

Functional diversification enabled grassy biomes to fill global climate space

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Abstract: Global change impacts on the Earth System are typically evaluated using biome classifications based on trees and forests. However, during the Cenozoic, many terrestrial biomes were transformed through the displacement of trees and shrubs by grasses. While grasses comprise 3% of vascular plant species, they are responsible for more than 25% of terrestrial photosynthesis. Critically, grass dominance alters ecosystem dynamics and function by introducing new ecological processes, especially surface fires and grazing. However, the large grassy component of many global biomes is often neglected in their descriptions, thereby ignoring these important ecosystem processes. Furthermore, the functional diversity of grasses in vegetation models is usually reduced to C₃ and C₄ photosynthetic plant functional types, omitting other relevant traits. Here, we compile available data to determine the global distribution of grassy vegetation and key traits related to grass dominance. Grassy biomes (where > 50% of the ground layer is covered by grasses) occupy almost every part of Earth's vegetated climate space, characterising over 40% of the land surface. Major evolutionary lineages of grasses have specialised in different environments, but species from only three grass lineages occupy 88% of the land area of grassy vegetation, segregating along gradients of temperature, rainfall and fire. The environment occupied by each lineage is associated with unique plant trait combinations, including C₃ and C₄ photosynthesis, maximum plant height, and adaptations to fire and aridity. There is no single global climatic limit where C₄ grasses replace C₃ grasses. Instead this ecological transition varies biogeographically, with continental disjunctions arising through contrasting evolutionary histories.

Significance statement: Worldviews of vegetation generally focus on trees and forests but grasses characterize the ground layer over 40% of the Earth's vegetated land surface. This omission is important because grasses transform surface-atmosphere exchanges, biodiversity and disturbance regimes. We looked beneath the trees to produce the first global map of grass-dominated biomes. Grassy biomes occur in virtually every climate on Earth. However, three lineages of grasses are much more successful than others, characterizing 88% of the land area of grassy biomes. Each of these grass lineages evolved ecological specializations related to aridity, freezing and fire. Recognizing the extent and causes of grass dominance beneath trees is important because grassy vegetation plays vital roles in the dynamics of our biosphere and human wellbeing.

1 **Introduction**

2 The global distribution of terrestrial biomes determines global patterns of carbon storage and
3 biodiversity (1). Delineation of biome distributions is crucial because it underpins evaluations
4 of vegetation feedbacks on climate (2), extinction threats for biodiversity (3), and strategies
5 for monitoring and reversing land-use change and degradation (4). Global studies of biome
6 distributions typically focus on forests and trees (4-6), following the long-established
7 paradigm in modern ecology of deterministic relationships between forest distributions and
8 environment (7). Within this paradigm, there is a widely held perception that grassy
9 vegetation only occupies semi-arid climates. However, it is increasingly recognized that biome
10 limits are not deterministically linked to climate but arise from multi-directional feedbacks
11 between plant functional traits, environment, and disturbance. These processes operate over
12 evolutionary and ecological timescales (8) creating biogeographic contingencies in biome-
13 environment relationships (9).

14 Grassy biomes require open-canopied tree layers (or no tree layer) to permit enough
15 light to penetrate for grass photosynthesis. As a result, grasses dominate the ground layer
16 when the rate of woody plant recruitment and growth is limited by climate, soil, drainage,
17 disturbance conditions or light competition (10-12). “Grassy biomes” defined in this way
18 include tropical savannas, montane grasslands, grassy deserts, temperate steppe grasslands,
19 boreal parklands, and many temperate woodlands. The distinction of whether the ground
20 layer is dominated by grasses (Poaceae) is fundamental to understanding global relationships
21 among plants, climate, and disturbance (13). While, both trees and grasses are clearly
22 important in driving vegetation dynamics, grass dominance causes a fundamental shift in
23 disturbance regimes, whereby the consumption of ground layer biomass by fire and grazing
24 reinforces grass dominance and maintains open tree canopies (10). Grass cover and biomass

25 in the ground layer also affects surface energy, carbon, nutrient and water cycling by, for
26 example, altering rates of decomposition, water infiltration and absorption of sunlight. Grass
27 dominance therefore leads to novel ecological processes and properties in the Earth System,
28 including frequent fire and grazing by mammals (14).

29 During the Cenozoic grasses displaced forests and shrublands by altering disturbance
30 regimes at large scales across tropical and temperate regions (14, 15). The global expansion
31 of grassy vegetation enabled major faunal and floral radiations (14, 16), and is linked to events
32 in human behavioral evolution (17, 18). Today, natural grassy biomes provide grazing lands,
33 water resources and numerous ecosystem services that directly support over a billion people
34 (19). Yet, despite this social and economic significance, and the profound disturbance
35 feedbacks engendered by grassy vegetation (20), understanding of grassy biomes is
36 geographically biased towards few regions (e.g., South and East African savannas, North
37 American grasslands), with the global limits of grassy biomes poorly defined.

38 When considering the limits to grassy biomes, the grass diversity present in a system
39 is generally reduced to a distinction between species using the C₃ or C₄ photosynthetic
40 pathways. If all else is equal, C₄ grasses should outcompete C₃ grasses under conditions of high
41 light and temperature as well as low CO₂ (21-23). This physiologically based model explains,
42 in general terms, how C₄ grasses dominate tropical regions and C₃ grasses dominate
43 temperate and high-altitude environments under current atmospheric CO₂ levels [ppm ≈ 408].
44 The physiological mechanisms underpinning this model have critical impacts for predicting
45 vegetation trajectories with global climate and atmospheric CO₂ changes (22) yet attempts to
46 parse the consequences of grass physiology for global vegetation is often reliant on sparsely
47 validated modelling (24). Further, a focus on photosynthetic type belies the rich phylogenetic
48 diversity within grasses independent of photosynthetic pathway (14). Grasses are unusual

49 among vascular plants because C₄ photosynthesis evolved in up to 24 independent lineages
50 (25), conferring unique ecological characters to each C₄ lineage inherited from its C₃ ancestors
51 (26). Photosynthetic type therefore interacts with different combinations of other functional
52 traits to determine plant performance under varied environmental conditions (27, 28), but
53 the influence of these interactions on the global biogeography of grassy biomes is unknown.

54 Here, we focus on grass-dominated systems to address three questions. First, what are
55 the global limits of grassy biomes? Second, to what extent is grassy biome structure
56 contingent on evolutionary history, whereby independent phylogenetic lineages characterize
57 grassy biomes on each continent? Finally, how do functional traits of the descendant species
58 of each lineage relate to climate and fire? Our findings have significant implications for the
59 representation of terrestrial vegetation processes in Earth System Models.

60

61 **Identifying grassy biomes.** Our dataset provides the first spatially explicit, functional
62 classification of grassy vegetation at the global scale (Figs. 1 and S1). Necessarily, our approach
63 that focusses on the ground layer contrasts with efforts to map biomes using remotely sensed
64 tree cover or biomass (4, 29). Such studies generally misclassify extensive areas of tropical
65 savanna as forest or degraded forest (30, 31). Global synthesis of grassy biomes has been
66 prohibited as satellite remote sensing does not see through a tree canopy. Therefore, we
67 mapped grassy formations by integrating and re-classifying 20 existing national and regional
68 vegetation maps produced using botanical data and detailed vegetation descriptions (see
69 Methods and SI).

70 What is a grassy biome? We defined vegetation units as grassy where the ground layer
71 is characterized by Poaceae and where grasses comprised > 50% of ground layer cover based
72 on descriptions within vegetation maps and associated literature (see Methods and SI). A

73 relatively small set of species often accounts for the majority of biomass in plant communities,
74 whether these are communities dominated by trees or grasses, and these species exert major
75 controls over ecosystem processes (32) and ecosystem services (33). Focusing on dominant
76 and characteristic species provides one way to explore links between evolutionary history and
77 ecosystem ecology at large scales (14). Through this process we identified 1,154 grass species
78 (~10% of the total grass flora) characterizing grassy vegetation.

79

80 **Results and Discussion**

81 **Global limits of grassy biomes.** Grasses can dominate ground layer vegetation in all but the
82 coldest and driest climates on Earth (Figs. 1 - 2). We estimate that vegetation with a grass-
83 dominated ground layer originally covered ~ 41% of the vegetated land surface, although
84 much is now under cultivation. Critically, grasses can dominate the ground layer in every
85 climate where woody vegetation can persist (Figs. 1 - 2). While steppe grasslands and prairies
86 occupy a large fraction of the global land area in dry temperate climates (Figs. 2, S2-S3), and
87 savannas and grasslands occupy most of the tropics, grass-dominated ground layers occupy
88 extensive areas in any other part of the vegetated global climate space (Fig. 2 and Fig. S4).

89 Members of 16 independently derived C₄ grass lineages dominate within at least one
90 vegetation unit worldwide (Fig. 1). However, two C₄ lineages and one C₃ lineage dominate
91 over 88% of the land area of grassy vegetation: C₄ Andropogoneae, 37% (1189 species in the
92 lineage); C₄ Chloridoideae, 14% (1601 species in the lineage); and C₃ BEP, 38% (Fig. 1). The vast
93 majority of C₃ BEP taxa belong to Pooideae (4234 species in the lineage). In contrast, C₃ species
94 of the PACMAD clade dominate only 2% of grassy biomes (Fig. 1); these are the closest
95 relatives of C₄ grasses and are restricted to warm, wet areas (Figs. S2-S4). Of the remaining

96 area of grassy vegetation, 6.6% is characterised by a mix of lineages, and the rest dominated
97 by 13 other, independently derived, C₄ lineages (Fig. 1 and Table S1).

98 The three dominant lineages sort in climate space. C₃ Pooideae dominate cooler, drier
99 climates, whereas C₄ Andropogoneae and Chloridoideae dominate grassy biomes in warmer
100 climates (Figs. 3, S3-S6). However, precipitation sorts the C₄ lineages, with peak dominance of
101 Andropogoneae occurring at ~ 1200mm MAP (Figs. 4, S3-S5), coinciding almost precisely with
102 the global peak in fire frequency (Fig. 4). This is also the climate space where disturbance-
103 driven feedbacks are considered to play a major role in maintaining open (i.e., grassy) or
104 closed (i.e., woody) vegetation (34). In contrast, the peak dominance of Chloridoideae occurs
105 at ~350mm MAP (Figs. 4, S3-S4), within semi-arid climate zones occupied by both dry savannas
106 and shrublands/thickets e.g., (35). Temperature seasonality also differs among the C₄ lineages,
107 with Chloridoideae dominating in regions with strong seasonality, and Andropogoneae
108 dominating in more aseasonal environments (Fig. S5).

109

110 **Continental disjunctions in C₃ and C₄ lineage distributions.** Globally, the mean growing
111 season temperature where dominance of grasses transitions from C₃ to C₄ types varies starkly
112 among continents, from 8.5-26.1 °C, with a global mean of 17.2 °C (Fig. 3). Lineages using C₃
113 and C₄ photosynthetic pathways are clearly sorted by growing season temperature and mean
114 annual temperature (Figs. 3 and S3-6). The C₃ Pooideae lineage has specialized and radiated
115 in cold environments by evolving physiological cold acclimation to protect tissues from
116 freezing damage, and vernalization to synchronize flowering with the growing season (36, 37).
117 Conversely, in tropical regions, the repeated evolution of C₄ photosynthesis appears vital in
118 expanding the range of grassy biomes, by enabling colonization of hot, high light, and
119 seasonally dry habitats across a wide span of rainfall (38, 39).

