RESEARCH ARTICLE

The contemporary distribution of grasses in Australia: A process of immigration, dispersal and shifting dominance

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Abstract

Aim: Little is known about the distribution of grasses throughout Australia. Using endemism as a basis for understanding biogeographical distributions, we hypothesised that contemporary species richness would be the result of environmental factors and dynamic ecological interactions spanning more than 25 Ma.

Location: Australia.

Taxon: Grasses.

Methods: We mapped the distribution of all Australian grass species and modelled climatic and landscape correlates according to photosynthetic type (C_3 or C_4), endemism, age in Australia, phylogenetic lineage and traits linked to dominance, using height as a proxy. Age classes comprised 'Ancient' (Gondwanan), and three others related to migration during the Sunda-Sahul Interchange (SSI): Early, Mid or Recent. In some analyses, 'Ancient', 'Early SSI' and 'Mid SSI' were combined into 'Pre-Recent SSI'.

Results: Overall, species richness of C_4 grasses increased with warmer mean annual temperatures, while richness of C_3 grasses was higher in cooler areas. Recent SSI species had strong associations with summer rains and were dominant in the continent's northeast, with Pre-Recent SSI species concentrated in the southeast, a pattern largely reflecting photosynthetic type (C_4 and C_3 respectively). Endemic and shared species distribution patterns support a migration sequence in which most C_3 Pooideae and Panicoideae genera arrived in Australia before the Pliocene aridifications, followed by C_4 Chloridoideae as aridification increased, with C_4 Andropogoneae immigrating most recently across Lake Carpentaria's open habitats in the later Pleistocene. Recent SSI shared species were significantly taller than Pre-Recent SSI endemic grasses.

Main Conclusions: The few grasses present in Australia before the Pliocene grew in cooler areas. The influx of taller Recent SSI grasses contributed to dramatic environmental changes—including creation of the northern savannas—with repercussions for resident taxa. Contemporary methods of fuel management could be promoting invasion by grass, thereby jeopardising the conditions suited to ancient taxa and threatening the region's evolutionary history.

KEYWORDS
C_3 grasses, C_4 grasses, grasslands, invasion, palaeoecology, Sahul, savanna, Sunda

1 | INTRODUCTION

Since the late Cretaceous (100–66 Ma), the grass family Poaceae has diversified and spread, penetrating all but the most extreme ecosystems across terrestrial Earth (Gallaher et al., 2022; Huang et al., 2022). Expedited by adaptable plant architecture and broad environmental tolerances (Linder et al., 2018), grasses transformed landscapes by introducing grazing and/or fire into wooded ecosystems and became the dominant ground cover over 25% of all terrestrial land (Strömberg & Staver, 2022).

The evolution of C_4 photosynthesis occurred in multiple lineages of C_3 grasses during the Eocene (56–34 Ma), according to studies based on recent technological advances in fossil and phytolith dating (Gallaher et al., 2022; Huang et al., 2022). The C_4 grasses eventually created new biomes of savannas and grasslands dominated by grazing mammals and grass-fire cycles (Bond, 2015; Ripley et al., 2015; Stromberg, 2011), particularly during the mid-Miocene (16–12 Ma) in the Americas, EurAsia and Africa (Edwards et al., 2010). In terms of biological invasions, C_4 grasses have been one of the most transformative plant groups; using rapid dispersal and protected buds to promote their own persistence and expansion, some can alter fire regimes, environmental conditions or resource availability (D'Antonio & Vitousek, 1992; Linder et al., 2018) with dramatic flow-on effects for native biota, described as an 'orgy of extinction' (Linder, 2014).

The ability of C_4 grasses to modify ecosystems is determined by the morphology they inherited from their C_3 ancestors (Edwards et al., 2010). The main C_4 grass groups (Chloridoideae, Paniceae, Andropogoneae) differ in architecture, inherent flammability and regrowth rates after disturbance, with the Andropogoneae most strongly associated with grass-fire cycles (Bocksberger et al., 2016; Ripley et al., 2015; Schmidt et al., 2011). In the Northern Hemisphere, the Andropogoneae are known ecosystem transformers linked with increased landscape flammability (Bond, 2015; Linder et al., 2018; Ripley et al., 2015) facilitated by their upright bulky growth, vertically continuous combustible tissue (Gao & Schwilk, 2018), rapid growth, fast resprouting (Ripley et al., 2015) and seed set synchronised with the wet season (Andrew & Mott, 2006; Scott et al., 2010).

Australia's contemporary grass flora has a unique combination of origins: Gondwanan-origin C_3 grasses, local-origin C_4 Eriachneae, and C_3 and C_4 immigrants from the Northern Hemisphere (Bryceson & Morgan, 2022). Until the Pliocene (5.3–2.6 Ma), Australasian ecosystems evolved largely in the absence of grasses, despite the existence of Eocene Poaceae fossils (Martin, 2006) and some relictual ancient C_3 grass genera. Only one C_4 grass genus evolved in situ in Australia—the *Eriachne* R. Br., which arose about 8 Ma (Gallaher et al., 2022). Grasses originating outside of Australasia migrated into the region once the continent had drifted close enough to the Southeast Asian region for wind dispersal to be effective, probably during periods of low sea levels (Bryceson & Morgan, 2022; Soons et al., 2004).

Savannas arose in Australia some 6–12 Ma later than elsewhere (Stromberg, 2011), with dominance in northwest Australia shifting from C_3 plants to C_4 grasses in open habitats around 3.5 Ma (Andrae et al., 2018). In the south, the earliest evidence for widespread grasslands dates from the late Pliocene/Pleistocene (Martin, 2006). Two-thirds of Australia's grass genera are thought to have been present only in the past few million years (Bryceson & Morgan, 2022), although today, grasslands and savannas cover 25% of Australia, supporting an extensive grazing industry (Cook et al., 2019).

The distributions of grasses across Australia have been mapped in previous studies using techniques that pre-dated the use of large online databases. Hartley (1958) outlined the distribution of the major C_4 grass tribes based on observations and species knowledge, while Hattersley (1983) analysed environmental drivers of grasses by manually quantifying and mapping herbarium records, but was hampered by a lack of data. However, simply updating these maps using computerised models of abiotic factors would provide only a limited understanding of our ecosystems, overlooking the role of evolutionary and biogeographical processes in determining why species live where they do, and their capacity to respond to change (Estes & Vermeij, 2022; Spencer, 2020).

