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Heteropogon-Themeda grasses evolve to occupy either tropical grassland or wetland biomes

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Abstract Species of the *Heteropogon-Themeda* clade are ecologically important grasses distributed across the tropics, including widespread species, such as the pantropical *Heteropogon contortus* and *Themeda triandra*, and range-restricted species such as *Heteropogon ritchiei* and *Themeda anathera*. Here, we examine habitat preferences of the grassland/savanna and wetland species by describing bioclimatic niche characteristics, characterizing functional traits, and investigating the evolution of functional traits of 31 species in the *Heteropogon-Themeda* clade in relation to precipitation and temperature. The climatic limits of the clade are linked to mean annual precipitation and seasonality that also distinguish seven wetland species from 24 grassland/savanna species. Tests of niche equivalency highlighted the unique bioclimatic niche of the wetland species. However, climatic factors do not fully explain species geographic range, and other factors are likely to contribute to their distribution ranges. Trait analyses demonstrated that the wetland and grassland/savanna species were separated by culm height, leaf length, leaf area, awn length, and awn types. Phylogenetic analyses showed that the wetland species had tall stature with long and large leaves and lack of hygroscopic awns, which suggest selective pressures in the shift between savanna/grassland and wetland. The two most widespread species, *H. contortus* and *T. triandra*, have significantly different bioclimatic niches, but we also found that climatic niche alone does not explain the current geographic distributions of *H. contortus* and *T. triandra*. Our study provides a new understanding of the biogeography and evolutionary history of an ecologically important clade of C_4 tropical grasses.

Key words: biogeography, biome shifts, niche divergence, Poaceae, precipitation, savanna, seasonality.

1 Introduction

Understanding associations between climatic niche, habitats, and functional traits of plant species can provide insights into their macroevolutionary patterns and trait evolution. A variety of combinations of environmental factors (e.g., precipitation, temperature, and disturbance) govern biome formations across the planet (Woodward et al., 2004). The environment exerts substantial control on the sorting of plant form and function via life-history strategies (Bazzaz, 1991). Life-history strategies in practice reflect ensembles of plant functional traits that combine to determine plant growth, survival, and reproduction (Westoby & Wright, 2006; Caruso et al., 2020). Functional traits are defined as morpho-physio-phenological traits that impact fitness indirectly via their effects on growth, reproduction, and survival (Violle et al., 2007) and just as environment sorts enable plants to acclimate to suitable climatic niches in different locations (Crisp et al., 2009; Aubin et al., 2016). However, plants are capable of dispersing along climatic gradients, which are associated with trait changes over time and the emergence of new

functional traits (Donoghue & Edwards, 2014; Funk et al., 2017).

Phylogenetically, both climatic characteristics and functional traits can be viewed in a species- or clade-specific context (Pearman et al., 2008; Donoghue & Edwards, 2014) and can be interpreted to infer evolutionary history. Two opposing ecological theories, niche conservatism (Wiens & Graham, 2005) and niche divergence (Donoghue & Edwards, 2014), have been tested as potential drivers of species distribution patterns, ecological speciation, and trait evolution (Ackerly, 2003; Pyron et al., 2015). Niche conservatism emphasizes the tendency of closely related species to retain the same climatic niche and responsive functional traits as their ancestors (Wiens & Graham, 2005; Liu et al., 2012). The process of niche conservatism results in subpopulations or species tracking and maintaining similar climatic niche in adjacent areas even if speciation occurs (Pyron et al., 2015). In contrast, niche divergence is viewed as a less prevalent but high-impact phenomenon (e.g., biome shifts; Donoghue & Edwards, 2014) as sister species undergo trait transitions that are slightly or completely different from their ancestors, to adapt to novel environments (Crisp et al., 2009; Gavrilets & Losos, 2009). Currently, a growing number of comparative studies have been conducted on different plant lineages (e.g., Crisp & Cook, 2012) that help infer the macroecological processes and plant adaptations that affect species distributions and how life histories and traits evolve and diversify in different environments (Woodward & Williams, 1987; Kelly et al., 2021).

Wetlands and grasslands/savannas dominate tropical C_4 grassy biomes, and they are shaped by precipitation, seasonality, seasonal inundation, fire, and grazing (Sankaran & Ratnam, 2013; Joyce et al., 2016; Lehmann & Parr, 2016). Grasslands and savannas cover a broad climatic range of rainfall and dry seasons of 4–9 months per year (Lehmann et al., 2011). Wetlands and seasonally inundated grasslands are generally characterized by higher rainfall than grasslands and savannas (Finlayson, 2005; Gopal, 2013) and are sensitive to changes in flooding and precipitation seasonality (PS) (Erwin, 2009; Joyce et al., 2016). In terms of geographic distribution, tropical savannas and grasslands occupy a greater land surface area than tropical wetlands: ~20% versus ~2%–6%, respectively, of the global land surface (Barrow, 1994; Scholes & Hall, 1996). However, savannas and wetlands are structured as mosaics (examples presented in Mantlana et al., 2008; Melack & Hess, 2010; Souza-Neto et al., 2016). Differences in climatic regimes and geographic proximity of wetlands and savannas provide the potential for biome shifts and niche divergence of species in savannas and wetlands (Donoghue & Edwards, 2014). Forrestel et al. (2015) demonstrated that shifts from grasslands to wetlands in the genus *Lasthenia* Cass. (Asteraceae) are evolutionarily labile and under selection due to changes in hydrological regimes. However, investigations of climatic niche evolution in savanna and wetland grasses are scarce despite these ecosystems being globally widespread.

Grass species proliferate, tolerate, and adapt to open ecosystems via a set of functional traits that represent life-history strategies. Distinct grass lineages have been found to have correlations between size-related traits, especially height and leaf area, and climatic factors (Liu et al., 2012; Jardine et al., 2020). In C_4 grassy biomes, wetland and savanna grass species have a set of functional traits correlated with both seasonal dryness and inundation or combinations of the two. With seasonal inundation, grasses must mitigate water saturation and anoxic conditions alongside the need to avoid shading due to rapid growth and high productivity (Moor et al., 2017). Wetland species are hypothesized to have specialized traits to cope with inundation such as larger stature, rapid growth, and adventitious roots (Bortherton & Joyce, 2015; Moor et al., 2017). In contrast, savanna and grassland species must tolerate periods of limited water availability, exposure to solar radiance, fire, and grazing (Skarpe, 1996; Sankaran, 2009). Further, fire and flooding have often been associated with different seed dispersal mechanisms that can aid in seed burial for plant establishment and fire escape (Peart & Clifford, 1987; Linder et al., 2018). Grass awns that are pivotal in dispersal show high variability in function and morphology (Cavanagh et al., 2019). Geniculate awns are functionally active and respond to moisture by twisting and moving on the soil surface (hygroscopic), while many species have passive awns or even no awns (Peart & Clifford, 1987; Cavanagh et al., 2019).

