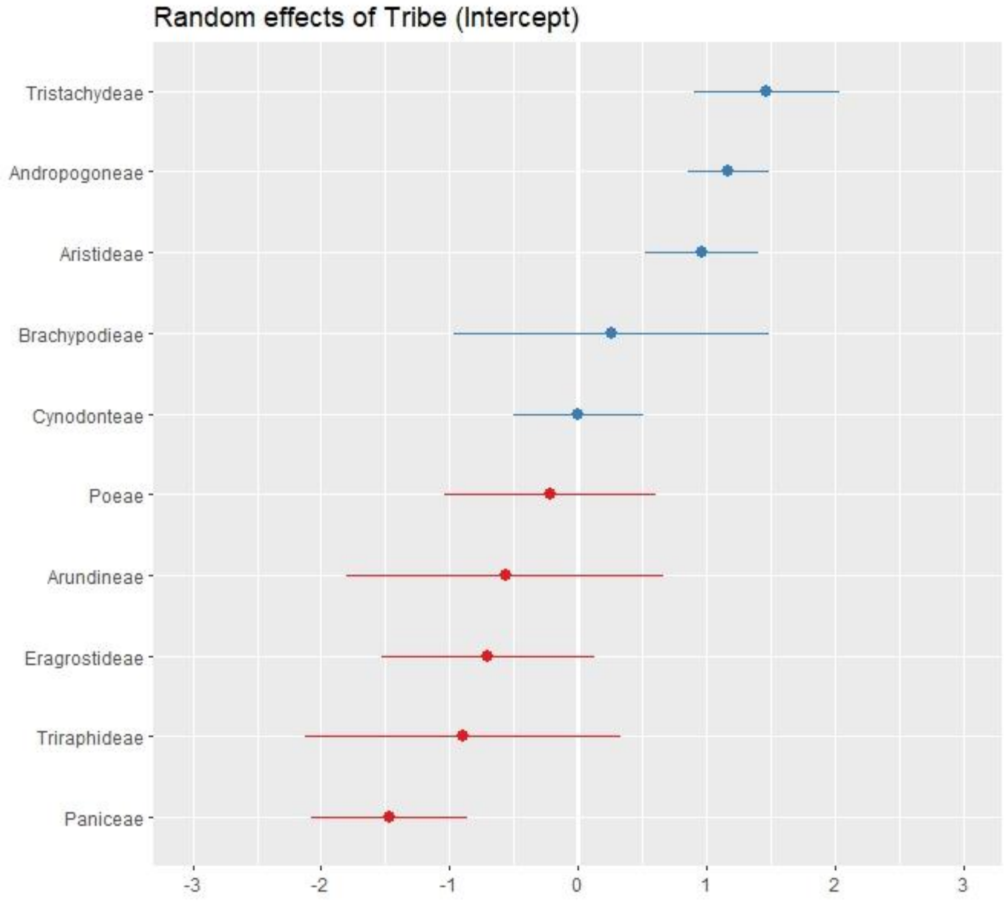

Figure 3.9 Tribe random effect intercept estimates from the linear mixed effect model, which assessed lemma awn length in response to plant height. The model was fitted to data for 67 long lemma awn grass species representing 10 tribes in African countries. Tribe Andropogoneae, Aristideae and Tristachydeae had an intercept > 0.0, whereas Arundineae, Eragrostideae and Paniceae, Poeae and Triraphideae had an intercept < 0.0, while intercept estimates for Brachypodieae and Cynodonteae overlapped zero.

Correlation between seed mass and lemma awn length for 38 species in 6 tribes did not find any significant relationship (β ± SE = 0.125 ± 0.143, p = 0.389) (Appendix B: Table S3.4). Tribes fitted as a random effect show that three tribes Andropogoneae, Aristideae and Tristachydeae had longer lemma awns and large seeds, whereas Cynodonteae, Eragrostideae and Paniceae tribes had short lemma awns and small seeds (Figure 3.10).

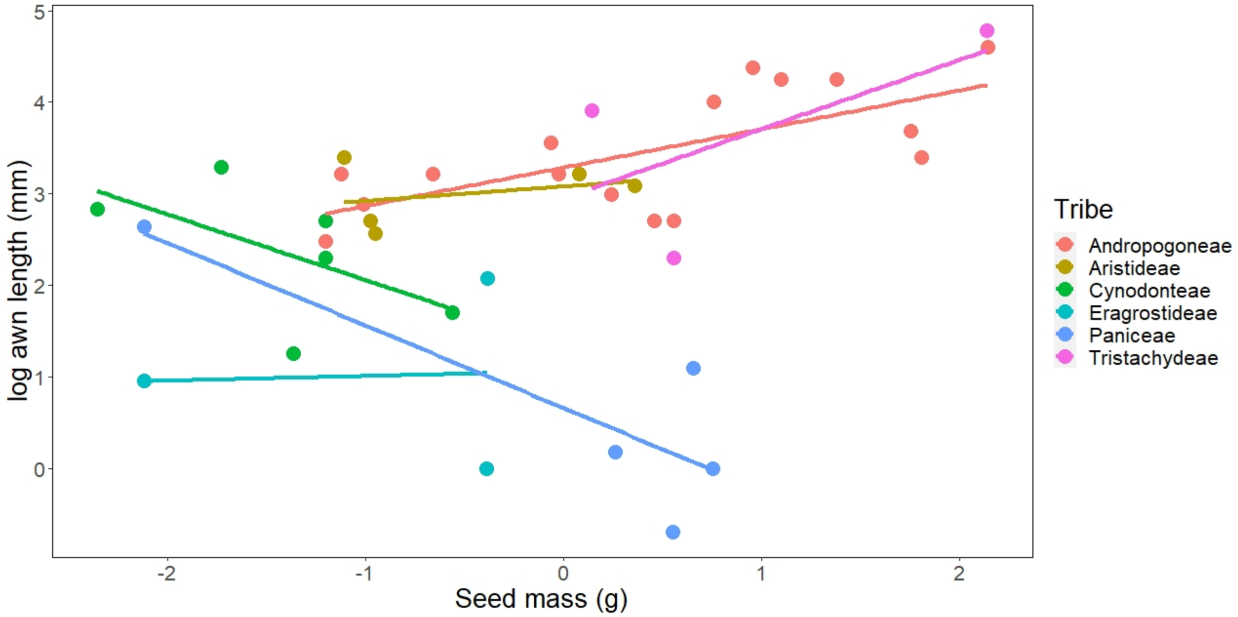

Figure 3.10 The tribes fitted as a random effect, which assessed log lemma awn length (mm) in response to log of seed mass (g). The model was fitted to data for 38 grass species representing 6 tribes in African countries. Three tribes Andropogoneae, Aristideae and Tristachydeae had longer lemma awns and large seeds, whereas Cynodonteae, Eragrostideae and Paniceae tribes had short lemma awns and small seeds.

3.5. │ Discussion

Four clear floral trait syndromes were identified separated largely by awn action, awn length, callus sharpness and the presence of hooks/prickles or bristles (Figure 3.3 and 3.5). Although the functionality of some floral traits (e.g. awn length and action) are not clear in the literature, and it is possible that the same trait can perform multiple functions, and each trait is linked to a different dispersal syndrome (Figure 3.1). Petersen & Kellogg (2022) mentioned that grass awn protect the seed from drought, herbivores, or fire by helping it become buried in soil.

The two groups with awns (A and B) differ in their awn action, with group B having only passive awns. Although both are associated with fire-prone ecosystems, group A is more strongly associated with them, and the probability of a fire-adapted grass having an active awn is almost 50% higher than what you would expect from a random association (31% instead of 21% - Appendix B: Table S3.2). Whether this is due solely to different dispersal modes, however, is not clear. Active awns are on average longer than passive awns (Figure 3.5), so this might increase wind dispersal opportunities, but the most obvious functional attribute of active awns in combination with a sharp callus is their ability to penetrate soft materials: useful for burying seeds in the soil to avoid lethal fire temperatures (Roux, 1969; Peart, 1979; Elbaum *et al*., 2007; Molano-Flores, 2012; Schrager-Lavelle *et al*., 2017). Petersen & Kellogg (2022) mentioned that grass awn protect the seed from drought, herbivores, or fire by helping it become buried in soil. Active awns (Group A) are also thought to be linked with epizoochory dispersal, as long active lemma awns are found buried into the hair of animals (Anderson *et al*., 2014; Petersen & Kellogg, 2022). Passive awn species are slightly equal to the active awn species, because both are found in fire-prone grasslands (14.67% compared with an expectation of 15% - Table S3.2). Nonetheless, awn length is significantly correlated with grass height, which lends support to the idea that they might be adaptations to promote effective wind-dispersal. Moreover, they are found less often than expected in grazer-dominated environments (Appendix B: Table S3.2). It is clear that group A is associated with four grass clades in particular: Andropogoneae, Aristideae, Poeae and Tristachydeae, so it could be that some other functional attributes associated with these clades are driving the relationship, and it is co-incidental. A final hypothesis is that the reason for the lack of association between awns and grazing environments are because awns themselves are an anti-grazer defense - preventing animals from damaging the seeds inside.

There are two “floral syndromes” that could be linked to epizoochory in particular: 1) the grass species with hooks/prickles and bristles in group D, which don’t have awns or sharp calluses; and 2) active awns with sharp calluses as seen in Group A – and these do not have hooks/bristles. Group D species are all from tribe Paniceae, subtribe Cenchrinae (the bristle clade) with only *Tragus* spp. from tribe Cynodonteae, subtribe Traginae (Soreng *et al*., 2022). This floral syndrome is never associated with awns and often has an inflorescence branch or spikelet dispersal unit. Support for the idea that group D would be dispersed by epizoochory is the strong association found with grazing environments (± 82% in Figure 3.6) of the species in this group and are “grazing” species according to our field classification. A second grazer-adapted group is group C, which also has no awns but also has no prickles or hooks. Again in Figure 3.6, ± 62%

of these species are associated with grazer-dominated environments and they are rare in fire-dominated systems. This is a very big group, and there is probably quite a bit of variability among species and hence the potential for different dispersal mechanisms, for which the appropriate traits may not have been measured. Our analysis shows that this group has small seeds (Figure 3.10) and is generally composed of short grasses, so endozoochory is likely one of the dispersal mechanisms used by these species (Rosas *et al*., 2008).

The grass floral structures (long active lemma awn, hooks or prickles, sharp callus and an awn that can be absent or present) have facilitated a rich diversity of dispersal modes (Peart, 1979; Clayton & Renvoize, 1986; Davidse, 1987; Peart & Clifford, 1987; Kellogg, 2015). Contrary to my expectation, I found that four tribes: Andropogoneae, Aristideae, Poeae and Tristachydeae have shown similarities in floral traits, such as long active lemma awns that have a sharp callus trait, because these two floral traits function together. Based on a literature review, grass with long lemma awns are thought to aid dispersal by wind and by sticking on animal's fur (epizoochory), whereas the sharp callus helps to attach to animals' and humans' bodies (drives long-distance dispersal) (Van der Pijl, 1982; Fischer *et al*., 1996; Clayton *et al*., 2015; Fish *et al*., 2015; Kellogg, 2015). Long-awned species were more likely to be found in frequently burned environments and were also usually taller than species without awns. Mashau *et al*. (2021) found that the grass tribe Andropogoneae is shown to be widely spread or has a larger range size in the sub-Saharan African region. Therefore, from the analysis, it appears that the fire-system grasses are likely to be wind or epizoochorous, and the grazing-system grasses are likely to be endo- or epizoochorous – but the way that seeds attach to animals is different in Group A (sharp callus and active awn) vs. Group D (hooks/prickles or bristles).

Mashau *et al*. (2021) found that tall grasses have larger range sizes, but some clades (Andropogoneae, Aristideae, Eragrostideae, Paniceae and Zoysieae) show this relationship more strongly. In this study it was found that there are some dispersal syndromes where grass height might not be important (e.g. endozoochory), so it makes sense that grasses in these clades would show less of a relationship (Figure 3.9). For example clades associated with grazing are Cynodonteae, Eragrostideae and Paniceae, but clade Cynodonteae had a negative height vs range size relationship (Mashau *et al*., 2021). Grass height shows a positive and significant relationship with long lemma awns, therefore taller grasses have longer lemma awns than short grasses (Figure 3.9). Tall grass tends to have long lemma awns, which facilitates dispersal mechanisms such as for wind-dispersed seeds and those with adaptations for epizoochory (Thomson *et al*., 2011). Tall grasses and grasses with awns also appear to be the first to establish in disturbed sites: for example, on the verge of a newly constructed road, as well as on the moderately compacted soils with the gravelly surface of older roads (Ullmann *et al*., 1995; Cilliers & Bredenkamp, 2000; Bredenkamp *et al*., 2006; Bettink, 2008). Grass height and long lemma awn traits prove to be a good predictor, which can help or influence the dispersal mode of grasses in sub-Saharan Africa, but further studies are still needed to test which dispersal syndromes are associated with these functional and floral traits.

The floral structures identified here are components of a larger life-history strategy scheme, and the habitat, leaf traits, and growth forms of grasses constrain the types of floral traits and dispersal syndromes that are appropriate. Moreover, although there are some clades with a variety of floral traits (e.g. Cynodonteae and Paniceae), these characters are largely conserved across the phylogeny. This might help explain why there is such a strong association between phylogeny and function in grasses (Griffith *et al*., 2020). Paniceae species are often highly palatable and attract high numbers of livestock, whereas most of the Andropogoneae species are unpalatable because they have hard, aromatic or essential oils in their leaves (Van Oudtshoorn, 2014). Additionally, I have shown here that many Andropogoneae also have unpalatable inflorescences with awns.

Finally, the tribes with long lemma awns, including Andropogoneae and Aristideae, are both older tribes, but they spread to their current dominance from the start of the Miocene, 10–20 million years ago (Strömberg, 2011). This implies that fire adaptations are more recent than grazing adaptations in the grass family, which would fit with the current understanding of the spread of tropical grasslands in Africa (Charles-Dominique *et al*., 2016), because Savannas began to spread across Africa during the Miocene period. Potentially, the diversity of the grass species floral syndromes is changing with time.

3.6 Conclusion

The study has highlighted the importance of understanding how floral traits link with specific dispersal syndromes in this significant plant family, and importantly, the degree to which they are associated with other key plant characters and the broader life history strategy schemes shown in tropical grasslands. This study's data suggest that the dispersal strategies shown in grasses depend on key functional attributes like grass height and leaf palatability, because these attributes will determine the effectiveness of the different dispersal modes: i.e. wind dispersal and whether dispersal agents like grazing animals utilise the plants. This might help explain observed associations between function and phylogenetic patterns in grasses. Long active lemma awns are revealed to be an important floral trait that facilitates the dispersal of the tall grasses in Africa.

Chapter 4 | Do dispersal syndromes and evolutionary history determine the range size of the subtribe Eleusininae (Poaceae: Chloridoideae: Cynodonteae) worldwide?

This chapter has been prepared for submission to the Journal of Vegetation Science

4.1 | Abstract

The subtribe Eleusininae (Poaceae), emerged and spread in the last 30.3 million years ago,. Lineage age and dispersal ability are two factors thought to explain the variation of range size and grasses show a wide range of floral structures and heights associated with different dispersal strategies. This study aims to assess how dispersal syndrome (inferred from floral structures and other functional traits) and evolutionary history affect range size in the grass subtribe Eleusininae – a tropical grass clade with variation in floral structures. Global location records for 97 grass species randomly sampled from 29 Eleusininae genera were used to quantify range size, and linear models were used to test the relationship between range size and interaction between plant height, and lemma awn state (absent/present), caryopsis length (mm) and genus age. Taller grass species with awned lemmas were found to have a larger range size, and this emphasises the importance of grass height and range size that depends on the dispersal syndrome. Again it was found that there is no relationship between genus age and the floral and functional traits used in this analysis. The study can help to explain some of the differences in biogeographic history between different lineages and also determine dispersal syndromes.

Keywords: caryopsis, dispersal mode, evolutionary history, lemma awn state, plant height, Poaceae, range size

4.2 | Introduction

Plant dispersal is the movement of seed or diaspore away from the parent. The dispersal of plant seeds is likely to influence the range size of certain species (Thomson *et al*., 2018) because it is the major mechanism for range expansion and invasion of a species into new suitable environments (Murray *et al*., 2002; Kristiansen *et al*., 2009). Different modes of dispersal have been identified depending on the agent used to move the diaspore: anemochory (wind dispersal) is more common in gymnosperms but is also a common dispersal mechanism in grasses; epizoochory (dispersal in animal coats, fur, skin, feathers and clothing) and endozoochory (in digestive tracts after ingestion) (Davidse, 1987; Rosas *et al*., 2008, Anderson *et al*., 2014, Kellogg, 2015; Sádlo *et al*., 2018) are both common dispersal modes in grasses, many of which have evolved along-side the mammalian herbivores that graze on them (Couvreur *et al*., 2005). Those dispersal modes (either wind, epizoochory or endozoochory) can influence changes in the different environment (habitat).

Both epizoochory and endozoochory can be effective mechanisms for dispersing seeds over long distances (Rosas *et al*., 2008; Anderson *et al*., 2014). Endozoochorous species need to survive ingestion, and the distances they are dispersed depends on the movements of the grazing animals, as well as the retention time (Couvreur *et al*., 2005). However, when ingested by animals that migrate large distances, such as elephant, wildebeest, and granivorous birds, occasional very long-distance dispersal events should be possible, and the seed is likely to germinate in a similar habitat to where its parent was eaten, potentially aiding establishment. Dispersal distances for epizoochorous species are less well studied, but again, very long-distance dispersal should be possible. Thomson *et al*. (2011) showed that epi- and endozoochorous species dispersed further, on average, than wind-dispersed species, and that taller plants tend to disperse seeds further, no matter what their dispersal syndrome. Both epi- and endozoochory are therefore important dispersal mechanisms that may play an important role in the evolution and ecology of the grass family (Rosas *et al*., 2008, Anderson *et al*., 2014). However, the degree to which this might impact range sizes of grass species with different dispersal syndromes has not been tested.

Range size is a geographical area that the species occupies (Brown *et al*., 1996; Morueta-Holme *et al*., 2013, Sheth *et al*., 2020). Range size is important for assessing extinction risk and adaptation capacity (Manne *et al*., 1999; Staude *et al*., 2020), due to the evolutionary and ecological processes controlling range size. Recent meta-analyses and reviews have identified a range of biotic and abiotic factors that can help to predict the range sizes of plants such as niche breadth, plant height, lifespan, latitude, habitat suitability, evolutionary history (age) and dispersal mechanism (Thomson *et al*., 2011; Gallagher, 2016; Sheth *et al*., 2020; Mashau *et al*., 2021; Alzate & Onstein, 2022). Dispersal strategy interacts with plant height to affect dispersal distance (Thomson *et al*., 2011). The degree to which plant height affects dispersal may depend on the dispersal mechanism: shorter plants could have very high dispersal distances if they are, for example, endozoochorously dispersed by wide-ranging animals (Rosas *et al*., 2008; Anderson *et al*., 2014).

Welker *et al*. (2020) demonstrated that the tribe Andropogoneae is the youngest grass tribe to have evolved and it has an extremely large range size. The distribution of grass lineages started to spread from their Gondwanan centre of origin after the breaking up of the southern supercontinent (Christin *et al*., 2014), 55–70 million years ago in the late Cretaceous or Paleocene period. The subtribe Eleusininae is estimated to have originated 30.3 million years ago (Hackel *et al*., 2018) and contains both species with cosmopolitan distributions (e.g. *Cynodon dactylon* (L.) Pers.), and ones with rare distributions (eg *Chloris ruahensis* Renvoize), and, unusually, there are a range of different floral structures represented within one subtribe. Therefore it represents an opportunity to distinguish between floral traits and evolutionary history as drivers of range size in grasses. From a meta-analysis of studies across the plant kingdom, Sheth *et al*. (2020) concluded that factors such as lineage age and niche breadth override dispersal ability in determining range size, but there is ample evidence for dispersal being an important driver of biogeographic patterns within particular plant groups (Hanski *et al*., 1993).