Braun-Blanquet's (1923) pioneering study of neo and palaeo flora of the French Massif Central was based on the premise that focussing on endemism enables better understanding of past ecological transformations, an approach supported by more recent research (Lazarina et al., 2019; Mishler et al., 2014; Stebbins & Major, 1965). Distributions of extant endemic and native taxa can reveal underlying drivers of speciation (Wiens & Donoghue, 2004) dispersal, opportunism and refuge, using endemism as the 'standard unit of historical biogeography' (Crisp et al., 2001). A similar perspective could deepen the exploration of ecological effects of grass migrations into Australia.

As a measure of potential ecological impact, two seminal plant ecology strategy schemes—Grime (1974) CSR classification and Westoby (1998) LHS —both highlight the competitive advantage of 'large size', with Westoby explicitly proposing plant height to be a main indicator of competitiveness. Analyses based on grass height have shown 'tallgrass', 'shortgrass' and 'grazing lawns' to be functionally and phylogenetically different grassland systems (Hempson et al., 2019; McNaughton, 1984). Tall grasses can dominate plant communities and change ecosystem dynamics (Canavan et al., 2019) and modern invasive C_4 grasses, for example, are typically taller and bulkier than native species (D'Antonio & Vitousek, 1992; Mashau et al., 2021). Understanding the distribution of grass height across the Australian landscape with respect to phylogeny, endemism and age class could help explain historical transformations and current functional dynamics of grass-dominated ecosystems.

Here, we accessed modern big data collections to map and model the distribution of contemporary native grasses in Australia and investigate ecological impacts. We modelled abiotic factors against locational records for grass species classified by phylogenetic origins, endemism and length of residency in Australia. A phylogenetic analysis was applied to the main C_4 clades to investigate possible speciation pathways by comparing the distributions of extant endemic and native taxa. Biogeographical distributions of four age classes were analysed through a broad ancient–recent perspective and a basic trait of plant architecture (height) was related to the distribution of main phylogenetic groups.

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This is the first study of the speciation patterns and potential ecological impacts of grasses on the evolution of Australian ecosystems in which, by necessity, we take a broad approach that will open avenues of deeper investigation. We hypothesised that contemporary species richness would be a factor of dynamic biogeographical processes (migration, speciation), abiotic factors and ecological interactions that span more than 25 Ma. We asked the following questions:

Are there relationships between species richness of grasses in Australia and abiotic factors, photosynthetic type, phylogenetic group, endemism and age class?

Are there relationships between plant height, phylogenetic group, age class and grassland type in Australia? How do these relate to its modern savannas?

2 | MATERIALS AND METHODS

The study region encompassed continental Australia, nearshore islands and Tasmania (SI-1). Using Atlas of Living Australia records, we mapped log-transformed species richness patterns across Australia for combinations of grass groups as per the categories below. We built a database using all Poaceae occurrence records downloaded from the Atlas of Living Australia (www.ala.org.au), a repository of verified occurrence observations and vouchered specimens from 16 major Australian herbaria. The final database comprised 648,003 records of 882 grass species from 151 genera (SI-3), of which C_3 genera comprised 40% of the species and C_4 genera the other 60%. Data cleaning and species richness derivation steps and rationale are outlined in SI-2 and SI-4.

2.1 | Categorising species

2.1.1 | Phylogenetic group and photosynthetic pathway

All C_4 grasses were sorted phylogenetically by Subfamily and/or Supertribe according to Soreng et al. (2017). Mapping and modelling were undertaken separately for C_3 genera, each of the main C_4 clades (Chloridoideae, Paniceae, Andropogoneae) and the Australasian-origin C_4 tribe Eriachneae. Further analysis focussed especially on C_4 grasses as their role in ecosystem change is well documented (Bond, 2015; Canavan et al., 2019; Linder et al., 2018; Stromberg, 2011).

2.1.2 | Endemism

The spread of grasses into Australia and their subsequent speciation into endemic lineages lies at the heart of this study. We mapped and compared shared and endemic distribution types to investigate pathways and adaptation. Instead of the term 'native', we use 'shared' for species distributed on more than one continent and 'endemic' for species found only in Australia, as shown conceptually in Figure 1.

2.1.3 | Age class

Age classes for genera were applied as per earlier work (Bryceson & Morgan, 2022) which combined dated phylogenies, with continental records of shared and endemic species, sourced from multiple studies and databases. Likely migration periods of biota from the ancient Southeast Asian region known as 'Sunda' across the Wallace Line (Wallace, 1863) into the Australia-Papua New Guinea conglomeration ('Sahul'), were delineated by four broad age classes: Ancient >25 Ma; Early Sunda–Sahul Interchange (SSI) 25–12 Ma; Mid SSI 12–3.5 Ma and Recent SSI <3.5 Ma. The age class delimitations were, respectively, informed by: Australia's separation from Antarctica (McLoughlin, 2001); the acceleration of rainforest species migration from Sunda (Crayn et al., 2015) and evidence of the first Australian C_4 grasslands (Andrae et al., 2018). Categories are summarised in SI-2.

The age class of each species was classified in line with its genus, as indicative of the earliest probable time of the species' occurrence in Australia, although we acknowledge that local diversification of some species may have occurred more recently. To partly accommodate this, some analyses combined the Ancient, Early SSI and Mid SSI age classes into a single, 'Pre-Recent SSI' group. Some speciation within Pre-Recent SSI genera has probably occurred in the past 3.5 Myr but it would be relatively minor compared to the surge of immigrant genera in the Recent SSI period. The two groups (Pre-Recent SSI and Recent SSI) should therefore provide a broad indication of shifts in distribution. Table SI-11 lists the genera by photosynthetic pathway, phylogenetic lineage, age class and distribution status (endemic or shared).
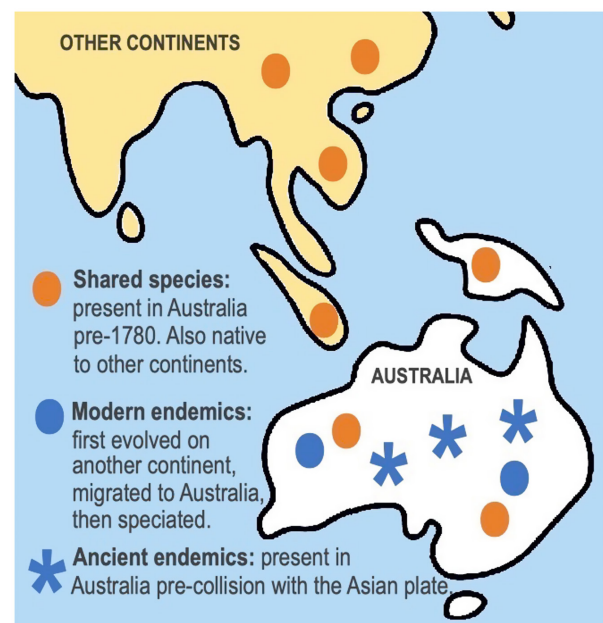

FIGURE 1 Terminology used for grasses in this study. Shared/endemic distribution status as informed by databases: AusGrass (Simon & Alfonso, 2011), GrassWorld (Simon et al., 2011); GrassBase (Clayton et al., 2006). See also SI-2.