120 The C₃ Pooideae occupy regions with lower winter temperatures and shorter droughts
121 than the C₄ lineages (Fig. S7). C₃ Pooideae dominate grassy biomes to much higher
122 temperatures in the Palearctic than the Nearctic realm, although distributions of C₄
123 Andropogoneae and Chloridoideae in these realms are similar (Fig. 3). Conversely, C₃ Pooideae
124 are confined to the geographically restricted colder parts of the Afrotropics and Indo-Malay
125 realms, and C₄ Andropogoneae dominate at much lower temperatures in these regions (Fig.
126 3). The sorting of C₃ and C₄ grass species along local and regional temperature gradients is well
127 established (40, 41), and the crossover temperature can be modified by ecosystem factors
128 (e.g., tree cover) (42). However, our observations are broadly consistent with model
129 predictions of carbon assimilation (22, 23, 43), as modeled crossover temperatures under low
130 light conditions and modern CO₂ levels occurs at ~20-22 °C.

131 In our data, some species of both Andropogoneae and Chloridoideae lineages have
132 adapted to low mean annual temperatures and may persist in grassy vegetation within cool
133 parts of each realm (e.g. Fig. 3). Given equal investment in the carbon-fixing enzyme Rubisco,
134 a relatively low canopy leaf area and sunny conditions, a C₄ canopy can theoretically achieve
135 higher total daily rates of photosynthesis than a C₃ at any temperature (37). In this case, the
136 primary limitation on canopy carbon uptake becomes light-mediated damage during low
137 temperature extremes (44), although C₄ photosynthesis is energetically expensive. Low
138 temperature tolerance may be absent from most C₄ species as C₄ photosynthesis evolved in
139 the tropics (38).

140

141 **Trait combinations of each lineage.** Chloridoideae are distinguished from Andropogoneae in
142 their occupation of regions with lower precipitation, higher daily variation in temperatures
143 and longer droughts (Fig. S7). Further, these lineages are differentially associated with fire

144 where Andropogoneae has the shortest fire return interval of 2 years, the peak occurrence of
145 Chloridoideae is at an interval of 8 years, while in Pooideae the modal fire return interval
146 exceeds 20 years (Fig. S7). Maximum plant heights of each lineage sort similarly, with values
147 peaking at 1.5 m for Andropogoneae and 0.6 m for both Chloridoideae and Pooideae (Fig. S7).
148 However, annual versus perennial life history is not globally relevant. The only significant areas
149 dominated by annual grasses occurring at the margins of the Sahara Desert and West Africa,
150 regions commonly considered as over-grazed.

151 80% of burned area globally occurs in the regions we see dominated by
152 Andropogoneae (20) and differs from other C₄ grass lineages with its greater average height
153 and consequent rapid growth rates. Where rainfall exceeds 800 mm MAP in the tropics, soils
154 are typically leached and infertile (45). Andropogoneae produce leaves with relatively high
155 C:N ratios (46, 47), which resist rapid decomposition. The tall, erect architecture of these
156 grasses produces a flammable well-connected fuelbed (48) and productive tropical
157 environments, with an annual dry season of > 5 months (13), are primed to burn as the grass
158 layer senesces. Experimental manipulations demonstrate that fire promotes dominance by
159 Andropogoneae (46) and we see this mirrored at a global scale. Grass persistence in these
160 competitive environments relies on the annual production of a new canopy and, in the
161 absence of woody investment, dead biomass must either rapidly decompose, burn or be
162 consumed by herbivores to avoid self-shading (11, 49). Andropogoneae are known to have
163 morphological adaptations enabling tolerances and persistence to fire that are not commonly
164 present in other grass lineages (49). Fire and other forms of repeated disturbance, such as
165 grazing, are therefore crucial for grass-dominated systems to persist in high rainfall
166 environments. While Andropogoneae appears to be the C₄ lineage most closely associated

167 with disturbance by fire, multiple lineages in the semi-arid African tropics appear linked to
168 grazing tolerance (Fig S8, (50, 51)), and this may be due to the strength and form of
169 environmental filtering associated with fire versus grazing, as well as the antiquity and
170 biogeography of grazing pressure relative to fire.

171

172 **Implications.** The Andropogoneae, Chloridoideae and Pooideae grass lineages dominate
173 globally, via mechanisms encompassing plant production and competition, resilience to
174 drought, freezing and disturbance. Why do three of the most diverse grass lineages
175 characterise grassy biomes? Does diversity beget ecological success or does success beget
176 diversity? Early diversification may have enabled ecological success, such that ecological
177 speciation allowed each lineage to radiate across broad environmental envelopes (an
178 ecological mechanism). Alternatively, a neutral mechanism of a long history of diversification
179 may have led to high diversity as Andropogoneae and Chloridoideae are the oldest C₄ lineages.
180 Across our dataset, evidence for this is equivocal. We list 8.8% of all grass species and within
181 lineages: Andropogoneae, 14.5%; Chloridoideae, 6.5%; Pooideae, 10.8%. Perhaps ecological
182 success facilitated diversification, such that large geographical ranges enabled by unique
183 adaptations made the isolation of populations and allopatric speciation more likely (a
184 geographic mechanism). The rapid spread of the cosmopolitan *Themeda triandra* from Asia to
185 Africa in < 500,000 years supports this idea (52). Resolving the relative role of these
186 mechanisms requires comparative phylogenetic analyses of the relationships among ecology,
187 functional traits, range sizes and diversification rates.

188 The biogeographic contingencies described here in crossover temperatures align with
189 emerging evidence that regional evolutionary and environmental histories have been

190 important modifiers of biome-climate relationships (9, 53). However, the rapid rates of
191 dispersal observed in grasses (52), along with their short generation times (49), raises critical
192 questions about whether the biogeographic contingencies observed in woody plants should
193 be mirrored in grassy communities.

194 Global change will rapidly modify the existing global distribution of grassy biomes.
195 First, environmental change can alter feedbacks between grasses and woody plants via
196 changes in the processes limiting the growth and mortality of woody plants. For example,
197 rising CO₂ is hypothesised to increase tree recruitment in savannas and forest margins (54,
198 55), while extreme drought events and warming may cause forest dieback on large scales (56),
199 where each process has feedbacks with fire leading to ongoing biome shifts (57). Second,
200 environmental changes will shift the community composition of grass communities. Our
201 analysis points to globally important ecotones between C₃ and C₄ likely to be influenced by
202 rising CO₂ and temperature (58), but these are better conceptualised as the boundary
203 between Pooideae and Chloridoideae in arid and semi-arid regions or regions of high grazing
204 pressure, and Pooideae and Andropogoneae in wetter regions. An experimental CO₂
205 manipulation in dry mixed prairie found elevated CO₂ favoured a Pooideae dominant over a
206 Chloridoideae dominant, with rising temperature having the opposing effect (59). Conversely,
207 in a mesic tallgrass prairie, an Andropogoneae dominant displaced a Pooideae dominant in
208 competition under elevated CO₂ via improved water relations (60). In each case, C₄
209 photosynthesis was one trait among many that influenced dynamic environmental responses.
210 Finally, the boundary between Andropogoneae and Chloridoideae is more likely to be
211 influenced by changes in rainfall amount and seasonality, along with shifting fire and grazing
212 regimes that can be directly altered by people at small and large scales.

213

214 **Conclusions.** The previous lack of synthesis in biome limits between grasses and woody plants
215 constrains our understanding of how ecological and evolutionary processes determine the
216 sensitivity of vegetation to global change. We have shown that divergent evolutionary
217 histories and unique functional trait combinations have enabled three major grass lineages to
218 dominate grassy biomes across global climate space. Local dominance by each lineage brings
219 differing sensitivities to alternative global change drivers.

220

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236 the figures.

237 **Methods**

238 **Classifying grassy biomes.** Data from 20 vegetation maps derived from botanical information,
239 or a combination of botanical and geographic information, were integrated to delineate grassy
240 biomes (references for these maps are listed in the Supplementary Information). The result
241 was a global map of grassy biomes resolved into 1,635 discrete vegetation units, each defined
242 by its characteristic grass species, which formed a list of 1,154 species (accounting for
243 synonymy) found commonly across global grassy biomes.

244 Vegetation maps are generally based on botanical survey and geographic analysis,
245 combined with expert input, that cluster species composition and vegetation structure to
246 define unique vegetation units. We compiled the ground layer information for the vegetation
247 units in each map to identify the grass species considered to characterize a vegetation unit.
248 To determine whether vegetation units were naturally dominated by grasses, we developed
249 a set of criteria. First, artificial vegetation units were defined as those plowed or sown for
250 agriculture and where humans are planting species that would not otherwise occur. We
251 retained data for this analysis of only natural formations. Second, based on the vegetation
252 descriptions we determined whether > 50% of the relative ground cover or biomass was
253 derived from grasses. We used this definition in place of 'Is there a continuous grassy ground
254 layer?' because low herbaceous cover in predominantly grassy vegetation would present a
255 problem with the classification of desertic and arid environments. Vegetation units were
256 considered grassy deserts where the total above-ground biomass was considered <50 g m²,
257 or where total ground cover <25%, throughout the year. Finally, we retained all formations
258 where grasses were the dominant component of the ground layer, irrespective of tree cover.
259 Numerous grassy biomes, such as tropical savannas and woodlands, may be characterised by
260 up to 80% tree cover, but behave functionally as savannas due to a contiguous grassy ground

261 layer (13, 35). Where necessary, we sourced additional information from published vegetation
262 descriptions and analyses to attribute key grass species to a grassy vegetation unit.
263 Additionally, vegetation units could be classified as mosaics with patches of closed canopy
264 vegetation intermingled with open vegetation, e.g. across the Steppe region of Russia.

265 **Mapping grassy biomes.** The vegetation maps we used as sources were developed
266 throughout the 20th century. While this method provides an incomplete global coverage, we
267 integrated available state-, country- and continent-level mapping to assemble what we
268 consider to be the most robust map possible of the limits of grassy vegetation, where both
269 vegetation characteristics and key constituent species could be identified. We were obliged
270 to use the WWF Ecoregions map (61) where no other mapping was available. We re-assessed
271 this global map to re-define units as grassy or not based on the criteria outlined above.

272 To quantify the global limits of grassy vegetation according to grass lineage, we gridded
273 the mapped data compilation at 0.5 degrees resolution. We calculated the proportion of each
274 0.5-degree grid cell occupied by grassy polygons. Using the grass phylogenetic and trait
275 information compiled, we then calculated the occupancy of grassy polygons by photosynthetic
276 type, annual/perennial life history, grass lineage, and mean maximum grass height. These data
277 are not the same as a classic concept of abundance or dominance but are a relative measure
278 of the likelihood of occupancy measured from zero to unity. We undertook a validation of our
279 map compilation described in the Supplementary Information and in Figure S9.