Mashau *et al*. (2021), **Chapter 2** of this study, using a range of southern African grass species, demonstrated that tall annual-biannual grasses had a larger range size than short perennial grass species. This emphasizes that plant height and lifespan are the key driver of the geographical range size in grass species found in sub-Saharan Africa. However, there was a large amount of variation in the responses between different grass clades, which Mashau *et al*. (2021) inferred might be due to differences in their dispersal strategies, environmental niches, and evolutionary history. For example, the importance of plant height in driving dispersal and range size depends on whether plants are wind or animal dispersed, and this could explain why certain grass lineages did not show the expected positive relationship with height. Moreover, Mashau *et al.* (2021) also found that species with large native ranges also had a higher probability of becoming invasive on other continents.

Mashau (**Chapter 3**) investigated what floral traits are correlated in the grass family, and identified floral trait syndromes that were more common in fire-prone areas and grazing lawns. I showed that the presence of awns was associated with other characters that imply wind dispersal and was also less common in systems with frequent grazers. In contrast, species in grazing environments tended to be smaller with smooth, hard seeds, except for a group with hooks and bristles, which was the most strongly associated with grazing. Small hard seeds have been proposed to be both more palatable, and more effective at surviving animal guts (Rosas *et al*., 2008) and hooks and bristles are known to enable ectozoochory (Tackenberg *et al*., 2006) - although species without these characters have also been found on animal fur (Rosas *et al*., 2008). Therefore, in grasses it appears that floral characters can be used to infer dispersal strategies, and might interact with other plant traits to affect dispersal distance and range size.

Based on the literature one would expect that animal-dispersed seeds would have larger range sizes than wind-dispersed seeds, and that the importance of grass height in driving dispersal distance (and therefore, potentially range size) would be higher for wind-dispersed seeds. I expect stronger relationships with grass height and range size for these species (Mashau *et al*., 2021).

Seed size is thought to be important for dispersal: it is expected that small-seeded species are likely to disperse further than large-seeded ones (Thomson *et al*., 2018). The positive relationship between seed mass and dispersal structure mass is thought to be useful to help larger seeds to disperse further (Edwards *et al*., 2006). However, there is evidence that smaller-seeded grasses (for example *Cynodon dactylon* (L.) Pers.) are more likely to be ingested by herbivores than large-seeded ones (Andropogoneae) (Anderson *et al*., 2014), so the association between seed mass and dispersal distance might only work for some dispersal syndromes.

In this study, I aim to assess how dispersal syndrome (inferred from floral structures and other functional traits) and evolutionary history affect range size in tropical grasses. Within subtribe Eleusininae there are 219 species in 29 genera, I assessed 97 grass species that belong to the subtribe Eleusininae. I expect i) a mean range size will vary between grasses with different floral trait syndromes: grasses with traits associated with endozoochory will have larger ranges than those associated with wind dispersal (height). ii) I also expect the relationship already established between grass height and range size to be stronger for grasses with floral trait syndromes associated with wind dispersal. and iii) Once I have accounted for other factors, I expect a positive relationship between grass genus age and range size.

4.3 | Materials and Methods

4.3.1 Identifying an appropriate grass clade and genus age

I chose the tribe Cynodonteae for this global phylogenetically controlled analysis because Mashau *et al*. (2021), **Chapter 2**, found that in Africa the grass tribe Cynodonteae did not show the expected relationship between range size and grass height, and proposed that this might be due to variations in dispersal syndrome within this clade. Within the tribe Cynodonteae: subtribe Eleusininae is an appropriate study group, as it is a relatively ancient grass clade. Hackel *et al*., (2018) estimate it originated 30.3 MYA and contains species with a range extending across the globe or a limited distribution, as well as species with a range of different floral structures. Species checklists were extracted from the World Checklist of selected plant families (WCSP, Govaerts *et al*., 2022) following the latest grass classification of the tribe Cynodonteae, subtribe Eleusininae (Soreng *et al*., 2017; Peterson *et al*., 2021). Within subtribe Eleusininae there are 219 species in 29 genera, to ensure a balanced design I randomly selected a maximum of 5 species per genus in the subtribe Eleusininae, which resulted in 97 species from 29 genera.

The phylogenetic classification and age of the 97 species of 29 genera under the subtribe Eleusininae were extracted from several articles (Appendix C: Table S4.1) (Filgueiras *et al*., 1999; Peterson *et al*., 2015, 2021; Hackel *et al*., 2018; Soreng *et al*., 2022). The phylogenetic tree from Hackel *et al*., (2018) was matched with the full data set (97 grass species from 29 genera) to produce an accurate genus age phylogenetic tree (in the case where species age is different within the genus, it's because those species have now moved from one genus to another due to recent DNA molecular analysis). Therefore unless there was accurate DNA information available, all species in the same genus were assigned the same age. This limited the scope of the analyses that could be done.

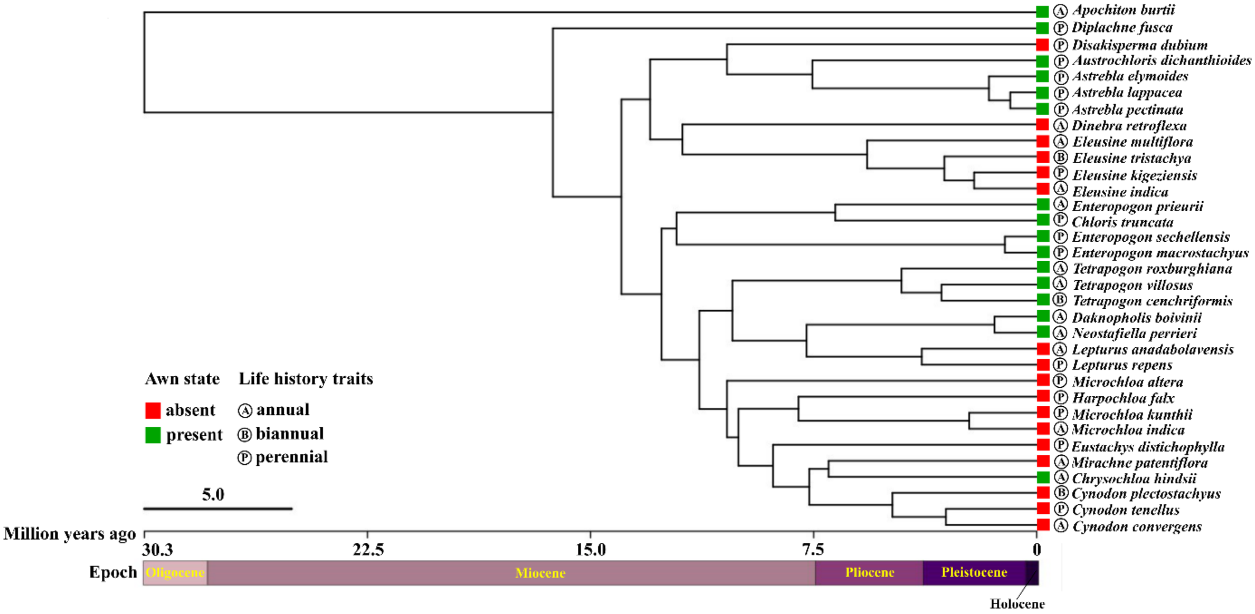

Figure 4.1 The phylogeny by Hackel *et al.* (2018) merged with the 97 grass species from 29 genera in the subtribe Eleusininae. There was only DNA data for 33 species in 19 genera; the other species were given the genus age. The phylogenetic tree indicates that the current species have a range of ages, that awns are ancestral characters in the Eleusininae, and that species without awns have evolved several times. Therefore, this is an appropriate subtribe to test the hypotheses about the importance of dispersal mode and genus age on range size.

4.3.2 | Plant traits data and species location records

From previous studies (**Chapter 2**, Mashau *et al*., 2021), I identified both plant height and plant lifespan as important determinants of range size. In **Chapter 3**, I identified six floral and life history traits, which are associated with dispersal ability in grasses (**Chapter 3**, Table 3.1 and Figure 3.1). The inflorescences of the grass species in this subtribe Eleusininae do not represent the full range of floral trait syndromes: there are no species with hooks/bristles, and no species with active awns. Therefore only group B and group C from **Chapter 3** are represented in this subtribe - i.e. possibly with wind (Group B) or endozoochorous (Group C) dispersal, although it is possible that the non-active awns are also able to disperse on animal fur. I, therefore, selected four grass functional traits to include in the analysis: plant height, lifespan scored as either annual-biannual (i.e. annual or biannual) or perennial, lemma awn (absent = 0 or present = 1), and caryopsis length, which I used as an index of seed mass (g). Accurate seed mass measurements are difficult to get for grass seeds because a valuable herbarium voucher or specimen is collected before seeding time. The lemma awn (absent/present), plant height, lifespan, caryopsis length trait measurement data were obtained from GrassBase (Clayton *et al*., 2015) https://www.kew.org/data/grasses-db.html (accessed 19 January 2022).

The geo-referenced data of 55 362 records of 97 grass species of the subtribe Eleusininae globally were extracted from the Global Biodiversity Information Facility (GBIF.org, 2019). The "CoordinateCleaner" package (Zizka *et al*., 2019) was used to clean the occurrence data. Grasses, and Chlorodoid grasses, in particular, are notoriously difficult to identify. However, as I used a dataset that was previously checked carefully by both L. Fish and A. C. Mashau I believe the instances of misidentification will not be numerous enough to disrupt the analysis.

4.3.3 │ Calculating range size

Gilles Dauby provided the development version of ConR packages used to estimate range size using the "EOO.computing" function in planar mode (Dauby *et al*., 2017; Dauby, 2020). An Equal Area Cylindrical Projection was used for all area calculations. Range sizes were estimated using the alpha hull = 200 km and buffer = 10 km method (for more information see Mashau *et al*., 2021). The shapefile in "natural_earth_10 m." was used as the country_map to exclude ocean areas (Appendix C: Figure S4.2). This method doesn't work with few location records, so species with 1 or 2 records have been arbitrarily assigned as 1 record = 200 km^2 and 2 records = 400 km^2 range sizes respectively. Range sizes of the full data set show a bimodal distribution (e.g. two distinct peaks or centres) (Appendix C: Figure S4.3). This is possibly due to the distributions of grasses being either within continents or across continents but it presented a problem for the statistical analysis as the response variable (range size) was not normal.

4.3.4 | Statistical analysis

General linear models were fitted to 97 grass species of 29 genera to assess the correlations between the predictor variables. The response variable (range size) and all continuous explanatory variables i.e. plant height (mm), caryopsis length (mm) and genus age (millions of years; Appendix C: Table S4.1) were log-transformed prior to analysis to improve the normality of the data, with lemma awn state fitted as a categorical explanatory variable (present/absent). However, as mentioned above, the range size had bimodal distribution, and the residuals were also not normally distributed (Appendix C: Figure S4.4).

Linear regression models were fitted to full dataset for 97 grass species of 29 genera under the subtribe Eleusininae across the globe. A model interaction term was included between height and lemma awn state to test whether the effect of height varied between plants with different dispersal syndromes. Residuals were not normally distributed, likely due to the bimodal distribution of range sizes, and hence I could not use (Appendix C: Figure S4.4) the log-likelihood to test whether predictor variables significantly affected range size. Therefore I did randomisation tests (Howell, 2015)) in a log-transformed data where I randomly resampled each of the predictor variables 5 000 times and ran the same linear model. I then tested whether the (normally distributed) coefficients of the random model were significantly different from the coefficients of the original model. I tested for a significant difference by counting the number of times it was larger than the predicted value from the linear out of the 5000 iterations. If it was different more than 95% of the time I considered the factor to be significant. Randomisation tests make no response about the distribution of the predicted variables, and therefore are more appropriate for significance testing in this instance.

Analysis of variance (ANOVA) was used to test the hypothesis that there are comparison between lemma awn state (absent/present), log height (mm), log caryopsis (mm) and log genus age. The Wilcoxon test is a non-parametric test and was used to compare two variables when the normality assumption is violated. This analysis was done in the R environment (R version 4.2.1; R Development Core Team, 2021).

4.4 | Results

4.4.1 │ Evolutionary history of the grass genera under the subtribe Eleusininae

The phylogeny classification tree of the 19 genera and 33 grass species under the subtribe Eleusininae were produced and therefore lemma awn state and lifespan traits were populated next to the species name. The phylogenetic tree indicates that the genera have a range of ages (Appendix C: Table S4.1), no test has been done, but through visual inspection the awned lemmas are ancestral characters in Eleusininae, and therefore species without awned lemmas have evolved several times (Figure 4.1). The lemma awn state is a labile character and also seems to be an age-component to the patterns: most of the grass species that evolved during the Miocene (10–20 million years ago) (Strömberg, 2011) had mixed characters of lemma awn state (present/absent), but grass species that evolved during the Pliocene and Pleistocene (which is about 0–7.5 million years ago) rarely had awns present.

4.4.2 │ Correlation between lemma awn state versus height, genus age and caryopsis

The ANOVA in Figure 4.2 reveals the relationship between three plant traits and lemma awn state (absent = 0/present = 1): species with lemma awns have greater mean caryopsis lengths than those without lemma awns ($F_{1,95} = 18.81$, $p < 0.001$; Fig. 4.2A). There was no difference in the mean plant heights of species when grouped by the presence or absence of lemma awns ($F_{1,95} = 0.2$, $p = 0.655$; Fig. 4.2B). In Figure 4.2C, species without lemma awns tend to have younger genera ages than those with lemma awns ($W = 1565$, $p < 0.001$).

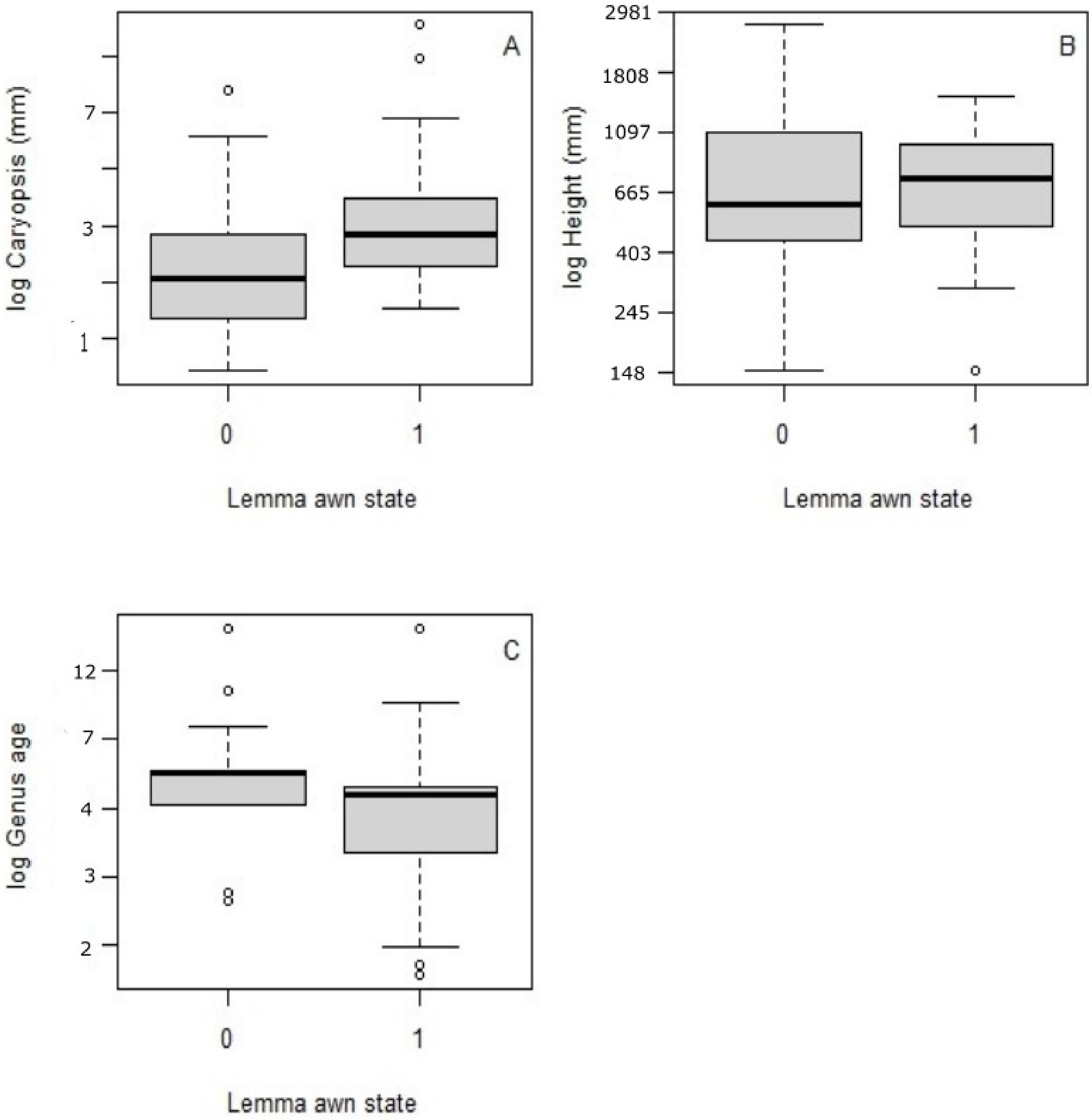

Figure 4.2 Boxplots show the relationship between lemma awn state (absent= 0 and present=1) among three functional and floral traits, A) grass species with awned lemmas tended to have a large caryopsis/grain (these floral traits show a significant positive relationship with lemma awn state where $p < 0.001$); B) there was no relationship with height ($p = 0.655$); C) genus age (million years ago) shows a slight difference in the species with lemma awn present/absent ($p< 0.001$).

4.4.3 │ Test whether the relationship between range size and plant height depends on lifespan, lemma awn state, caryopsis and genus age

There was some evidence to suggest that perennial grasses have smaller range sizes than annual-biannual grasses (coefficient = -1.389, p = 0.071), which would be consistent with results from Mashau *et al*. (2021) **Chapter 2**. I also found an interaction between the lemma awn state and log height (coefficient = 2.253, p = 0.049), which confirmed the hypothesis that the importance of grass height for range size depends on the dispersal syndrome (Table 4.1, Appendix C: Figure S4.1). The species with the largest range sizes had awns and were tall (Figure 4.3). There was no evidence that caryopsis size or genus age affected range size (Table 4.1, Figure 4.4, Figure 4.5).

Table 4.1 Normal linear model was fitted to test range size (km^2, log-scale) estimated using alpha values of 200 km, log height (mm), lemma awn state (absent = 0/present = 1), log caryopsis (mm), lifespan (two-level factor: "annual-biannual" or "perennial") and genus age data for 97 grass species of the subtribe Eleusininae globally. This model includes an interaction between plant height and lemma awn state. Because the response variable was not normal, the P-value here reports on the results of a randomisation test: it represents the proportion of times that the true parameter was different from a parameter produced with a randomised dataset..