2.2 | Mapping and model building

We explored distribution patterns for the different combinations of photosynthetic pathway, species age class, distribution status and phylogenetic classification. Species richness patterns were compared to environmental variables using multi-linear regression. Our process is fully detailed in SI-4 to SI-7.

We gridded Australia, nearshore islands and Tasmania into 1,146 100×100 km cells. Species richness was calculated for each grass category in each cell using a species richness estimator that accounts for differences in sampling effort. The grid size selected allowed us to examine broad patterns in grass distributions, with an inevitable reduction in finer-scale detail. Species richness was log-transformed to meet assumptions of normality. We then built multi-linear regression models to describe the variation in 100×100 km log-transformed species richness for each grass category to environmental variables. From 26 environmental variables representing major climatic and landscape gradients across Australia (Table SI-5a), we developed a subset of variables by excluding those that measured similar environmental aspects and were strongly correlated (Pearson's correlation value of $>|0.7|$; Table SI-5b). We retained seven variables: mean annual temperature, aridity, temperature seasonality, summer rainfall, winter rainfall, topographic heterogeneity and per cent clay in the soil (Table SI-5c, Figure SI-5b).

Due to the gridded nature of the 100×100 km cells, all grass groups showed significant spatial autocorrelation which was addressed (see SI-6). We tested four spatial autocorrelation terms using generalised least squares (GLS) implemented in the function *gls* from the R package *nlme* (3.1.147) and chose the one associated with the model that had the lowest AICc value (see SI-7). Overall model fit to the data was assessed by calculating the adjusted R^2.

2.3 | Plant height

We collated plant height data for each species as a surrogate for competitive ability (Grime, 1974; Westoby, 1998). For each species, grass height was obtained preferentially from Australian sources—(ABRS, 2020; Simon & Alfonso, 2011)—followed by Clayton et al. (2006) where necessary. For height, we used 'culm height' (following Forrestel et al., 2017), using the mean where a range was reported. Species with missing height data were excluded, leaving 864 species for this component of the study. Statistical comparisons (ANOVA and post-hoc analysis) were carried out in R (R Core Team, 2013).

3 | RESULTS

The database compiled for this study identified 882 species of Australian grasses in 151 genera in the following groups: 'age class' had 42 Ancient species, 99 Early SSI, 244 Mid SSI, 480 Recent SSI and 17 'uncertain' species; 'photosynthetic pathway' had 355 C_3 and 527 C_4 species; 'distribution origin' had 137 shared and 745 endemic species. (For further details, see SI-3 and SI-11.)

3.1 | Environmental factors

For most of the 15 grass groups analysed, species richness increased with summer rainfall and topographic heterogeneity but decreased with increasing aridity (see SI-8). C_3 species richness was highest in cooler temperatures; C_4 richness highest in warmer. Species richness for C_3 grasses also decreased with increasing aridity and temperature seasonality. The environmental niches of shared and endemic species largely aligned, but endemics responded more positively to all parameters.

For each C_4 phylogenetic group, species richness was generally linked with environmental factors with R^2 values ranging from 0.33 to 0.64, apart from shared C_4 Paniceae (0.18). Species richness declined in response to temperature seasonality and increasing aridity, except for two groups which registered strong increases: Australian-origin C_4, and Endemic Chloridoideae. In all other groups, Recent SSI endemic C_4 species were more tolerant of temperature seasonality than their shared counterparts. All results by photosynthetic type, age class, endemism and phylogenetic origin are detailed in SI-8.

3.2 | Species richness distributions

Figure 2 shows species richness patterns of all Australian grasses grouped by photosynthetic type, endemism and phylogenetic clade.