280 **Phylogenetic and plant trait information.** We cross-referenced our species list to a taxonomy
281 of accepted scientific names (GrassBase, <http://www.kew.org/data/grasses-syn/cite.htm>)
282 and a recent accepted phylogeny from the Grass Phylogeny Working Group (25) to eliminate
283 synonymy and link species to descriptions of evolutionary history and functional traits.
284 Functional traits considered were: C₃/C₄ photosynthetic pathway, maximum plant height,

285 annual/perennial life history, and tolerance of climatic extremes and fire frequency. C₃ species
286 were divided amongst two groups: a polyphyletic group belonging to the PACMAD clade
287 (including the C₃ sister groups for all C₄ lineages); and the monophyletic BEP clade, a C₃
288 outgroup to PACMAD, including bamboos, rice relatives and Pooideae species. C₄ grass species
289 were attributed to one of 24 independently evolved grass lineages. Maximum plant size is a
290 major axis of plant trait variation at a global scale (62), with maximum culm height in
291 herbaceous grasses reflecting annual rates of height growth, as most grasses annually senesce
292 their canopy (49). Height also describes differences in life history strategies related to light
293 competition and flammability and grazing tolerance (49). We included annual/perennial as
294 while most grasses reach sexual maturity in < 1 growing season, perennial grasses can be long-
295 lived. Plant longevity is an effective strategy for occupying space in competitive environments
296 (63). We summarized these data for each grassy vegetation unit based on the grass species
297 listed as characteristic of each unit.

298 For the Poaceae species that we listed, we extracted all available georeferenced
299 occurrence records from the Global Biodiversity Information Facility (GBIF) web portal
300 (<http://www.gbif.org/>; accessed January 2014) and cleaned these data to ensure longitude
301 and latitude values were viable and to two decimal places. Species distributions were
302 standardised against descriptions of distributions in Grassbase using TDWG regions. For this
303 subset of species produced via distribution records, median fire return intervals were
304 calculated at a species level following the methods of Archibald *et al.* 2010 (64). Information
305 on fire date was extracted for each GBIF location from the MODIS global monthly burnt area
306 (MCD45A1) satellite data product. To calculate climatic extremes for these same species, the
307 WorldClim dataset (www.worldclim.org) was used to obtain species median values of
308 minimum temperature (BIO6 variable) and seasonal drought length (calculated as the number

309 of successive months where mean annual precipitation was below 30mm). These species level
310 data were used to construct frequency histograms to examine lineage level variation in fire
311 regimes and climate extremes (Fig S7).

312 **Environmental data used in global analyses.** Our analysis aimed to elucidate lineage, climate
313 and disturbance relationships, and whether biogeography impacts the C₃-C₄ crossover
314 temperature. We used the WorldClim dataset at a 0.5 degree resolution to match the
315 vegetation map, and extracted mean annual precipitation (MAP), rainfall seasonality, mean
316 annual temperature (MAT) and temperature seasonality (www.worldclim.org). We used a
317 rainfall concentration index to describe rainfall seasonality based on (35). Growing season
318 temperature (GST) was calculated for each grid cell to quantify regional and global C₃-C₄
319 crossover temperatures. GST was calculated as the mean temperature across months with a
320 greater than or equal to 5 degree mean temperature and at least 25 mm rainfall, and was
321 calculated using WorldClim monthly climate normals (65).

322 A median fire return interval (FRI) is the number of years between fire events that
323 represents the time period available for plants to grow. We used fire interval data from the
324 16 year MODIS fire datasets to fit Weibull distributions to 0.5° gridded data for the globe by
325 using the method outlined in Archibald *et al.* 2010 (64). Tropical grasslands and savannas have
326 the world's shortest fire return times, due to rapid rates of fuel accumulation and a climate
327 that supports frequent fire (annual dry seasons, warm climate and reliably seasonal rainfall)
328 (20). Our dataset of estimated fire return times, while spatially biased, is therefore robust for
329 grassy biomes.

330 Globally consistent data on present or past herbivore pressures are simply not
331 available. We were obliged to restrict our analyses to Africa where efforts have been made to
332 map mammalian herbivore pressures of both wildlife and livestock (66). We combined

333 herbivore and fire data to assess links between lineage composition and disturbance. Soils
334 data are not of sufficient quality to be meaningfully incorporated in analyses of this scale,
335 despite being known to mediate local scale vegetation patterns (35). In our global analyses,
336 we excluded grassy vegetation units defined as flooded, saline or edaphic, where the limits of
337 these units are generally decoupled from climate.

338 **Analyses.** First, we mapped the distribution of grassy biomes in geographic space according
339 to lineage and photosynthetic type to calculate the land area occupied by different grass
340 lineages in a “rank-abundance” style (Fig. 1). Grassy biome distributions were aligned with
341 MAT (in 1°C intervals) and MAP (in 100 mm intervals) to construct “Whittaker” style plots of
342 the limits of grassy biomes and of C₃ and C₄ photosynthetic types (Figure 2). These data were
343 further decomposed to represent the climate space of 17 grass lineages including Pooideae
344 that dominate grasslands (Figure S4). Data were also analysed by climate intervals of MAT and
345 MAP to calculate the proportion of grassy land area occupied by each grass lineage within
346 each climate interval, to consider the potential for deterministic links between climate and
347 biomes (Figs. S3-S4).

348 Generalised additive models relating the distribution of lineages to growing season
349 temperature, MAT and MAP across continents were fitted using the mgcv R package and the
350 function predict.gam (67). Crossover temperatures plus standard deviations were calculated
351 based on the temperature at which the predicted abundance of C₄ dominance reached 50%.

352 Random forest regressions ([https://cran.r-](https://cran.r-project.org/web/packages/randomForest/randomForest.pdf)
353 [project.org/web/packages/randomForest/randomForest.pdf](https://cran.r-project.org/web/packages/randomForest/randomForest.pdf)) were used to examine the
354 climate niche of key grass lineages and to infer correlations between four key climate
355 predictors (MAP, MAT, temperature seasonality and rainfall seasonality). Models were
356 constructed for six groups of interest: the C₃ BEP, PACMAD and Pooideae lineages; and the

357 independent C₄ lineages Andropogoneae, Chloridoideae and MPC (Melinidinae + Panicinae +
358 Cenchrinae) (25). Model fit was checked via a mean of squared residual test. The relative
359 importance of each environmental correlate was computed with a mean decrease of accuracy
360 test. The computed coverage response plots for each grass group was an adaptation of the
361 evaluation strip method developed by (68). These plots demonstrate the non-linear
362 relationships between environmental gradients and the various grass lineages. To produce
363 these plots, an environmental dataset was simulated where the focal environmental variable
364 is varied over its full environmental range and where, for each interval, the observed median
365 of each of other environmental variables (median over areas where the focus environmental
366 variable is within the interval) is returned. The displayed curve in each case is the prediction
367 of our Regression Random Forest model over this simulated dataset. The process used bi-
368 variate response curves, where two variables rather than one vary simultaneously. The 90th
369 quantile of a kernel density function (function kde2d from the R package ade4) was used to
370 plot limits of grass lineages relative to herbivore abundance and fire frequency.

371

372 **List of figures in main text**

373

374 **Figure 1.** Global distributions of grassy biomes and dominant grass lineages.

375

376 **Figure 2.** Grassy biomes in global climate space.

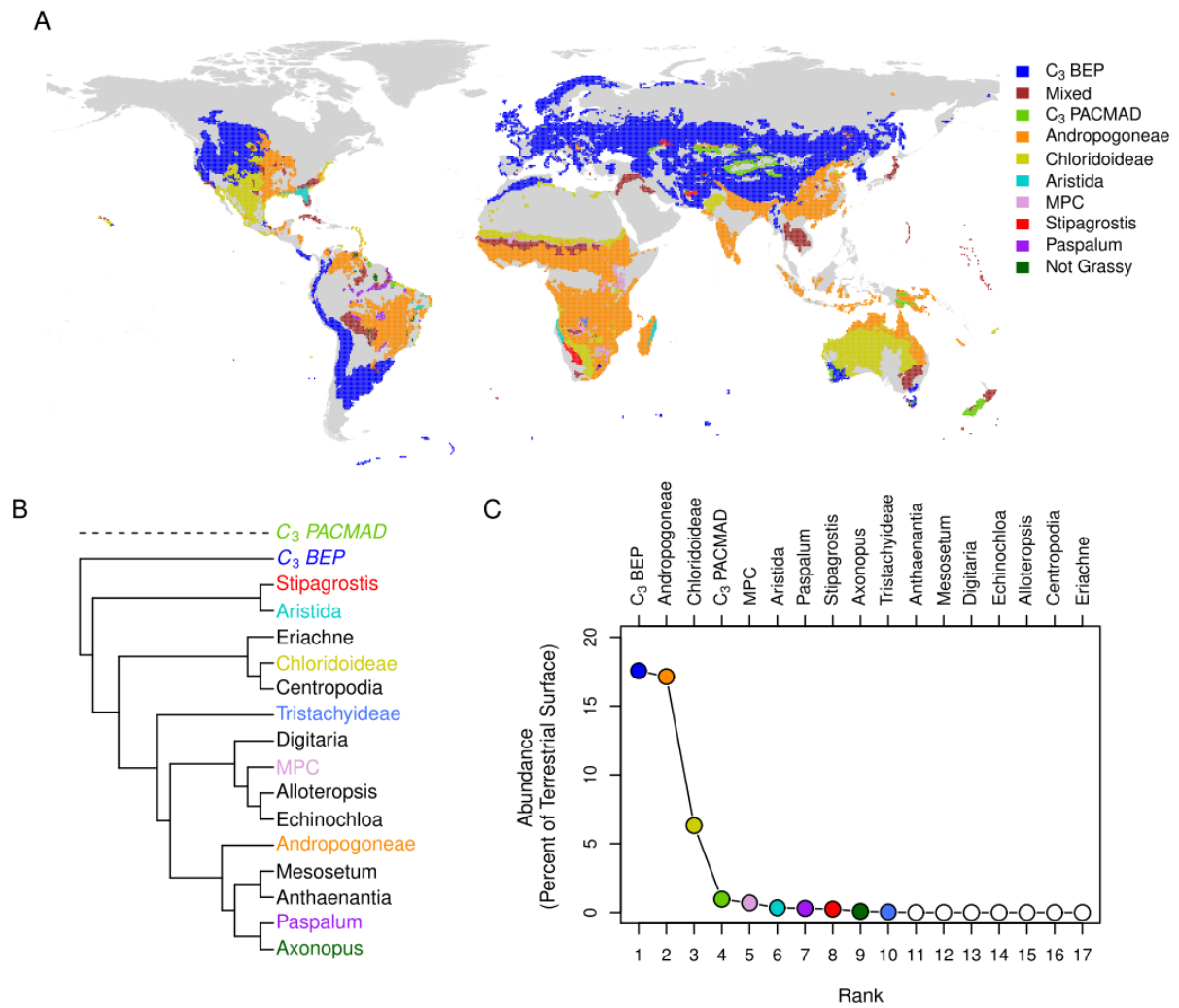
377

378 **Figure 3.** Continental disjunctions in lineage-growing season temperature relations.