Parameters:	Coefficient	P-value
Intercept	8.911	0.062
1og Height	0.599	0.412
Lemma awn state (present/absent)	-13.487	0.071
log Caryopsis	-0.882	0.173
Lifespan (perennial)	-1.389	0.071
log Genus age	-0.871	0.208
log Height: Lemma awn state	2.253	0.049

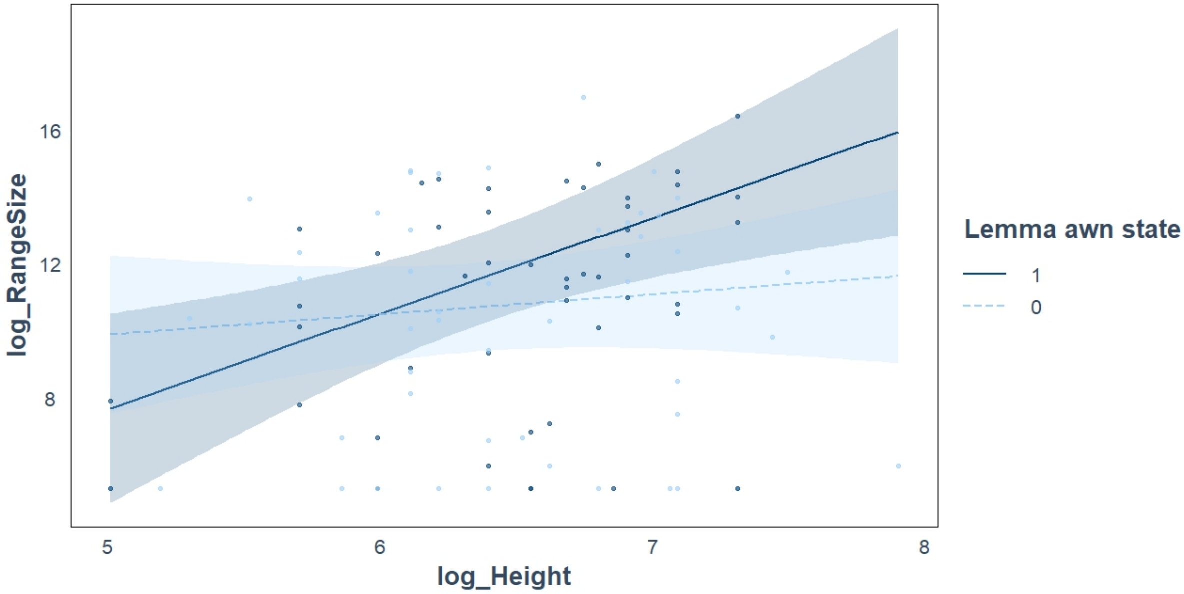

Figure 4.3 Correlation relationships between range size (km^2, log-scale) and plant height (mm, log-scale) for 97 grass species in the subtribe Eleusininae globally with lemma awn state, awn present (solid symbols and line) or awn absent (light symbols and dash line). The shaded areas represent the 95% confidence interval for plant height and lemma awn state coefficient estimates.

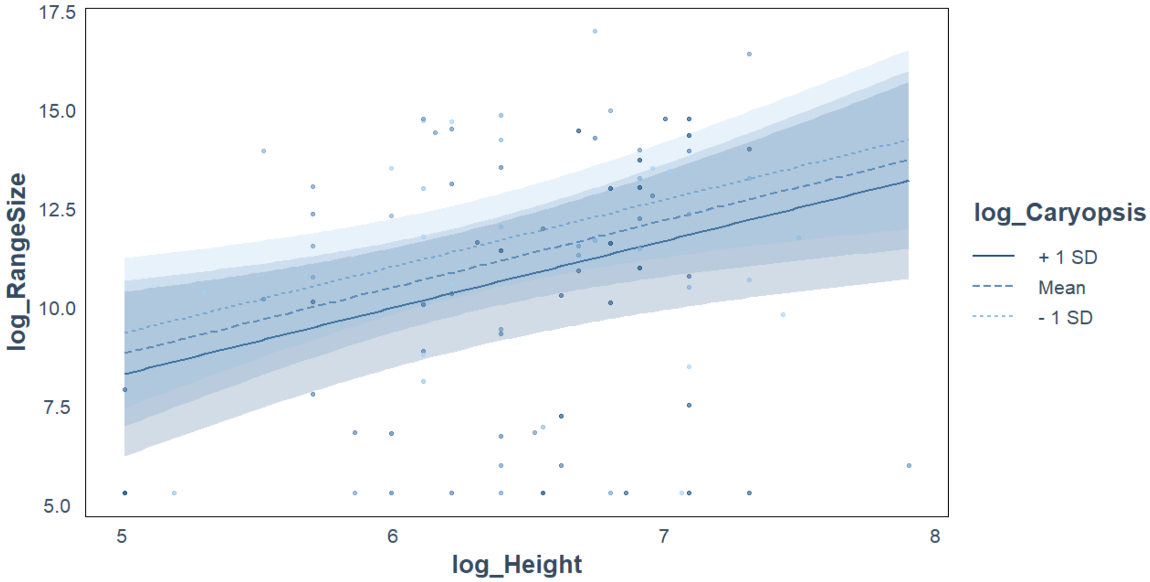

Figure 4.4 Correlation relationships between range size (km^2, log-scale) and plant height (mm, log-scale) for 97 grass species in the subtribe Eleusininae globally: the linear model was run on continuous caryopsis (mm, log scale) data, but for visualisation I plotted the response to the mean size, as well as the mean+-1 standard deviation. The relationship with height does not vary with caryopsis size. The shaded areas represent the 95% confidence interval for plant height and log caryopsis coefficient estimates.

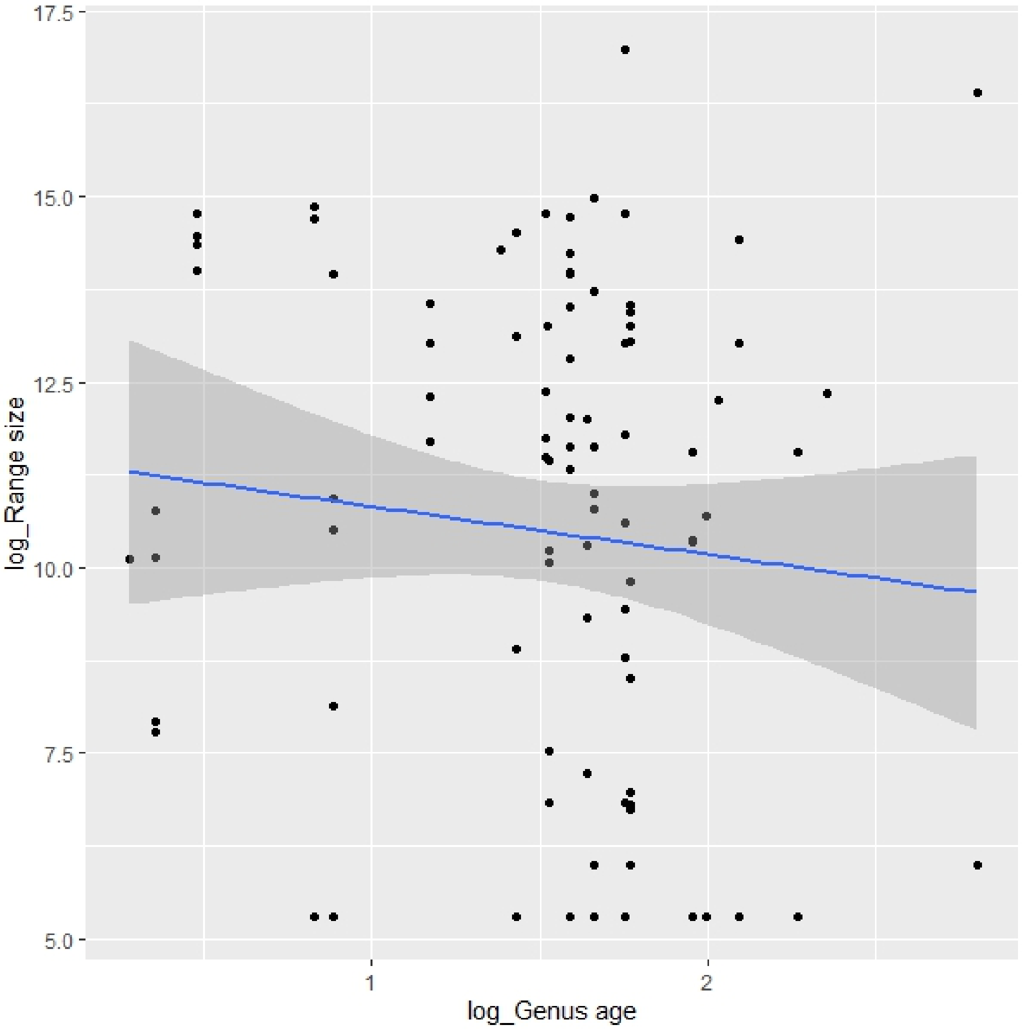

Figure 4.5 Correlation relationships between range size (km^2, log-scale) and log genus age (million years ago) of the 97 grass species of 29 genera, shows that there is no significant relationship between these two variables. The shaded areas represent the 95% confidence interval for the range size and log genus age coefficient estimates (coefficient = -0.817, p-value = 0.199). Many species have the same age because they could only be assigned a genus age. This might limit the strength and power of the analysis.

4.5 | Discussion

This study demonstrated that grass species with a larger range size in subtribe Eleusininae are the ones which are taller with awned lemmas that can be dispersed by wind. Examples of these species in the subtribe Eleusininae are *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth. and *Tetrapogon roxburghiana* (Schult.) *P.M.Peterson*. Wind dispersal is common in grasses, especially in places with few animals (Jurado *et al*., 1991) and it facilitates long-distance dispersal across the globe. In fact, Linder *et al.* (2018) when discussing how grasses managed to spread and colonise the globe so quickly during the Miocene, highlights the role of wind dispersal and awns. It is true that some of the tribes with many cosmopolitan species – such as the Andropogoneae tend to have awns, as well as being large plants (**Chapter 2**). The Andropogoneae are one of the youngest grass clades (having evolved in the early Miocene 10–20 million years ago) (Strömberg, 2011; Welker *et al*., 2020), which implies that dispersal characteristics are more important than age in driving range size in grasses.

This analyses on subtribe Eleusininae confirmed this – there was no significant relationship between the age of the grasses and range size, despite the fact that the age of grass species in our analysis ranged from <2 to >30 million years ago. The strong relationship observed in Mashau *et al*. (2021) **Chapter 2** between lifespan and range size was again confirmed in this analysis. This might also explain why I found no relationship with genus age – as some of the oldest species in the analysis were also perennial and smaller (Figure 4.1, Table 4.1). Therefore, within grasses, the conclusions of Sheth *et al*. (2020) do not hold true: dispersal mode appears to be more important than species age. Sheth *et al*. (2020) did find that habitat suitability was more important than any of these other factors, and although I did not test it here, the evolutionary history of this subtribe shows that there are geographical constraints within species (Gallagher, 2016). There is a challenge that the potential for global dispersal can be very different for different species – some have to cross major biogeographic barriers before encountering suitable habitats, and others do not. This means that rare events (super long-distance dispersal) and chance (where they evolve) could have substantial effects on range size, and are not accounted for in the study design. For example, habitat suitability restricts species (*Cynodon convergens* F.Muell. found in Australia only) from dispersing from one continent to another (Appendix C: Figure S4.3). Moreover, some biogeographic barriers are uninhabitable for all grasses (e.g. oceans) and hence have to be crossed via dispersal, introducing the potential for chance events to play a substantial role in shaping distribution ranges – but at the same time, broader niche breadth should have a consistent positive effect on range size – as it increases the total area of the planet that is potentially inhabitable, and hence the likelihood that a rare long-distance event (and any other dispersal event) may encounter suitable habitat. The configuration of suitable habitats also matters – e.g. north and southern temperate zones vs. north and south tropics.

There is evidence that large seeds and dispersal structures might increase dispersal distances, and also that small seeds might promote endozoochory and bigger dispersal distance and range size (Thomson *et al*., 2018). There is mixed evidence in the literature regarding how seed size correlates with animal ingestion. Anderson *et al*. (2014) found that small seeds of grass species (for example *Eragrostis* spp. and *Sporobolus* spp.) are found in the dung of grazers. Rosas *et al*. (2008) demonstrated that some small-seeded and small-statured plant species are incidentally consumed while bison are foraging on grasses. Moreover, granivorous waterbirds are thought to disperse *Dactyloctenium giganteum* Fisher & Schweick. on their feet (personal communication I. P. J. Smit). Endozoochory is a dispersal mode which is associated with small, smooth, hard seeds or spikelets (Shiponeni & Milton, 2006). Thomson *et al*. (2011) prove that there may be a negative relationship between plant height and endozoochory species, smaller plant seeds are more likely ingested by grazing animals (Anderson *et al*., 2014). More importantly, however, they are probably also less likey to be damaged going through an animal gut (Rosas *et al*., 2008).

The findings have shown that lemma awns and plant height are important for range size, it is difficult to conclude whether animal-dispersed grasses should have larger or smaller range sizes than wind-dispersed grasses. Certainly the combination of awns and height seem to be two important traits that might contribute to explaining the large distributions of many Andropogoneae, but except in the subtribe Eleusininae, the floral traits are strongly phylogenetically conserved and links among grass lineages (Kellogg, 2015).

Sheth *et al*. (2020) found that habitat suitability and niche breadth are important determinants of range size globally. Including information on the environmental niche of different grass species would be an important way forward but is difficult to do without developing circular reasoning (larger range-sized species could have larger niche breadths simply because they have larger range sizes, i.e. it is a consequence, and not a cause, of their large ranges). Well the details matter… to have a large global range size and narrow niche breadth seems less probable than a large global range size and broad niche breadth. But not impossible at all. How niche breadth is quantified obviously is key – if it is inferred from range size, then totally circular. So, it needs to be quantified independently. Therefore, it would then make sense to check what proportion of potentially inhabitable habitat is actually inhabited, and then relate this to traits or syndromes that may influence dispersal.

4.6 | Conclusion

This study provides the taxonomical and biogeographical understanding of how range size and floral traits and dispersal mode varies across the globe. Although focused on the subtribe Eleusininae, these results can be extrapolated to other grass tribes, and help explain some of the differences in biogeographic history between different lineages.

Chapter 5 | General discussion

General overview of the study, geographical distribution of the southern African grasses, grass clades co-vary according to their floral traits, conservation and management implications, limitations of this study and needs for future research and conclusion.

5.1 | General overview of the study

The geographical range size is the main tool used to predict species extinction risk across the globe (Brown *et al*., 1996; Purvis *et al*., 2000; Alzate & Onstein, 2022). Therefore, it is important to understand the drivers of the species range size (Brown *et al*., 1996; Gaston & Fuller, 2009; Mashau *et al*., 2021; Alzate & Onstein, 2022). Several biotic and abiotic factors affect range sizes. The study shows that plant height and lifespan predict the range size of southern African grasses distributed/found over the sub-Saharan region. Moreover, grasses with larger native range sizes and shorter lifespans are more likely to become invasive after being introduced to other continents (**Chapter 2** see Figure 2.7). The annual-biannual grasses had a significantly higher probability of being invasive than perennial grasses (**Chapter 2** see Figure 2.6). Overall this study helps to understand the main drivers of range size in grasses (Sheth *et al*., 2020) and how grass range size varies across sub-Saharan Africa and also globally.

The range size estimations for the whole of sub-Saharan Africa, the geo-reference data (occurrence) were extracted from Botanical Database of southern Africa (BODATSA, 2019) and Global Biodiversity Information Facility (GBIF.org, 2019). The well-curated herbarium specimens from three SANBI herbaria (and Kew Herbarium (K), UK, including the species identifications recently confirmed in preparation of Fish *et al*. (2015) were also useful in this work. In addition to herbarium specimens, “an identification guide to southern Africa grasses” by Fish *et al*. (2015) and database information mentioned above, the Plants of the World Online (POWO, 2019) (http://plantsoftheworldonline.org/ and GrassBase (Clayton *et al*., 2015) (https://www.kew.org/data/grasses-db.html were used to extract the grass functional and floral traits (plant height (mm), lifespan (perennial, annual-biannual), fertile spikelet length (mm), lemma awn length (mm), lemma awn action, callus sharpness, dispersal unit, and hooks/prickles). The taxonomic goal of defining floral characters that help to distinguish different species is very different from the ecological goal of defining floral functional traits that describe the mechanisms by which grass species reproduce and disperse. However, in this case the ways that the taxonomists defined the floral characters also assisted with the difficult job of identifying key functional traits, and ascertaining useful metrics of seed size and dispersal ability. This study therefore exemplifies the value of mining taxonomic and herbarium data for ecological research questions.

5.1.1 Geographical distribution of the southern African grasses

The grass family (Poaceae) covers approximately 31–43% of the land surface globally (Gibson, 2009; Linder *et al*., 2018; Archibald *et al*., 2019), and started to spread during the Miocene period (10–20 million years ago) to achieve their current dominance (Strömberg, 2011). This study proves that plant height is an important driver of grass biogeography with implications for understanding the spread of certain grass clades both during the Miocene and today. The C_4 clades Andropogoneae, Aristideae, Eragrostideae, Paniceae and Zoysieae, generally, had a strong positive relationship with plant height, but the Cynodonteae is an exception. Cynodonteae species are generally shorter than the other C_4 clades (**Chapter 2** see Figure 2.5). The C_3 tribes Danthonieae and Poeae had smaller range sizes than the other tribes once grass height and lifespan had been accounted for (**Chapter 2** see Appendix A: Figure S2.5). Moreover, the C_3 tribes are predominantly limited to cooler environments in the southern Cape of Africa (Humphreys & Linder, 2013), so height and dispersal ability should not affect their ranges, which are constrained by habitat availability (Gallagher, 2016).

The evolution and maintenance of mesic savanna grasslands are forced by fire and herbivory globally (Forrestel *et al*., 2015; Archibald & Hempson, 2016; Linder *et al*., 2018). Both fire and herbivore pressure are thought to have increased with the spread of grasslands during the Miocene (Forrestel *et al*., 2015; Archibald & Hempson, 2016; Linder *et al*., 2018). The sorting of grass community phylogeny is influenced by fire frequency across South Africa (Visser *et al.*, 2012; Forrestel *et al*., 2015). Most grass species do not have permanent above-ground structures that need protection (hemicryptophyte growth form); therefore, they are resistant to fire (Visser *et al*., 2012; Archibald & Hempson, 2016). Frequent fires enable certain clades, particularly Andropogoneae, to dominate, and through this process these are sometimes called “fire-climax” grasslands. Fire-tolerant or flammable grasses accumulate a lot of above-ground biomass quickly because they often grow fast and tall (Visser *et al*., 2012; Archibald & Hempson, 2016).

Visser *et al*. (2012) demonstrated that Andropogoneae species richness is higher in areas frequently burnt, in mesic savannas and grasslands, in low grazing intensity and average temperatures, but cold in winter, see Figure 5.1 (Everson *et al.*, 1988; Visser *et al.*, 2012). Frequent fires help many grass species of the Andropogoneae to dominate in grass communities (Everson *et al.*, 1988; Visser *et al.*, 2012). Species of the Paniceae are commonly found in warm regions, in mesic habitats such as wetlands and river edges and woody savannas with high grazing intensity (Visser *et al.*, 2012). Wet habitats within either arid or mesic grasslands with low fire frequencies, warm winters and hot summers, basic soil and high grazing pressure are associated with species richness of Chloridoideae in South Africa (Taub, 2000; Cabido *et al.*, 2008; Visser *et al.*, 2012). In general, or on a broad scale, species of the Chloridoideae are geographically associated with arid environments (Taub, 2000; Cabido *et al.*, 2008; Visser *et al.*, 2012). Lastly, the species richness of Aristidoideae is associated with hot, arid grasslands with heavy grazing or disturbances (Figure 5.1). This study has built on previous work showing that not only is aridity a driver of phylogenetic turnover, but also fire and grazing can result in different communities – and that these fire and grazing communities have different floral structures. Those floral structures can be used to infer dispersal strategies and might interact with other plant traits to affect dispersal distance and range size.