3.2.1 | All grasses

Our results show a north–south divide in the distribution of C_3 and C_4 grasses, and an east–west, shared–endemic, tall–short divide among the C_4 grasses. The overall picture shows highest species richness in the east and few records of grasses in the west (Figure 2a–c), and a north–south, C_4–C_3 pattern (Figure 2d,e). In particular, shared species richness was highest along the Queensland coast and lowest in the continent's south and southwest (Figure 2b). By comparison, endemic species richness was very high in the northern half of Australia, suggesting there has been high speciation along the Queensland, northern coast, Western Australian coast (Kimberley and Pilbara) and in Central Australia (Figure 2c) driven by the dominance of C_4 grasses (Figure 2e) which had about twice the maximum species richness of C_3 species (Figure 2d). In contrast to C_4 distributions, highest C_3 richness occurred in southeast Australia. In Western Australia, large areas recorded few records and, as a whole, C_4 endemic species tended to dominate the northern coastal areas of the state, whereas C_3 species dominated the southwest (Figure 2d,e).
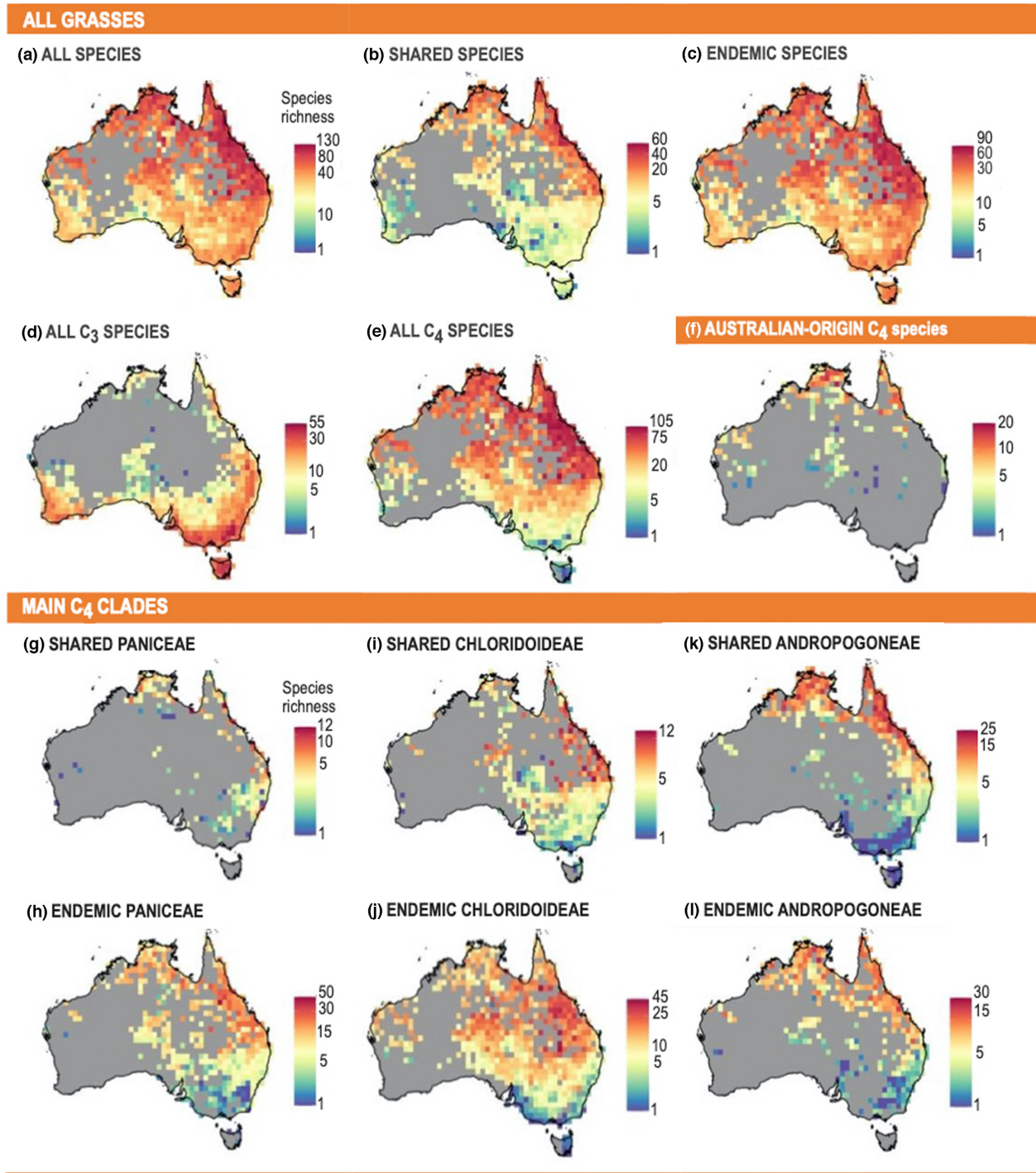
FIGURE 2 Species richness of Australian grasses, in relation to endemism, photosynthetic pathway, age class and phylogeny. Endemic species = distributed in Australia only; Shared species = also distributed on other continents. Legends indicate species richness mapped on a log-transformed scale and are individual to each map. Grey cells = insufficient species numbers to register a signal. Clades as per Soreng et al. (2017). Map: Australian Albers Equal Area projection.

3.2.2 | Main C_4 phylogenetic analysis

C_4 grass species showed a clear east–west divide, with highest species richness in all groups along the Queensland coast, reducing with latitude. Of all groups, Shared Paniceae were the most range-restricted (Figure 2g–l). Paniceae endemics showed disjunct distributions in

Central Australia, the Top End/Kimberley and the Pilbara (Figure 2h). In the Chloridoideae, shared species richness was highest along the Queensland coastal hinterland (Figure 2i), whereas endemic species were distributed across most of the eastern half of Australia, with high species richness along the Tropic of Capricorn into the inland (Figure 2j). In Central Australia, endemic Chloridoideae species

richness was far higher than other phylogenetic groups. Both shared and endemic Andropogoneae had highest species richness along the north Queensland and Northern Territory coasts (Figure 2k,l). Endemic and shared distributions were similar (aligning with the environmental analysis detailed in SI-8), but shared species richness decreased sharply with temperature seasonality away from the coastal strip. The southernmost Andropogoneae species here was *Themeda triandra*.

3.2.3 | Age class

Comparing the distributions of genera and species revealed speciation 'hot spots', with C_3 speciation in the Ancient species (Figure 3a) in southwest Australia, shifting in the Early SSI group (Figure 3b) to the southern coastline, then in the Mid SSI group (Figure 3c) to the southeast (C_3) and north (C_4). In the Recent SSI (Figure 3d), diversification was highest in the country's north.

Ancient and Early SSI groups were mostly clustered around the southern parts of the continent, with additional occurrences in Central Australia (disjunct for Ancient species; Figure 3a). In the Ancient group, a cluster in the Top End of the Northern Territory represents speciation in a few genera of the subfamily Micrairoideae. The southeast and southwest were similarly rich in genera, but the highest speciation was found in the west with little diversification in the east. Compared to the Ancient group, distributions of genera In the Early SSI group (Figure 3b) were broader (particularly in the southeast), with the high diversity found along the Queensland coast due to the Paniceae C_3 Boiviinellae 'forest shade' clade (SI-10). The high species richness in the south is mainly attributable to speciation in one genus, *Austrostipa*. The Mid SSI group (Figure 3c) shows a broad shift, with genera and species spread throughout northern regions. In this age class, genus richness is higher in the southeast, echoed by strong speciation in C_3 species in the southeast (*Deyeuxia*, *Lachnagrostis* and *Rytidosperma*) and secondarily in a few C_4 genera along northern coasts (*Eriachne*, *Aristida* and *Panicum*). Distribution of the Recent SSI species (Figure 3d) resembles the distribution in Figure 2e, showing the dominance of the influx of C_4 species in the past 3.5 Ma. Grasses attributed to this period had at least five times the genus richness and three times the species richness of any other age class, indicating a wave of immigration and speciation. In stark contrast to the Ancient group, species richness in the southwest was very low.

The distribution of Australian-origin C_4 grass genera (Figure 3e) shows the range of the Eriachnineae subtribe, in particular, the speciation of the genus *Eriachne* in northern and western Australia. Alongside the endemic Chloridoideae (Figure 2j), this was the only C_4 group with substantial presence in far Western Australia.