The *Heteropogon* Pers.-*Themeda* Forssk. clade is an ecologically and morphologically diverse lineage of the grass tribe Andropogoneae, a major group in C_4 grassy biomes (Kellogg, 2015; Welker et al., 2020). The clade is relatively young (~8–10 million years), originating and diversifying during the time of the Miocene C_4 grassland expansion (Arthan et al., 2021), and comprises approximately 31 species (POWO, 2019). The ecological success of the clade is represented by two globally significant species: *Heteropogon contortus* (L.) P.Beauv. ex Roem. & Schult. and *Themeda triandra* Forssk. (Snyman et al., 2013; POWO, 2019). Both species share a broad distribution range across Africa, Asia, Australia, and North America (Barkworth et al., 2003; POWO, 2019), but only *H. contortus* occurs in South America (Goergen & Daehler, 2001). *Heteropogon triticeus* (R.Br.) Stapf ex Craib, *Themeda arundinacea* (Roxb.) A. Camus, *Themeda caudata* (Nees ex Hook. & Arn.) A. Camus, and *Themeda villosa* (Lam.) A. Camus are only found in mesic environments of Southeast Asia (Ratnam et al., 2016; POWO, 2019). Species with even more restricted distributions include *Themeda anathera* (Nees ex Steud.) Hack. in the Himalaya mountains and *Heteropogon ritchiei* (Hook.f.) Blatt. & McCann endemic to southern India. Morphological variation (e.g., plant height and size-related leaf traits; Clayton et al., 2006 onwards) presumably represents adaptation to different climatic niches and habitat types.

Diversity in geographic range, habitats, and phenotypes of the clade lead to questions about relationships between climatic niche, habitats, and responsive functional traits and provides an opportunity to explore macroevolution and trait evolution within C_4 grassy biomes at the species level. Here, we examine the *Heteropogon-Themeda* clade and seek to build on the most recent phylogenetic work of the *Heteropogon-Themeda* clade to understand relationships between the climate and key functional traits of the clade, to answer the following questions: (1) What is the interspecific

bioclimatic variation of *Heteropogon* and *Themeda* species and how does bioclimatic variation explain their distribution patterns? In this aspect, we also focus on two widespread species, *H. contortus* and *T. triandra*, to examine differences in climatic niches. (2) Do wetland and grassland/savanna species occupy distinct bioclimatic and functional trait spaces? (3) How do functional traits evolve between grassland/savanna and wetland species?

2 Material and Methods

2.1 Species occurrence records and selection of bioclimatic data

Species occurrence records for all *Heteropogon* and *Themeda* species were obtained from two main databases: Global Biodiversity Information Facility (GBIF) (www.gbif. org) using the "rgbif" package (Chamberlain et al., 2020) in R software (R Core Team, 2021) and the Botanical Information and Ecology Network (BIEN) databases (Enquist et al., 2016). Additional records were obtained from the Tropicos database (www.tropicos.org), plant specimen labels deposited in Bangkok Forest (BKF), Kew (K), Leiden (L), and Paris (P) herbaria, data collected by Morales-Fierro (2014), and fieldwork data from Thailand in 2018. Species records from regions not covered by these databases were compiled from floras (Shouliang & Phillips, 2006a, 2006b). Here, species occurring in a single locality are defined as endemic. All occurrence data sets were cleaned using R scripts and the "CoordinateCleaner" package (Zizka et al., 2019) by erasing records from the sea and out of range.

Nineteen climatic variables were extracted from the cleaned occurrence points at a resolution of 10 min from the WorldClim database (Hijmans et al., 2005) using the

"raster" package (Hijmans & van Etten, 2012). Boxplots were used to inspect data patterns and outliers, which were then deleted. Principal component analysis (PCA) was performed using the "FactoMineR" package (Lê et al., 2008). All variables were standardized and centered. To avoid over-parameterization, highly correlated variables ($r^2 \geq 0.75$) were dropped from the data set by considering the first two principal components of PCA and Pearson's coefficients (Figs. S1A, S1B). The PCA was used to select four bioclimatic driver variables also known to be significant regulating factors of C_4 grassy biomes (Lehmann et al., 2011; Bocksberger et al., 2016): temperature seasonality (TS), mean annual precipitation (MAP), PS, and precipitation of driest quarter (PDryQ).

2.2 Trait selection and habitat classification

Simple size-related functional traits (e.g., leaf length, width, or area) are accessible from databases and herbarium specimens and effective in explaining some ecological functions of plants (Pérez-Harguindeguy et al., 2016). Six vegetative and six reproductive traits were compiled from GrassBase (Clayton et al., 2006 onwards), Morales-Fierro (2014), measurements from herbarium specimens (K, BKF), and the literature (Deshpande, 1988; Shouliang & Phillips, 2006a, 2006b; Veldkamp, 2016). The traits were selected based on their ecological importance in grassy ecosystems as described in Table 1. Vegetative traits include five quantitative traits: culm height, leaf length, leaf width, leaf area, and leaf width to length ratio, and one qualitative trait, the presence of stilt roots, was recorded. Maximum culm height, recorded from floras as the typical maximum distance between the ground level and the apex of the inflorescence, is used as the maximum plant height (Clayton et al., 2006 onwards). Leaf length is measured from the base to the apex of the blade, and leaf width is the widest part of the blade. Reproductive traits include five

Table 1 Grass functional traits and their ecological importance

Functional traits	Ecological importance	Citations
Culm height	Competition: light acquisition	Liu & Osborne (2014), Moles et al. (2009)
Leaf length	Competition: productivity	Wright et al. (2004)
Leaf width	Drought avoidance	Wright et al. (2017)
Leaf area	Competition: productivity	Linder et al. (2018), Pan et al. (2020)
	Reduce hydrological stress	Li et al. (2020), Pan et al. (2020), Wright et al. (2004)
	Solar irradiance	Gallaher et al. (2019)
Leaf width to length ratio (Leaf ratio)	Drought avoidance	Gallaher et al. (2019), Wright et al. (2014)
Spikelet length	Dispersal	Linder et al. (2018)
Callus length	Seed establishment	Silberbauer-Gottsberger (1984)
Caryopses length	Seed establishment and dormancy	Cayssials & Rodríguez (2013), Linder et al. (2018)
Caryopses width	Seed establishment and dormancy	Cayssials & Rodríguez (2013), Linder et al. (2018)
Awn length	Seed establishment and dispersal	Peart & Clifford (1987), Linder et al. (2018)
Awn type	Seed establishment and dispersal mode	Cavanagh et al. (2019), Peart & Clifford (1987)
Presence of stilt root	Mitigate water saturation	Moor et al. (2017), Pan et al. (2020)

quantitative traits: sessile spikelet length, caryopsis length, caryopsis width, callus length, and awn length, and one qualitative trait, awn type (geniculate, straight, or awnless). Spikelet measurements include the whole spikelet, but not the callus or pedicel. The measurement of caryopses follows Zhang et al. (2014). Awn is measured from the point of the attachment to the lemma to the apex. Maximum, minimum, and mean values were calculated for each trait across species (Tables S1, S2).