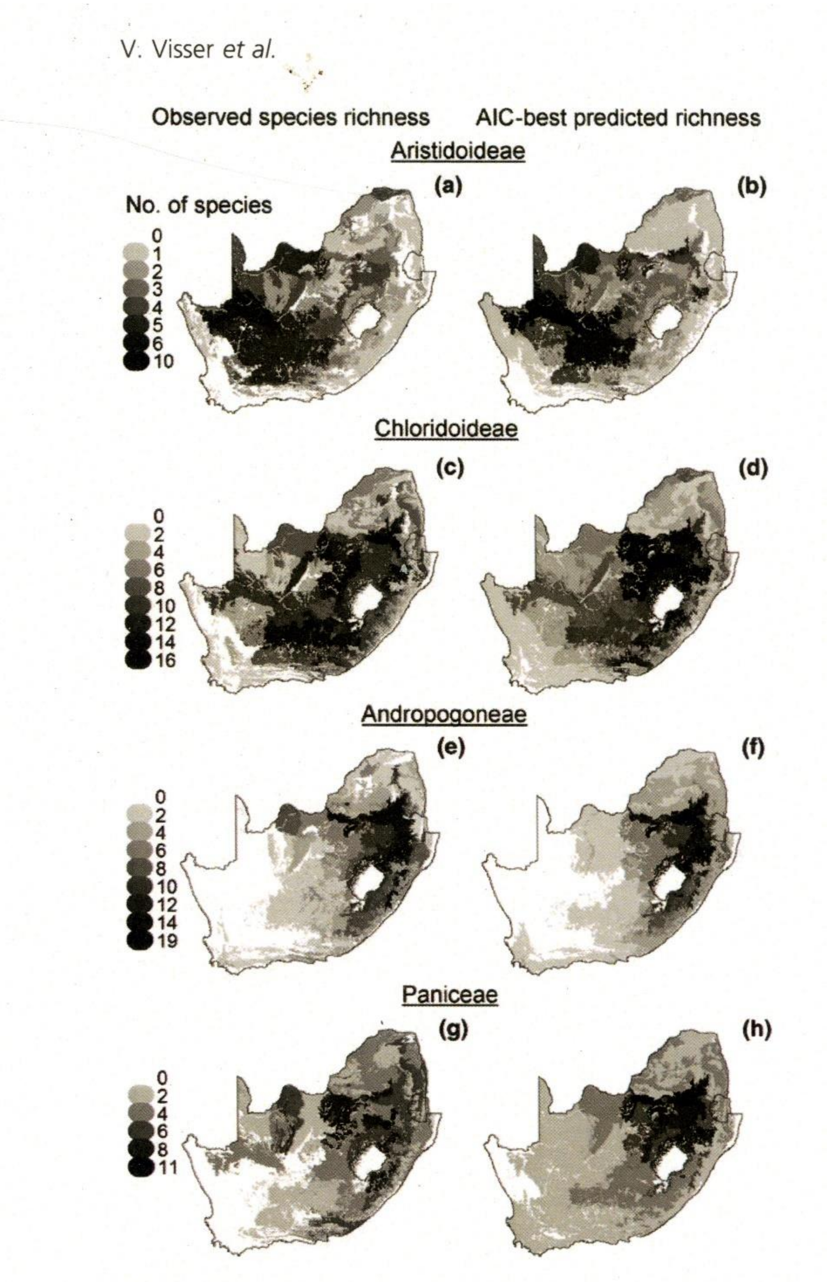

Figure 5.1 From Visser *et al*. (2012), Figure 2. Predicted distribution of species richness for the four major C_4 grass clades. Darker colours represent a high number of species for a particular clade in South Africa.

5.1.2 Grass clades co-vary according to their floral traits

Grass flowering structures vary widely and are often the main morphological characters in distinguishing different grass clades (Kellogg, 2000, 2015). In **Chapter 3**, I identified four clear floral trait syndromes separated largely by awn length and the presence of hooks/prickles or bristles. Long-awned species were more likely to be found in frequently burned environments and were also usually taller than species without awns. Grazer-dominated systems appear to select two different floral trait syndromes. The diversity of grass flowering structures and their functions provide interesting knowledge of evolution and biogeography. A long lemma awn is shown to be an important floral trait that facilitates the dispersal of tall grasses in Africa.

The dispersal of grass seeds is closely associated with the structure and composition of the spikelets (Schrager-Lavelle *et al*., 2017). Epizoochorous, endozoochorous and wind-dispersed seeds have all been reported in this family (Rosas *et al*., 2008) (**Chapter 3**, Figure 3.1). In **Chapter 4,** this study demonstrated that grass species with a large range size in the subtribe Eleusininae are the ones which are taller and had awned lemmas that can be dispersed by the wind. Examples of these species in the subtribe Eleusininae are *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth. and *Tetrapogon roxburghiana* (Schult.) *P.M.Peterson*. Wind dispersal is common in grasses, especially in places with few animals (Jurado *et al*., 1991) and it facilitates long-distance dispersal (less than 1 m) across the globe. Again in **Chapter 4**, the analyses on subtribe Eleusininae confirmed this – there was no significant relationship between the age of the grasses and their range size. Therefore, within the grasses, the conclusions of Sheth *et al*. (2020) do not hold true: dispersal mode appears to be more important than species age.

5.1.3 Conservation and management implications

The understanding of the geographical range of grass species in southern Africa helps to determine the spatial distribution and conservation status of the grasses. Therefore, all these outcomes will give more information on why there are rare species (species that have very limited ranges or that exist in low number) and what constrains them from dispersing to other areas. As an example, this study suggests that some C_3 grasses from the Western Cape are rare not because of dispersal constraints, but because their preferred habitat and climate only occurs in a limited area..

This study's findings 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. This study can provide useful information to the Biological Invasion Division at the South African National Biodiversity Institute (SANBI) on how to quantify geographical distribution and also on risk assessment of introduced species. Currently the SANBI risk profiling mechanism does not consider native range size in their assessment (https://www.sanbi.org/biodiversity/building-knowledge/biodiversity-monitoring-assessment/biological-invasions/the-alien-species-risk-analysis-review-panel-asrarp). Therefore, this study will help conservationists and managers to improve their strategic plans for the conservation and management of southern African grasses across the globe.

5.1.4 Limitations of this study and needs for future research

While it was possible to use the existing literature to infer a lot about dispersal strategies in grasses it would be worthwhile investigating the dispersal mechanisms more by doing field experiments, to see whether the floral traits identified as endozoochory and ectozoochory facilitate grass dispersal potential and long-distance dispersal. Specifically, one could do observational studies, recording the prevalence of different grass seeds in animal coats, compared with their prevalence in the community to determine how important awns, bristles, and hooks are for epizoochorous dispersal, and one could look at the seeds which germinate in dung to assess which ones are ingested and can survive in animal guts. Dispersal by birds has seldom been investigated, but birds often use grass inflorescences as nesting material, and might therefore be important medium-distance dispersal agents.

That wind-dispersed species had a larger range size than endozoochory species is not necessarily predictable. Endozoochory is an important dispersal mechanism that can help with a better understanding of the contemporary and evolutionary role of herbivores and grass species worldwide (Rosas *et al.*, 2008; Anderson *et al*., 2014). More studies are still needed as to why endozoochorous species become dominant in certain environments where there is a high population of herbivores (Anderson *et al*., 2014). One can identify the plants that are found in such an environment and assess whether they are palatable or not. Moreover, this study has improved our ecological and taxonomic understanding of how floral traits differ among the range of tribes in one family across African countries. It can help in understanding dispersal limitations in grasses and predicting which species are likely to flourish in a particular grassland habitat..

There are important traits that could help us to understand the distribution of grass species around the globe but that this thesis does not cover. The relationship between latitude and range size (Rapoport's rule; Stevens, 1989) has been explained regarding the larger seasonal variation experienced at higher latitudes that enables organisms to succeed in a wider range of environments (Morin & Lechowicz, 2011; Morueta-Holme *et al*., 2013). Therefore, there is great interest in how latitude and habitat suitability determine range size, and this is also important for predicting how range sizes will vary in the future as a product of environmental change. It is important to assess or predict how seed size affects the dispersal of grasses in Africa, but in this study, the seed size trait was not fully tested or studied due to insufficient data. I suggest that it is better to use caryopsis length than seed mass because fewer mass data are available. Moreover, a meta-analysis of Alzate & Onstein (2022) showed that dispersal positively affects range size, but the effect dependent on the latitude, range size metric and taxonomic breadth of their study clades: plants and animals in marine, terrestrial and freshwater realms. Moreover, despite potential differences in habitat connectivity, they didn't find an effect on the dispersal-range size relationship. Contrary to these Sheth *et al*. (2020) also demonstrated that factors predicting geographic range size in plants showed that niche breadth is consistently important. Including information on the environmental niche of different grass species would be an important way forward but is difficult to do without developing circular reasoning (larger range-sized species could have larger niche breadths simply because they have larger range sizes, i.e. it is a consequence, and not a cause, of their large ranges). Further studies are needed to assess the niche breadth, floral and functional traits, and how these may affect the relationship between dispersal and range size by shifting the habitat suitability and dispersal ability over time (Jaramillo, 2019; Alzate & Onstein, 2022).

Finally, future research could also explore the correlation between evolutionary history, range size, and extinction risk. Tanentzap *et al*. (2018) found that range size is a proximate explanation for why clade age and diversification rate were associated with extinction risk in plants, as young species tend to occupy narrower geographic and adaptive spaces (Castiglione *et al*., 2017). Unfortunately in this study, I found that there is no relationship between genus age and range size, perhaps because the data available were only at a genus level insufficient to find the existing relationship.

The grass clades Danthonieae and Poeae are the C_3 clades which had rare species (*Pentameris* spp. and *Trisetopsis* spp.); these species had the dispersal ability, but habitat suitability is the key factor due to environmental restrictions (Humphreys & Linder, 2013). Maybe in the future one can assess on how rarity correlates with range size.

5.2 | Conclusion

Practicing the traditional morphological identification on herbarium specimens can help to improve species descriptions and fill the distribution gaps, and these will continue to be most useful for solving ecological problems. Herbarium specimens also help to give a lot of information about the distribution and evolution of species. Herbarium specimen information is fed into the global biodiversity information facility (GBIF), GrassBase, Plants of the World Online (POWO) and even a checklist database to support ecological research. The understanding of the link between range size, floral traits and plant dispersal can help to test hypotheses on how each trait affects dispersal (Alzate & Onstein, 2022) in any plant family across the globe. Dispersal is an important process driving ecological and evolutionary patterns (Onstein *et al*., 2017; Alzate *et al*., 2019; Sheard *et al*., 2020): because it affects how quickly plant populations get isolated from one another, and also how often new plant populations can arise in different geographic regions. Finally, understanding dispersal mechanisms and geographical distribution (range size) can provide useful information for risk assessment – both for risk of invasion and for risk of extinction.

REFERENCES

Alzate, A. & Onstein, R. E. (2022). Understanding the relationship between dispersal and range size. *Ecology Letters*, 00, pp. 1–21. https://doi.org/10.1111/ele.14089

Alzate, A., Van der Plas, F., Zapata, F. A., Bonte, D. & Etienne, R. S. (2019). Incomplete datasets obscure associations between traits affecting dispersal ability and geographic range size of reef fishes in the tropical eastern Pacific. *Ecology and Evolution*, 9, pp. 1567–1577.

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

Archibald, S. & Hempson, G. P. (2016). Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 371, 20150309. https://doi.org/10.1098/rstb.2015.0309

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/10.1002/97811 19081 111.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, pp. 760–771. https://doi.org/10.1111/j.1365-2699.2011.02612.x

Bettink, K. (2008). Bushland weedwatch: Tambookie grass (*Hyparrhenia hirta*). *Bushland News*, 65, pp. 3–4.

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 and Evolution*, 26, pp. 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

Bouchenak-Khelladi, Y., Verboom, G. A., Savolainen, V. & Hodkinson, T. R. (2010). Biogeography of the grasses (Poaceae): A phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society*, 162, pp. 543–557. https://doi.org/10.1111/j.1095-8339.2010.01041.x

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

Bredenkamp, G. J., Brown, L. R. & Pfab, M. F. (2006). Conservation value of the Egoli Granite Grassland, an endemic grassland in Gauteng, South Africa. *Koedoe*, 49, pp. 59–99.

Bremer, K. (2002). Gondwanan evolution of the grass alliance of families (Poales). *Evolution*, 56, pp. 1374–1387.

Bremer, K. & Janssen, T. (2006). Gondwanan origin of major monocot groups inferred from dispersal-vicariance analysis. *Aliso: A Journal of Systematic and Evolutionary Botany*, 22, pp. 22–27.

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, pp. 597–623. https://doi.org/10.1146/annur ev.ecols ys.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, pp. 19–28. https://doi: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, pp. 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, pp. 214–224. https://doi.org/10.1111/j.1365-2745.2010.01759.x

Cabido, M., Pons, E., Cantero, J. J., Lewis, J. P. & Anton, A. (2008). Photosynthetic pathway variation among C4 grasses along a precipitation gradient in Argentina. *Journal of Biogeography*, 35, pp. 131–140.

Canavan, S., Meyerson, L. A, Packer, J. G., Pysek, P., Maurel, N., Lozano, V., Richardson, D. M., Brundu, G., Canavan, K., Cicatelli, A. 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, pp. 37–58. https://doi.org/10.1007/s1053 0-018-1815-z

Castiglione, S., Mondanaro, A., Melchionna, M., Serio, C., Di Febbraro, M., Carotenuto, F. & Raia, P. (2017). Diversification rates and the evolution of species range size frequency distribution. *Frontiers in Ecology and Evolution*, 5, pp. 147.

Charles-Dominique, T., Davies, T. J., Hempson, G. P., Bezeng, B. S., Daru, B. H., Kabongo, R. M., Maurin, O., Muasya, A. M., Van der Bank, M. & Bond, W. J. (2016). Spiny plants, mammal browsers, and the origin of African savannas. *Proceedings of the National Academy of Sciences of the United States of America*, 113, pp. E5572–E6557. https://doi.org/10.1073/pnas.1607493113

Christin, P.-A., Spriggs, E., Osborne, C. P., Strömberg, C. A. E., Salamin, N. & Edwards, E. J. (2014). Molecular dating, evolutionary rates, and the age of the grasses. *Systematic Biology*, 63, pp. 153–165. https://doi.org/10.1093/sysbio/syt072

Cilliers, S. S. & Bredenkamp, G. J. (2000). Vegetation of road verges on an urbanization gradient in Potchefstroom, South Africa. *Landscape and Urban Planning*, 46, pp. 217–239.

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

Clayton, W. D. & Renvoize, S. A. (1986). *Genera graminum: grasses of the world*. London: Her Majesty's Stationery Office.

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

Cousens, R. D., Hill, J., French, K. & Bishop, I. D. (2010). Towards better prediction of seed dispersal by animals. *Functional Ecology,* 24, pp. 1163–1170. https://doi.org/10.1111/j.1365-2435.2010.01747.x

Couvreur, M., Cosyns, E., Hermy, M. & Hoffmann, M. (2005). Complementarity of epi- and endozoochory of plant seeds by free ranging donkeys. *Ecography,* 28, pp. 37–48.

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, pp. 11292– 11303. https://doi.org/10.1002/ece3.3704

Davidse, G. (1987). Fruit dispersal in the Poaceae. In: T. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth (eds.), *Grass systematics and evolution*, pp. 143–155. Smithsonian Institution, Washington D.C., USA

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

Diacon-Bolli, J. C., Edwards, P. J., Bugmann, H., Scheidegger, C. & Wagner, H. H. (2013). Quantification of plant dispersal ability within and beyond a calcareous grassland. *Journal of Vegetation Science,* 24, pp. 1010–1019.

Diaz, 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, pp. 167–171. https://doi.org/10.1038/natur e16489

Donaldson, J. E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z., & Parr, C. L. (2018). Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*, 55, pp. 225–235.

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, pp. 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, pp. 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, pp. 551–559. https://doi.org/10.1109/TIT.1983.1056714

Edwards, E. & Smith, S. (2010) Phylogenetic analyses reveal the shady history of C_4 grasses. *Proceedings of the National Academy of Sciences of Sciences of the United States of America*, 107, pp. 2532–2537. https://doi.org/10.1073/pnas.0909672107

Edwards, W., Dunlop, M., Rodgerson, L. (2006). The evolution of rewards: seed dispersal, seed size and elaiosome size. *Journal of Ecology*, 94, pp. 687–694.

Elbaum, R., Zaltzman, L., Burgert, I. & Fratzl, P. (2007). The role of wheat awns in the seed dispersal unit. *Science*, 316, pp. 884–886.

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, pp. 849–858. https://doi.org/10.1111/geb.12306

Everson, C. S., Everson, T. M. & Tainton, N. M. (1988). Effects of intensity and height of shading on the tiller initiation of six grass species from the Highland sourveld of Natal. *South African Journal of Botany*, 54, pp. 315–318.

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

Filgueiras, T., Peterson, P. M. & Herrera-Arrieta, Y. (1999). *Rheochloa* (Poaceae: Chloridoideae), A new genus from Central Brazil. *Systematic Botany*, 24, pp. 123–127.

Fischer, S. F., Poschlod, P. & Beinlich, B. (1996). Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology*, 33, pp. 1206–1222.

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*, 36, pp. vi–749, South African National Biodiversity Institute, Pretoria.

Forrestel, E. J., Donoghue, M. J. & Smith, M. D. (2015). Functional differences between dominant grasses drive divergent responses to large herbivore loss in mesic savanna grasslands of North America and South Africa. *Journal of Ecology*, 103, pp. 714–724. https://doi.org/10.1111/1365-2745.12376

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

Garnier, L. K. M. & Dajoz, I. (2001). Evolutionary significance of awn length variation in a clonal grass of fire-prone savannas. *Ecology*, 82, pp. 1720–1733.

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, pp. 219–230.

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

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

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

Gibbs Russell, G.E., Watson, L., Koekemoer, M., Smook, L., Barker, N.P., Anderson, H.M. & Dallwitz, M.J. (1990). Grasses of southern Africa. *Memoirs of the Botanical Survey of South Africa*, 58, pp. 1–437.

Gibson, D. J. (2009). *Grasses and Grassland Ecology*. Oxford University Press, Oxford.

Godó, L., Valkó, O., Borza, S. & Deák, B. (2022). A global review on the role of small rodents and lagomorphs (clade Glires) in seed dispersal and plant establishment, *Global Ecology and Conservation*, 33, e01982, https://doi.org/10.1016/j.gecco.2021.e01982.

Govaerts, R., Dransfield, J., Zona, S., Hodel, D. R. & Henderson, A. (2022). *World Checklist of Poaceae*. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet, http://wcsp.science.kew.org/ Retrieved 10 January 2022

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 27, pp. 857–871. https://doi.org/10.2307/2528823

Griffith, D. M., Osborne, C. P., Edwards, E. J., Bachle, S., Beerling, D. J., Bond, W. J., Gallaher, T. J., Helliker, B. R., Lehmann, C. E., Leatherman, L. & Nippert, J. B. (2020). Lineage-based functional types: characterising functional diversity to enhance the representation of ecological behaviour in Land Surface Models. *New Phytologist*, 228, pp. 15–23.

Grossenbacher, D., Briscoe Runquist, R., Goldberg, E.E. & Brandvain, Y. (2015). Geographic range size is predicted by plant mating system. *Ecology Letters*, 18, pp. 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 C3 shade clades and support for a Miocene to Pliocene origin of C4 grassy biomes. *Journal of Biogeography*, 45, pp. 750–761.

Hanski, I., Kouki, J. & Halkka, A. (1993). Three explanations of the positive relationship between distribution and abundance of species. In: Ricklefs, R. & Schluter, D., (eds.), *Species diversity in ecological communities: historical and geographical perspectives*. Chicago, IL, USA: The University of Chicago Press, pp. 108–116.

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F. J., Kruger, L. M., Moxley, C., Owen-Smith, N., Peel, M. J. S., Smit, I. P. J. & Vickers, K. J. (2015). Ecology of grazing lawns in Africa. *Biological Reviews*, 90, pp. 979–994. https://doi.org/10.1111/brv.12145

Hempson, G. P., Archibald, S., Donaldson, J. E. & Lehmann, C. E. R. (2019). Alternate grassy ecosystem states are determined by palatability-flammability trade-offs. *Trends in Ecology & Evolution*, 34, pp. 286–290.

Hempson, G. P., Parr, C. L., Lehmann, C. E. R. & Archibald, S. (2022). Grazing lawns and overgrazing in frequently grazed grass communities. *Ecology and Evolution*, 12(9), pp. e9268.

Howell, D. C. (2015). Randomization Test Correlation Coefficients. https://www.uvm.edu/~statdhtx/StatPages/ResamplingWithR/RandomCorr/randomization_Correlation.html [Accessed 02 June 2022].

Huang, S. Q., Yang, C. F., Lu, B. & Takahashi, Y. (2002). Honeybee-assisted wind pollination in bamboo *Phyllostachys nidularia* (Bambusoideae: Poaceae)? *Botanical Journal of the Linnean Society*, 138, pp. 1–7. https://doi.org/10.1046/j.1095-8339.2002.00001.x

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, pp. 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, pp. 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, Gland, Switzerland and Cambridge.