3.3 | Plant height

Plant height was analysed in a number of ways: by photosynthetic type; by comparing Pre-Recent groups (combined Ancient, Early SSI
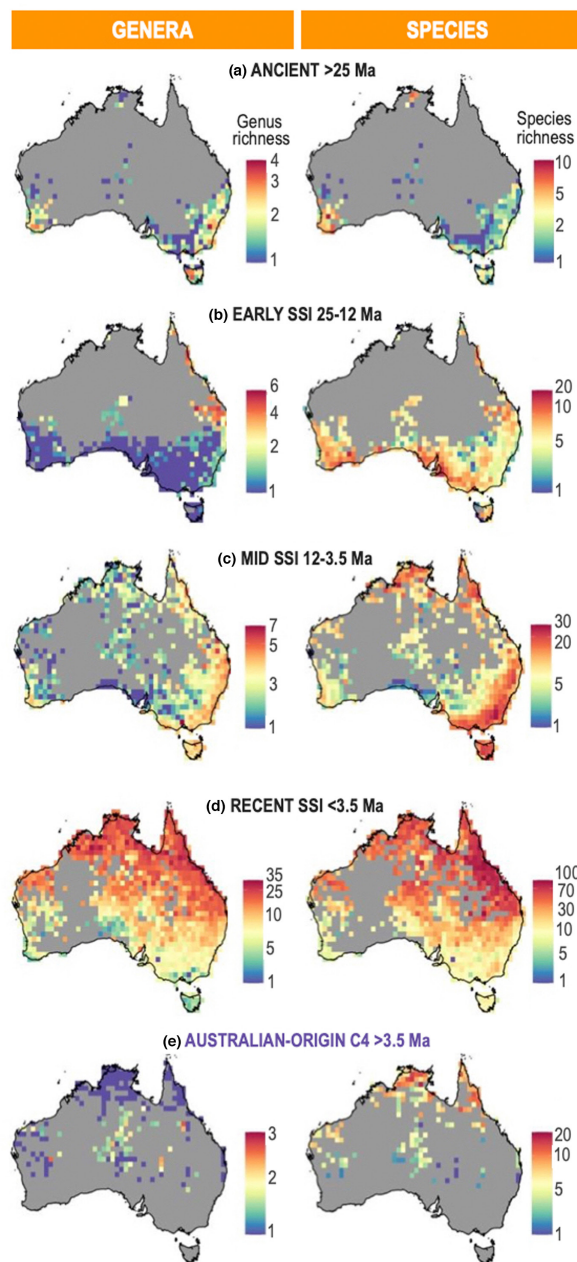

FIGURE 3 Comparison of distribution and richness between genera and species of Australian grasses in four age classes. Legends indicate species richness mapped on a log-transformed scale and are individual to each map. Grey cells = insufficient species numbers to register a signal. Age classes as per Bryceson and Morgan (2022). Species are classified according to the age class of their genus. Note that the Ancient age class represents Australian-origin C_3 grasses. Map: Australian Albers Equal Area projection.

and Mid SSI) with Recent SSI; by endemism; by phylogeny (Figure 4) and by age class (Figure 5). At the broadest level, there was no clear evidence of a height difference between C_3 and C_4 grasses ($p > 0.05$; Figure 4a). However, there was strong evidence that Recent species were significantly taller than Pre-Recent species ($p = 0.03$; Figure 4b). There was very strong evidence that the tallest grasses

were Recent C_4 species ($p=0.02$; Figure 4c), likely to be driven by the Andropogoneae tribe in which the shared grasses were significantly taller than any other group ($p<0.001$; Figure 4e). Endemic Andropogoneae grasses were also significantly taller than all others ($p=0.004$) except the shared Paniceae. The tallest grasses are therefore synonymous with the range of the Andropogoneae (Figure 2k,l) through the northern savannas, in regions of high summer rainfall, low aridity and low seasonality. Shared species were significantly taller than endemic species in the Recent C_3 group ($p<0.01$; Figure 4d) and the Andropogoneae tribe ($p=0.03$; Figure 4e). See full details in SI-9.

Each age class was also characterised according to height categories (Figure 5) and the results reveal an increasing presence of tall grasses in Australia through time, particularly evident in the shortest (0–45 cm) and taller (over 150 cm) categories. More than half of Ancient species were shorter than 50 cm, and nearly 90% were shorter than 100 cm (only one species was taller than 150 cm). In each subsequent age class, only 20% of species at most were shorter than 50 cm, and at least 35% were taller than 100 cm. Twenty per cent of Recent SSI grasses were taller than 150 cm, 10% taller than 200 cm (45 species, including 32 Andropogoneae).

4 | DISCUSSION

We found that environmental drivers and photosynthetic type alone were inadequate to explain the distribution of contemporary species richness of grasses in Australia. However, when combined with patterns of speciation (shared vs endemic), length of time in Australia (Pre-Recent SSI vs Recent SSI) and phylogenetic group, a more dynamic synthesis emerged. The spread of the Recent SSI species from the northeast coast across the country into a range of environments (including the semi-arid) encompasses both photosynthetic types. In their wake, grasses in the older age classes may have been outcompeted or become niche-restricted. More importantly, Recent SSI grasses did not simply move into vacant niches but, in the case of the Andropogoneae, likely changed ecosystem dynamics and landscape processes, enabled by their taller height. We expand on these explanations below.

4.1 | Exploiting environmental opportunities

The restriction of C_3 grasses to southern or coastal regions aligns with rainfall and temperature limitations identified by other studies (Edwards et al., 2010; Hattersley, 1983). The overlapping distributions of C_3 and C_4 grasses also confirmed Hattersley's findings (1983), with the dominance of C_4 grasses abating as summer rainfall decreased towards southern latitudes (Bowman et al., 2010). The Australian C_4 distributions generally echo rainfall and temperature patterns reported from other continents, including examples from Africa (Bocksberger et al., 2016; Schmidt et al., 2011), North America (Cotton et al., 2016; Teeri & Stowe, 1976) and South America (Cabido et al., 2007). This congruence is unsurprising given that more than 90% of C_3 and C_4 species were derived from lineages that likely originated on continents outside of Australia (Bryceson & Morgan, 2022).