Habitat data for each *Heteropogon* and *Themeda* species were compiled from the literature (Table 2; Deshpande, 1988; Shouliang & Phillips, 2006a, 2006b; Veldkamp, 2016), labels from herbarium specimens, and online herbarium databases from K (apps.kew.org), L (bioportal.naturalis.nl), and P (science.mnhn.fr) herbaria. Data on local community composition, seasonality, soil types, and geology were also obtained in habitat categorization to help identify major habitats: grassland and savanna, or wetland. Terminology was standardized for grassland and savanna, for example, woodland and savanna are interchangeable terms that refer to a habitat where C_4 grasses are the main ground cover and sparse trees are present within the area (Table 2). Some habitats not described in the literature as grasslands/savannas or wetlands, such as coastal areas or rock outcrops (Goergen & Daehler, 2001), were excluded from the habitat classification.

2.3 Statistical analyses of climatic niche and traits among *Heteropogon-Themeda* species

2.3.1 Climatic niche and trait analyses among habitat groups
PCA was used to analyze and illustrate bioclimatic niche groupings, based on the four selected bioclimatic variables, between habitat groups using the "FactoMineR" package (Lê et al., 2008). To understand trait groupings, factor analysis of mixed data (FAMD) was performed in "Facto-MineR" package by using continuous (plant height, leaf area, leaf ratio, maximum sessile spikelet length, and maximum awn length) and discrete characters (habit, presence of stilt root, presence of awn, and awn type). Missing data were addressed using the function "imputePCA" in the "missMDA" package (Josse & Husson, 2016). To test statistical differences, all bioclimatic and functional trait mean values from all species were scaled and centered. The Kruskal–Wallis test was chosen as the statistical test for continuous traits, given the size of the data set of 29 species. Dunn's and Wilcoxon's tests were performed as post hoc analyses to compare between habitat groups.

2.3.2 Climatic niche and trait analyses between widespread species, *Heteropogon contortus*, and *Themeda triandra*
The climatic space occupied by *H. contortus* and *T. triandra* was compared. Occurrence records of each species were divided into continents according to The World Geographical Scheme for Recording Plant Distributions (WGSRPD) (Brummit, 2001). The Tropics of Capricorn and Cancer (between 23.44 and −23.44 latitude) were used to separate tropical and temperate regions. Records from islands were discarded, but records from Madagascar were combined with those from Africa. This resulted in five tropical data sets for *H. contortus* from Africa, America, Asia, Australia, and the

Middle East along with three tropical data sets for *T. triandra* from Africa, Asia, and Australia. A data set of *Themeda quadrivalvis* (L.) Kuntze sampled from the Middle East was included in this analysis as it is nested in the *T. triandra* clade despite its annual habit (Dunning et al., 2017; Arthan et al., 2021). The temperate data set was separated from the tropical data set and compared with each other to determine the differences in climatic niche. The similar bioclimatic data from the previous section (TS, MAP, PS, and PDryQ) were used in the PCA to compare the climatic niche space of *H. contortus* and *T. triandra*. Similar settings of niche equivalency and similarity tests described above were used to compare bioclimatic niche occupancy between *H. contortus* and *T. triandra* + *T. quadrivalvis* populations. Analysis of variance was used to test statistical differences among traits, and PCA was used to group these two widespread species by traits using the "FactoMineR" package (Lê et al., 2008).

2.3.3 Climatic niche overlap, niche equivalency, and niche similarity tests among *Heteropogon-Themeda* species
"ENMTools" (Warren et al., 2021) and "ecospat" package222s (Di Cola et al., 2016) were used to compute the climatic niche overlap between species. The PCA-env method (Broennimann et al., 2011) was implemented in the "ecospat" package to quantify niche overlap between species estimated by Schoener's *D* (Schoener, 1970) and Warren's *I* matrices (Warren et al., 2021). Higher *D* and *I* values indicate greater overlap between species pairs. Species with fewer than five occurrence records were not included in equivalency and similarity tests.

Observed niche overlap values in the previous step were statistically compared with a null distribution of niche overlap values calculated from background points. Niche equivalency tests the similarity of two species in their climatic space and hence any potential for functional equivalence and mutual replacement. Niche similarity tests take climatic differences into account to test if the two species are more different than expected by chance. Both tests were performed according to Warren et al. (2021), using background points within a 5 km buffer radius and non-parametric tests with 1000 pseudoreplicates to create null distributions. The null distribution of sampled *D* and *I* values from the background environment was set to compare with empirical *D* and *I* values. The two species considered as significantly different have distinct climatic niche occupations. These analyses were repeated with all possible pairs of species and species grouped by habitat types.

2.4 Phylogenetic comparative methods
2.4.1 Phylogenetic reconstruction
Andropogoneae plastome alignment from Arthan et al. (2021) was combined with four other *Themeda* accessions, *Themeda avenacea* (F. Muell.) T. Durand & B. D. Jacks., *Themeda intermedia* (Hack.) Bor, *Themeda novoguineensis* (Reeder) Jansen, and *Themeda trichiata* S. L. Chen & T. D. Zhuang, from Dunning et al. (2017) to produce a phylogenetic tree. The phylogenetic tree includes 25 ingroup species, representing 81% of the 31 species in the genera *Heteropogon* and *Themeda* (Table 2). Bayesian analyses were run using

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Table 2 Summary of habitat classifications and key references of *Heteropogon-Themeda* species