Janzen, D. H. (1984). Dispersal of small seeds by big herbivores – foliage is the fruit. *American Naturalist*, 123, pp. 338–353.

Jaramillo, C. (2019). 140 million years of tropical biome evolution. In: Gómez, J. & Pinilla–Pachon, A. O. (eds.), The Geology of Colombia, Volume 2 Mesozoic. Bogotá: *Servicio Geológico Colombiano, Publicaciones Geológicas Especiales* 36, pp. 209–236. https://doi.org/10.32685/ pub.esp.36.2019.06

Jurado, E., Westoby, M. & Nelson, D. (1991). Diaspore weight, dispersal, growth form and perenniality of central Australian plants. *Journal of Ecology*, 79, pp. 811–830.

Kellogg, E. A. (2000). The grasses: a case study in macroevolution. *Annual Review of Ecology and Systematics*, 31, pp. 217–238.

Kellogg, E. A. (2015). Flowering plants. Monocots: Poaceae. In: K. Kubitzki (ed.), *The families and genera of vascular plants*. Springer, Germany. 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, pp. 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). doi: 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, pp. 1879. https://doi.org/10.1038/ncomms2836

Lehmann, C. E. R., Archibald, S. A., Hoffmann, W. A., & Bond, W. J. (2011). Deciphering the distribution of the savanna biome. *New Phytologist,* 191, pp. 197–209. https://doi.org/10.1111/j.1469-8137.2011.03689.x

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, pp. 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, pp. 258–261. https://doi.org/10.1038/20436

Mashau A. C., Hempson, G. P., Lehmann, C. E. R., Vorontsova, M. S., Visser, V. & Archibald, S. (2021). Plant height and lifespan predict range size in southern African grasses. *Journal of Biogeography,* 48, pp. 3047–3059. https://doi.org/10.1111/jbi.14261

McLoughlin, S. (2001). The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany*, 49, pp. 271–300. https://doi.org/10.1071/BT00023

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

Molano-Flores, B. (2012). Diaspore morphometrics and self-burial in *Hesperostipa spartea* from loam and sandy soils. *The Journal of the Torrey Botanical Society*, 139, pp. 56–62.

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, pp. 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, pp. 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, pp. 1–13. doi: 10.1111/ecog.04609

Morin, X. & Lechowicz, M. J. (2011). Geographical and ecological patterns of range size in North American trees. *Ecography,* 34, pp. 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., Ŝímová, 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, pp. 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, pp. 291–310. https://doi.org/10.1046/j.1442-9993.2002.01181.x

Nielsen, S. (2000). Numerical Ecology. In: Legendre, P. & Legendre, L., second ed., Elsevier, Amsterdam, p. 853, 1998. *Ecological Modelling*, 132, pp. 303–304. https://doi.org/10.1016/S0304-3800(00)00291-X

Niklas, K. J. (2004). Plant allometry: is there a grand unifying theory? *Biological Reviews*, 79, pp. 871–889. https://doi.org/10.1017/S1464 79310 4006499

Oksanen, J. (2015). Vegan: An introduction to ordination. Retrieved from http://cran.ma.ic.ac.uk/web/packages/vegan/vignettes/introvegan.pdf

Onstein, R. E., Baker, W. J., Couvreur, T. L. P., Faurby, S., Svenning, J. C. & Kissling, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nature Ecology and Evolution*, 1, pp. 1903–1911.

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, pp. 441–446. https://doi.org/10.1111/nph.12942

Pagel, M. (1997). Inferring evolutionary processes from phylogenies. *Zool Scripta*, 26, pp. 331–348. https://doi.org/10.1111/j.1463-6409.1997.tb004 23.x

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

Pakeman, R. J., Digneffe, G. & Small, J. L. (2002). Ecological correlates of endozoochory by herbivores. *Functional Ecology*, 16, pp. 296–304. https://doi.org/10.1046/j.1365-2435.2002.00625.x

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

Peart, M. H. (1979). Experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology*, 67, pp. 843–863.

Peart, M. H. (1981). Further experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* 69, pp. 425–436.

Peart, M. H. & Clifford, H. T. (1987). The influence of diaspore morphology and soil-surface properties on the distribution of grasses. *Journal of Ecology*, 75, pp. 569–576.

Petersen, K.B. & Kellogg, E.A. (2022). Diverse ecological functions and the convergent evolution of grass awns. *American Journal of Botany*, 109, pp. 1331–1345. https://doi.org/10.1002/ajb2.16060

Peterson, P. M., Romaschenko, K. & Herrera-Arrieta, Y. (2015). A molecular phylogeny and classification of the Eleusininae with a new genus, *Micrachne* (Poaceae: Chloridoideae: Cynodonteae). *Taxon*, 64, pp. 445–467.

Peterson, P. M., Romaschenko, K., Herrera-Arrieta, Y. (2021). Phylogeny, classification, and biogeography of *Afrotrichloris*, *Apochiton*, *Coelachyrum*, *Dinebra*, *Eleusine*, *Leptochloa*, *Schoenefeldia*, and a new genus, *Schoenefeldiella* (Poaceae: Chloridoideae: Cynodonteae: Eleusininae). *Journal of Systematics and Evolution*, 60, pp. 630–639. doi.org/10.1111/jse.12803.

POWO. (2019). Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published online: http://www.plantsoftheworldonline.org/ [Accessed 28 August 2020].

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, pp. 513–523. https://doi.org/10.1111/j.1466-8238.2011.00703.x

Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B*, 267(1456), pp. 1947–1952.

Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I. & 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, pp. 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, Vienna, Austria. http://www.R-project.org/

Ripley, B., Visser, V., Christin, P. A., Archibald, S., Martin, T. & Osborne, C. (2015). Fire ecology of C3 and C4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology*, 96, pp. 2679–2691.

Rosas, C. A., Engle, D. M., Shaw, J. H. & Palmer, M. W. (2008). Seed dispersal by *Bison bison* in a tallgrass prairie. *Journal of Vegetation Science*, 19, pp. 769–778. https://doi.org/10.3170/2008-8-18447

Roux, E. (1969). *Grass. A Story of Frankenwald.* Oxford University Press, Cape Town, South Africa.

Royal Botanical Garden Kew. (2008). *Seed Information Database* (SID), v 7.1. Available at: http://data.kew.org/sid/.

Ruiz-Sanchez, E., Peredo, L. C., Santacruz, J. B. & Ayala-Barajas, R. (2017). Bamboo flowers visited by insects: do insects play a role in the pollination of bamboo flowers? *Plant Systematics and Evolution*, 303, pp. 51–59. https://doi.org/10.1007/s00606-016-1351-1

Sádlo, J., Chytrý, M., Pergl, J. & Pyšek, P. (2018). Plant dispersal strategies: A new classification based on the multiple dispersal modes of individual species. *Preslia*, 90, pp. 1–22. https://doi.org/10.23855/preslia.2018.001

Sajo, M. D. G, Furness, C. A. & Rudall, P. J. (2009). Microsporogenesis is simultaneous in the early-divergent grass *Streptochaeta*, but successive in the closest grass relative. *Ecdeiocolea.Grana*, 48, pp. 27–37.

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, pp. 490–500. https://doi.org/10.1111/j.1365-2028.2011.01283.x

Schrager-Lavelle, A., Klein, H., Fisher, A. & Bartlett, M. (2017). Grass flowers: an untapped resource for floral evo-devo. *Journal of Systematics and Evolution*, 55, pp. 525–541. https://doi.org/10.1111/jse.12251

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

Sheard, C., Neate-Clegg, M. H. C., Alioravainen, N., Jones, S. E. I., Vincent, C., MacGregor, H. E. A., Bregman, T. P., Claramunt, S. & Tobias, J. A. (2020). Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications*, 11, pp. 2463. https://doi.org/10.1038/s41467-020-16313-6

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

Shiponeni, N. N. & Milton, S. J. (2006). Seed dispersal in the dung of large herbivores: implications for restoration of renosterveld shrubland old fields. Biodiversity Conservation, 15, pp. 3161–3175.

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

Soderstrom, T. R. & Calderón, C. E. (1971). Insect pollination in tropical rainforest grasses. *Biotropica*, 3, pp. 1–16. https://doi. org/10.2307/2989701

Solofondranohatra, C. L., Vorontsova, M. S., Hempson, G. P., Hackel, J., Cable, S., Vololoniaina, J. & Lehmann, C. E. R. (2020). Fire and grazing determined grasslands of central Madagascar represent ancient assemblages. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20200598.

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, pp. 11204–11212. https://doi.org/10.1002/ece3.3568

Soreng, R. J., Peterson, P., Romaschenko, K., Davidse, G., Teisher, J. K., Clark, L., Barberá, P., Gillespie, L. J. & Zuloaga, F. (2017). A worldwide phylogenetic classification of the Poaceae (Gramineae) II: an update and a comparison of two 2015 classifications. *Journal of Systematics and Evolution*, 55, pp. 259–290. https://doi.org/10.1111/jse.12262

Soreng, R. J., Peterson, P. M., Zuloaga, F. O., Romaschenko, K., Clark, L. G., Teisher, J. K., Gillespie L. J., Barberá, P., Welker, C. A. D., Kellogg, E. A., Li, D. Z. & Davidse, G.

(2022). A worldwide phylogenetic classification of the Poaceae (Gramineae) III: An update. *Journal of Systematics and Evolution*, 60, pp. 476–521. https://doi.org/10.1111/jse.12847

Spriggs, E. L., Christin, P. A. & Edwards, E. J. (2014). C4 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, pp. 16–25. https://doi.org/10.1111/geb.13003

Staver, A. C. & Bond, W. J. (2014). Is there a "browse trap"? Dynamics of herbivore impacts on trees and grasses in an African savanna (ed. A. Austin). *Journal of Ecology*, 102, pp. 595–602. https://doi.org/10.1111/1365-2745.12230

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

Strömberg, C. A. E. (2005). Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences of the United States of America*, 102, pp. 11980–11984.

Strömberg, C. A. E. (2011). Evolution of grasses and grassland ecosystems. *Annual review of Earth and planetary sciences*, 39, pp. 517–544. https://doi.org/10.1146/annur ev-earth-040809-152402

Tackenberg, O., Römermann, C., Thompson, K. & Poschlod, P. (2006). What does diaspore morphology tell us about external animal dispersal? Evidence from standardized experiments measuring seed retention on animal-coats. *Basic and Applied Ecology*, 7, pp. 45–58.

Tanentzap, A. J., Igea, J., Johnston, M. G. & Larcombe, M. J. (2018). Range size dynamics can explain why evolutionarily age and diversification rate correlate with contemporary extinction risk in plants. *Peer Community in Evolutionary Biology, BioRxiv*. https://doi.org/10.1101/152215

Taub, D. R. (2000). Climate and the US distribution of C4 grass subfamilies and decarboxylation variants of C4 photosynthesis. *American Journal of Botany*, 87, pp. 1211–1215.

Taylor, S. H., Hulme, S. P., Rees, M., Ripley, B. S., Woodward, F. I. & Osborne, C. P. (2010). Ecophysiological traits in C3 and C4 grasses: a phylogenetically controlled screening experiment. *New Phytologist*, 185, pp. 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, pp. 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

Thomson, F. J., Letten, A. D., Tamme, R., Edwards, W. & Moles, A. T. (2018). Can dispersal investment explain why tall plant species achieve longer dispersal distances than short plant species? *New Phytologist*, 217, pp. 407–415. https://doi.org/10.1111/nph.14735

Ullmann, I., Bannister, P. & Wilson, J. B. (1995). The vegetation of roadside verges with respect to environmental gradients in southern New Zealand. *Journal of Vegetation Science*, 6, pp. 131–142.

Van der Pijl, L. (1982). *Principles of dispersal in higher plants*, 3rd revised and expanded edn. Springer, Berlin.

Van Oudtshoorn F. (2014). *Guide to Grasses of Southern Africa*. Briza Publications, Pretoria.

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, pp. 104–114. https://doi.org/10.1111/nph.13574

Visser, V., Woodward, F. I., Freckleton, R. P. & Osborne, C. P. (2012). Environmental factors determining the phylogenetic structure of C4 grass communities. *Journal of Biogeography*, 39, pp. 232–246. https://doi.org/10.1111/geb.12445

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, pp. 679–692. 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, pp. 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, pp. 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, pp. 213–227.

Wilson, A.M. & Thompson, K. (1989). A comparative study of reproductive allocation in 40 British grasses. *Functional Ecology*, 3, pp. 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, pp. 744–751. http://doi.org/10.1111/2041- 210X.13152

APPENDIX A

Table S2.1 Model selection for the phylogenetic generalised least squares models fitted to assess relationships between range size (km^2, log-scale) and plant height (mm) and lifespan (two-level factor: "annual-biannual" or "perennial") for 350 southern African grasses. d.f. = degrees of freedom, AIC = Akaike's Information Criterion, and ΔAIC = difference in AIC values between the best model and the model with lowest AIC value. Parameter estimates for models fitted to range size estimated using alpha values of 100 km, 200 km and 300 km are shown for comparison.

		Alpha = 100 km		Alpha = 200 km		Alpha = 300 km	
Models	d.f.	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
Range size ~ Height + Lifespan	3	1386.38	0.00	1308.69	0.00	1286.20	0.00
Range size ~ Height * Lifespan	4	1388.38	2.00	1310.64	1.95	1288.13	1.93
Range size ~ Lifespan	2	1409.96	23.58	1337.72	29.03	1316.09	29.88
Range size ~ Height	2	1408.24	21.86	1340.46	31.78	1318.11	31.91

Table S2.2 Parameter estimates for the best phylogenetic generalised least squares model fitted to range size (km^2, log-scale) data for 350 southern African grasses. Plant height (mm) and lifespan (two-level factor: "annual-biannual" or "perennial") were included as additive predictors in this model. Note that the parameter estimates for lifespan = "annual-biannual" is included in the model intercept. Statistical significance of parameter estimates is represented as follows: *** = < 0.001, ** = < 0.01, * = < 0.05 and + = < 0.10. Parameter estimates for models fitted to range size estimated using alpha values of 100 km, 200 km and 300 km are shown for comparison.

	Alpha = 100 km	Alpha = 200 km	Alpha = 300 km
Parameter	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)
Intercept	5.809 ±1.326 ***	6.819 ±1.226 ***	7.351 ±1.195 ***
Height	0.882 ±0.172 ***	0.876 ±0.154 ***	0.860 ±0.150 ***
Lifespan			
Perennial	-1.032 ±0.209 ***	-1.098 ±0.185 ***	-1.064 ±0.179 ***

Table S2.3 Model selection for the linear mixed effect models fitted to test relationships between range size (km^2) and plant height (mm) and lifespan (two-level factor: "annual-biannual" or “perennial”), with genus within tribe fitted as a random effect for 757 species (12 tribes) of southern African grasses. Range size and plant height were natural log-transformed prior to analysis. Table headers as per Table S2.1. Parameter estimates for models fitted to range size estimated using alpha values of 100 km, 200 km and 300 km are shown for comparison.

		Alpha = 100 km		Alpha = 200 km		Alpha = 300 km	
Models	d.f.	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
Range size ~ Height + Lifespan + (1|Tribe/Genus)	6	3361.54	0.00	3198.29	0.00	3132.45	0.00
Range size ~ Height * Lifespan + (1|Tribe/Genus)	7	3363.06	1.52	3200.10	1.81	3134.43	1.98
Range size ~ Height + (1|Tribe/Genus)	5	3375.66	14.11	3221.91	23.62	3156.82	24.37
Range size ~ Lifespan + (1|Tribe/Genus)	5	3396.27	34.72	3241.12	42.83	3175.94	43.50

Table S2.4 Parameter estimates for the best linear mixed effect model fitted to range size data for 757 grass species representing 144 genera and 12 tribes in southern Africa. Plant height (mm) and lifespan (two-level factor: “annual-biannual” or “perennial”) were included as additive predictors in this model. The effect of genus nested within tribe was fitted as a random intercept term. Note that the parameter estimates for lifespan = “annual-biannual” is included in the model intercept. Statistical significance of parameter estimates is represented as follows: *** = < 0.001, ** = < 0.01, * = < 0.05 and + = < 0.10. Parameter estimates for models fitted to range size estimated using alpha values of 100 km, 200 km and 300 km are shown for comparison.

	Alpha = 100 km	Alpha = 200 km	Alpha = 300 km
Parameter	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)
Fixed effects			
Intercept	5.226 ±0.935***	6.365 ±0.859 ***	6.96 ±0.89 ***
Height	0.877 ±0.140 ***	0.872 ±0.127 ***	0.85 ±0.13 ***
Lifespan			
Perennial	-0.769 ±0.190 ***	-0.870 ±0.170 ***	-0.84 ±0.17 ***
Random effects	Variance	Variance	Variance
Genus: Tribe	0.504	0.464	0.494
Tribe	0.149	0.355	0.488
Residual	4.545	3.607	3.777

Table S2.5 Parameter estimates for linear models fitted to species range size estimates for each of 12 grass tribes. Plant height (mm, log-transformed) and plant lifespan (annual-biannual vs. perennial) were fitted as predictors, except in the models for the Arundineae, Oryzeae and Tristachydeae, which each had two or fewer annual species. Column “n” shows the total number of species in each tribe, with representation by annual-biannual vs. perennial species shown in parentheses. Statistical significance of the intercept, height and lifespan parameter estimates is represented as follows: *** = < 0.001, ** = < 0.01, * = < 0.05 and + = < 0.10. Overall model fit (r^2) and significance (p) are also shown. Note that species range size estimates analysed in these models were all calculated using an alpha value of 200 km.

Tribe	n	Intercept	Height	Lifespan	r^2	p
Andropogoneae	97 (13/84)	6.807 **	1.005 **	-1.625 ***	0.187	< 0.001
Aristideae	60 (19/41)	1.270	1.633 **	-1.443 *	0.178	0.004
Arundineae	7 (2/5)	3.512	1.276 *		0.644	0.030
Cynodonteae	70 (22/48)	15.639 ***	-0.514	-0.715	0.040	0.251
Danthonieae	112 (15/97)	9.970 ***	0.080	-0.826	0.024	0.266
Ehrhartideae	23 (6/17)	7.374 $^{+}$	0.685	-1.542 *	0.191	0.121
Eragrostideae	102 (44/58)	5.173 *	1.095 **	-0.736	0.086	0.011
Oryzeae	7 (2/5)	-50.316 *	9.077 **		0.788	0.008
Paniceae	173 (64/109)	8.159 ***	0.640 *	-0.651 *	0.045	0.020
Poeae	45 (7/38)	-2.796	2.099 **	-1.017	0.209	0.007
Tristachydeae	19 (1/18)	2.865	1.158		0.071	0.267
Zoysieae	42 (8/34)	6.734 *	0.878 *	-0.369	0.113	0.097

Table S2.6 Model selection for the binomial generalised linear mixed effect models fitted to assess relationships between grass species invasiveness and native range size (km^2), plant height (mm), lifespan (two-level factor: "annual-biannual" or "perennial") and tribe fitted as a random effect. Invasiveness was scored according to the three categories in Visser *et al*. (2016), with introduced and naturalised categories scored as 0, and invasive as 1. Range size and plant height were natural log-transformed prior to analysis. See Table S2.1 for header descriptions. Parameter estimates for models fitted to range size estimated using alpha values of 100 km, 200 km and 300 km are shown for comparison.