The low model fit for endemic species in all three Pre-Recent SSI age classes is perhaps to be expected given the great changes
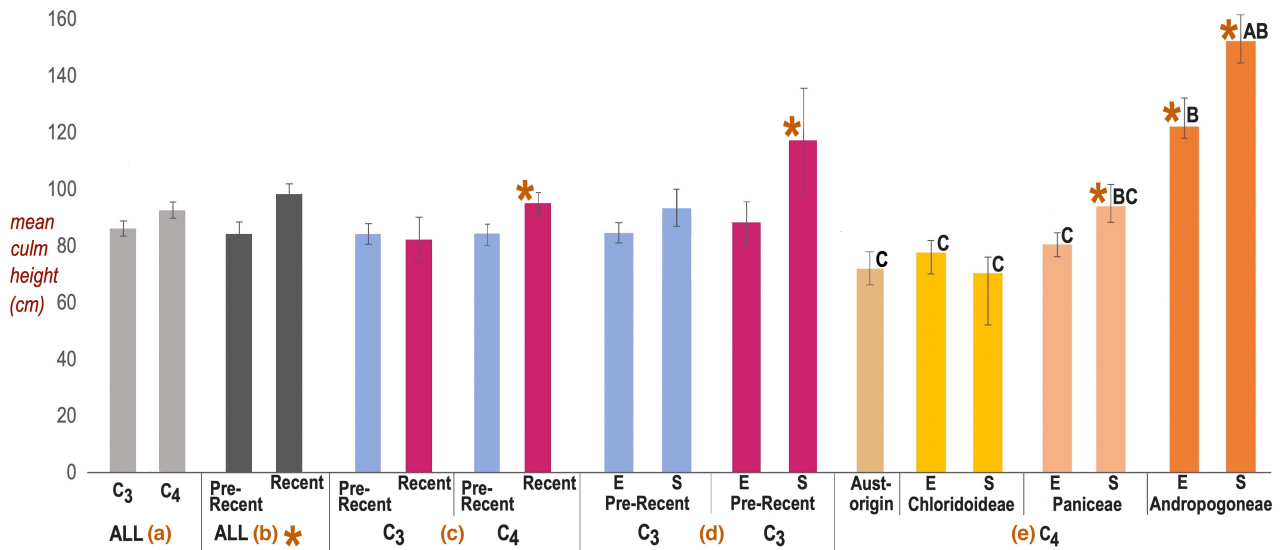

FIGURE 4 Height of Australian grasses. Mean culm height (+-SE) in relation to photosynthetic type, species distribution range, and phylogenetic group. (a) All species, according to photosynthetic type. (b) All species, according to age class. (c) Photosynthetic type according to age class. (d) Distribution range in C_3 grasses according to age class. (e) Distribution range in C_4 grasses according to main C_4 phylogenetic groups. Photosynthetic type=C_3 or C_4. Distribution range=E Endemic (Australia only) or S Shared with other continents. Age classes: Pre-Recent=Ancient, Early SSI and Mid SSI combined. Recent=Recent SSI. Phylogenetic group: sub-family Chloridoideae; tribe Paniceae; sub-tribe Andropogoneae. $n=835$ species. *=statistically significant differences. In group (e), letters denote statistically distinct groups (full details in Table SI-9a).
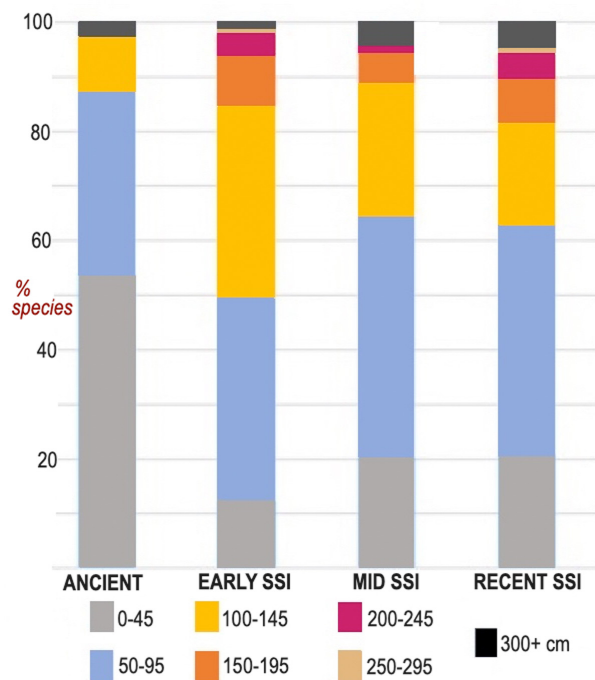
FIGURE 5 Characterising Australian grasses according to height and age class. Proportion of species in each age class according to culm height as per legend. Age classes as per Bryceson & Morgan (2022): Ancient >25 Ma; Early Sunda-Sahul Interchange (SSI)=25–12 Ma; Mid SSI=12–3.5 Ma; Recent SSI=<3.5 Ma.

in climate and soils in Australia over the past 30 Ma, suggesting that distributions of these species could be partly relictual. The marked negative response to clay soils in the Ancient group may be due to the more recent origin of these soils (sedimentary) and the niche conservatism of the Ancient genera. Compared to the Ancient group, Early SSI species richness declined with aridity and temperature seasonality and showed a clear tendency to increase with summer rain, which would support immigration via northeast Queensland. The comparatively restricted ranges of the Ancient, Early SSI and Mid SSI grasses echoes niche-conserved Gondwanan-origin flora in the southeast and centres of plant species richness (Crisp et al., 2001), likely reflecting their limited environmental tolerances rather than competition with the Recent SSI C_3 grasses.

4.2 | Broad biogeographical patterns

4.2.1 | Continental opposites

In the wider Australian flora, Crisp et al. (1999) found almost no species in common between southwest Western Australia and the Wet Tropics. Our results indicate that this also applies to Australian grasses, with the highest species richness occurring in coastal Queensland.

Sniderman et al. (2013) found evidence of high plant diversity in the southeast in the Early Pleistocene equivalent to that of southwest Western Australia today, indicating there has been simplification of

the eastern flora through extinction. In grasses, rainfall and edaphic barriers may account for the current east–west pattern whereby only the short-statured Chloridoideae and *Eriachne* penetrated the central sandy deserts into Western Australia, in contrast to the broad distribution of C_4 grasses through the eastern half of the mainland.

The southeast spread of C_4 grasses was likely propelled by repeated glacial periods, similar to earlier radiations in Europe and Pakistan (Stromberg, 2011). These conditions would have enabled them to disperse across the east and south during Pleistocene climate cycles (Mooney et al., 2017), competing with resident flora and potentially increasing flammability. By the Last Glacial Maximum, the region was dominated by steppe grasslands (Nelson et al., 2016). Future work could explore potential links between the rich floristic diversity in southwest Australia and the absence of tall grasses, especially in comparison to the country's east. Today, few C_4 species remain in higher latitudes in Australia, with low growing-season temperatures shown to kill C_4 grasses (Teeri & Stowe, 1976); the widespread and cold-tolerant *Themeda triandra* Forsskal (Dunning et al., 2017) is a notable exception and its southernmost record in Australia was in the Huon Valley, Tasmania at 42.866° S (AVH, 1983 cat. no. HO62710).