Species	Sample size	Habitat types	Key references to the habitat classification	Phylogenetic analyses
Heteropogon contortus	7069	Savanna & Grassland	Grice & McIntyre (1995) Daehler & Carino (1998) Ratnam et al. (2016)	✓
Heteropogon fischerianus	1	Savanna & Grassland	Deshpande (1988)	✓
Heteropogon melanocarpus	544	Savanna & Grassland	Vesey-Fitzgerald (1970) Srivastava (2004) Strohbach (2013) Nanjarisoa et al. (2017)	✓
Heteropogon ritchiei	6	Savanna & Grassland	Puri & Patil (1960) Lekhak & Yadav (2012) Rahandale & Rahandale (2014)	✓
Heteropogon triticeus	3244	Savanna & Grassland	Kirkpatrick et al. (1987) Scott et al. (2009) Ens et al. (2015) Sookchaloem et al. (2015)	✓
Themeda anathera	55	Savanna & Grassland	Muhammad et al. (2012) Shaheen et al. (2015) Amjad et al. (2016)	✓
Themeda arguens	516	Savanna & Grassland	Kirkpatrick et al. (1988) Neldner et al. (1997) Djufri & Wardiah (2017) Sutomo (2020) Sutomo et al. (2020)	✓
Themeda arundinacea	56	Wetland	Yadava (1990) Lehmkuhl (1994) Dangol & Maharjan (2012) Pala et al. (2012) Ratnam et al. (2016) Naskar & Bera (2018)	✓
Themeda avenacea	581	Savanna & Grassland	Kennedy et al. (2001) Lang (2008) Lewis et al. (2008) Fensham et al. (2015)	✓
Themeda caudata	72	Wetland	Bhatia (1958) Xiwen & Walker (1986) Ghosh (2012) Biswas et al. (2016)	✓
Themeda cymbaria	23	Savanna & Grassland	Kothandaraman et al. (2020) Mondal & Sukumar (2015) Pulla et al. (2016) Sankaran (2009) Subashree & Sundarapandian (2017)	✓
Themeda gigantea	24	Wetland	Marler & Ferreras (2017) Veldkamp (2016) Li et al. (2011) Xiwen & Walker (1986)	✗
Themeda helferi	6	Savanna & Grassland	Kumar et al. (2018) Shouliang & Phillips (2006b)	✗
Themeda hookeri	33	Savanna & Grassland	Li et al. (2016) Liu et al. (2019) Veldkamp (2016) Xiwen & Walker (1986) Zhao et al. (2020)	✓
Themeda huttonensis	4	Savanna &	Shouliang & Phillips (2006b)	✓

Table 2 Continued

Species	Sample size	Habitat types	Key references to the habitat classification	Phylogenetic analyses
		Grassland		
Themeda idjenensis	7	Wetland	Veldkamp (2016)	✗
Themeda intermedia	52	Wetland	Gressitt (1982)	✓
			Paijmans (1983)	
			Manner & Lang (2006)	
			Mylliemngap & Barik (2019)	
Themeda minor	1	Savanna & Grassland	Chen-feng et al. (2004)	✓
			Liu et al. (2004)	
Themeda mooneyi	5	Savanna & Grassland	Mahata et al. (2019)	✓
			Murthy (2003)	
Themeda novoguineensis	18	Wetland	Eden (1974)	✓
			Gillison (1983)	
			Gressitt (1982)	
Themeda pseudotremula	1	Savanna & Grassland	Potdar et al. (2003)	✗
Themeda quadrivalvis	1457	Savanna & Grassland	Shukla et al. (2010)	✓
			Patzelt (2011)	
			Keir & Vogler (2006)	
			Vogler & Owen (2008)	
Themeda sabarimalayana	1	Savanna & Grassland	Sreekumar & Nair (1987)	✓
Themeda saxicola	1	Savanna & Grassland	Karthikeyan et al. (1989)	✗
			Bor (1951)	
Themeda strigosa	2	Savanna & Grassland	Bor (1960)	✓
			Karthikeyan et al. (1989)	
Themeda tremula	37	Savanna & Grassland	Amarasinghe & Pemadasa (1982)	✓
			Pemadasa (1990)	
			Pemadasa & Mueller-Dombois (1979)	
Themeda triandra	46 703	Savanna & Grassland	Snyman et al. (2013)	✓
			Morgan & Lunt (1999)	
			Lunt (1995)	
			Trollope (1982)	
			Mott & Tothill (1984)	
			O'Connor (1997)	
Themeda trichiata	3	Savanna & Grassland	Shouliang & Phillips (2006b)	✓
Themeda unica	1	Savanna & Grassland	Shouliang & Phillips (2006b)	✓
Themeda villosa	245	Wetland	Ratnam et al. (2016)	✓
			Biswas et al. (2016)	
			Dutta & Sarma (2018)	
			Rawat (2005)	
			Mylliemngap & Barik (2019)	
Themeda yunnanensis	0	Savanna & Grassland	Chao (2009)	✗
			Tain et al. (2007)	
			Shouliang & Phillips (2006b)	

MrBayes v.3.2.7a (Ronquist et al., 2012) in CIPRES (Miller et al., 2010). The GTR + Γ + I was the best model estimated from jModelTest v.2.1.6 (Darriba et al., 2012). Two Markov Chain Monte Carlo (MCMC) runs were set with 100 000 000 generations each, 2000 generation samplings, and 25% burn-in. Dating analyses followed Arthan et al. (2021) using BEAST2 v.2.6.1 (Bouckaert et al., 2014), with the divergence time between *Zea mays* L. and the other Andropogoneae at 25 Ma.

Effective sample size values for most parameters were more than 200 as explored by Tracer v.1.7.1 (Rambaut et al., 2018).

2.4.2 Continuous trait analyses—Bioclimatic variables and functional traits

We investigated how the four climate variables and functional traits evolved in the context of habitat preferences of species in the *Heteropogon-Themeda* clade. The evolution of climatic occupancy was analyzed by PCA values

of the four climatic variables from Section 2.3 with the function "fastanc" in the "phytools" package (Revell, 2012). For functional traits, the phylogenetic signal was estimated using Blomberg's *K* (Blomberg et al., 2003) and Pagel's *λ* (Pagel, 1999) values with maximum likelihood estimation with 1000 simulations in the "phytools" package (Revell, 2012) with the "phylosig" function. The maximum clade credibility tree was pruned to include only the *Heteropogon-Themeda* clade. The phylogenetic tree was painted with habitat types by all-rate-different (ARD) with the "make.simmap" function from "phytools" packages with 500 simulations. Each simulated tree reconstructed shifts in habitat type at different positions along the branches. All trait values were log-transformed before fitting trait evolution models, except for maximum awn length, which was squared-root transformed as it contained zero values (awnless species). The "OUwie" package (Beaulieu et al., 2012) was then used to test six different Brownian motion (BM) and Ornstein Uhlenbeck (OU) models on the simulated trees: BM (simple Brownian motion), BMS (different evolutionary rates between habitat groups), OU1 (one optimum across habitat groups), OUM (more than one optimum across habitat groups and with a single pull strength), OUMA (more than one optimum across habitat groups; multiple pull strengths; a single evolutionary rate), and OUMV (more than one optimum across habitat groups; a single pull strength; multiple evolutionary rates). Trait optimum value (θ), strength of selection (*α*), and rates of evolution (σ²) were estimated from the analyses. The OU model is a model of macroevolution. Note that the strength of selection explained by the *α* statistic describes current trait value evolution towards the optimum value (θ) over time (Butler & King, 2004). The *α* statistic is derived from the OU model predicting and simulating changes in trait values along the branches of the phylogeny over large timescales (Butler & King, 2004; Cooper et al., 2016) as opposed to more conventional measures such as $R = h^2 S$ making use of genetic data between generations (Stinchcombe et al., 2017).