		Alpha = 100 km		Alpha = 200 km		Alpha = 300 km	
Models	d.f.	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
Invasive ~ Range size + Lifespan + (1|Tribe)	4	233.37	0.00	233.82	0.00	234.51	0.00
Invasive ~ Range size + (1|Tribe)	3	235.59	2.23	235.45	1.63	236.02	1.51
Invasive ~ Range size + Height + Lifespan + (1|Tribe)	5	234.81	1.44	235.64	1.83	236.43	1.91
Invasive ~ Range size + Height + (1|Tribe)	4	237.59	4.22	237.38	3.57	237.87	3.36
Invasive ~ Height + Lifespan + (1|Tribe)	4	247.30	13.94	247.24	13.43	247.30	12.79
Invasive ~ Lifespan + (1|Tribe)	3	248.79	15.43	248.79	14.98	248.79	14.28
Invasive ~ Height + (1|Tribe)	3	255.22	21.86	255.17	21.35	255.22	20.71

Table S2.7 Parameter estimates for the best binomial generalised linear mixed effect model fitted to invasion category data for 250 grasses native to South Africa but invasive on other continents. Range size (km^2) and lifespan (two-level factor: “annual-biannual” or “perennial”) were included as additive predictors in this model. Range size was natural log-transformed prior to analysis. Note that the parameter estimates for lifespan = “annual-biannual” is included in the model intercept. Statistical significance of parameter estimates is represented as follows: *** = < 0.001, ** = < 0.01, * = < 0.05 and + = < 0.10. Parameter estimates for models fitted to range size estimated using alpha values of 100 km, 200 km and 300 km are shown for comparison.

	Alpha = 100 km	Alpha = 200 km	Alpha = 300 km
Parameter	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)
Fixed effects			
Intercept	-7.911 ±1.968 ***	-8.743 ±2.289 ***	-8.888 ±2.399 ***
Range size	0.555 ±0.152 ***	0.576 ±0.167 ***	0.565 ±0.168 ***
Lifespan			
Perennial	-0.727 ±0.352 *	-0.670 ±0.349 $^+$	-0.655 ±0.345 $^+$
Random effects	Variance	Variance	Variance
Tribe	0.284	0.180	0.074

Table S2.8 Parameter estimates for the best linear mixed effect models fitted to range size (km^2) estimates for 757 grasses native to southern Africa, with invasion status on other continents fitted as a fixed effect. There are four categories of invasion status: "not introduced" (included in the estimate in this model), "introduced", introduced and now "naturalised", and introduced and now "invasive". Genus was nested within tribe in the random effects. Statistical significance of parameter estimates is represented as follows: *** = < 0.001, ** = < 0.01, * = < 0.05 and + = < 0.10. Parameter estimates for models fitted to range size estimated using alpha values of 100 km, 200 km and 300 km are shown for comparison.

	Alpha = 100 km	Alpha = 200 km	Alpha = 300 km
Parameter	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)
Fixed effects			
Intercept	9.677 ±0.161 ***	10.809 ±0.211 ***	11.383 ±0.226 ***
Invasion category			
Introduced	2.179 ±0.192 ***	1.948 ±0.174 ***	1.880 ±0.166 ***
Naturalised	2.532 ±0.298 ***	2.270 ±0.270 ***	2.218 ±0.258 ***
Invasive	3.291 ±0.299 ***	2.976 ±0.270 ***	2.836 ±0.258 ***
Random effects	Variance	Variance	Variance
Tribe: Genus	0.371	0.360	0.361
Tribe	0.099	0.318	0.401
Residual	3.683	2.978	2.702

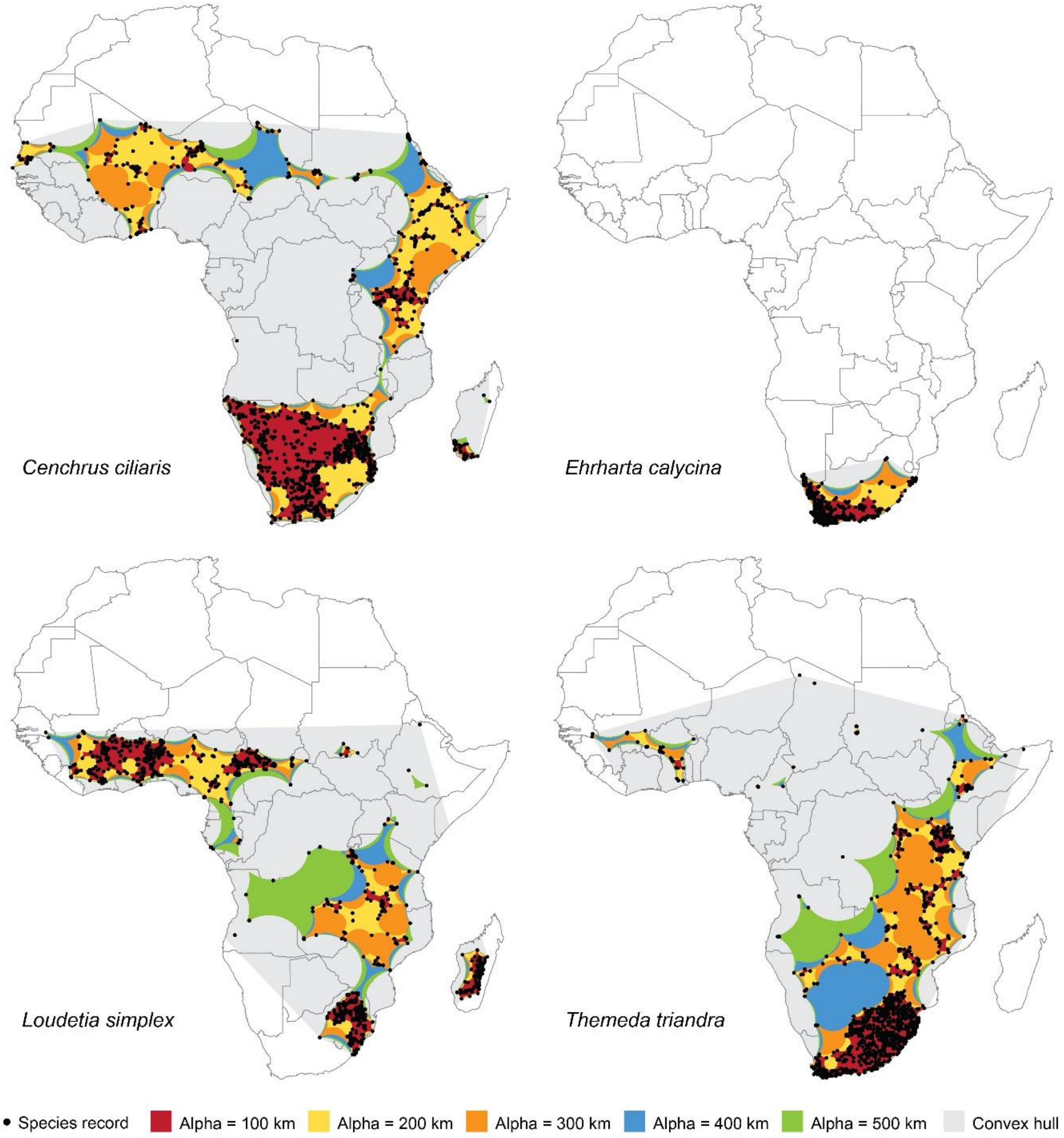

Figure S2.1 Maps showing range size estimates of four southern African grasses when estimated using different alpha hull values and extent of occurrence (EOO: Convex hull). The alpha hull range size estimate approaches the EOO or convex hull estimate as the alpha hull value is increased. Note that the estimated distribution ranges for different alpha values are stacked on top of each other, with ranges estimated by lower alpha values forming part of the estimate for higher alpha values.

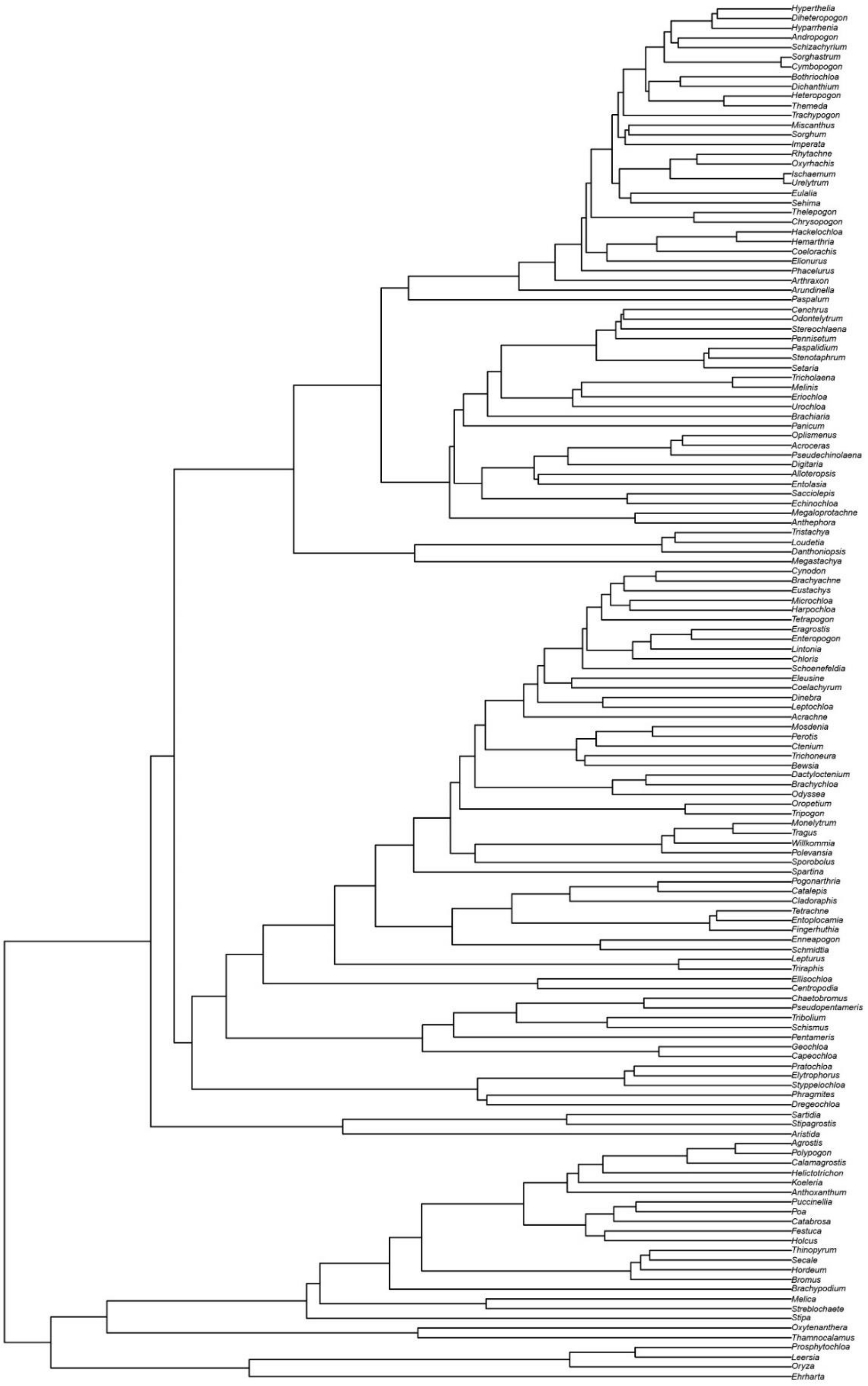

Figure S2.2 The genus-level phylogenetic tree from Spriggs *et al*. (2014), which included 120 of the 144 genera, covering 350 of the 757 native grass species from southern Africa in the dataset.

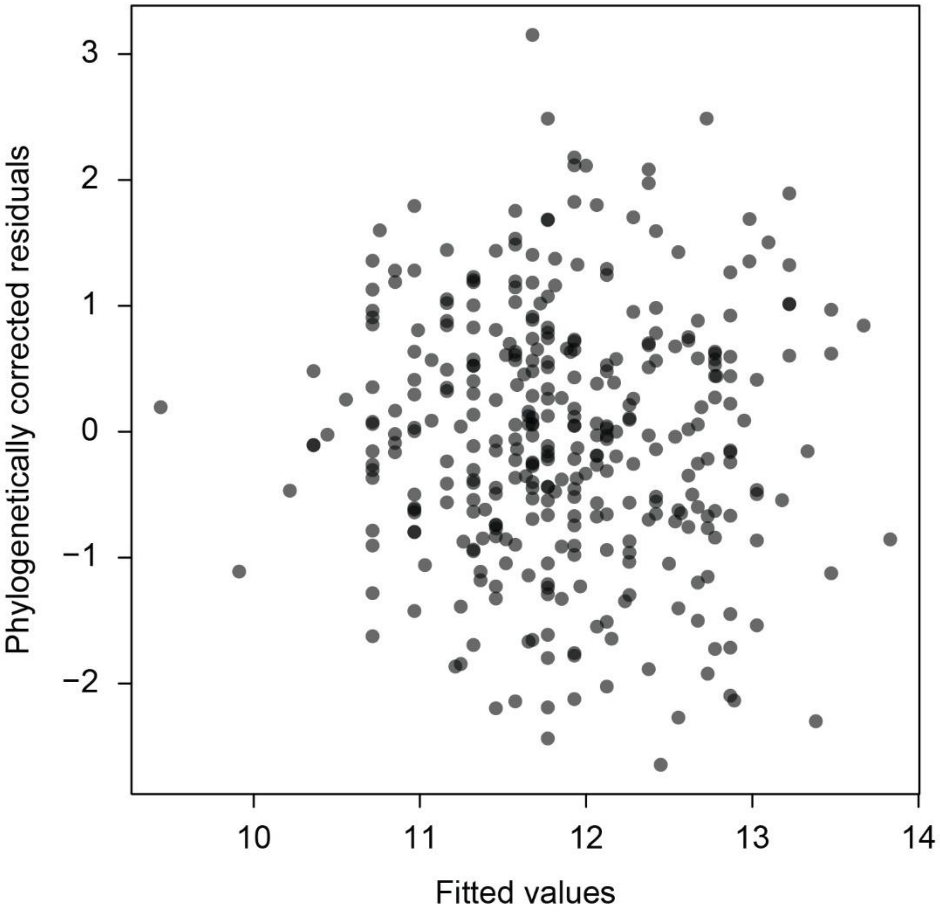

Figure S2.3 Plot of phylogenetically corrected residual vs. fitted values for the phylogenetic least squares regression model fitted to range size estimates of 350 southern African grass species.

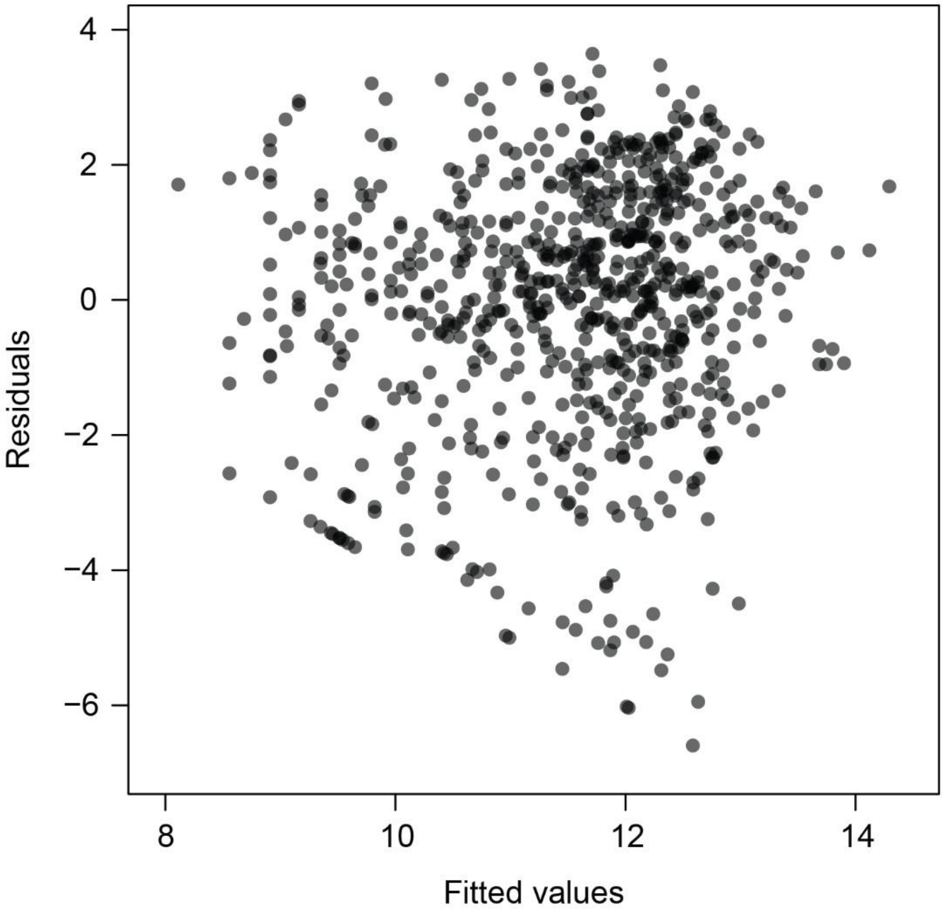

Figure S2.4 Plot of residual vs. fitted values for the linear mixed effects model fitted to range size estimates of 757 southern African grass species with plant height and lifespan fitted as fixed effects, and genus nested within tribe as the random effects.

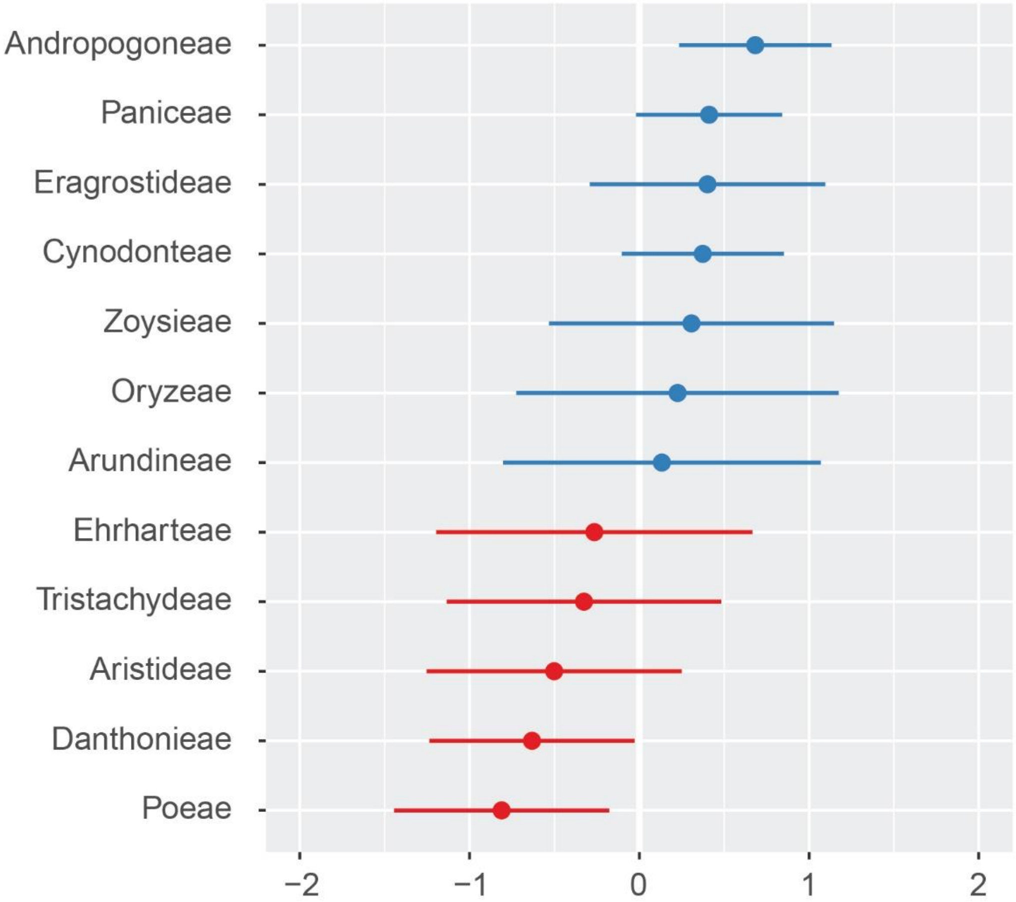

Figure S2.5 Tribe random effect intercept estimates from the best linear mixed effect model, which assessed range size in response to plant height and lifespan. The model was fitted to data for 757 grass species representing 144 genera and 12 tribes in southern Africa. Tribe Andropogoneae an intercept > 0.0, whereas Danthonieae and Poeae had intercepts < 0.0, while intercept estimates for the remaining tribes overlapped zero.