4.2.2 | North–south track

A north-to-south dispersal route from Sunda to Sahul is supported by the close phylogenetic relationships found between Queensland coastal rainforest species and New Guinea. The diversity of Sunda rainforest lineages decreased with increasing latitude, suggesting that some moved south relatively recently (Crayn et al., 2015; Sniderman & Jordan, 2011). These patterns also apply to the concentration of species richness in Early SSI genera (C_3 Panicoideae). Recent SSI grasses along the Queensland coast could indicate a stage in a migration pathway and a starting point for radiation and speciation into the interior, similar to that identified for angiosperms (Crisp et al. 1999). Future work could geographically and environmentally track the evolution of endemic grass genera and species from these internationally shared subtribes, as outlined in Bryceson & Morgan (2022). Past existence of a Timor–Kimberley dispersal track (Joyce et al., 2021) is not evident in our study.

4.3 | Speciation and endemism

4.3.1 | Niche shifting

The high ratio of endemic to shared C_3 species suggests prima facie that they may have become established in Australia before C_4 grasses. This conclusion is supported by fossil pollen strata analyses from northwest Australia that show the presence of C_3 grasses from the late Miocene-early Pliocene, possibly facilitated by the wetter climate (Sniderman et al., 2016) before intensification of the Asian-Australian monsoon created conditions conducive to C_4

grasses (Andrae et al., 2018). Our comparisons between shared and endemic distributions suggest broadscale niche-shifting occurred along a rainfall spectrum. The high degree of adaptation in the endemic Chloridoideae in dry regions and the rainfall-associated spread of the Paniceae (C_3 and C_4) compare starkly to the near-duplicate ranges of shared and endemic Andropogoneae species along the monsoonal coasts—this may reflect greater plasticity in the former group, but could also point to the more recent arrival and superior competitiveness of the latter (Bryceson & Morgan, 2022).

4.3.2 | Sequence of migration and speciation

This study supports the sequence of colonisation outlined in earlier work (Bryceson & Morgan, 2022) and deepens our understanding of the temporal and spatial sequences of speciation. The current distribution of grass genera with different antiquities is a clue to their respective environmental constraints and to changes over time that may have stimulated speciation. For example, the ancestors of *Austrostipa* arriving in Australia during the Early SSI probably speciated widely in vacant niches in conditions similar to those currently experienced in southern Australia, while the pattern of Mid SSI C_4 grass speciation in the north indicates that warmer, high-light niches had become available with the continent's closer proximity to the equator.

Based on the difference between shared and endemic distributions as a rough indicator of available dispersal time, the C_4 Paniceae's disjunct distribution suggests that it may have radiated during the Pliocene wet period (Sniderman et al., 2016) but contracted when aridification resumed. By contrast, the distribution of shared and endemic Chloridoideae shows a more continuous pattern of expansion through the inland, suggesting speciation occurred after the resumption of aridification and intensification of the Asian monsoon (Bowman et al., 2010).

In Australia, the Andropogoneae comprises only three endemic genera but includes 31 genera that are also distributed throughout the Northern Hemisphere, implying recent arrival of the group (Bryceson & Morgan, 2022). The tall height of Andropogoneae species is a strong competitive trait, fostering wind-borne dispersal and improving chances of reaching safe germination sites in microsites created by fire (Scott et al., 2010; Soons et al., 2004). The subtribe's high species richness clustered around the Gulf of Carpentaria could be a vestige of recent dispersal and rapid speciation across novel, open habitats of the Lake Carpentaria system in times of low sea levels (Hope et al., 2004) into environments that required minimal niche-shifting.

The migration to Australia of the Andropogoneae genus *Themeda* c 1 Ma (Dunning et al., 2017) is consistent with this scenario, and the phylogenetic shallowness of the Andropogoneae in Australia (Bryceson & Morgan, 2022)—despite the rich diversity in Southeast Asia (Arthan et al., 2017)—suggests that most of the subtribe arrived at a similar time. The rapid and continuing evolution of the Andropogoneae (Welker et al., 2020) indicates that the group could still be adapting to new niches in Australia.

4.3.3 | Speciating into the inland

The concentration of C_4 shared species richness along the Queensland coast may reflect the physiological limits of the Andropogoneae and Paniceae, already at the fringe of their global distribution (Bryceson & Morgan, 2022). The intolerance of Paniceae and shared Chloridoideae to temperature seasonality likely restricted them to warmer coastal regions. It is possible that the taller Paniceae may have forced the diversifying Chloridoideae into peripheral niches where they overcame the limitations of temperature extremes, speciating in a pattern similar to other colonisations of Australia's arid regions (Byrne et al., 2008; Crisp et al., 1999), not unlike their ancestral association with areas of infrequent fires and high temperatures in Africa (Visser et al., 2012).

Australia's arid centre has been described as a sink, with species moving in during wetter periods and becoming isolated during late Pliocene aridifications (Crisp et al., 1999). The inland refuges with high plant endemism of mainly genetically conserved Gondwanan lineages (Crisp et al., 2001) are a stark contrast to the endemism pattern of Australia's Recent SSI C_4 grasses which range from the east coast across drier regions into Western Australia. This breadth is highlighted by the splintering of the globally distributed Chloridoideae genus *Eragrostis* into 47 short-statured endemic species, implying high genetic plasticity able to exploit the subtle niche variability of drier regions, as also expressed by intricate distribution patterns in eucalypt clades (Ladiges et al., 2003).

4.4 | Ancient lineage following different cues

In Crete, Lazarina et al (2019) found that while the distributions of neo-endemics and palaeo-endemics overlap, different drivers shape their respective species richness patterns. This could explain the co-occurrence of the Eriachneae (Australia's only autochthonous C_4 grass tribe; Sage et al., 2011) and Recent SSI C_4 groups, with both groups responding to different climate factors, suggesting that their distributions are tracking different environmental histories.

Eriachneae's ancestral habitat is thought to be similar to its extant sister, the *Micraira* Mueller (Teisher et al., 2019), an unusual C_3 grass able to 'resurrect' after dry periods in rocky outcrops in northern Australia (Gaff & Latz, 1978). Its unique C_4 biochemistry—Eriacinoid (Sage et al., 2011)—coupled with an inherited tolerance to dry conditions, has enabled dispersal into the arid country multiple times (Teisher et al., 2019), traversing 1000 mm in rainfall gradients and 20 degrees of latitude throughout diverse habitats in northern Australia (Lazarides, 1995). Open habitats existed well before C_4 grasses became a significant presence ~3.5 Ma (Andrae et al., 2018) and the Eriachneae possibly had a head start in colonising the aridifying regions, enabling it to persist against incoming C_4 groups

(Hewitt, 2000). *Eriachne's* short stature and low biomass may have meant that, like *Triodia* R.Br. species, it was too slight to register a signal in fossil pollen assemblages (Toon et al., 2015), so it is likely that the C_4 grasses identified in northwest/central Australian leaf waxes (Andrae et al., 2018) were from Recent SSI Chloridoideae.

