Climate and the distribution of grasses in West Africa

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Abstract

Questions: Which environmental variables influence grass diversity in West Africa? What are the effects of climate and grass functional traits on the spatial patterns (richness and abundance) of the grass clades Andropogoneae, Paniceae and Chloridoideae?

Location: West Africa, demarcated by the Atlantic Ocean in the west and south (20° W and 4° N), the Sahara desert in the north (25° N) and the border between Niger and Chad in the east (20° E).

Methods: Based on 38 912 georeferenced occurrence records, we modelled the distribution of 302 grass species (51% of West African grass diversity). We integrated species richness, abundance and functional traits (life cycle, photosynthetic type and height) to determine the contribution of the most speciose grass clades (Andropogoneae, Paniceae and Chloridoideae) to overall grass diversity in West Africa.

Results: Precipitation is the variable most often influencing the species distribution models of grasses in West Africa. Richness and relative abundance of the tribe Andropogoneae show a centre of diversity in Sudanian savanna regions. The height of Andropogoneae species, generally >150 cm, is driving this ecological dominance. Species richness of the tribe Paniceae is more dispersed and shows two main centres of abundance: The southern regions with higher mean annual precipitation and tree density are dominated by C_3 Paniceae species. The Sahelian regions in the north are dominated by short Paniceae species with the C_4 NAD-ME photosynthetic subtype, as well as Chloridoideae possessing the same functional attributes.

Conclusions: Our study provides insight into the environmental correlates of grass species richness in West Africa and contributes to the much-needed research on tropical rangelands. Moreover, the integration of evolutionary history significantly improves our understanding of large-scale biodiversity patterns.

Introduction

Tropical rangelands (grasslands and savanna) represent about 20% of the Earth's terrestrial vegetation cover (Scholes & Archer 1997) and have been shown to be a major carbon sink (Grace et al. 2006). Furthermore, they provide habitat for wildlife and support the livelihood of nearly one fifth of the world's population (Solbrig et al. 1996). However, the spatial extent and biodiversity of those biomes are threatened by climate change through increased CO_2 levels (Higgins & Scheiter 2012) or reduced precipitation (Hély et al. 2006), as well as intense human exploitation (Hoekstra et al. 2004). Despite this high level of vulnerability, conservation efforts are still hampered due to a limited understanding of the functioning of rangelands and a general lack of recognition of their value (Parr et al. 2014). The plant family Poaceae, the fifth most species-rich family of flowering plants, forms a major component and is one of the key elements of their structure (Heywood et al. 2007). Thus, understanding the factors that determine the geographic distribution and community assembly of grasses is crucial to predict the potential dynamics of grassy biomes under changing environmental conditions.

Previous studies have suggested that the geographic distribution of grasses is determined by the correlation between temperature and photosynthetic pathway (e.g. Batanouny et al. 1988). The C_4 photosynthetic pathway is a set of biochemical and morphological traits, evolved from the C_3 pathway multiple times in the plant kingdom. It increases photosynthetic efficiency at low CO_2 levels and reduced photorespiration, resulting in higher net photosynthetic rates (Sage 2004). At the same time, the C_4 pathway is more energy intensive and therefore has a competitive advantage over the C_3 pathway only in hot, dry or saline environments and under high light intensities (Sage 2004).

However, Edwards et al. (2010) argued that the observed temperature differences between C_3 and C_4 grasses is mainly based on a comparison of distantly related species, specifically species from the BEP clade (Bambusoideae, Ehrhartoideae and Pooideae; exclusively C_3) and the PACMAD clade (Panicoideae, Aristidoideae, Chloridoideae, Micrairioideae, Arundinoideae and Danthonioideae; mixed C_3/C_4) that likely diverged more than 50 million years ago (Appendix S1). Members of the PACMAD clade have been shown to be generally warm-season, regardless of their photosynthetic pathway. Thus, the observed ecological differences between the photosynthetic types may in fact reflect the divergent evolutionary histories of the two clades (Edwards & Still

2008). Moreover, three biochemical subtypes have been identified among C_4 grasses. These subtypes are named after the enzyme used in the decarboxylation reaction: NAD-malic enzyme (NAD-ME), NADP-malic enzyme (NADP-ME) and PEP carboxykinase (PCK). Their distribution was shown to correlate with precipitation rather than temperature (e.g. Ellis et al. 1980; Schmidt et al. 2011b): NAD-ME plants are usually found in arid regions, NADP-ME in mesic regions, while PCK plants show no clear preferences. Given the association of these C_4 subtypes with particular grass subfamilies, the correlation between the distribution of taxonomic groups and precipitation may actually reflect a suite of adaptive traits unique to each group. Those traits complement the biochemical subtypes (Taub 2000; Cabido et al. 2008) and highlight the role of historical contingency. Good candidates could be functional traits related to resource capture and utilization, such as plant height and leaf traits (Oyarzabal et al. 2008), or strategies to cope with stress and disturbance, such as the perennial life cycle (Sarmiento 1992).

In regions where the mean annual temperature is above 20 °C, the threshold enabling C_4 plants to dominate over C_3 plants (Cerling et al. 1997), the spatial distribution of grasses should mainly be driven by precipitation and functional traits (including the photosynthetic pathway). West Africa is an ideal example of a region dominated by grassy biomes with uniformly high temperatures. However, the only broad-scale study of grass diversity for West Africa to date focused on determining grass communities based on herbarium specimens and records in countries' floras (Clayton & Hepper 1974). Species distribution modelling (SDM) now affords the opportunity to assess the association between species occurrence data and environmental parameters to quantify ecological niches and derive potential geographic distributions (Guisan & Zimmermann 2000; Peterson 2006). This approach is particularly useful when collection records are scarce (Guisan & Zimmermann 2000). Despite indications that stacked SDMs may over-predict species richness compared to observations (Guisan & Rahbek 2011), combining SDMs of multiple species is a valuable approach to bridge the sampling bias and gaps in distribution records of poorly sampled tropical areas. This approach has been successfully used to infer species richness and community assembly (de la Estrella et al. 2012; Mateo et al. 2012; Pottier et al. 2013).