379

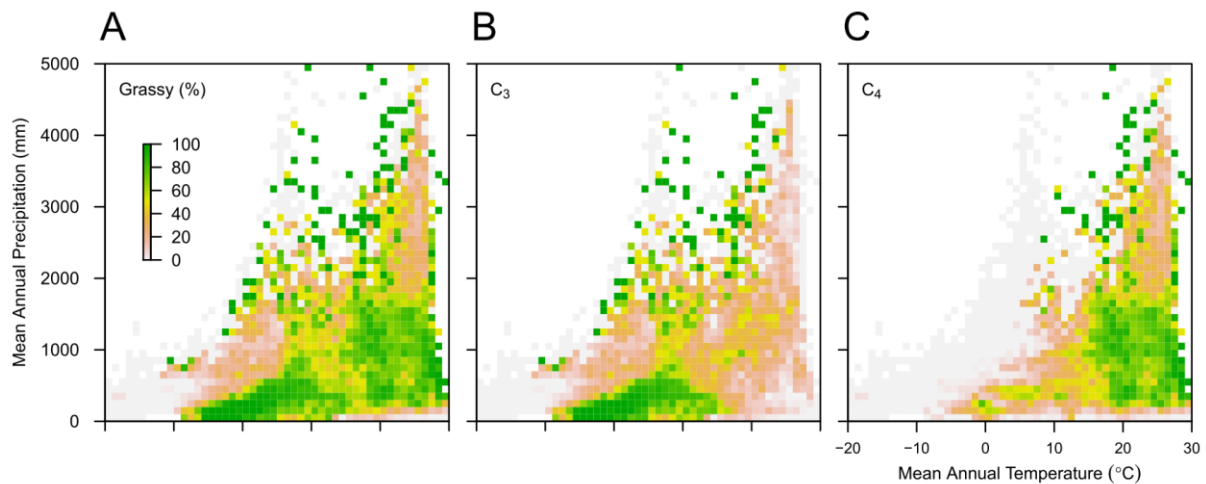
380 **Figure 4.** Global relationships between rainfall, fire and height.

381 **Figure 1: Global distributions of grassy biomes and dominant grass lineages.** A. Grassy
 382 biomes coded by the C₄ and C₃ grass lineages dominating each vegetation formation. B.
 383 Relationships among the dominant C₄ grass lineages, with colours matching those used on the
 384 map. The phylogeny is based on (25) and for simplicity excludes C₃ PACMAD sister clades. C.
 385 Rank-abundance curve for C₄ and C₃ grass lineages at the global scale, ordered by the
 386 proportion of the terrestrial surface dominated by each lineage.



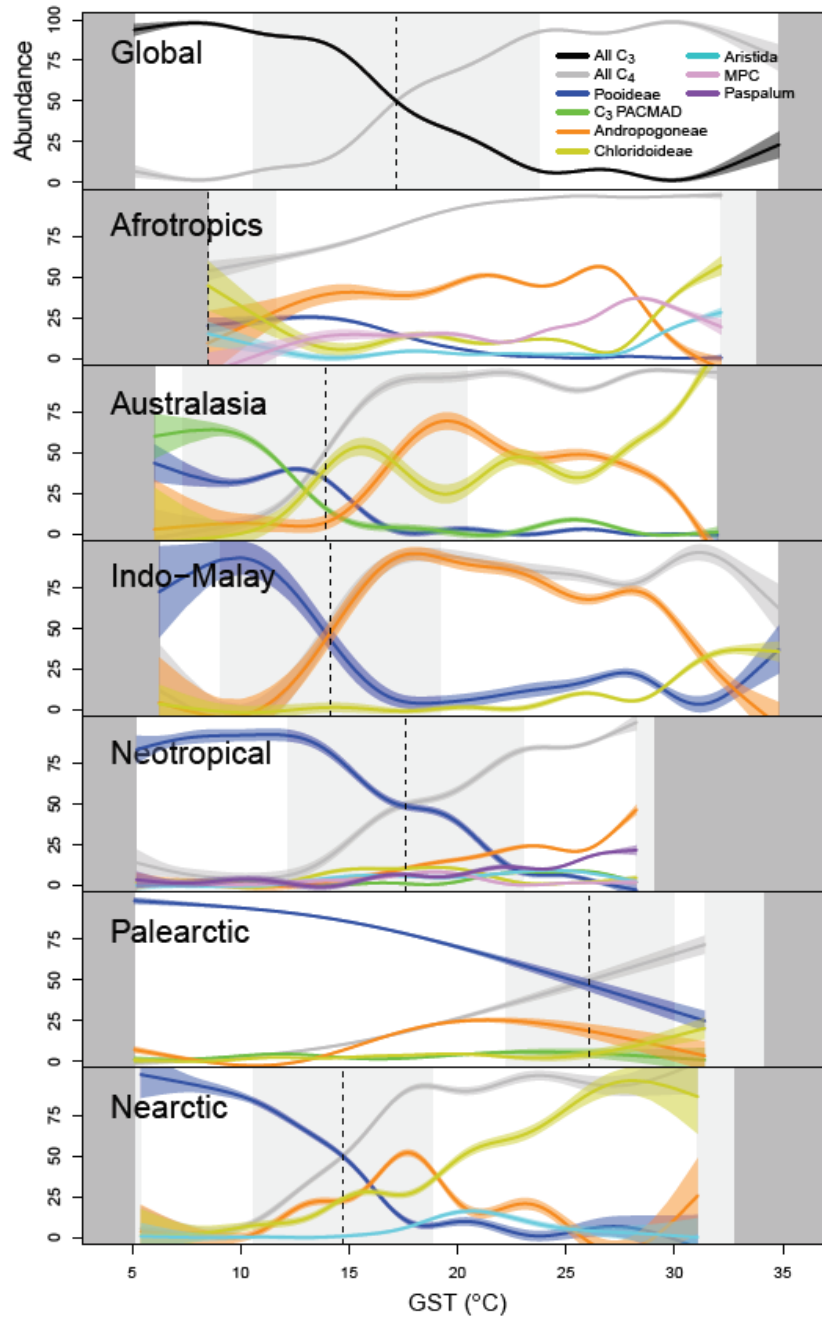
387

388 **Figure 2: Grassy biomes in global climate space.** Based on data at a 0.5-degree resolution,
389 where data has been binned in 1° mean annual temperature (MAT) and 100 mm mean annual
390 precipitation (MAP) intervals. Colour ramp shows the relative proportion of the global climate
391 space for that MAP x MAT bin occupied by grassy biomes. Grey shading represents the
392 vegetated land area. Data shown here link to Figure S1 showing the total vegetated land area
393 within each climate interval.



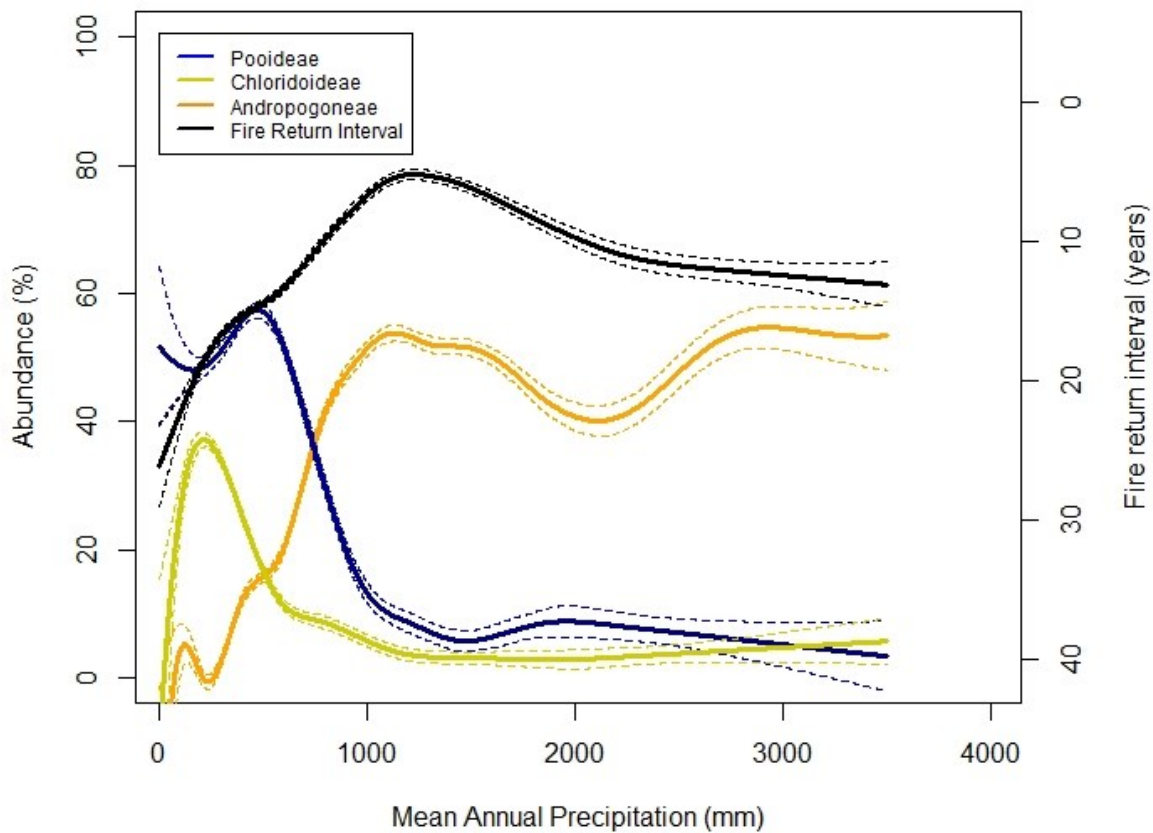
394

395 **Fig. 3. Continental disjunctions in lineage-growing season temperature relationships.** The
396 distribution of grass lineages relative to growing season temperature (GST) in degrees Celsius
397 globally (top panel) and then showing the variation in estimated C₃-C₄ crossover temperatures
398 by geographic realm. Distributions was fitted using generalized additive models and the
399 crossover temperature calculated as the point where modelled C₄ grass abundance is 50%,
400 based on the mapping in Figure 1. The fitted lines and confidence intervals are shown in
401 different colours for each lineage, with the legend on the figure.



402

403 **Figure 4. Global relationships between rainfall, fire and grass lineages.** The global
404 relationships of grass lineage abundance relative to MAP using a generalised additive model,
405 showing 95% confidence intervals. The right-hand axis is the global relationship between fire
406 return interval and MAP for grassy biomes and is inverted to reflect the inverse relationship
407 with MAP. The global peak in fire activity coincides with the global peak in dominance of
408 *Andropogoneae* grassy biomes. In contrast longer fire return times are associated with
409 dominance by *Pooideae* and *Chloridoideae*.



410

411

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567

568 **Supplementary Figures, Tables and Information for:**

569 **Functional diversification enabled grassy biomes to fill global climate space**

570

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578 **Contents**

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582 4. References to dataset development

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584 b. References for plot data for map validation

585

586 **Development and validation of map compilation**

587 Rarely, if ever, has this rich body of vegetation mapping research been integrated with Earth
588 system science or evolutionary studies. This is perhaps because vegetation mapping is
589 considered a descriptive natural science in an age of big data. The contiguous land mass
590 covering the countries of China, Mongolia, the former Soviet Union, Afghanistan, Turkey and
591 Europe are represented by detailed botanical data. The regions of Africa, North America,
592 Mexico, Panama, Venezuela, Brazil, Argentina, Papua New Guinea, Indonesia, northern and
593 western Australia are also well documented by botanical data. However, there is a general
594 paucity of adequate vegetation mapping available across India, South-East Asia (Burma,
595 Thailand, Laos, and Vietnam), Central America, and parts of South America (Chile, Peru,
596 Bolivia, Uruguay, Paraguay, Ecuador, and Columbia). It is worth noting that given anticipated
597 impacts of global change on the distribution and dynamics of vegetation, an absence of
598 publicly available vegetation mapping for key regions such as South East Asia and the Andes
599 should be of concern to many.