In arid Western Australia, Eriachneae co-occurs with Recent SSI Chloridoideae grasses but along the Queensland coast, low species richness may indicate it has been outcompeted by taller C_4 grasses, especially considering its wide environmental tolerances. *Eriachne* is the only grass recorded among fire-intolerant palaeo-endemic vegetation in Central Arnhem Land (Woinarski et al., 2006) where fire, rather than climate, has caused contraction into refuges. This suggests a degree of co-evolution, with Eriachneae species unlikely to have been 'ecosystem transformers'.

4.5 | Effects on other taxa

The magnitude of the stimulus from immigrating grasses on the evolution of grazing animals in Australia is still unclear, though the extinct *Diprotodon* in south-central Queensland is thought to have grazed on C_4 plants and tracked them seasonally (Price et al., 2017). The dietary switch from browsing to grazing in the evolution of modern kangaroos in northern Australia was stimulated by the increasing presence of grasses (C_3 and C_4) in the landscape (Couzens & Prideaux, 2018) and today some marsupials—including pademelons, wallabies and wombats—create grazing lawns in southeast regions (Ingram & Kirkpatrick, 2013). Our limited investigations indicate that the relationship between early grazing marsupials and the immigrating C_3 grasses (particularly forest-adapted Paniceae/Boiviinellae group, see SI-10) is an avenue for further study. However, the pre-historic absence of large herds of grazing mammals (Cook et al., 2019) enabled Recent SSI grasses to spread untrammelled, consumed instead by the 'global herbivore', lightning-strike fire (Bond & Keeley, 2005).

It is likely that other taxa migrated with the dispersing grasses, building the biodiversity of the new biomes. For example, the grass-finches and mannikins (subfamily Estrildinae)—obligate graminivores descended from a tropical group—are migrants to Australia and their range aligns with the monsoonal tallgrass savanna (Franklin et al., 2000), the Andropogoneae. Modelled scenarios of habitat suitability through the Lake Carpentaria region during the Last Glacial Maximum (Schidelko et al., 2013) suggests they likely tracked the distribution of the C_4 grasses. Rodent migrations from New Guinea during Pleistocene sea-level lows (Rowe et al., 2008) similarly coincided with the grass migrations. High ant species richness has been linked with frequently burned savanna (Andersen et al., 2014) and species of the Southeast Asian grass-skipper butterfly (*Neohesperi*) are now endemic to the northern savannas (Braby, 2008).

Ancient Australian-origin taxa, such as parrots, cockatoos (Franklin et al., 2000) and skinks (Potter et al., 2018) also spread into the novel grassy ecosystems, and the savanna region hosts the highest biomass of termites in the country (Eldridge et al., 2011).

However, it is also likely that shrubby environments that supported some of the now-extinct megafauna, including the giant flightless Mihirung (*Genyornis*), were adversely affected by the invading grasses (Miller et al., 2005).

4.6 | Creating the savannas

Although not all C_4 grasses are associated with ecosystem change, the taller Recent SSI grasses (mostly Andropogoneae) brought a new component into Australian ecosystems: a fast-growing ground layer of flammable dry matter capable of carrying fire into mid-storey canopies that were otherwise unreachable by the short tufty grasses. We concur with other research showing that monsoon areas have been dominated and transformed by tall Andropogoneae grasses (Ma et al., 2013; Scott et al., 2012).

While the creation of Australian savanna and grassland ecosystems deserves much fuller investigation than can be provided here, we propose that it is likely that Andropogoneae caused 'savannisation' of northern Australian landscapes, relatively recently. In African and South American fire-maintained tropical savannas, resprouting from extensive underground storage organs is common to plants from more than 30 families, an adaptation as yet absent from Australian savannas (Maurin et al., 2014), highlighting the youthfulness of the biome. Karp et al. (2021) reported no increase in fire with the arrival of C_4 grasses in northwest Australia before 1 Ma, which we contend shows that the increase occurred later than their research parameters—before 1 Ma, either fire was insufficiently frequent to enable Andropogoneae grasses to become dominant, and/or the migration of most Andropogoneae occurred more recently (Bryceson & Morgan, 2022). A number of studies report fire increasing in the north of Australia since ~150 ka, which were later likely accelerated by the arrival of humans (Johnson, 2016; van der Kaars et al., 2000).

Whenever this landscape transformation began in Australia, it could have happened very quickly, given frequent fire. Bond et al. (2004) modelled turning fire 'off', finding that in Australia, C_4 grasses would still occupy the inland but that their dominance would be greatly reduced in the mesic monsoon area. In Hawaii, invasive grasses dominated ecosystems in a matter of decades, with grass coverage increasing after each fire and persisting to the detriment of species that had not co-evolved with intense or frequent fires (D'Antonio & Vitousek, 1992).

5 | CONCLUSIONS

Today, Australia is the world's most fire-prone country, with most frequent fires occurring in the Andropogoneae-dominated savanna country (Murphy et al., 2018). Contemporary methods of fuel management could be promoting invasion by grasses (Corey et al., 2019). We support concerns that burning to promote species richness or phylogenetic diversity might inadvertently jeopardise the conditions

suited to ancient flora (which may be less diverse or species-rich), and thereby threaten part of the region's evolutionary history (Costion et al., 2015; Woinarski et al., 2006).

Much of Australia's grass diversity is of Recent SSI origin. This study adds another piece to the map of global grass distributions and their environmental drivers. Grass distribution in Australia is not static; rather, it can be understood as a process of immigration and dispersal through adaptation, niche-shifting and physical dominance. The relatively large scale of this study (100×100km cells) means that finer-scale niche patterns are obscured and conclusions must necessarily be broad. Nonetheless, the distribution patterns uncovered—and their environmental and phylogenetic correlates—provide a springboard for more detailed studies.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Downloadable via https://researchdata.canberra.edu.au/datasets/jkh8n7grbw doi: 10.17632/jkh8n7grbw.1. Code for analysis and reproduction of plots is located at https://github.com/khemming/australian_poaceae.

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BIOSKETCH

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Author contributions: SRB conceived the ideas with KH and JWM. KH collected species distribution data; SRB collected plant height data and classified species data; KH managed data and created models and maps. SRB interpreted the results in consultation KH, RPD and JWM. SRB led the writing and all authors worked through multiple iterations.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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