In this study, we examine the spatial patterns of grass diversity in West Africa and their environmental, taxonomic and functional correlates, drawing on extensive species occurrence databases and environmental data. This enables us to assess regional patterns of grass diversity with a precision (both spatially and taxonomically) that is

usually not achieved in global studies. More specifically, we compare the potential spatial distribution of the three most abundant grass taxonomic groups (Andropogoneae, Paniceae, Chloridoideae, hereafter referred as clades) and their relation to climate and functional traits (life cycle, plant height, photosynthetic types and subtypes). Following previous studies, we predict that: (1) in West Africa precipitation is the main determinant of grass species' spatial distribution; (2) the clades Andropogoneae, Paniceae and Chloridoideae should be dominant in different habitats; and (3) this partitioning is not necessarily only linked to C_3/C_4 photosynthetic metabolism, but driven by clade-specific morphological and physiological adaptations. Our study provides insights into the environmental correlates of grass species diversity in West Africa and contributes to the much-needed research on tropical grassy biomes. Moreover, we show how the consideration of evolutionary history significantly improves our understanding of large-scale biodiversity patterns.

Methods

Study region and environmental variables

Our study focuses on western sub-Saharan Africa, covering about 8.5 million km^2, and is demarcated by the Atlantic Ocean in the west and south (20° W and 4° N), the Sahara desert in the north (25° N) and the border between Niger and Chad in the east (20° E; Fig. 1). The climate is tropical and strongly seasonal (unimodal in the north, bimodal in the south) with marked rainfall gradients from the western coast and the Cameroon coast (annual rainfall = 4500 mm) to the north (annual rainfall <100 mm).

The vegetation of this region has been classified into 30 different ecoregions (Olson et al. 2001). We aggregated the original ecoregions into five coarse groups: desert, Sahelian savanna, Sudanian savanna, Forest-savanna mosaic and forest (from north to south; Fig. 1; see Appendix S1 for the original ecoregions and biomes).

We compiled a set of 23 environmental variables at a 2.5 arc-min resolution, including altitude, 19 bioclimatic layers of the WORLDCLIM data set (Hijmans et al. 2005), CGIAR-CSI global potential evapotranspiration and global aridity (Zomer et al. 2008), and tree cover continuous fields (DeFries et al. 2000; for the complete list of layers and acronyms see Appendix S1). To avoid problems associated with collinearity which may result in model over-fitting (Dormann et al. 2007), it is useful to reduce the number of variables used in the models. Therefore we performed a Pearson's pair-wise correlation analysis (Appendix S1) and retained only one per set of highly correlated variables (Pearson's $r \geq 0.8$; de la Estrella et al. 2012). We obtained a working data set of eight variables (alt, bio1, bio8, bio11, bio12, bio17, PET, Tcov – Appendix S1). Data layer manipulations were performed in R (R Foundation for Statistical Computing, Vienna, AT) using the raster package (v 2.3-40, http://CRAN.R-project.org/package=raster).

Species sampling

We compiled georeferenced species records for Poaceae from three databases: (1) West African Vegetation database (17 675 records) of the Senckenberg Research Institute (Janßen et al. 2011), (2) Flotrop (76 751 records) com-
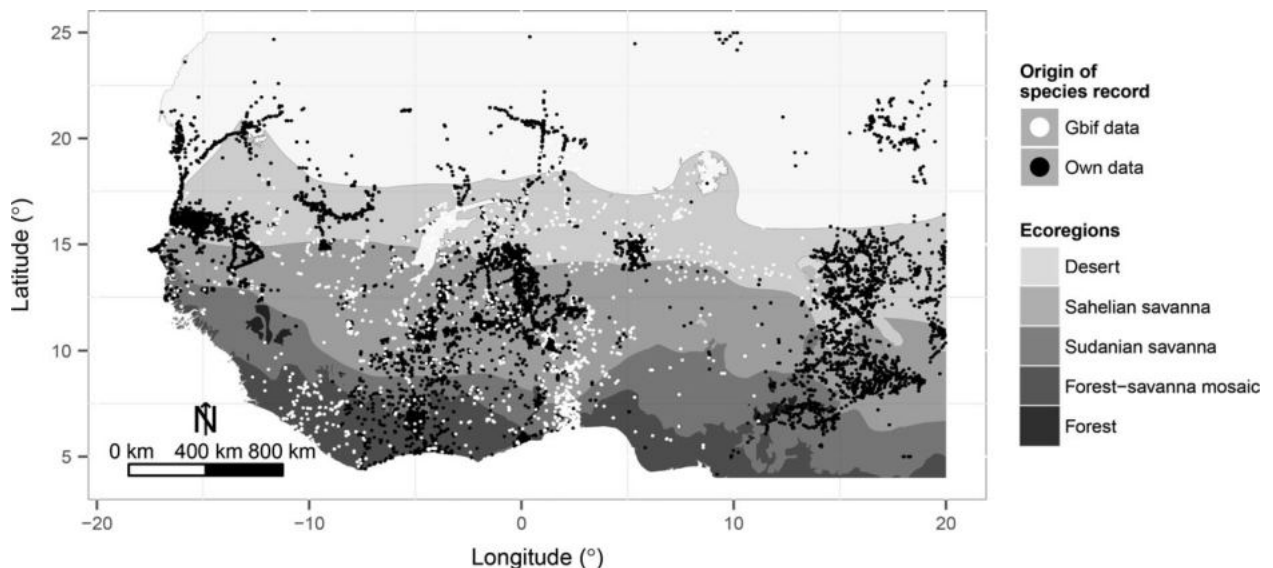