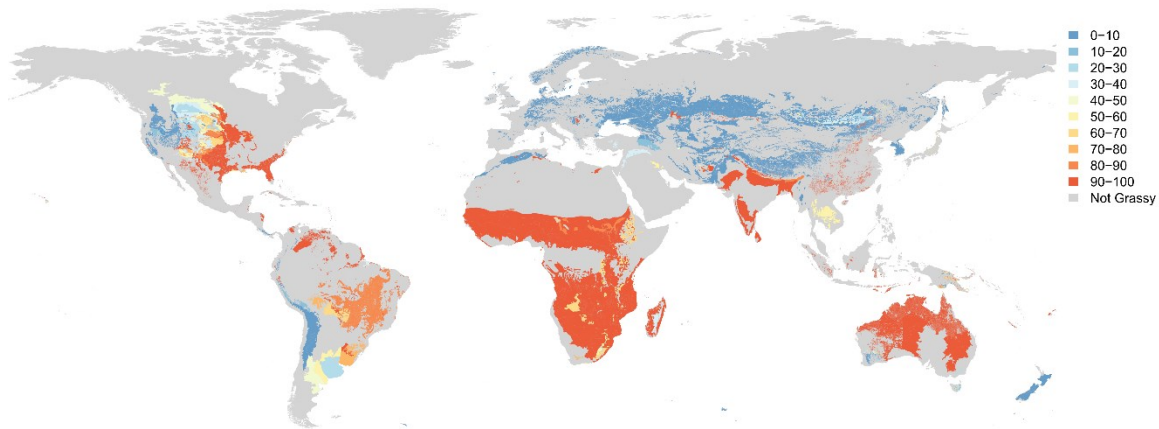
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601 We undertook a validation process between plot data describing *in situ* grass abundance and
602 our global species list. Using publicly available data that intersected with vegetation unit
603 descriptions we found that, at the level of independent evolutionary lineages of grasses (i.e.,
604 subfamily), we had strong confidence in the geographic and environmental relationships we
605 elucidate here (Fig. S9). To validate the classification of common grass species across regions,
606 we compared the species list in each vegetation unit to a plot level database developed for
607 validation purposes (Fig. S9). Plot data were sourced from the literature and vegetation
608 databases and assembled by the authors (see references in the Supplementary Information).

609 110 vegetation units contained enough plot level data for validation analyses. To determine
610 what taxonomic levels agree with plot data, the comparison was conducted at the species and
611 subfamily levels. We also examined the agreement of our map and plot datasets at a
612 functional level by comparing the attribution of photosynthetic type. From the 507 common
613 grass species across these vegetation units, 88% of these species were present in the plot
614 dataset of those appropriate vegetation types. This is a very high degree of overlap in species
615 in our mapping classifications and plot data, especially considering the difference in scale
616 between local species plots and large vegetation units. Furthermore, we found that vegetation
617 types generally had similar percentages of characteristic grass species represented in their
618 plot datasets, although the agreement was worse for particularly large and broadscale
619 vegetation units. To validate the higher taxonomic classifications and plant functional type
620 classifications of our map units, we compared the proportion each classification in plots
621 (weighted by abundance) to the proportion of that classification in our map. Because these
622 data are on the interval (0,1) we used beta regression to model this relationship. Beta
623 regression can be interpreted much like logistic regression, except that it allows continuous
624 values in the dependent variable. Proportions of Poaceae subfamilies and functional types
625 showed that plot values were strongly predictive of classified values in our map (Fig. S9).

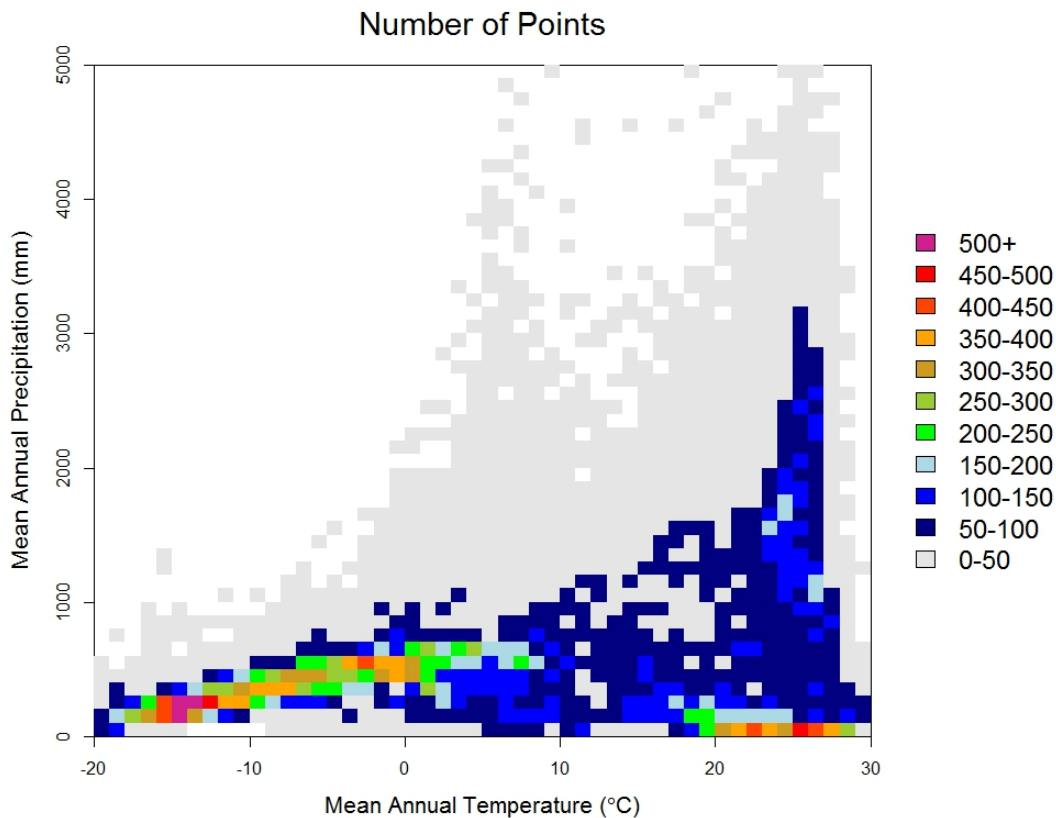
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627 **Figure S1: Global distribution of grassy biomes.** The global map was derived as a composite
628 from national and regional maps of vegetation that was gap-filled using the Ecoregions map
629 (see Methods in the main text and references for all maps at the end of the Supplementary
630 Information). Coloured areas show the extent of grassy biomes globally and dominance of
631 these by C₃ grasses and C₄ grasses mapped at the scale of identified vegetation units (i.e.,
632 polygons). Red = High proportion of C₄ grasses. Blue = High proportion C₃ grasses. Datum:
633 WGS84.
634



635
636

637 **Figure S2. Global vegetated land area as related to Mean annual temperature and mean**
638 **annual precipitation.** Mean annual precipitation is in 100 mm bins, while temperature is in
639 1oC bins. The color ramp represents the number of 0.5 degree points in 100mm x 1oc unit of
640 climate space. Note the grey background that highlights the global extent of climate space
641 where these temperature – precipitation combinations are essentially rare on the vegetated
642 land surface. The color ramp from dark blue to purple represents an increasing density of
643 points in a given climate bin.
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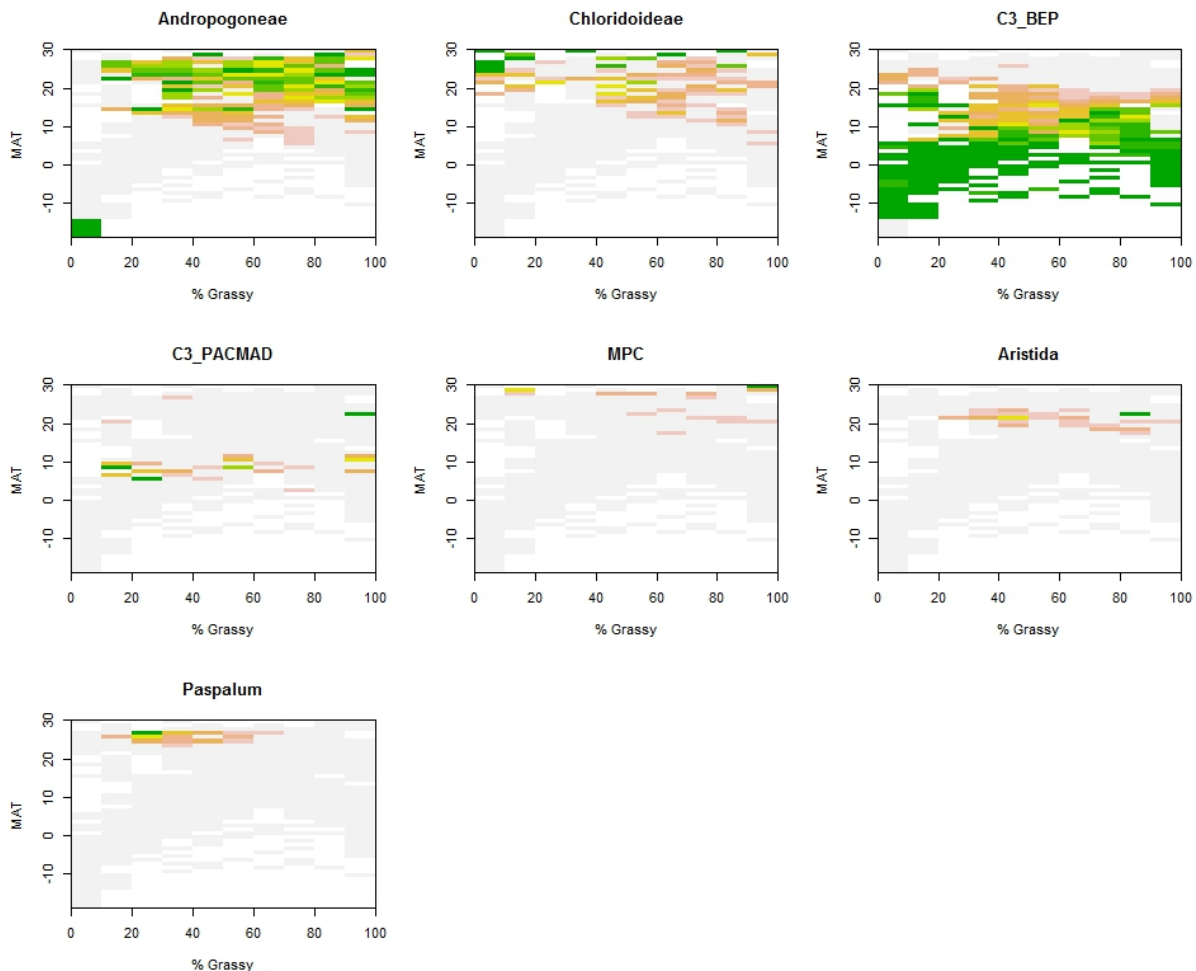
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648

649 **Figure S3: Global abundance of the main grass lineages by temperature and rainfall.** Colour
650 scale indicates the proportion of 0.5° grid squares dominated by each lineage at the global
651 scale for each of (A) mean annual temperature and (B) Mean annual precipitation. These plots
652 demonstrate that, in cool, dry regions where the C3 Pooideae lineage is concentrated, it tends
653 to be the only grass lineage present, and this lineage dominates that climate space. These can
654 be considered as deterministic grasslands. In contrast, the heterogeneity of the dominance of
655 C₄ Andropogoneae and C₄ Chloridoideae lineages across climate space could suggest that the
656 grassy biomes where these lineages are found are not deterministic, and dominance may be
657 driven by processes other than climate.