2.4.3 Discrete trait analyses—Awn evolution analyses

Awn type transitions and rates were analyzed using BayesTraits v.3.0.2 (Pagel et al., 2004). Character coding in this study treats the geniculate state as 0. The non-hygroscopic straight state and the awnless state are coded with 1 and 2 as derived characters, respectively. A set of 1000 post-burn-in Bayesian trees was sampled from the phylogenetic analyses to account for phylogenetic uncertainty. The trees included ingroups and additional outgroups, *Andropogon distachyos* L., *Hyparrhenia subplumosa* Stapf, and *Schizachyrium sanguineum* (Retz.) Alston. The multistate mode and the MCMC method in BayesTraits were selected to run with nine different transition models. 100 000 000 generations, 10 000 000 burnin, tree sampling every 1000 generations, and exponential hyperprior of 10 were set for the MCMC analyses. Median log-likelihood values (−lnL) were calculated from each transition model. Likelihood ratio tests were used for model comparisons to find the best transition model.

To reconstruct the probabilities and patterns of change along the phylogenetic tree, the best model estimated for the MCMC analyses was applied to the same set of 1000 post-burnin trees. We tested the best model against three other models, ARD, equal rates, and symmetrical rates, to confirm that the previous model was the best model. The function "make.simmap" from the "phytools" package (Revell, 2012) was used in stochastic mapping. Simulations were run with 100 replicates per tree, which yielded 100 000 simulated trees in total. All trees were summarized using the "describe.simmap" function, yielding an average number of shifts and probabilities between states at nodes. The summary tree was visualized using pie charts to represent the probabilities of each awn state at the nodes.

3 Results

3.1 Summary of species occurrence records and habitat categorization

A total of 60 585 occurrence records were obtained, of which 46 703 were for *Themeda triandra*. Within the study group, we recognize six endemic species: *Heteropogon fischerianus* Bor, *Themeda minor* L. Liou, *Themeda pseudotremula* Potdar et al., *Themeda sabarimalayana* Sreek. & V. J. Nair, *Themeda saxicola* Bor, and *Themeda unica* S. L. Chen & T. D. Zhuang having a single record each (Table 2).

Twenty-four species exist in a variety of savannas including dipterocarp deciduous forest, *Acacia* woodlands, *Eucalyptus* woodlands, *Melaleuca* savanna, and Miombo woodland. Seven wetland species were identified from the literature by indicative descriptions such as "seasonally flooded," "riverine forest," "alluvial grassland," "flood plain," "water-logged depressions," or "river basin" (Gopal, 2013; Joyce et al., 2016).

3.2 Climatic niche and functional traits separation among habitat groups

The bioclimatic envelopes of the wetland species were characterized by higher MAP and PDryQ and lower seasonality than the grassland/savanna group (*P* < 0.05; Figs. 1A–1D; Table 3). According to the PCA, 88.8% of variance explained the separation between the wetland and the grassland/savanna groups (Fig. 1E; Table S3). The wetland species exist in the area with high rainfall that was sufficient to create a seasonally inundated area or wetland (Joyce & Wade, 1998). Average lower PS in wetlands suggested a shorter dry season in the habitat as compared to grasslands/savannas. Most grassland/savanna species have high rainfall seasonality values of more than 50 (Fig. 1C), with dry seasons lasting more than 5 months. Standing water of wetlands is maintained during the dry phase as rainfall during the "dry" season is not very low (Fig. 1D). The wetland species are spread out by the variance of MAP and precipitation of the driest quarter along the PC1. Broad precipitation ranges can be found within single species such as *Themeda villosa* that ranges from 670 to around 2500 mm/year. One wetland species, *Themeda arundinacea*, is positioned close to the grassland/savanna group in climatic space (Fig. 1E) as it occupies lower precipitation envelopes than other wetland species.

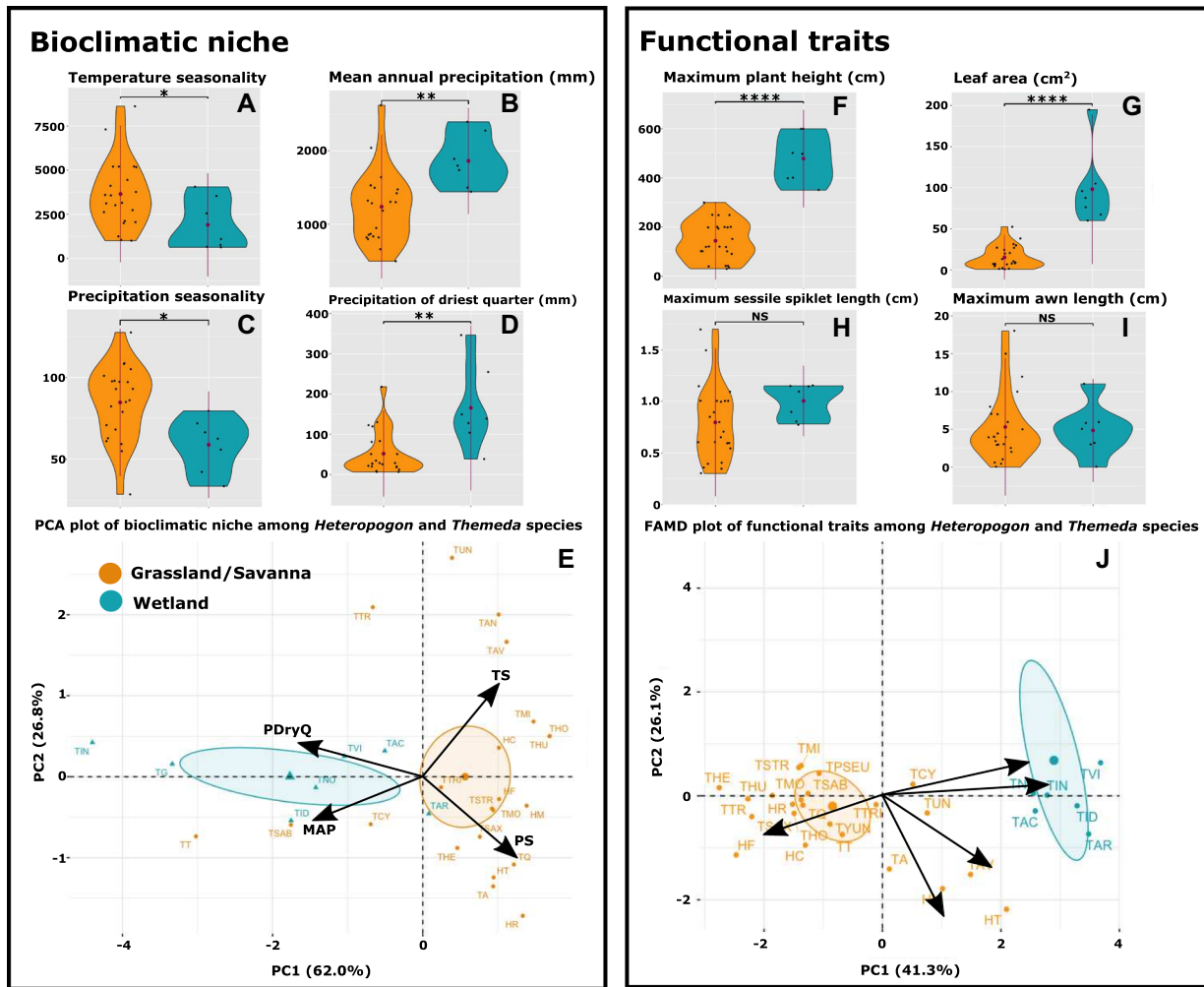In the PCA of functional traits, some vegetative traits were highly correlated; thus, we chose one of them to explain