Fig. 1. Area of study with occurrence points (38 530) from GBIF data, herbarium data and vegetation survey data. The underlying colours represents the five main biomes adapted from Olson et al. (2001).

piled by the Centre de cooperation internationale en recherche agronomique pour le développement (CIRAD; Daget & Gaston 2001), and (3) SIG-Ivoire (5498 records) compiled at the Conservatoire et Jardin botaniques de la ville de Genève (Chatelain et al. 2011). These databases were complemented by specimen data from four different herbaria (FR – 2750; OUA – 2442; K and P – 271). Additional records for species present in our data set were extracted from the global biodiversity information facility excluding records with imprecise spatial resolution or mistakes (e.g. wrong country, locality in the sea; GBIF – 8173 records). In total, our data set comprised 113 560 records representing 495 species (the contribution of each institution is summarized in Appendix S1). All species names were checked against the African Plant Database (Klopper et al. 2007) and synonyms were resolved. From these records, we retained unique species presences for each 2.5 arc-min grid cell. For species distribution modelling only species with a minimum of ten unique records were kept (since a very low number of localities leads to high uncertainties in the models; Wisz et al. 2008). This resulted in a reduced data set of 302 species represented by 38 912 records (from ten to 1371 records per species; Fig. 1, Appendix S1). This sampling corresponds to 51.3% of the entire West African grass flora, as recorded in the Flora of West Tropical Africa (Hepper 1972).

For each of the 302 species, information about their taxonomic relationship, photosynthetic pathway (C_3 or C_4 and subtypes PCK, NADP-ME and NAD-ME), life cycle (annual/perennial) and height were collected (Appendix S1). Each species was assigned to a subfamily and a tribe following Watson & Dallwitz (http://delta-intkey.com/grass/, v Nov 2009), Sánchez-Ken & Clark (2010) and Morrone et al. (2012). In total, eight grass subfamilies and 16 tribes are included in our data set (see Appendix S1 for a cladogram of the Poaceae subfamilies and their associated photosynthetic type). We focus particularly on the subfamily Chloridoideae and the tribes Andropogoneae and Paniceae of Panicoideae subfamily (together representing 89% of the Panicoideae species in our data set). Both tribes are monophyletic and characterized by a set of traits that support their separation: Andropogoneae are mostly tall perennials utilizing exclusively the C_4 subtype NADP-ME, while Paniceae are mostly short annual or perennial plants and use C_3 as well as the three subtypes of C_4 photosynthesis. We focus on these clades because they represent more than 80% of the species in our study (Andropogoneae 90 spp., Paniceae 92 spp., Chloridoideae 72 spp.), and are thus likely to be well sampled and are good surrogates for the broad-scale patterns in grass diversity. Moreover, it makes our study more comparable to other studies that also focus on those groups. The photosynthetic type for 191 species was obtained from the literature (Downton 1975; Ellis 1977) and own studies (Schmidt et al. 2011a). Species with unknown photosynthetic type (111 spp.) were assigned the type of the genus, when there was no evidence of more than one type/subtype present within the genus. In cases where genera were known to have more than one photosynthetic type (e.g. *Panicum, Sporobolus*), the photosynthetic type was inferred as ambiguous (19 spp.). This resulted in a data set including 29 C_3 species, and 254 C_4 species (148 of the NADP-ME, 21 of the NAD-ME, 36 of the PCK subtypes, six indiscernible between NAD-ME and PCK, and 43 of unknown subtype). Furthermore, we extracted data on the life cycle (annual/perennial) and plant height from GrassBase [The Online World Grass Flora. http://www.kew.org/data/grasses-db.html (accessed July 2009)]. Our data set contained 134 annuals, 152 perennials and 16 species with an ambiguous life cycle. Finally, we classified the species based on their maximum height into two classes: plants with a maximum height up to 1.5 m (short) and plants above 1.5 m in height (tall). These classes include 187 and 115 species, respectively.

To quantify the climatic tolerances of the grass tribes, we extracted the climate data for each species with two or more records and plotted the species accumulation curve of each tribe against the key environmental gradients.

Species distribution model and bias-corrected null model

To model the potential species distributions, we selected the program Maxent (v 3.3.3e; Phillips et al. 2006), which was specifically developed for presence-only data and has been shown to outperform most other modelling applications (Elith et al. 2006). It is also least affected by georeferencing errors (Graham et al. 2008) and performs best when only few presence records are available (Wisz et al. 2008). However SDM predictions are partly dependent on the algorithm used. Therefore, to support the results obtained with Maxent we also used an ensemble modelling approach implemented in the R package biomod2 (Thuiller et al. 2009 - see detailed method and results in Appendix S2). Presence-only data are often affected by sample selection bias, where some areas in the landscape are sampled more intensively than others (Phillips et al. 2009). Therefore, to correct for any such geographical sampling bias and add to the predictive performance of the model we used the 'target group absences' technique (Phillips et al. 2009; Mateo et al. 2010). We forced Maxent to randomly draw 4000 pseudo-absences from the 5721 grid cells with a grass species record instead of drawing them from the whole extent of the study region. To further assure that the target group data are not biased in environmental space (Fielding & Bell 1997), we performed a chi-

square test on the distribution of the sampled cells and the whole study area along the eight environmental variables.

As a measure of accuracy we used the AUC (area under the curve) value derived from a ROC (threshold receiver operating characteristic) curve. However, as the power of the AUC has been contested (Lobo et al. 2008), we chose a bias-corrected null model approach, as proposed by Raes & ter Steege (2007), to validate our models. This method determines the significance of a SDM based on n records by testing its AUC value against the 95th percentile of a null distribution of expected AUC values. The null distribution is obtained by modelling 1000 sets of n presence records drawn from the study region. Following Raes & ter Steege (2007), we modelled individual null distributions for ten to 35 records, 40–50 records (with intervals of five records), 60–100 (with intervals of ten), 150–300 (with intervals of 50), 400–1000 (with intervals of 100) and for 1300 records. Both the 'presence' records and 4000 'pseudo-absence' records were drawn from the cells with a grass species record.