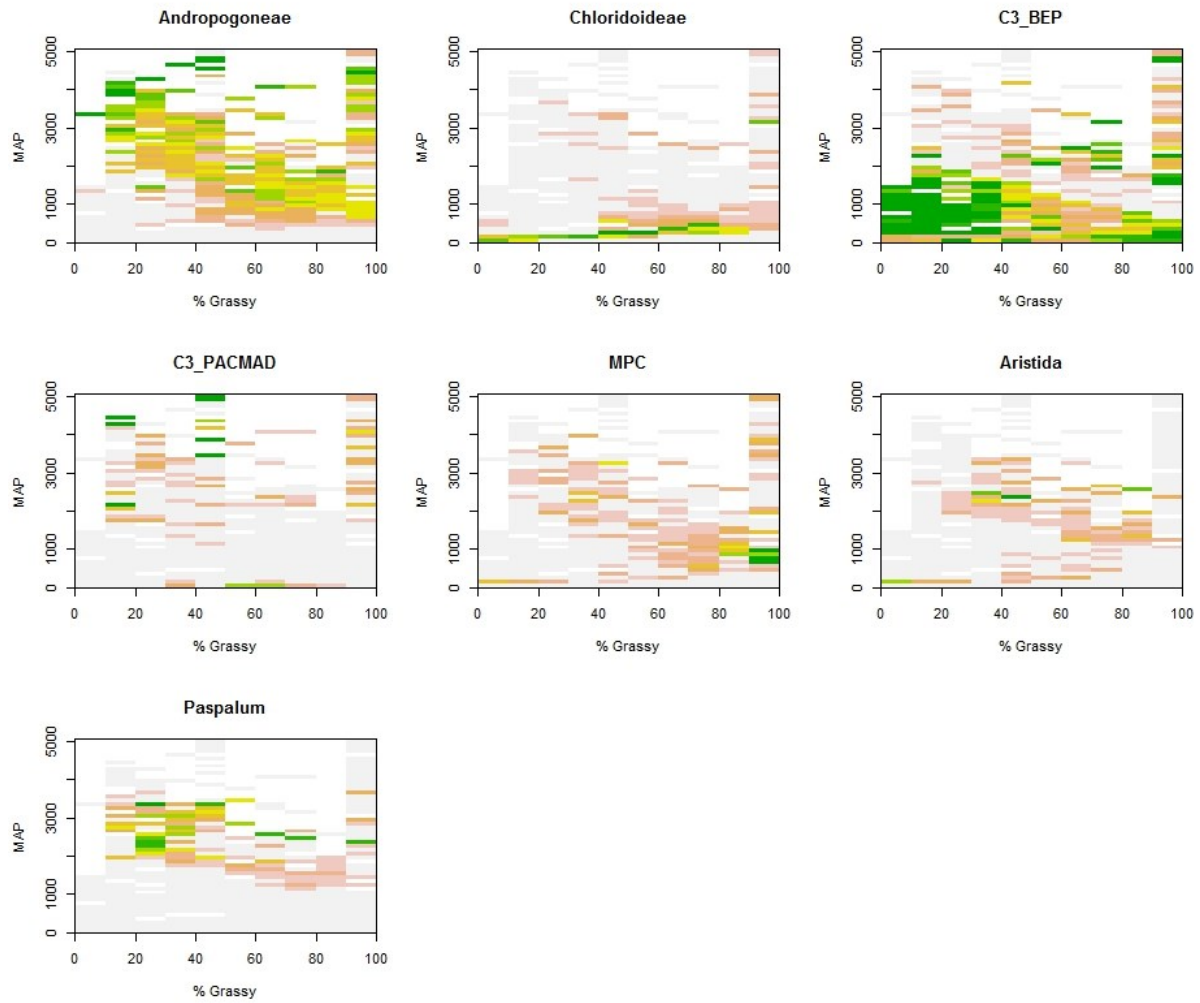
658 **A. Dominance by mean annual temperature**



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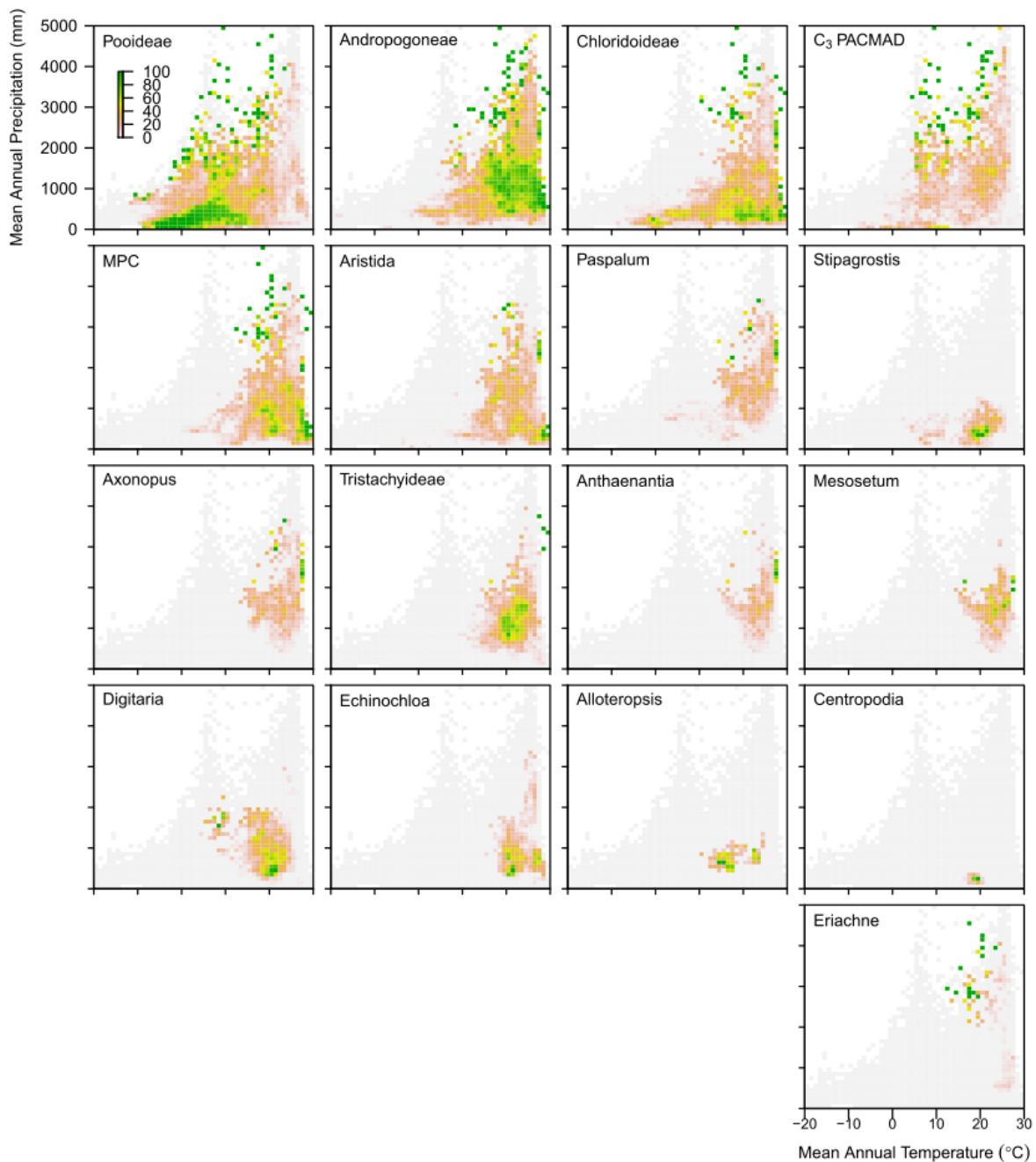
B. Dominance by mean annual precipitation



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662

663 **Figure S4: Concentration of 17 grass lineages in climate space.** This figure builds on S1 – S2
664 by again highlighting the climate space characterised by different grass lineages. It is very clear
665 that C3 PACMAD dominance is highly restricted to warmer wetter parts of climate and we
666 know from S1 that geographically these combinations of temperature and precipitation are
667 limited. These figures also again highlight the wide distribution of Pooideae, Andropogoneae
668 and Chloridoideae.

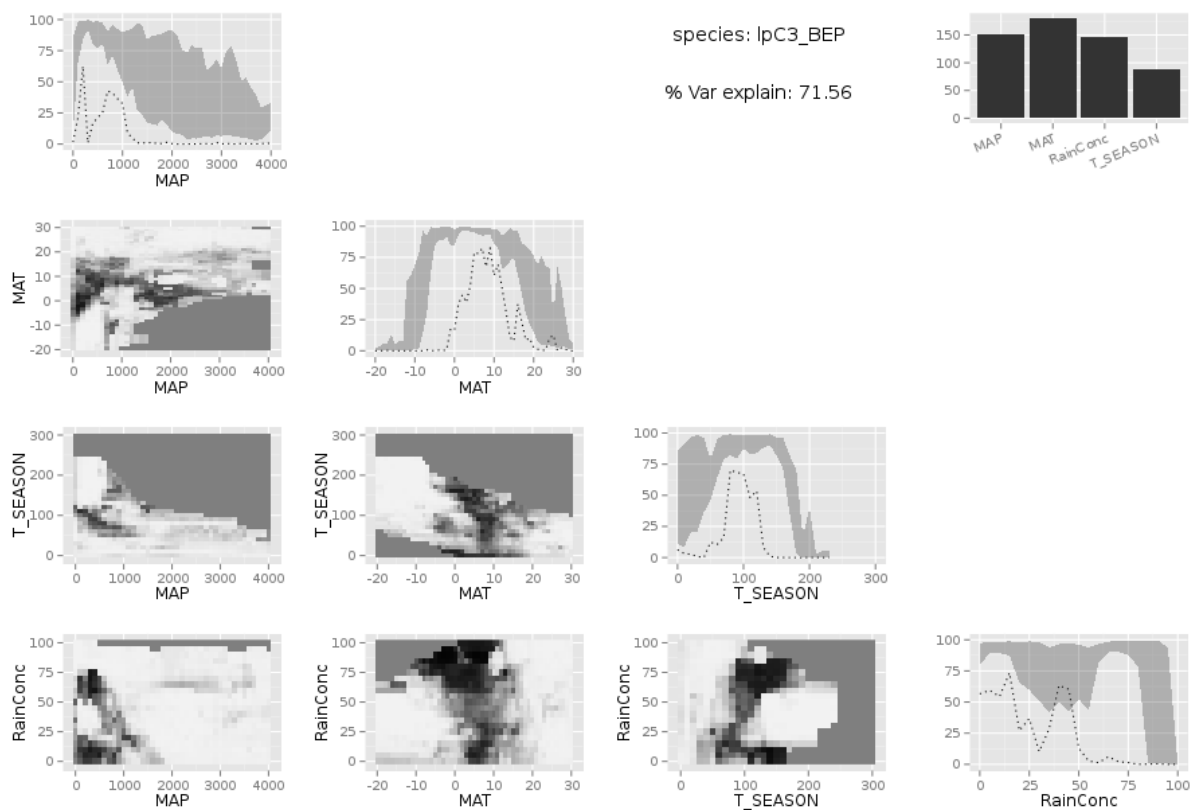


669

670 **Figure S5: Plots from Random Forest analyses of the relative importance of mean**
671 **temperature, mean precipitation, temperature seasonality and rainfall seasonality in the**
672 **limits of the three key lineages of grasses. A) C3 BEP, B) C4 Andropogoneae, and C) C4**
673 **Chloridoideae. Model fits against data are shown for the land area over which each lineage**
674 **dominates against each climate variable.**