Fig. 1. Box plots representing bioclimatic ranges (**A**–**D**) and functional traits (**F**–**I**) between grassland/savanna (orange) and wetland (blue) and principal component analysis (PCA) of bioclimatic variables (**E**) and functional traits (**J**) of *Heteropogon* and *Themeda* species distinguishing bioclimatic overlap and trait space between grassland/savanna and wetland groups. Asterisks above the plots represent statistical significance between the groups.

HC = *Heteropogon contortus*, HF = *Heteropogon fischerianus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TAN = *Themeda anathera*, TA = *Themeda arguens*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TMI = *Themeda minor*, TMO = *Themeda mooneyi*, TNO = *Themeda novoguineensis*, TPSEU = *Themeda pseudotremula*, TQ = *Themeda quadrivalvis*, TSAB = *Themeda sabarimalayana*, TSAX = *Themeda saxicola*, TT = *Themeda triandra*, TTR = *Themeda tremula*, TUN = *Themeda unica*, TVI = *Themeda villosa*, TYUN = *Themeda yunnanensis*.

functions in the grasslands/savannas and wetlands. The vegetative traits did not correlate with reproductive ones in the PCA (Figs. S2A–S2B), while no significant differences were detected among reproductive traits (data not shown). The wetland species have taller culms (479 ± 37.6 cm) than the grassland/savanna species (144 ± 16.2 cm). Likewise, the wetland species also have greater leaf area (98.2 ± 17.2 cm²) than the grassland/savanna species (15.3 ± 2.75 cm²) ($P < 0.05$; Figs. 1F, 1G; Table 3). In contrast, the maximum length of the spikelet and the awn did not differ significantly between the two habitat types ($P > 0.05$; Figs. 1H, 1I). The FAMD biplot showed that 67.40% of the morphological variance explained the grassland/savanna versus wetland

groupings (Fig. 1J), demonstrating that distinct sets of functional traits represent the grassland/savanna versus wetland species, but the grassland/savanna species encompass greater trait variation than the wetland group.

3.3 Climatic niche and functional traits separation between two widespread species *Heteropogon contortus* and *T. triandra*

The bioclimatic envelope of *H. contortus* is typified by greater seasonality than *T. triandra* (Figs. 2A–2D; Table 4). *Themeda triandra* occupies a significantly narrower climatic niche than *H. contortus*, especially in terms of seasonality (Figs. 2A, 2C). PCA of climate variables explained 85.96% of variance

Table 3 Statistical differences in functional traits between the grassland/savanna and wetland species tested by the Kruskal–Wallis test and post hoc comparisons using Dunn's and Wilcoxon's tests

	Grassland/savanna (mean [SE])	Wetland (mean [SE])	Kruskal–Wallis test	Dunn's test	Wilcoxon test	Significance difference
Bioclimatic variables						
Temperature seasonality	3650 (413)	1897 (554)	5.03	−2.24	121	P < 0.05
Mean annual precipitation	1239 (104)	1862 (136)	8.44	2.91	20	P < 0.005
Precipitation seasonality	84.8 (4.80)	58.9 (6.16)	6.24	−2.50	126	P < 0.05
Precipitation of the driest quarter	52.2 (11.4)	166 (38.7)	9.67	3.11	16	P < 0.005
Functional traits						
Maximum plant height (cm)	144 (16.2)	479 (37.6)	15.9	−2.24	121	P < 0.001
Leaf length (cm)	40.2 (5.12)	129 (21.4)	15.1	3.89	2.5	P < 0.001
Leaf area (cm²)	15.3 (2.75)	98.2 (17.2)	15.8	3.97	0	P < 0.001
Leaf width to length ratio	0.027 (0.003)	0.014 (0.001)	6.67	−2.58	138	P < 0.05
Maximum sessile spikelet length (cm)	0.796 (0.073)	1.000 (0.065)	3.60	1.90	44	P > 0.05
Maximum awn length (cm)	5.31 (0.927)	4.86 (1.29)	0.01	0.09	82	P > 0.05

separating *H. contortus* from *T. triandra* (Fig. 2E). *Themeda triandra* is generally greater in stature and produces longer leaves than *H. contortus* (Figs. 2F–2G; Table 4), but the leaf area does not significantly differ between the species (Fig. 2H). The leaf width to length ratio showed that *H. contortus* had a higher leaf ratio than *T. triandra* (Fig. 2I). Trait space distinguished *H. contortus* from *T. triandra* by 90.60% of the trait variation included in this study (Fig. 2J).

3.4 Comparisons of climatic niche overlap, equivalency, and similarity among species

Low to intermediate *D* and *I* values ranged from 0 to 0.56 and from 0 to 0.74, respectively, following the criteria from Broennimann et al. (2011). The highest climatic niche overlap from niche equivalency tests was found between *Themeda arguens* (L.) Hack. and *Themeda quadrivalvis* (*D* = 0.54, *I* = 0.74, *P* < 0.05). *H. contortus* and *Heteropogon ritchiei* shared the most and the least similar bioclimatic envelopes with other species, respectively (Table 5).

Bioclimatic niche overlap between the wetland and grassland/savanna groups was overall low, with a *D* value of 0.190 and an *I* value of 0.410 (Fig. S3). Niche equivalency and similarity tests rejected the null hypothesis, indicating that the group climatic niche spaces are not identical or similar. Wetland species pairs showed greater bioclimatic niche overlap compared to the grassland/savanna species in niche equivalency and similarity tests (Table 5). For example, the bioclimatic niche of *Themeda caudata* was shared with most wetland species (Table 5). However, the bioclimatic niche also differed among some wetland species; for instance, *T. arundinacea* and *T. villosa* had very low *D* values (Table 5).