Species richness and relative abundance

The single species SDMs were stacked, summing the probabilities predicted by Maxent to derive species richness maps, as recommended by Dubuis et al. (2011). Differences in climatic tolerances between clades (e.g. due to different photosynthetic types) should lead to divergent distribution patterns among clades along climatic gradients. For example, one would expect C_4 grasses to be more diverse in arid environments, while C_3 plants should exhibit greater diversity in mesic habitats. To assess regional differences in the prevalence of grass tribes, we infer the contribution of each of the major taxonomic groups to the grass flora throughout the study region. For each grid cell, we calculated the relative abundance of each tribe (i.e. the fraction of the total species richness; Fig. 2). We normalized these values by the expected relative abundance (based on the proportion of tribes in the data set) to account for the differences in their total species diversity. The degree of divergence from the null expectation (even contribution of all clades) allows us to identify regions where particular taxonomic groups are over- or underrepresented.

Influence of functional traits on spatial distribution

We calculated the correlation between the spatial distribution of the relative abundance (i.e. the fraction of the total species richness per grid cell) of the three clades (Andropogoneae, Paniceae, Chloridoideae), mean annual precipitation, photosynthetic types and subtypes, life cycle (annual and perennial) and height classes (short and tall). Then, we used semi-partial correlation, included in the R
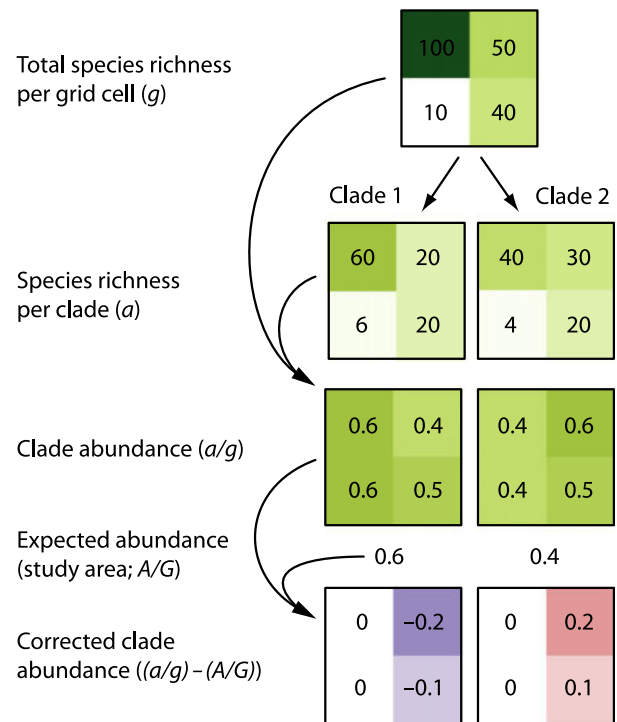

Fig. 2. Calculation of the corrected relative abundances. The relative species richness of each group ('Clade abundance') in a grid cell is corrected by subtracting the corresponding abundance in the regional data. While the relative species richness might represent potential sampling biases, the corrected clade abundance indicates over- or underrepresentation in relation to the total diversity of each clade in the data set.

package ppcor (http://CRAN.R-project.org/package=ppcor), to measure the association between annual precipitation and the spatial distribution of the taxonomic groups, while removing the influence of the photosynthetic type, life cycle or height. Semi-partial correlation statistically resolves the correlations among intercorrelated variables and calculates the correlation between two variables while the others are held constant (Sokal & Rohlf 1995). High values indicate that the correlation is not influenced by the third variable; by contrast low values indicate that the variable held constant influences the correlation.