675

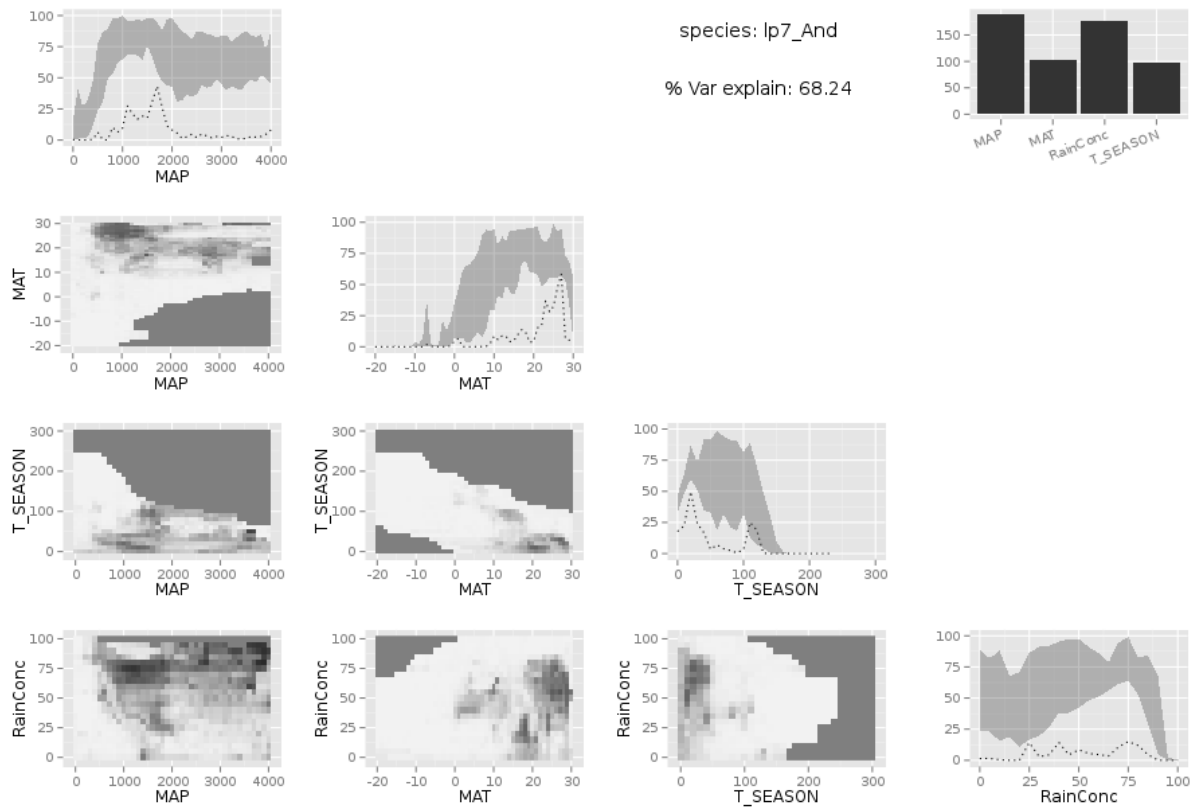
676 **A. C₃ BEP**



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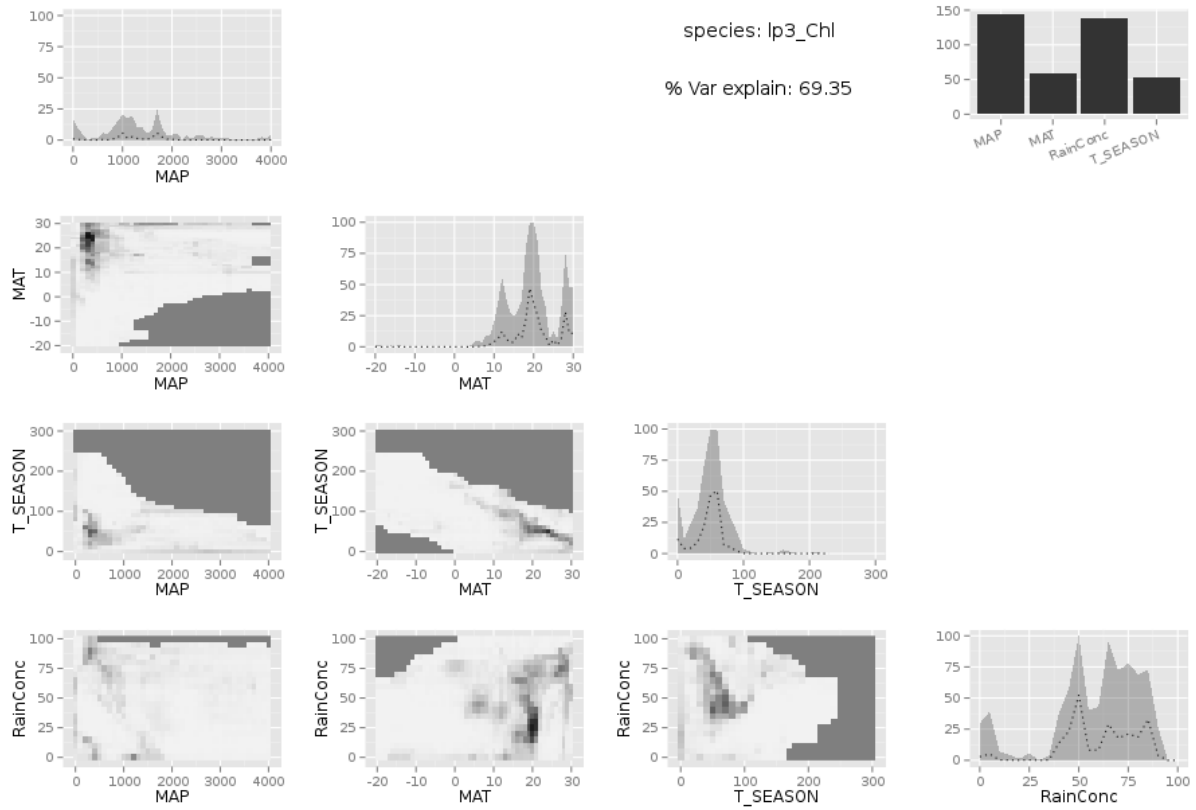
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679 **B. C₄ Andropogoneae**



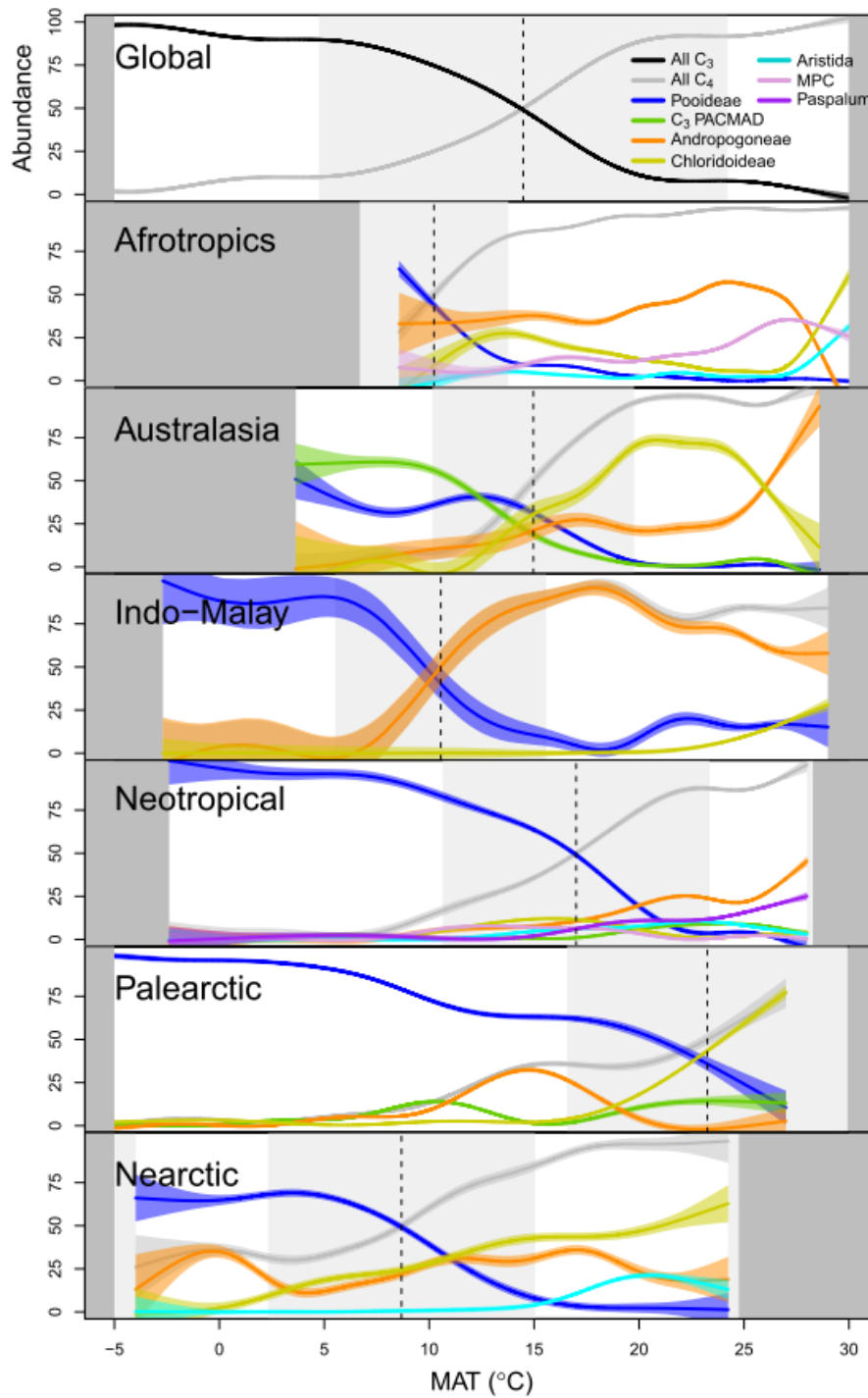
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681 C. C₄ Chloridoideae