Variations in the bioclimatic envelopes occupied by the *Heteropogon-Themeda* clade partly explained distribution patterns at interspecific levels. Low *D* and *I* values were obtained between endemic species or between endemic and wide-ranging species, showing that the most narrow-ranging species occupy a unique climate space (Table 5). The climate space of *Themeda anathera* is dissimilar to that of the other species as shown by the significantly low *D* and *I* matrices in niche similarity tests (Table S4). This is also particularly true for other narrow-ranging species, *H. ritchiei*, *Themeda cymbaria* Hack., *Themeda helferi* Hack., *Themeda hookeri* (Griseb.) A. Camus, and *Themeda idjenensis* Jansen. However, most *D* and *I* values are significantly different from null distributions in equivalency tests (Table S4).

Overall, climatic niche analyses of *H. contortus* and *T. triandra* quantified a low, but significantly different climatic niche overlap of 0.29 and 0.39 for *D* and *I* values, respectively. When the continents are considered separately, the PCA explained 81.40% and 87.40% of the variance between *H. contortus* and *T. triandra* populations (Fig. 3). African *T. triandra* shares the most similar bioclimatic niche with South American *H. contortus* (*D* = 0.67, *I* = 0.79, *P* > 0.05; Table S5; Fig. S4). Asian and Australian *T. triandra* have lower overlap with the South American *H. contortus* when compared to the African *T. triandra* (*D* = 0.38 and 0.33, *I* = 0.61 and 0.48, *P* < 0.05; Table S5; Fig. S4). Asian and Australian groups are positioned in the more mesic and arid portions of the PCA surface (Fig. 3). High inter- and intraspecific overlaps between the temperate and tropical populations of both species showed no statistical differences (Table S6).
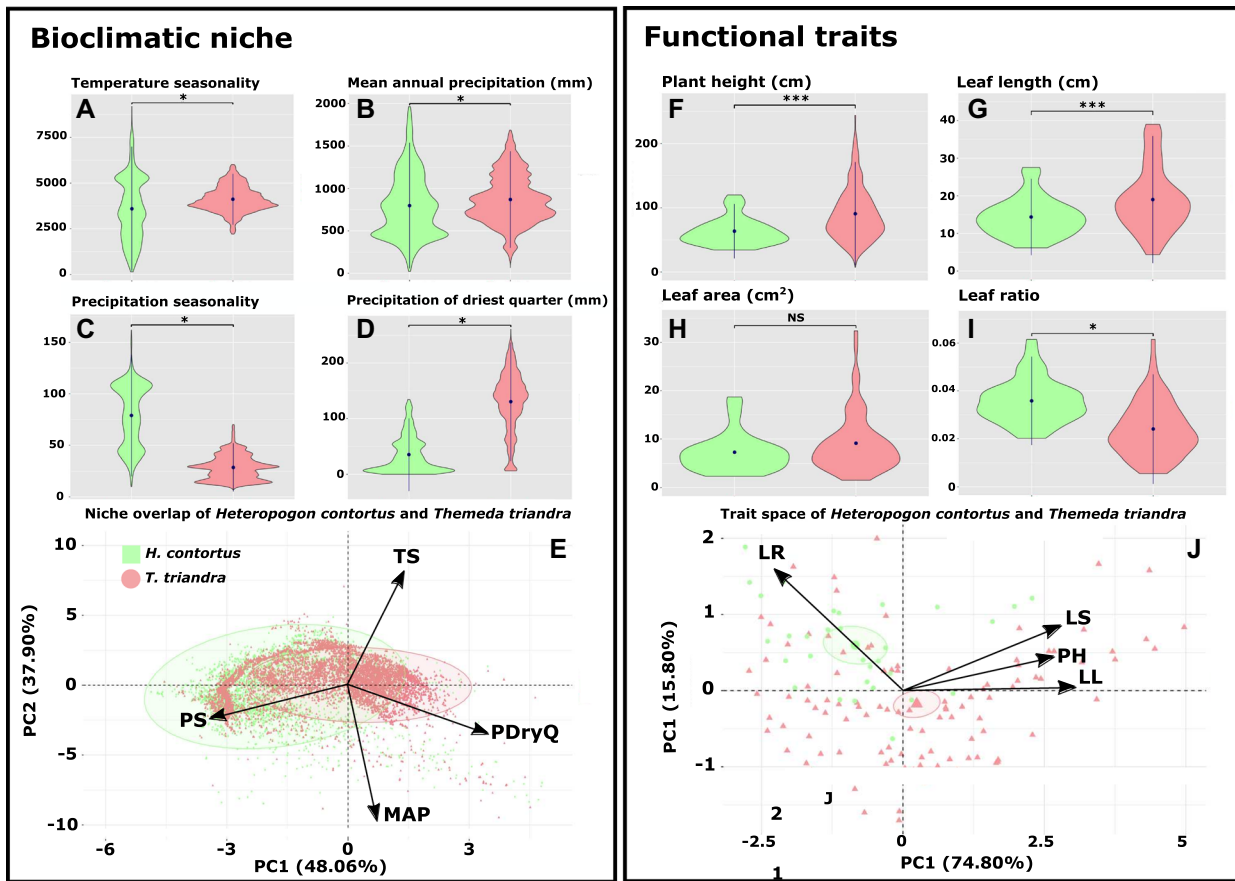
Fig. 2. Box plots showing significant differences in bioclimatic factors (**A–D**) and height- and size-related leaf traits, except leaf area (**F–I**) of two widespread species *Heteropogon contortus* and *Themeda triandra*. Bioclimatic niche space (**E**) and trait space (**J**) of two species were shown by principal component analyses. Bioclimatic niche: MAP = mean annual precipitation, PDryQ = precipitation of driest quarter, PS = precipitation seasonality, and TS = temperature seasonality; functional traits: LL = leaf length, LR = leaf ratio, LS = leaf size, and PH = plant height.