Results

Climatic tolerances

Species accumulation curves show the distribution of species diversity for each grass tribe along environmental gradients in West Africa (Fig. 3, Appendix S3). Note that from here we focus only on the four factors that were identified as important contributors in the species distribution models (Fig. 4 below) and showed the strongest divergences along the environmental gradients: mean annual precipitation, mean temperature of wettest quar-
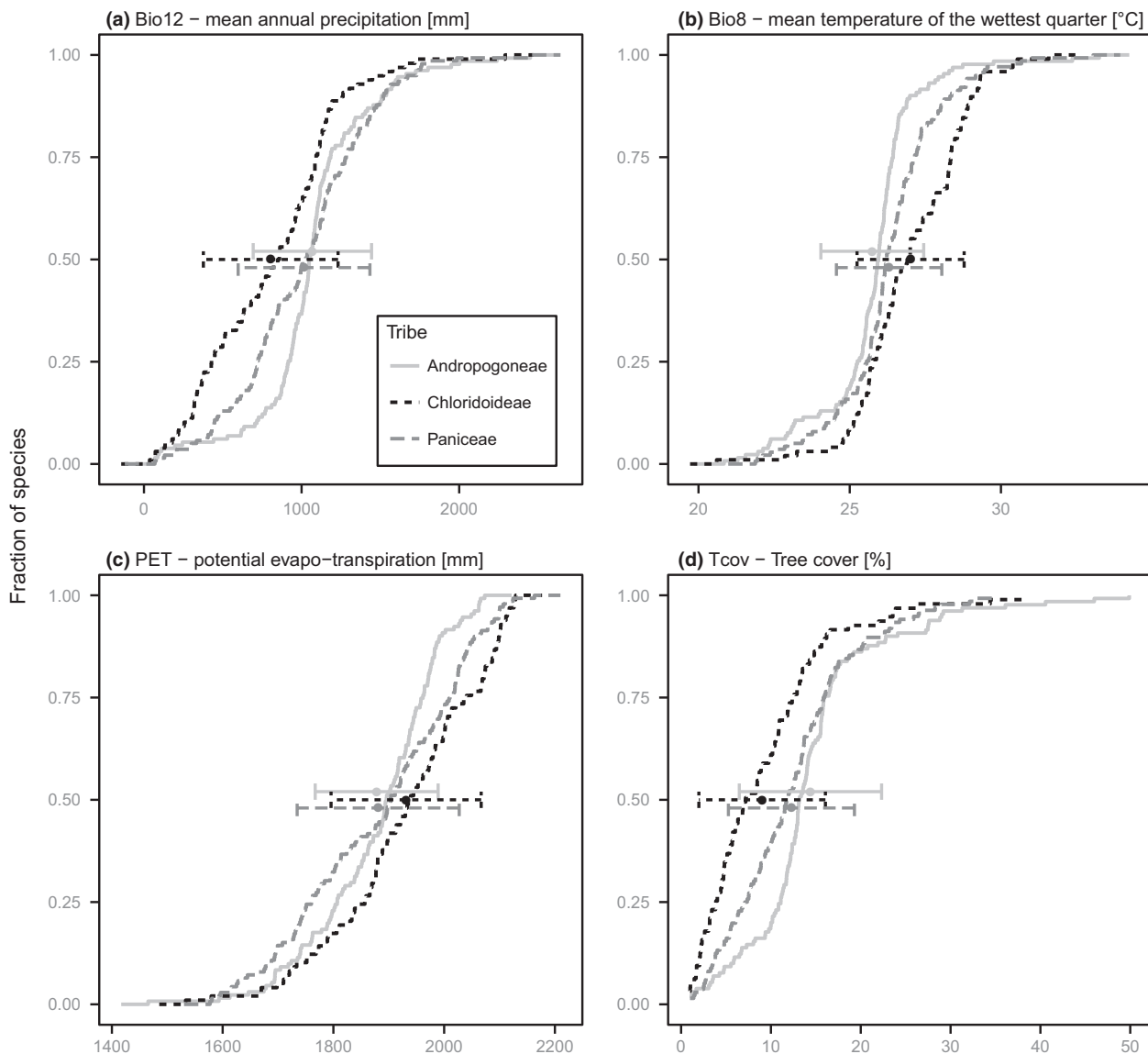
Fig. 3. Cumulative distribution curves of each clade along four environmental gradients (a) mean annual precipitation, (b) mean temperature of the wettest quarter, (c) potential evapo-transpiration, (d) Tree cover. All species with a minimum of two collections were included. Each dot in the curve represents the mean value of collection localities of one species. The dot with error bar indicates, for each clade, the mean value of the clade and SD.

ter, potential evapotranspiration and tree cover. The Paniceae and Andropogoneae occupy overall similar environments, but with markedly narrower tolerances in the Andropogoneae. In contrast to the other clades, Chloridoideae occupy regions with low precipitation and tree cover, and high temperatures.

Species distribution modelling and predicted richness

Mean annual precipitation (Bio12) and precipitation of driest quarter (Bio17) contributed most to the models and had the highest permutation importance (Fig. 4). The variable importance extracted from the five models run with biomod2 are comparable, thus we show here only the results from Maxent (see Appendix S2). These results were found to be consistent across the tribes, Andropogoneae and Paniceae, and the subfamily Chloridoideae, although in the case of the latter altitude (ALT) and potential evapotranspiration (PET) contribute similarly (Appendix S3).

Of the 302 modelled species, 299 (99%) had a distribution pattern that differed significantly from the random expectation (Appendix S3). The stacked SDMs derived from the biomod2 models were highly correlated with the Maxent results (see Appendix S2), thus we present here only the latter results. The highest grass species richness can be found in the Sudanian savanna region of Ivory
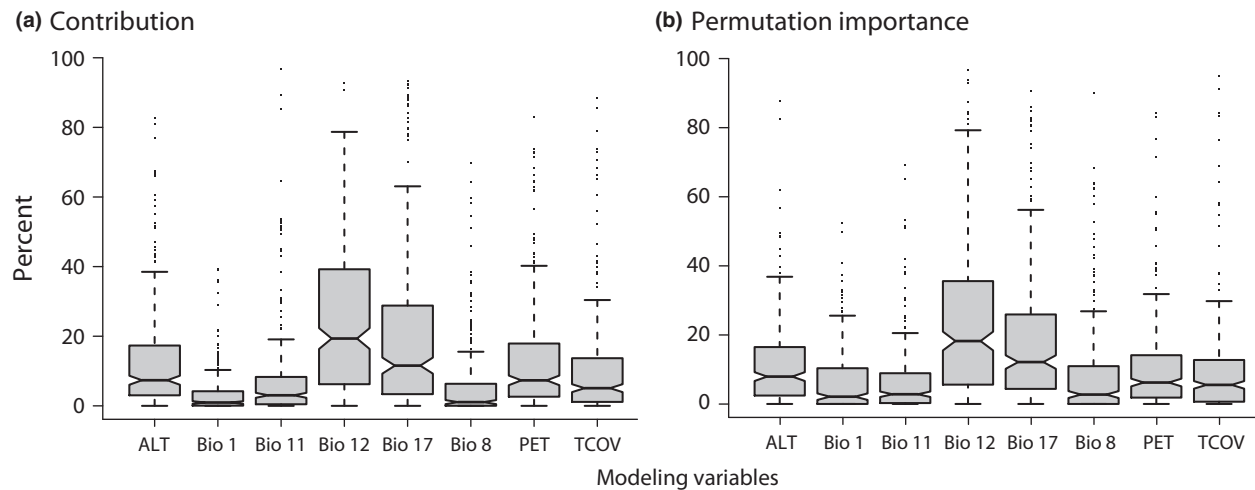
(a) Contribution

(b) Permutation importance

Fig. 4. Relative contribution and permutation importance of each environmental variable in the models. The boxplots represent the first (top) and third (bottom) quartile of the data, the median is represented by the line and outliers by dots. The contribution depends on the path of the model and reflects how much the variable added to the model gain. The permutation importance is based on the final model and calculated by randomly permuting the values of that variable among the training points and measuring the resulting decrease in training AUC (Phillips et al. 2006). Mean annual precipitation (Bio12) and precipitation of the driest quarter (Bio17) are the most important variables in the models, which indicates the strong influence of precipitation on grass distribution at our study scale.