682

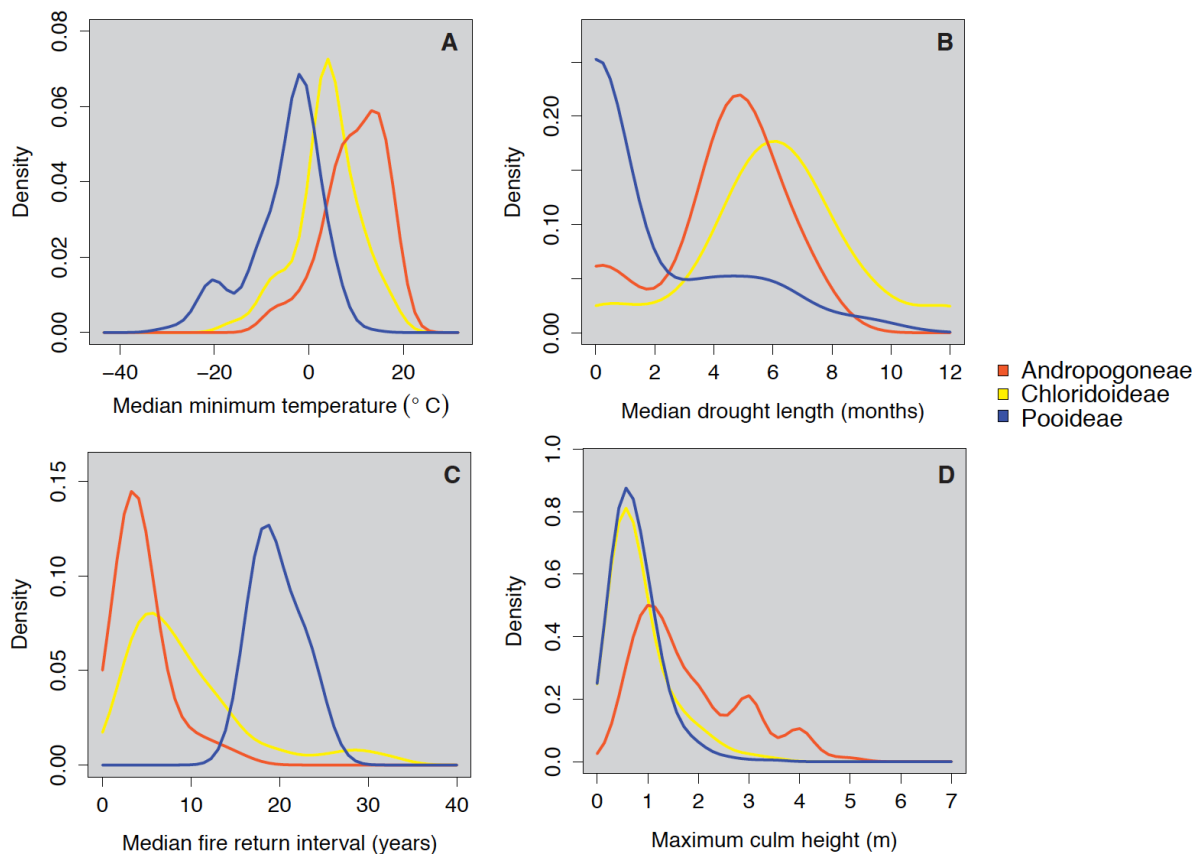
683 **Figure S6. Lineage – temperature associations.**



684

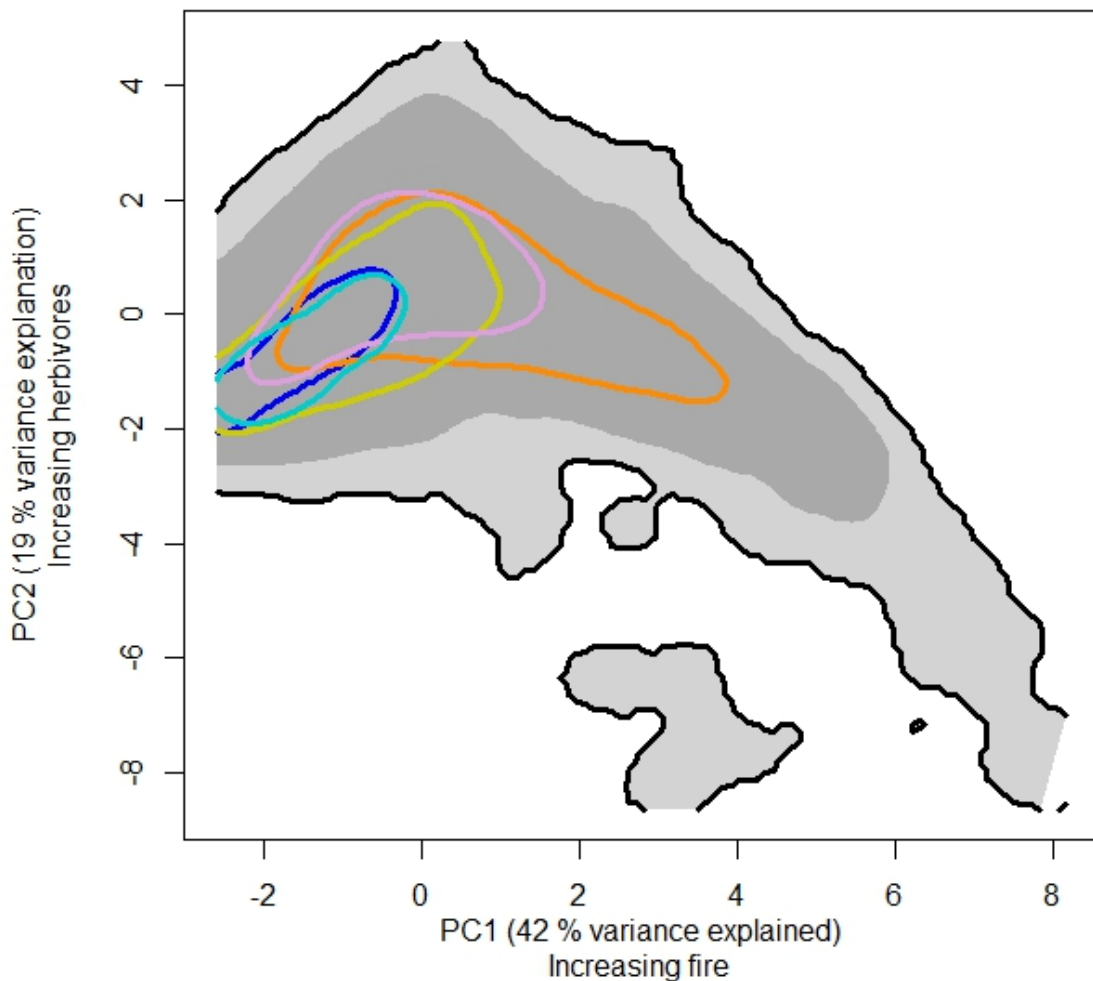
685 **Fig. S7: Trait-environment associations.** Density plots of traits that characterise the realised
686 ecological niche of dominant grass lineages: A) Median minimum annual temperature ($^{\circ}\text{C}$)
687 across the range of each species; B) Median drought length (months); and C) Median fire
688 return interval (years), calculated by mapping GBIF occurrence data for each species onto
689 Earth Observation data layers (see Methods). D) Maximum height of the culm (flowering stem)
690 for each species, as a measure of plant size at maturity (see Methods). In each case, species
691 from each lineage recorded within vegetation units in our dataset were mapped across their
692 whole range (i.e. beyond the area over which they dominate ground cover).

693



694

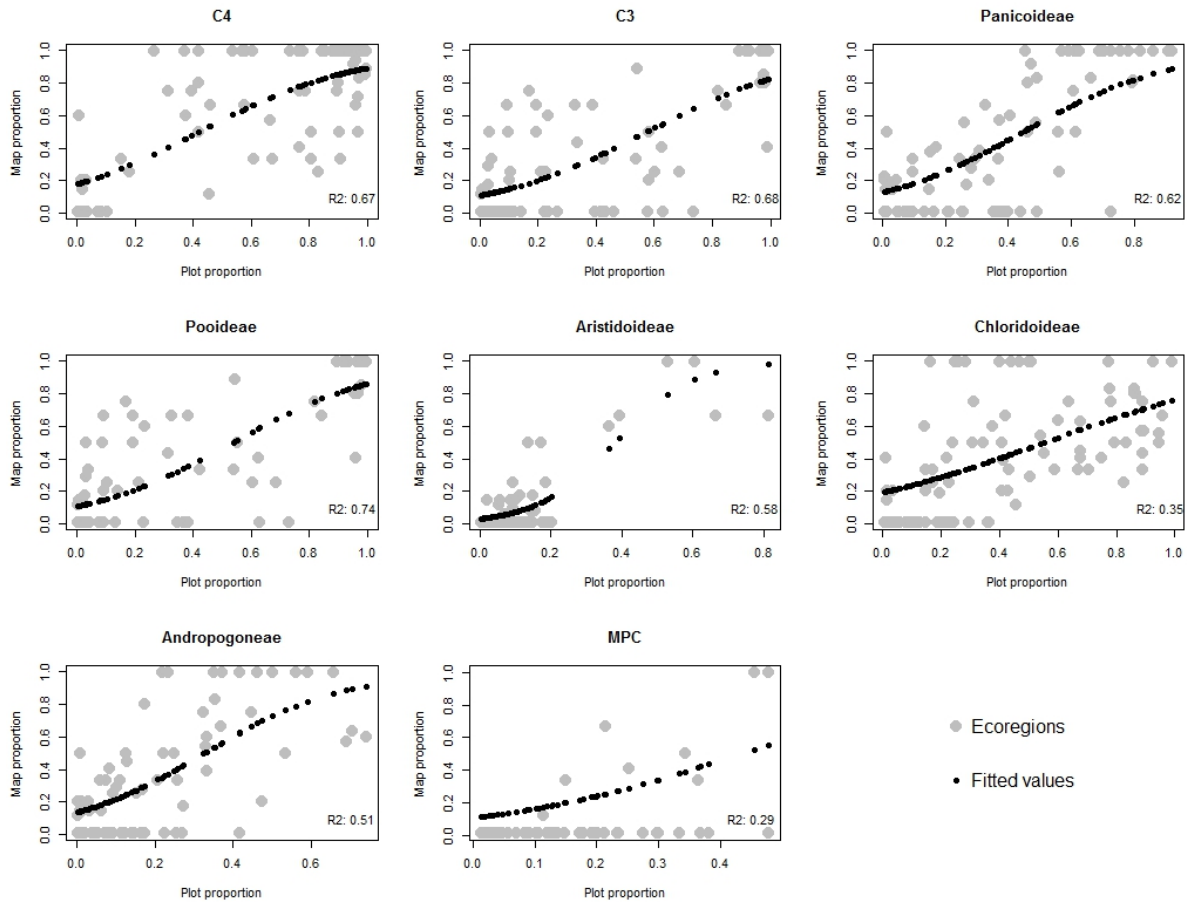
695 **Figure S8. Ordination of fire frequency and herbivore biomass with the 90th quantile of**
696 **lineage distributions shown via different colours.** This ordination shows the limits of five
697 grass lineages relative to the prevalence of fire and modelled herbivore biomass. Colours
698 representing lineages are consistent with figures in the main text. Key here is that one lineage
699 stretches into environments of more frequent fire (Andropogoneae = orange), while a number
700 of lineages are clustered and overlapping with respect to variation in herbivore biomass.
701 However, it is worth noting the globally poor data on herbivore biomass in contrast to fire that
702 is relatively easily quantified by satellites as changes in surface reflectance and heat.



703

704

705 **Figure S9. Validation of mapping approach to determine function and lineage level**
706 **distributions of grassy biomes.** Shown are figures relating plot level versus map level
707 estimates of different grass groups (as shown on each plot). Logistic regression was used to
708 quantify relationships and the deviance explained of the analyses are shown on each plot.



709

710

711 **Table S1: Land area occupied by each grass lineage.** Each column represents a slightly
712 different way to calculate the relative coverage of grassy biomes by different grass lineages.
713 Polygon calculations are based on the mapped polygons while grid cells represent the
714 conversion of data from Both calculations use a WGS84 projection.

LINEAGE	Percentage of grassy (from polygons)	Percentage of grassy (from grid cells)
Andropogoneae	38.99	36.66
C3 BEP	32.51	37.57
Chloridoideae	13.93	13.51
Mixed	10.66	6.56
MPC	1.38	1.48
C3 PACMAD	0.92	2.06
Aristida	0.64	0.73
Stipagrostis	0.62	0.53
Paspalum	0.18	0.64
Tristachyideae	0.09	0.09
Axonopus	0.07	0.17

715

716 **Appendix S1: Supplemental Data References**

717

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