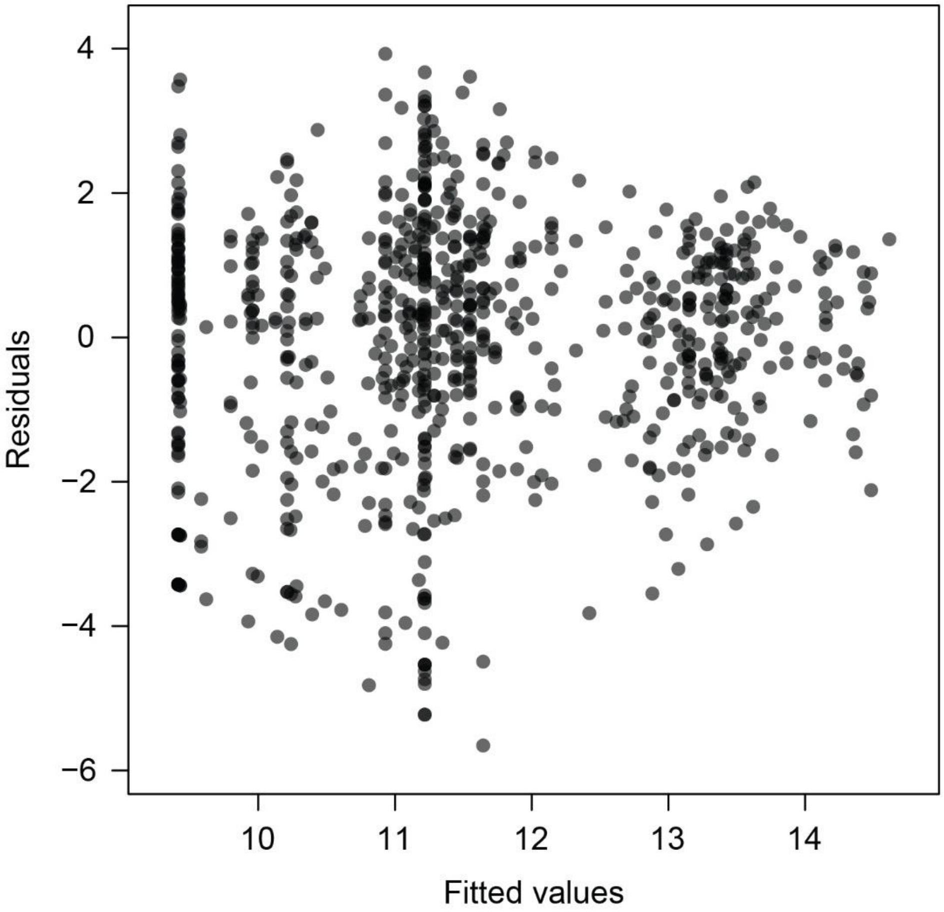

Figure S2.6 Plot of residual vs. fitted values for the linear mixed effects model fitted to range size estimates of 757 southern African grass species with invasion categories as a single fixed effect, and genus nested within tribe as the random effects.

Appendix B

Table S3.1 Different grass species can share similar floral traits in non-metric multi-dimensional scaling (NMDS).

Floral traits	**NMDS1**	**NMDS2**	**R^2**	**P-value**
Lemma awn action	-0.920	0.391	0.92	< 0.001
Callus sharpness	-0.996	0.087	0.83	< 0.001
Hooks/Prickles	0.313	0.950	0.36	< 0.001
Dispersal unit	-0.040	0.999	0.79	< 0.001
Fertile spikelet length	-0.692	-0.722	0.28	< 0.001
Lemma awn length	-0.973	0.231	0.92	< 0.001

Table S3.2 Pearson's Chi-squared test shows how ordinal traits relate to fire and grazing categories of 163 species. Callus sharpness ($p < 0.001$) and awn action ($p < 0.001$) traits are significantly associated with particular fire and grazing grasses. But hooks/prickles ($p = 0.084$) and dispersal unit ($p = 0.321$) traits are not significant with any category. Blue colour if the expected percentage is lower than observed, and red colour if the expected percentage is higher than observed.

Ordinal variables	**Category (number of species)**			**Expected percentage**	**Pearson's Chi-squared test**		
	Fire	**Intermediate**	**Grazing**		**X-squared**	**Df**	**p-values**
Hooks/Prickles					4.958	2	0.084
0 = absent	49	29	74	93%			
1 = present	2	0	9	7%			
Callus sharpness					17.918	4	0.001
0 = none	23	16	65	64%			
1 = blunt	20	8	15	26%			
2 = sharp	8	5	3	10%			
Lemma awn action					24.923	4	0.001
0 = none	23	14	68	64%			
1 = passive	9	7	8	15%			
2 = active	19	8	7	21%			
Dispersal unit					7.000	6	0.321
0 = seed	1	1	8	6%			
1 = floret	18	10	37	40%			
2 = spikelet	27	14	30	44%			
3 = inflorescence branch	5	4	8	10%			

Table S3.3 Parameter estimates for the linear mixed effect model fitted to lemma awn length (mm, log-scale) data for 67 African lemma awned grass species and plant height (mm, log-scale). The effect of the 10 tribes were fitted as a random intercept term.

Parameter	Estimate	Std. Error	d.f.	t-value	p-value
Fixed effects					
Intercept	-1.792	1.571	65.656	-1.141	< 0.258
Height (mm; log-scale)	0.556	0.226	63.014	2.451	< 0.05
Random effects	Variance				
Tribe	1.018				
Residual	0.642				

Table S3.4 Parameter estimates for the linear mixed effect model fitted to lemma awn length (mm, log-scale) data for 38 African grass species for which I had reliable seed mass data and plant height (mm, log-scale). The effect of the 6 tribes were fitted as a random intercept term.

Parameter	Estimate	Std. Error	d.f.	t-value	p-value
Fixed effects					
Intercept	2.404	0.454	5.851	5.292	< 0.002
Seed mass(g; log-scale)	0.125	0.143	35.541	0.872	< 0.389
Random effects	Variance				
Tribe	1.088				
Residual	0.679				

Table S3.5 The mean annual rainfall (mm) of the collection sites.

Collected sites	Mean Annual Rainfall in mm (MAR)
Ezemvelo	624
Pullen Farm	874
Madikwe	478
Satara	477
Mwekwera	1256
Berg-en-Dal	689
Black Rock	876
Camdeboo	323
Commando Drift	572
Cape Vidal	1134
Giants Castle	871
Golden Gate	725
Great Fish	708
Gariep Dam	437
Ithala	813
Kogatende	1130
Koppies Dam	597
Kirawira	870
Lower Sabie	591
Luchaba	756
iMfolozi	838
Marakele	529
Mkambati	1060
Maria Moroka	559
Mokala	349
Mountain Zebra	452
Ndumo	692
Pilanesburg	524
Soit	570
Spioenkop	706
Seronera	837
St Lucia	1099
Tembe	709
Tsolwana	766
Willem Pretorius	555

Table S3.6 The species abbreviations (code) and full names used in this chapter.

Code	**Species (taxa)**	**Tribe**	**Category**
LOUSIM	*Loudetia simplex*	Tristachydeae	Fire
ARIRUF	*Aristida rufescens*	Aristideae	Grazing
HYPHIR	*Hyparrhenia hirta*	Andropogoneae	Intermediate
SCHPAP	*Schmidtia pappophoroides*	Eragrostideae	Grazing
CHRORI	*Chrysochloa orientalis*	Cynodonteae	Grazing
CRAAFR	*Craspedorhachis africana*	Cynodonteae	Intermediate
CYNDAC	*Cynodon dactylon*	Cynodonteae	Grazing
CYNINC	*Cynodon incompletus*	Cynodonteae	Grazing
DACAEG	*Dactyloctenium aegyptium*	Cynodonteae	Grazing
DACAUS	*Dactyloctenium australe*	Cynodonteae	Grazing
ELEIND	*Eleusine indica*	Cynodonteae	Grazing
ENNCEN	*Enneapogon cenchroides*	Eragrostideae	Grazing
ERAAET	*Eragrostis aethiopica*	Eragrostideae	Grazing
ERAATR	*Eragrostis atrovirens*	Eragrostideae	Grazing
ERABOI	*Eragrostis boinensis*	Eragrostideae	Grazing
ERACAPE	*Eragrostis capensis*	Eragrostideae	Fire
ERACAPU	*Eragrostis capuronii*	Eragrostideae	Grazing
ERACHA	*Eragrostis chapelieri*	Eragrostideae	Fire
ERACILIAN	*Eragrostis cilianensis*	Eragrostideae	Intermediate
ERACILIAR	*Eragrostis ciliaris*	Eragrostideae	Grazing
ERACUR	*Eragrostis curvula*	Eragrostideae	Grazing
ERACYL	*Eragrostis cylindriflora*	Eragrostideae	Grazing
ERAGUM	*Eragrostis gummiflua*	Eragrostideae	Fire
ERAHET	*Eragrostis heteromera*	Eragrostideae	Grazing
ERALAT	*Eragrostis lateritica*	Eragrostideae	Intermediate
ERALEH	*Eragrostis lehmanniana*	Eragrostideae	Grazing
ERAOBT	*Eragrostis obtusa*	Eragrostideae	Grazing
ERAPAT	*Eragrostis patentipilosa*	Eragrostideae	Grazing
ERAPLANA	*Eragrostis plana*	Eragrostideae	Grazing
ERARAC	*Eragrostis racemosa*	Eragrostideae	Intermediate
ERATENE	*Eragrostis tenella*	Eragrostideae	Grazing
ERATENU	*Eragrostis tenuifolia*	Eragrostideae	Grazing
POGSQU	*Pogonarthria squarosa*	Zoysieae	Fire
CENCIL	*Cenchrus ciliaris*	Paniceae	Grazing
CENECH	*Cenchrus echinatus*	Paniceae	Grazing
STEDIM	*Stenotaphrum dimidiatum*	Paniceae	Grazing
STESEC	*Stenotaphrum secundatum*	Paniceae	Grazing
TRABER	*Tragus berteronianus*	Cynodonteae	Grazing
TRAKOE	*Tragus koelerioides*	Cynodonteae	Grazing
CENMEZ	*Cenchrus mezianus*	Paniceae	Grazing
CENPSE	*Cenchrus pseudotriticoides*	Paniceae	Fire
PHYSAG	*Phyllorachis sagittata*	Phyllorachideae	Grazing

STEOOS	*Stenotaphrum oostachyum*	Paniceae	Grazing
THUINV	*Thuarea involuta*	Paniceae	Grazing
ELECOR	*Eleusine coracana*	Cynodonteae	Grazing
AXOCOM	*Axonopus compressus*	Paspaleae	Grazing
UROARR	*Urochloa arrecta*	Paniceae	Intermediate
URODIS	*Urochloa distachya*	Paniceae	Grazing
BRAHUM	*Brachiaria humbertiana*	Paniceae	Grazing
BRASUB	*Brachiaria subrostrata*	Paniceae	Grazing
BRAUMB	*Brachiaria umbellata*	Paniceae	Grazing
CYRDEL	*Cyrtococcum deltoideum*	Paniceae	Grazing
DIGBIC	*Digitaria bicornis*	Paniceae	Grazing
DIGCIL	*Digitaria ciliaris*	Paniceae	Intermediate
DIGDEB	*Digitaria debilis*	Paniceae	Intermediate
DIGDIA	*Digitaria diagonalis*	Paniceae	Fire
DIGDID	*Digitaria didactyla*	Paniceae	Grazing
DIGERI	*Digitaria eriantha*	Paniceae	Grazing
DIGLON	*Digitaria longiflora*	Paniceae	Grazing
DIGMAC	*Digitaria macroblephara*	Paniceae	Grazing
DIGMON	*Digitaria monodactyla*	Paniceae	Fire
DIGNAT	*Digitaria natalensis*	Paniceae	Grazing
DIGPSE	*Digitaria pseudodiagonalis*	Paniceae	Intermediate
DIGTHO	*Digitaria thouarsiana*	Paniceae	Intermediate
DIGTRI	*Digitaria tricholaenoides*	Paniceae	Fire
ERASUP	*Eragrostis superba*	Eragrostideae	Grazing
OPLBUR	*Oplismenus burmanni*	Paniceae	Fire
PANAEQ	*Panicum aequinerve*	Paniceae	Grazing
PANCIN	*Panicum cinctum*	Paniceae	Intermediate
PANCOL	*Panicum coloratum*	Paniceae	Intermediate
PANDRE	*Panicum dregeanum*	Paniceae	Fire
PANIBI	*Panicum ibitense*	Paniceae	Fire
PANLUR	*Panicum luridum*	Paniceae	Fire
MEGMAX	*Megathyrsus maximus*	Paniceae	Fire
PANPER	*Panicum perrieri*	Paniceae	Fire
PANSUB	*Panicum subhystrix*	Paniceae	Fire
PANVOE	*Panicum voeltzkowii*	Paniceae	Intermediate
PASDIL	*Paspalum dilatatum*	Paspaleae	Grazing
PASSCR	*Paspalum scrobiculatum*	Paspaleae	Intermediate
PERPAT	*Perotis patens*	Cynodonteae	Grazing
SACCUR	*Sacciolepis curvata*	Paniceae	Grazing
SETHUM	*Setaria humbertiana*	Paniceae	Grazing
SETINC	*Setaria incrassata*	Paniceae	Fire
SETPUM	*Setaria pumila*	Paniceae	Grazing
SETSPH	*Setaria sphacelata*	Paniceae	Grazing
SETVER	*Setaria verticillata*	Paniceae	Grazing

STEUNI	*Stenotaphrum unilaterale*	Paniceae	Grazing
TRIBRA	*Trichanthecium brazzavillense*	Paniceae	Fire
MELREP	*Melinis repens*	Paniceae	Grazing
TRINAT	*Trichanthecium natalense*	Paniceae	Fire
SPOAFR	*Sporobolus africanus*	Zoysieae	Grazing
SPOCEN	*Sporobolus centrifugus*	Zoysieae	Grazing
SPOFIM	*Sporobolus fimbriatus*	Zoysieae	Grazing
SPOIOC	*Sporobolus ioclados*	Zoysieae	Grazing
SPONIT	*Sporobolus nitens*	Zoysieae	Grazing
SPOPAN	*Sporobolus paniculatus*	Zoysieae	Intermediate
SPOPIL	*Sporobolus pilifer*	Zoysieae	Fire
SPOPYR	*Sporobolus pyramidalis*	Zoysieae	Grazing
SPOSTA	*Sporobolus stapfianus*	Zoysieae	Grazing
SPOVIR	*Sporobolus virginicus*	Zoysieae	Grazing
BRAMAD	*Brachypodium madagascariense*	Brachypodieae	Fire
FESCAM	*Festuca camusiana*	Poeae	Fire
HARSCH	*Harpachne schimperi*	Eragrostideae	Grazing
ALLSEM	*Alloteropsis semialata*	Paniceae	Fire
MELMIN	*Melinis minutiflora*	Paniceae	Fire
UROTRI	*Urochloa trichopus*	Paniceae	Intermediate
UROOLI	*Urochloa oligotricha*	Paniceae	Grazing
UROPAN	*Urochloa panicoides*	Paniceae	Intermediate
ARISTE	*Aristida stenostachya*	Aristideae	Grazing
AGRELL	*Agrostis elliotii*	Poeae	Fire
ARISIM	*Aristida similis*	Aristideae	Fire
ARITEN	*Aristida tenuissima*	Aristideae	Fire
CYMCAE	*Cymbopogon caesius*	Andropogoneae	Fire
CYMPOS	*Cymbopogon pospischilii*	Andropogoneae	Fire
HYPRUF	*Hyparrhenia rufa*	Andropogoneae	Grazing
SCHBRE	*Schizachyrium brevifolium*	Andropogoneae	Intermediate
SCHEXI	*Schizachyrium exile*	Andropogoneae	Grazing
SCHSAN	*Schizachyrium sanguineum*	Andropogoneae	Fire
ANDITR	*Andropogon itremoensis*	Andropogoneae	Fire
ANDSCH	*Andropogon schirensis*	Andropogoneae	Fire
ANDTRI	*Andropogon trichozygus*	Andropogoneae	Intermediate
BOTINS	*Bothriochloa insculpta*	Andropogoneae	Grazing
BOTRAD	*Bothriochloa radicans*	Andropogoneae	Fire
EULVIL	*Eulalia villosa*	Andropogoneae	Intermediate
SARVER	*Sarga versicolor*	Andropogoneae	Fire
EUSPAS	*Eustachys paspaloides*	Cynodonteae	Grazing
MELDEN	*Melica dendroides*	Meliceae	Grazing
MICCAF	*Microchloa caffra*	Cynodonteae	Grazing
MICKUN	*Microchloa kunthii*	Cynodonteae	Grazing

UREAGR	*Urelytrum agropyroides*	Andropogoneae	Fire
UROSER	*Urochloa serrata*	Paniceae	Fire
ARIADS	*Aristida adscensionis*	Aristideae	Intermediate
ARINEM	*Aristida nemorivaga*	Aristideae	Intermediate
ARIJUN	*Aristida junciformis*	Aristideae	Intermediate
ARISCA	*Aristida scabrivalvis*	Aristideae	Grazing
BEWBIF	*Bewsia biflora*	Cynodonteae	Fire
CHLGAY	*Chloris gayana*	Cynodonteae	Grazing
CHLHUM	*Chloris humbertiana*	Cynodonteae	Grazing
CHLVIR	*Chloris virgata*	Cynodonteae	Intermediate
CTECON	*Ctenium concinnum*	Cynodonteae	Intermediate
DAKBOI	*Daknopholis boivinii*	Cynodonteae	Grazing
STYHIT	*Styppeiochloa hitchcockii*	Arundineae	Fire
TRIGRA	*Trichoneura grandiglumis*	Cynodonteae	Grazing
TRIAND	*Triraphis andropogonoides*	Triraphideae	Fire
ANDEUC	*Andropogon eucomus*	Andropogoneae	Fire
FINAFR	*Fingerhuthia africana*	Eragrostideae	Fire
TRIHUM	*Tristachya humbertii*	Tristachydeae	Grazing
TRIISA	*Tristachya isalensis*	Tristachydeae	Intermediate
TRISUP	*Tristachya superba*	Tristachydeae	Fire
DIHAMP	*Diheteropogon amplectens*	Andropogoneae	Fire
HETCON	*Heteropogon contortus*	Andropogoneae	Intermediate
HYPNEW	*Hyparrhenia newtonii*	Andropogoneae	Fire
THETRI	*Themeda triandra*	Andropogoneae	Intermediate
CHRSER	*Chrysopogon serrulatus*	Andropogoneae	Intermediate
HYPDIS	*Hyperthelia dissoluta*	Andropogoneae	Fire
TRASPI	*Trachypogon spicatus*	Andropogoneae	Fire
TRILEU	*Tristachya leucothrix*	Tristachydeae	Fire
TRIREH	*Tristachya rehmanii*	Tristachydeae	Fire
UROBRI	*Urochloa brizantha*	Paniceae	Fire
URODEF	*Urochloa deflexa*	Paniceae	Fire
ARICON	*Aristida congesta*	Aristideae	Grazing
LOUFIL	*Loudetia filifolia*	Tristachydeae	Fire
IMPCYL	*Imperata cylindrica*	Andropogoneae	Grazing

Appendix C

Table S4.1 The phylogenetic classification and age (in million years ago) of the 29 genera under the subtribe Eleusininae that were extracted from several articles (Filgueiras *et al*., 1999; Hackel *et al*. 2018; Peterson *et al*., 2015, 2021; Soreng *et al*., 2017, 2022).