Coast, Ghana, Togo, Benin and western Nigeria, while the lowest predicted richness was found in the Sahara region (Fig. 5). In the south, grass richness decreases sharply towards more forested regions. It should be noted, however, that the accuracy of species richness predictions from S-SDM may vary along environmental gradients (Pottier et al. 2013). Thus, such predictions should be interpreted with care, even if the individual SDMs are accurate.

All clades (Andropogoneae, Paniceae and Chloridoideae) show similar patterns of species richness in West Africa, with the highest diversity in mesic savanna habitats (Sudanian savanna; Fig. 6a,c,e). However, the tribe-specific relative abundances reveal pronounced differences (Fig. 6b, d, f). Andropogoneae contribute more to grass richness in the savanna belt of the Sudanian region and the savanna–forest mosaic bordering the closed tropical forest, whereas the Chloridoideae contribute more to species richness in the Sahel region. The Paniceae show a high relative abundance in two different regions: the savannas of the Sahel in the north and the rain forest of upper and lower Guinea in the south. Six of the 16 Paniceae genera of our data set have species occurring in both regions, four genera are present mostly in the north, six only in the south (including the five exclusively C_3 Paniceae genera of our data set).

Correlation with precipitation and functional traits

The distribution of the Panicoid tribes (Andropogoneae and Paniceae) and the chloridoids along the precipita-

tion gradient are diametrically opposed, with the proportion of panicoids positively (Pearson's $r = 0.69$ and 0.52) and that of the chloridoids negatively ($r = -0.82$) correlated with mean annual precipitation (Table 1). The proportion of C_3 grasses and the C_4 subtypes NADP-ME are positively correlated with mean annual precipitation (C_3 $r = 0.83$, NADP-ME $r = 0.55$), the C_4 subtype NAD-ME is negatively correlated ($r = -0.83$), while the C_4 subtype PCK is not correlated with mean annual precipitation ($r = -0.04$). Life cycle is not correlated with mean annual precipitation (annual $r = -0.10$, perennial $r = 0.14$), while plant height is highly correlated ($r = 0.76$; short being negatively correlated, and tall being positively correlated; Appendix S3). The results of the semi-partial correlation (Table 1) suggest that for Andropogoneae, the spatial distribution is still highly correlated with annual precipitation when the C_4 subtype NADP-ME is held constant (semi-partial $r = 0.45$), but not when plant height is held constant (semi-partial $r = 0.003$). The correlation of the spatial distribution of Paniceae with mean annual precipitation stays high when the C_4 subtype NADP-ME is held constant (semi-partial $r = 0.43$), but is reduced when the C_3 pathway, the C_4 subtype NAD-ME and plant height are held constant (semi-partial $r = 0.08$, $r = 0.22$ and $r = 0.13$). For Chloridoideae, the correlation with annual precipitation is lower when the C_4 subtype NAD-ME, as well as plant height, are held constant (semi-partial $r = -0.17$, and $r = -0.28$).
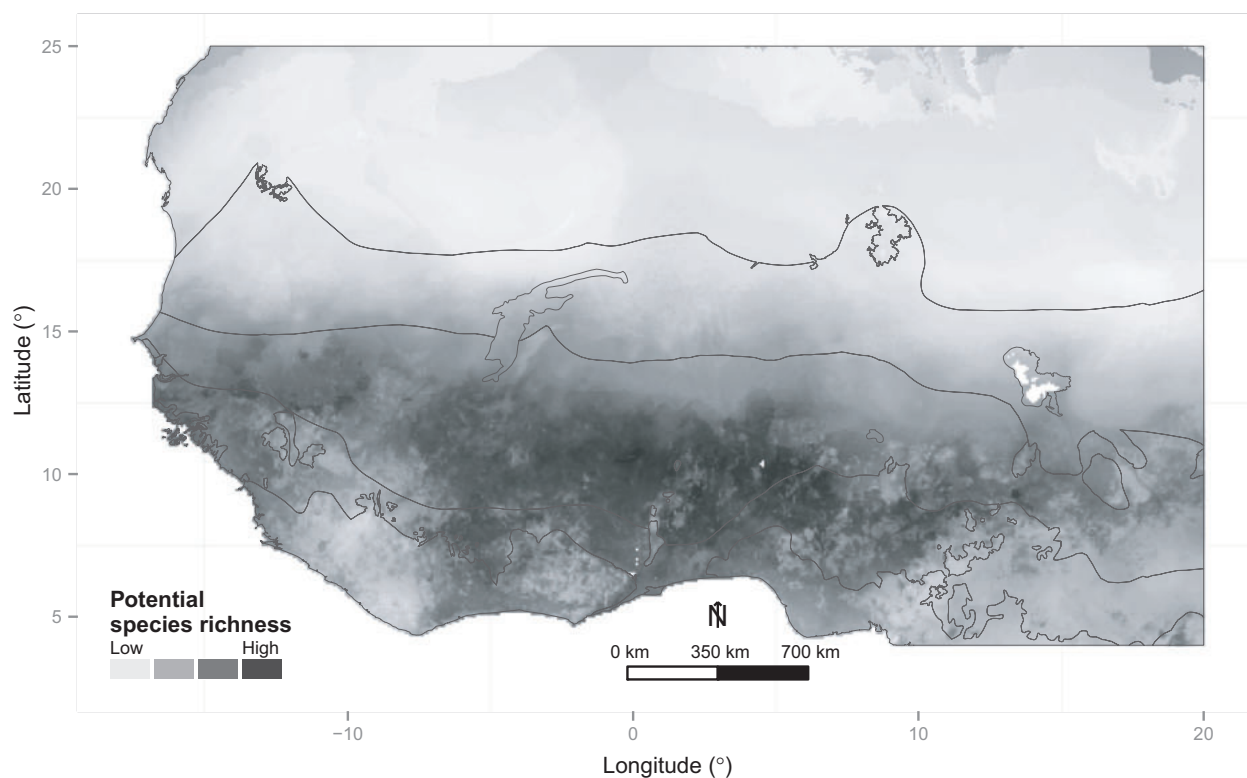
Fig. 5. Potential grass species richness in West Africa derived from 299 stacked significant species distribution models (S-SDM). Darker tones indicate higher species richness.

Discussion

We assessed the correlations between spatial distribution, traits and climate for grasses in West Africa. Overall, mean annual precipitation is the most important factor determining the spatial patterns of grass diversity in West Africa, confirming the results of previous studies on African vegetation classes (Greve et al. 2011) and determinants of savanna tree cover (Sankaran et al. 2005). Furthermore, our results corroborate the findings of Edwards & Smith (2010), who showed that mean annual precipitation (as a proxy for water availability) is the most important climatic factor influencing the distribution of grasses at regional to global scales. While rainfall in West Africa is strongly seasonal (with one rainy season in the north and two in the south), mean annual precipitation is highly correlated with the mean precipitation of the wettest quarter (Bio16 – representing precipitation during the growing season) and precipitation seasonality.

The analysis of the major taxonomic groups of the West African grass flora reveals different optima along the precipitation gradient, suggesting a possible divergence in their climatic tolerances. As expected, the difference between panicoids and chloridoids is minimal along the

temperature gradient (mean annual temperature: 26.3 °C for Paniceae and 25.8 °C for Andropogoneae v 27.1 °C for Chloridoideae), but was found to be more pronounced along the precipitation gradient (mean annual precipitation: 994 mm and 1048 mm vs. 778 mm). This differentiation between panicoids and chloridoids has been previously observed on a global scale (Edwards & Smith 2010), for North America (Taub 2000) and for Argentina (Cabido et al. 2008).

While both Andropogoneae and Paniceae seemingly cover the same environmental space along the precipitation gradient (Fig. 3), the steeper accumulation curve for the Andropogoneae indicates a narrower realized climate niche. Both species richness and relative abundance patterns are highly congruent in the Andropogoneae, indicating dominance in the Sudanian savannas. Andropogoneae have the NADP-ME subtype of C_4 photosynthesis, which has been shown to be more competitive at high water availability than the other subtypes due to higher quantum yield (Wan & Sage 2001).

Our results indicate that the correlation between the distribution of Andropogoneae and precipitation is in fact dependent on their height. Tall grasses are more competitive for light, but are also dependent on disturbances (such
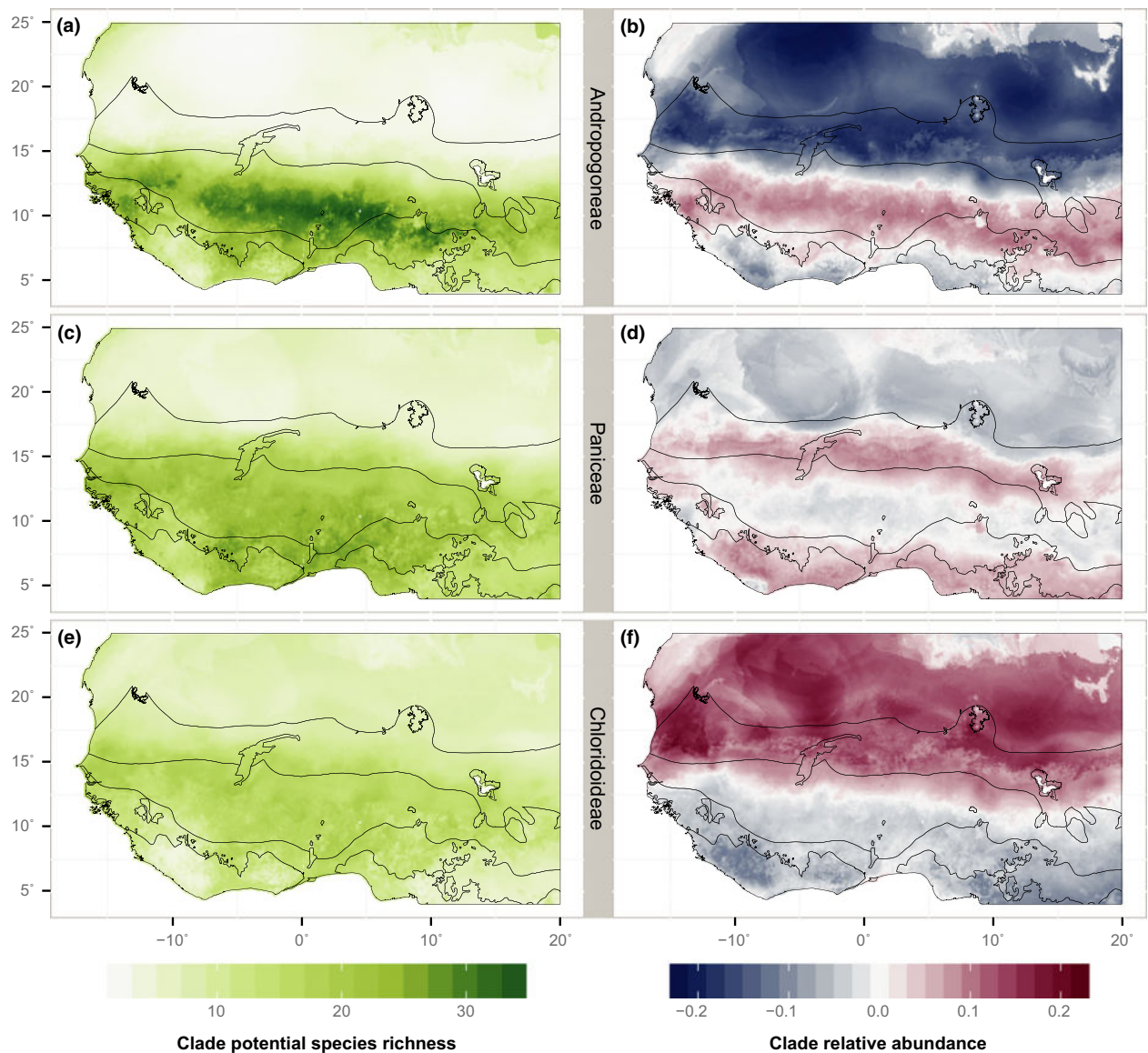
Fig. 6. Spatial patterns of potential species richness (**a**, **c**, **e**) and corrected relative abundance (**b**, **d**, **f**) for Andropogoneae, Paniceae and Chloridoideae derived from stacked species distribution models.