Taxa	**Genus age**
Afrotrichloris hyaloptera Clayton	5.26
Afrotrichloris martinii Chiov.	5.26
Apochiton burttii C.E.Hubb.	1.32
Astrebla elymoides F.Muell. ex F.M.Bailey	1.62
Astrebla lappacea (Lindl.) Domin	1.62
Astrebla pectinata (Lindl.) F.Muell. ex Benth.	1.62
Astrebla squarrosa C.E.Hubb.	1.62
Austrochloris dichanthioides (Everist) Lazarides	7.62
Chloris flabellata (Hack.) Launert	4.17
Chloris halophila Parodi	4.17
Chloris jubaensis Cope	4.17
Chloris ruahensis Renvoize	4.17
Chloris truncata R.Br.	4.17
Chrysochloa hindsii C.E.Hubb.	5.15
Chrysochloa hubbardiana Germ. & Risop.	5.15
Chrysochloa orientalis (C.E.Hubb.) Swallen	5.15
Chrysochloa subaequigluma (Rendle) Swallen	5.15
Coelachyrum brevifolium Hochst. & Nees	5.76
Coelachyrum lagopoides (Burm.f.) Senaratna	5.76
Coelachyrum longiglume Napper	5.76
Coelachyrum piercei (Benth.) Bor	5.76
Coelachyrum poiflorum Chiov.	5.76
Cynodon convergens F.Muell.	4.9
Cynodon coursii A.Camus	4.9
Cynodon plectostachyus (K.Schum.) Pilg.	4.9
Cynodon simonii P.M.Peterson	4.9
Cynodon tenellus R.Br.	4.9
Daknopholis boivinii (A.Camus) Clayton	1.43
Dinebra marquisensis (F.Br.) P.M.Peterson & N.Snow	5.87
Dinebra polycarpha S.M.Phillips	5.87
Dinebra polystachyos (R.Br.) E.A.Kellogg	5.87
Dinebra retroflexa (Vahl) Panz.	5.87
Dinebra xerophila (P.M.Peterson & Judz.) P.M.Peterson	5.87
Diplachne fusca (L.) P.Beauv. ex Roem. & Schult.	16.43
Diplachne gigantea Launert	16.43
Disakisperma dubium (Kunth) P.M.Peterson & N.Snow	4.57
Disakisperma eleusine (Nees) P.M.Peterson & N.Snow	4.57

Disakisperma obtusiflorum (Hochst.) P.M.Peterson & N.Snow	4.57
Disakisperma yemenicum (Schweinf.) P.M.Peterson & N.Snow	4.57
Eleusine indica (L.) Gaertn.	5.76
Eleusine kigeziensis S.M.Phillips	5.76
Eleusine multiflora Hochst. ex A.Rich.	5.76
Eleusine semisterilis S.M.Phillips	5.76
Eleusine tristachya (Lam.) Lam.	5.76
Enteropogon longiaristatus (Napper) Clayton	5.26
Enteropogon macrostachyus (Hochst. ex A.Rich.) Munro ex Benth.	5.26
Enteropogon prieurii (Kunth) Clayton	3.98
Enteropogon rupestris (J.A.Schmidt) A.Chev.	5.26
Enteropogon sechellensis (Baker) T.Durand & Schinz	5.26
*Eustachys distichophyll*a (Lag.) Nees	2.42
Eustachys floridana Chapm.	2.42
Eustachys neglecta (Nash) Nash	2.42
Eustachys paranensis A.M.Molina	2.42
Eustachys tenera (J.Presl) A.Camus	2.42
Harpochloa falx (L.f.) Kuntze	8.09
Harpochloa pseudoharpechloa (Chiov.) Clayton	8.09
Leptochloa barbata (Desv.) Nicora	9.67
Leptochloa coerulescens Steud.	5.87
Leptochloa longa Griseb.	9.67
Leptochloa southwoodii N.Snow & B.K.Simon	5.87
Leptochloa viscida (Scribn.) Beal	5.87
Lepturus anadabolavensis A.Camus	4.61
Lepturus androyensis A.Camus	4.61
Lepturus geminatus C.E.Hubb.	4.61
Lepturus humbertianus A.Camus	4.61
Lepturus repens (G.Forst.) R.Br.	4.61
Lintonia brizoides (Chiov.) C.E.Hubb.	5.85
Micrachne fulva (Stapf) P.M.Peterson	7.07
Micrachne obtusiflora (Benth.) P.M.Peterson	7.07
Micrachne patentiflora (Stent & J.M.Rattray) P.M.Peterson	7.07
Micrachne pilosa (Van der Veken) P.M.Peterson	7.07
Micrachne simonii (Kupicha & Cope) P.M.Peterson	7.07
Microchloa altera (Rendle) Stapf	10.52
Microchloa annua (Kupicha & Cope) Cope	2.29
Microchloa ensifolia Rendle	2.29
Microchloa indica (L.f.) P.Beauv.	2.29
Microchloa kunthii Desv.	2.29
Neostapfiella chloridiantha A.Camus	1.43
Neostapfiella humbertiana A.Camus	1.43
Neostapfiella perrieri A.Camus	1.43
Oxychloris scariosa (F.Muell.) Lazarides	8.09

Pommereulla cornucopiae L.f.	4.9
Rheochloa scabriflora Filg., P.M.Peterson & Y.Herrera	5.87
Schoenefeldia gracilis Kunth	5.26
Schoenefeldia transiens (Pilg.) Chiov.	5.26
Stapfochloa berroi (Arechav.) P.M.Peterson	4.9
Stapfochloa canterae (Arechav.) P.M.Peterson	4.9
Stapfochloa ciliata (Sw.) P.M.Peterson	4.9
Stapfochloa lamproparia (Stapf) H.Scholz	4.9
Stapfochloa parvispicula (Caro & E.A.SÃ¡nchez) P.M.Peterson	4.9
Tetrapogon bidentatus Pilg.	3.23
Tetrapogon cenchriformis (A.Rich.) Clayton	3.23
Tetrapogon chlorideus (J.Presl) P.M.Peterson	3.23
Tetrapogon roxburghiana (Schult.) P.M.Peterson	4.59
Tetrapogon villosus Desf.	3.23
Trigonochloa rupestris (C.E.Hubb.) P.M.Peterson & N.Snow	7.34
Trigonochloa uniflora (Hochst. ex A.Rich.) P.M.Peterson & N.Snow	7.34

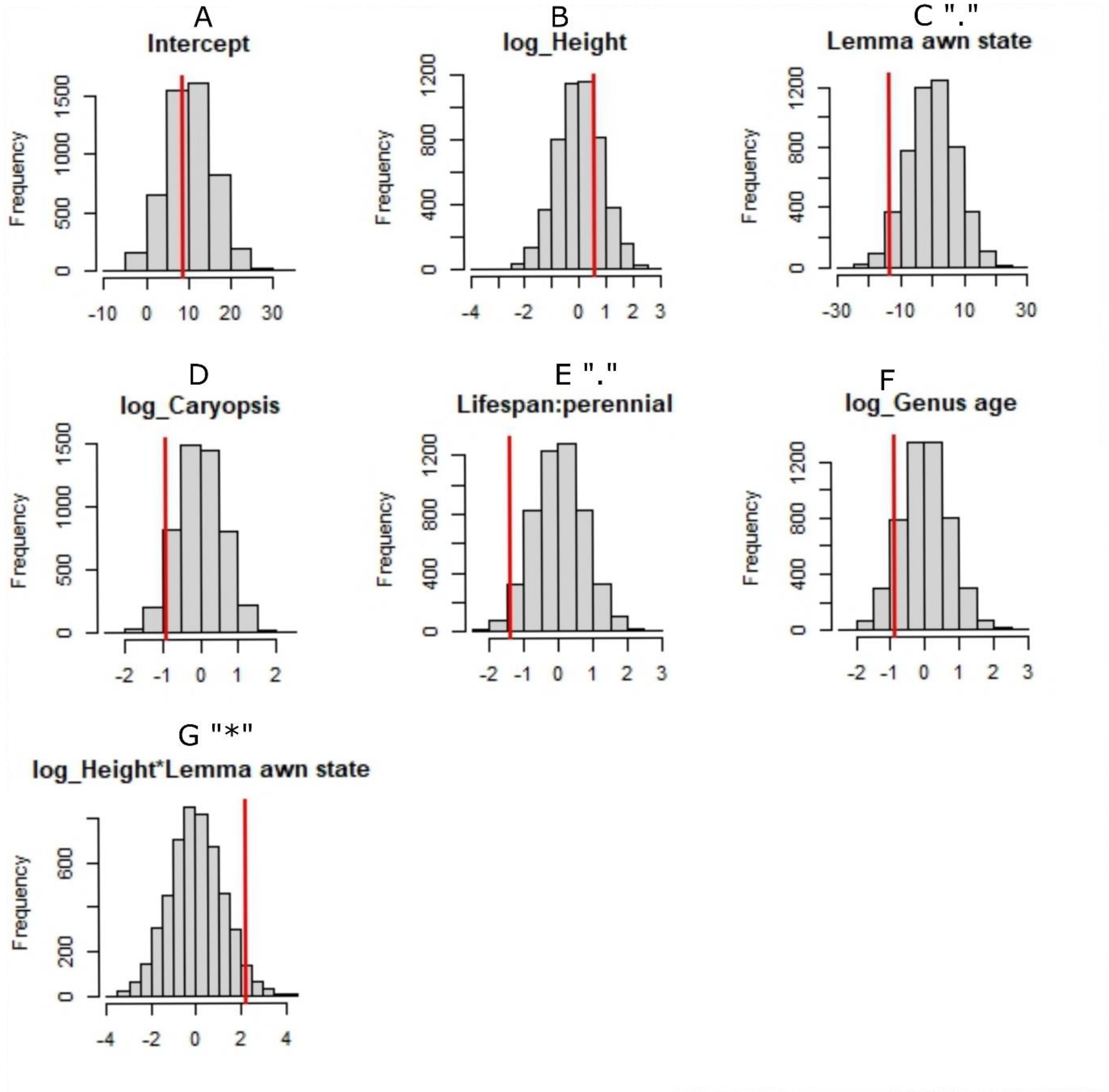

Figure S4.1 Histograms showing the parameters which are significantly different from random. The red line indicates significant differences from the mean of the grey histogram. The symbols above each histogram: “*”= mean significant and “.” mean marginally significant.

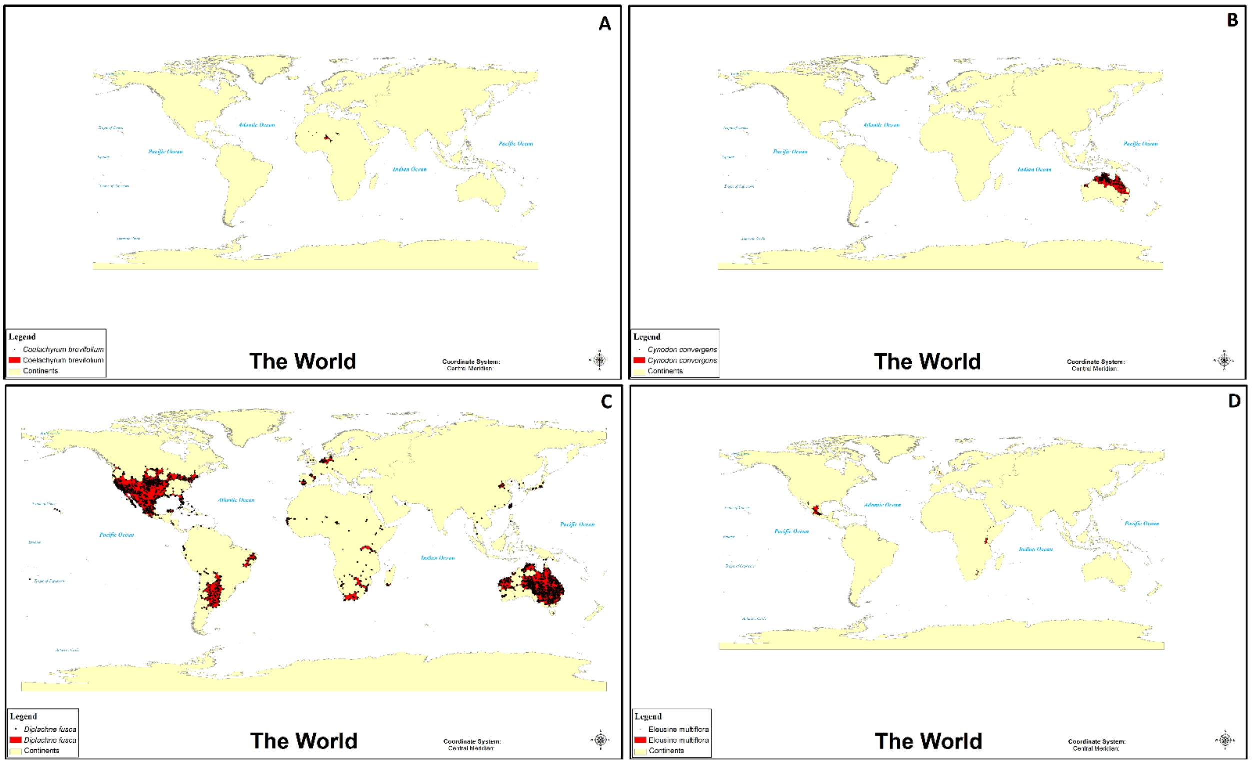

Figure S4.2 Maps showing range size estimates of four kinds of grass species globally. The estimation of range sizes was done using the alpha hull = 200 km and buffer = 10 km method. Shapefiles and distribution points were stacked together. Maps: A) *Coelachyrum brevifolium* Hochst. & Nees; B) *Cynodon convergens* F.Muell.; C) *Diplachne fusca* (L.) P.Beauv. ex Roem. & Schult.; D) *Eleusine multiflora* Hochst. ex A.Rich.

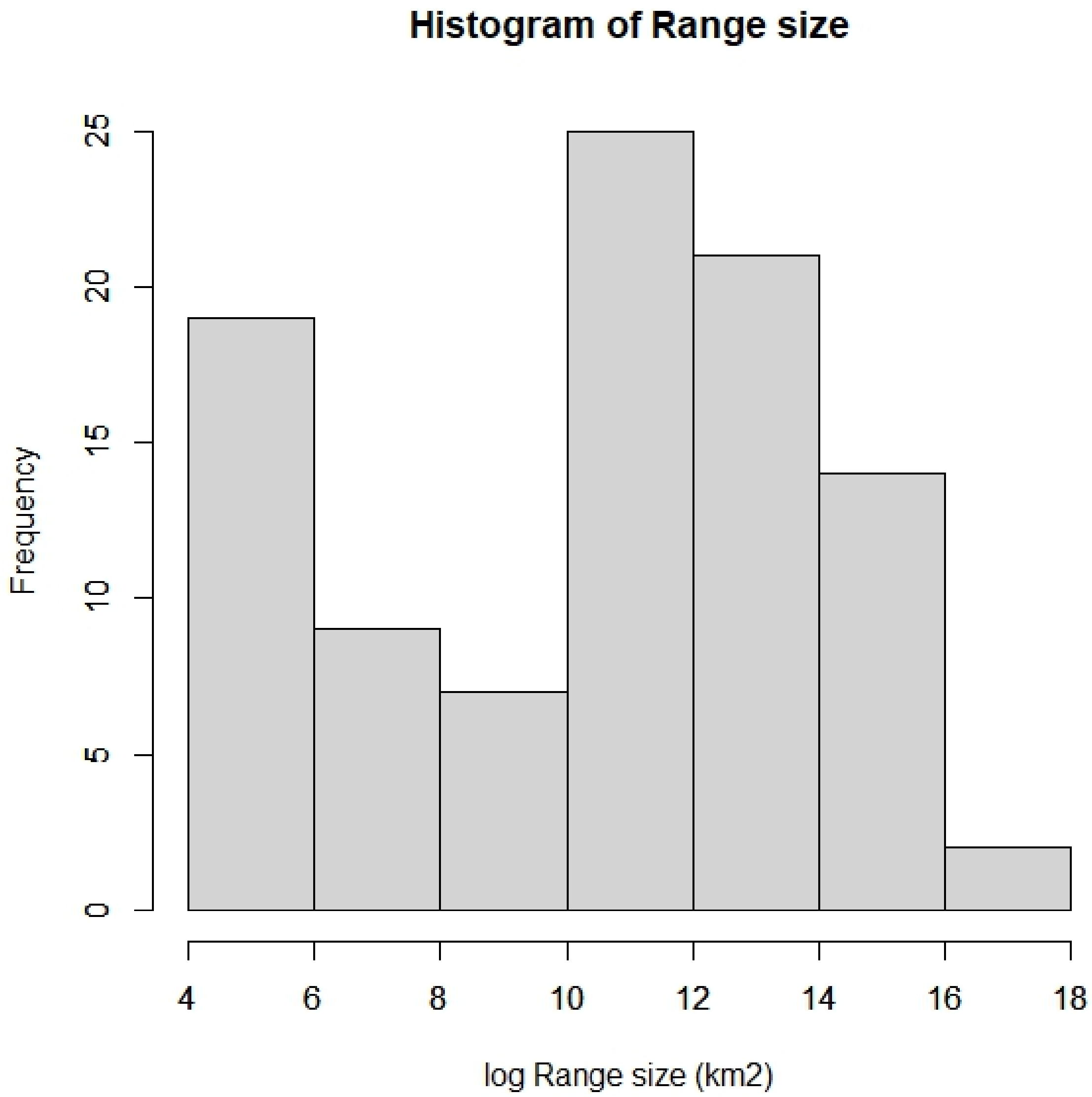

Figure S4.3 Histogram showing a bimodal distribution of the log range size (km^2) of the full data set of 97 grass species in 29 genera of the subtribe Eleusininae around the globe.

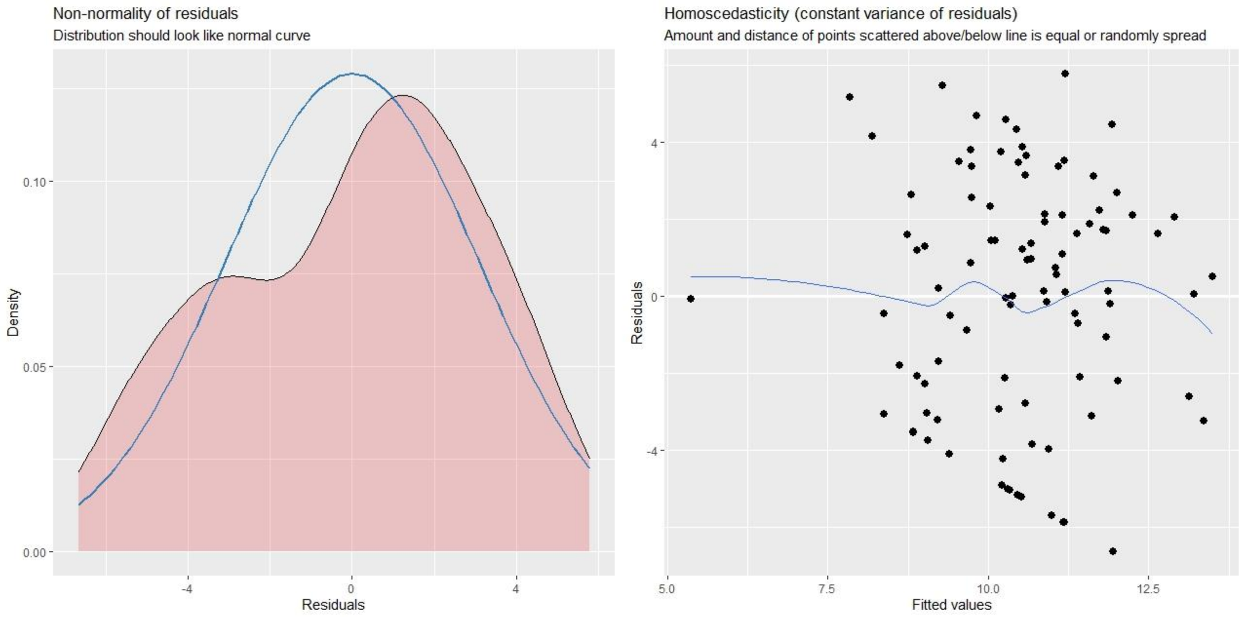

Figure S4.4 The residuals and fitted values for the normal linear model fitted to range size estimates of 97 grass species of the subtribe Eleusininae globally. The binomial distribution is still present so maximum likelihood methods were not appropriate