Table 1. Correlations between mean annual precipitation (MAP) and the spatial distribution of the clades Andropogoneae, Paniceae and subfamily Chloridoideae, and semi-partial correlation while removing the influence of photosynthetic type, life cycle and size. In the semi-partial correlation results, values highlighted in bold indicate that the variable held constant is influencing the correlation with MAP. '–' indicates that the semi-partial correlation does not apply, because there is no correlation between the functional trait and MAP.

	Correlation with MAP	Semi-Partial Correlation with MAP When Functional Trait Held Constant					
		Photosynthetic Type				Traits	
		C3	NADP-ME	NAD-ME	PCK	Life cycle	Height
Andropogoneae	**0.691**	NA	0.459	NA	NA	–	**0.003**
Paniceae	**0.529**	**0.088**	0.430	**0.220**	–	–	0.136
Chloridoideae	**−0.829**	NA	NA	**−0.178**	–	–	−0.284

as fire and herbivory) as leaf litter from previous years would have a negative impact on the young, shade-intolerant shoots (Bond et al. 2003). In fact, tall grasses may induce fires through their high yield and low decomposition rates, thus contributing to shaping their ideal environment (Bond et al. 2003). For example, the invasive *Andropogon gayanus* in Australia has been shown to alter the natural vegetation by contributing to an increase in fire intensities (Rossiter et al. 2003). Thus, Andropogoneae have evolved morphological and physiological characters that allow them to promote disturbances and outcompete other grasses and closed-canopy trees, which may explain their dominance in the mesic savannas of West Africa. Thus, incorporating fire as an additional predictor may further improve the accuracy of potential distribution models in Andropogoneae.

Some Paniceae species possess the same features that allow the Andropogoneae to dominate in Sudanian savannas, i.e. the NADP-ME subtype and tall growth, but nevertheless contribute much less to grass diversity in that region. In contrast, they show a bimodal pattern of high contributions in the north (Sahelian savannas) and south (mosaic of forest and savannas, forest regions), which may be due to the higher morphological and physiological variability compared to the Andropogoneae. Most importantly, the Paniceae express all subtypes of C_4 photosynthesis, as well as C_3 photosynthesis. This variability allows them to extend into a wider range of habitats than the Andropogoneae, and to dominate when they are not outcompeted by Andropogoneae. This is supported by Osborne (2008), who showed that Paniceae represent a larger fraction of grass diversity in moist and aseasonal climates of the tropics. In our data set, the genera contributing to the dominance of Paniceae in the forested regions are now recognized as the subtribe Boivinelineae, which includes species with broad lanceolate leaves and mostly C_3 photosynthesis (Morrone et al. 2012). Paniceae also contribute substantially in the drier northern regions, where water availability is insufficient for the Andropogoneae.

Our results show that the Chloridoideae are overrepresented in Sahelian savannas and the Sahara Desert, regions with low precipitation and high temperatures. This is confirmed by fossil phytolith assemblages (a collection of siliceous plant remains used in palaeovegetation reconstruction) composed mostly of chloridoid phytoliths, which have been shown to be good proxies for the AET/PET ratio (the ratio of annual actual evapotranspiration to annual potential evapotranspiration) of Sahelian savannas in West Africa (Bremond et al. 2005). The contribution of the subfamily Chloridoideae is congruent with its tolerance profile. The adaptation of the Chloridoideae to dry and hot habitats is linked to their generally small size and the C_4

NAD-ME pathway, which has been shown to confer better drought resistance (Ghannoum et al. 2002).

We conclude that precipitation is the main climatic factor influencing the broad-scale distribution patterns of grasses in West Africa. Nevertheless, the different grass clades have evolved both physiological and morphological adaptations allowing each to dominate the grass flora under specific conditions along the rainfall gradient. Plant size explains the correlation of precipitation with the three taxonomic groups, indicating that in addition to the photosynthetic type, other traits need to be considered when studying the spatial distribution of grasses. Moreover, we argue that broad-scale analyses of species richness should ideally be complemented by evaluations of specific clades to gain better insight into the distribution of diversity and the regional composition of the flora.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supporting information for the Methods section (Tables S1, S2, S3, S4; Figs S1, S2, S3).

Appendix S2. Supporting information for the methods and results of Biomod (Figs S4, S5, S6).

Appendix S3. Supporting information for the Results section (Figs S7, S8, S9, S10).