Table 4 Statistical differences in bioclimatic characteristics and functional traits between *Heteropogon contortus* and *Themeda triandra* tested by analysis of variance (ANOVA) and post hoc comparisons using the Tukey's honest significant difference test

	H. contortus (mean [SE])	*T. triandra* (mean [SE])	ANOVA test F-value	Tukey's honest significant difference test	Significance difference
Bioclimatic variables					
Temperature seasonality	3593 (20.2)	4115 (3.31)	2040	522.455	$P < 0.05$
Mean annual precipitation	797 (4.46)	869 (1.33)	351.2	71.940	$P < 0.05$
Precipitation seasonality	78.9 (0.351)	28.6 (0.056)	63 892	−50.307	$P < 0.05$
Precipitation of driest quarter	34.8 (0.399)	130 (0.249)	20 206	95.441	$P < 0.05$
Functional traits					
Maximum plant height (cm)	63.6 (3.64)	91.3 (1.64)	15.5	0.301	$P < 0.05$
Leaf length (cm)	14.4 (0.793)	21.0 (1.40)	10.29	0.299	$P < 0.001$
Leaf area (cm²)	7.26 (0.624)	9.13 (0.708)	2.02	0.167	$P > 0.05$
Leaf width to length ratio	0.036 (0.001)	0.026 (0.002)	21.75	−0.432	$P < 0.001$

Table 5 Matrix of background or similarity tests between species pairs of the *Heteropogon-Themeda* clade[†] in two directions

	HC	TT	TAV	HM	TQ	HT	TA	THO	TAN	TCY	TTR	HR	THE	TMO	TVI	TC	TIN	TAR	TG	TNO	TID
HC																					
TT																					
TAV																					
HM																					
TQ																					
HT																					
TA																					
THO																					
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TTR																					
HR																					
THE																					
TMO																					
TVI																					
TC																					
TIN																					
TAR																					
TG																					
TNO																					
TID																					

Savanna and wetland species are labeled by orange and blue boxes, respectively. Nonparametric tests were analyzed with 1000 pseudoreplicates by comparing with empirical *D* (upper diagonal) and *I* (lower diagonal) values. White and gray boxes indicate that the species pairs are significantly similar ($P > 0.05$) or dissimilar ($P < 0.05$), respectively; [†]Some species are discarded from the analyses as they provide less than five presence records that ENMTools package does not allow in the analyses;   HC = *Heteropogon contortus*, HM = *Heteropogon melanocarpus*, HR = *Heteropogon ritchiei*, HT = *Heteropogon triticeus*, TAN = *Themeda anathera*, TA = *Themeda arguens*, TAR = *Themeda arundinacea*, TAV = *Themeda avenacea*, TC = *Themeda caudata*, TCY = *Themeda cymbaria*, TG = *Themeda gigantea*, THE = *Themeda helferi*, THO = *Themeda hookeri*, TID = *Themeda idjenensis*, TIN = *Themeda intermedia*, TNO = *Themeda novoguineensis*, TQ = *Themeda quadrivalvis*, TT = *Themeda triandra*, TTR = *Themeda tremula*, TVI = *Themeda villosa*.
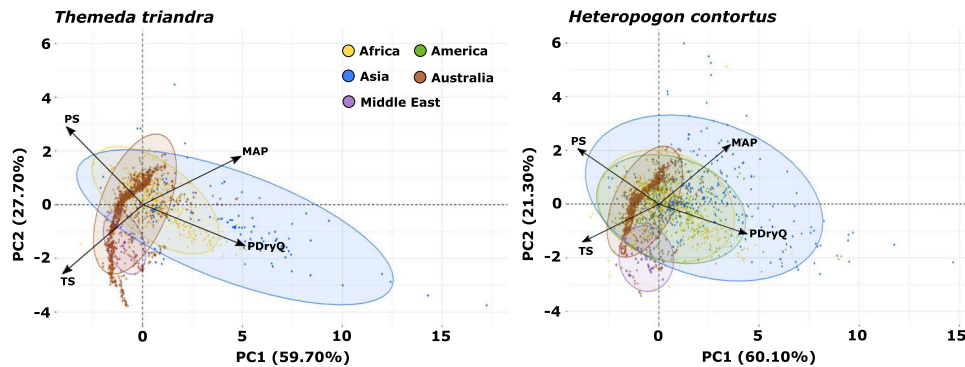

Fig. 3. Principal component analyses of climatic niche space using the four bioclimatic variables between *Heteropogon contortus* and *Themeda triandra* populations from Africa, America, Asia, Australia, and the Middle east. MAP = mean annual precipitation, PDryQ = precipitation of driest quarter, PS = precipitation seasonality, and TS = temperature seasonality.

3.5 Evolution of climatic niches and functional traits of the grassland/savanna and wetland species

Both bioclimatic niche and functional trait evolution had low phylogenetic signals as estimated by the *K* and λ indices (Table 6). The maximum likelihood estimation of bioclimatic variables on the phylogeny predicted intermediate levels of PS (PS ~ 90; Fig. 4C) and annual precipitation, but a low level of precipitation during the driest quarter (~60 mm; Fig. 4D) at the ancestral node of the wetland clade comprising *T. arundinacea*, *T. caudata*, *Themeda intermedia*, and *T. villosa* (Figs. 4C, 4D). Shifts into wetter conditions occur twice, one in the *T. arundinacea*, *T. caudata*, *T. intermedia*, and *T. villosa* clade,

Table 6 Comparative phylogenetic analyses of functional traits showing estimates of phylogenetic signal based on the maximum likelihood method with 1000 simulations

Traits	Phylogenetic signal K	λ	Best model	AICc	AICc weight	θ₁ (grassland/ savanna)	θ₂ (wetland)	α₁ (grassland/ savanna)	α₂ (wetland)	σ₁² (grassland/ savanna)	σ₂² (wetland)
Maximum plant height	0.18*	0	BM	22.94	< 0.01	-	-	-	-	0.061	0.061
			BMS	13.46	<0.01	-	-	0.975	0.975	0.204	0.204
			OU	19.99	<0.01	0.325	2.219	-	-	0.029	0.155
			OUM	8.72	0.02	0.072	2.111	11.967	11.967	1.443	1.443
			OUMA	**1.55**	**0.96**	0.102	2.094	0.754	0.861	0.105	0.105
			OUMV	10.25	0.01	0.081	2.112	9.244	9.244	1.318	0.399
Maximum leaf length	0.10*	0	BM	20.30	<0.01	-	-	-	-	0.070	0.070
			BMS	10.14	0.02	-	-	0.815	0.815	0.192	0.192
			OU	14.92	<0.01	0.333	1.634	-	-	0.030	0.164
			OUM	6.95	0.12	0.079	1.536	7.277	7.277	1.069	1.069
			OUMA	**3.17**	**0.79**	0.121	1.517	0.673	0.727	0.097	0.097
			OUMV	8.38	0.06	0.093	1.536	3.538	3.538	0.569	0.410
Leaf area	0.14*	0	BM	28.95	<0.01	-	-	-	-	0.263	0.263
			BMS	14.58	<0.01	-	-	1.578	1.578	1.059	1.059
			OU	**5.10**	**0.50**	0.683	1.591	-	-	0.142	0.634
			OUMA	9.02	0.07	0.103	1.344	27.121	27.121	9.634	9.634
			OUMV	5.46	0.42	0.153	1.353	1.332	1.320	0.534	0.534
						0.112	1.353	21.510	21.510	9.157	2.145
Leaf width to length ratio	0.10*	0	BM	46.50	<0.01	-	-	-	-	0.135	0.135
			BMS	16.81	<0.01	-	-	20.222	20.222	3.491	3.491
			OU	32.18	<0.01	-1.670	0.405	-	-	0.034	0.397
			OUM	18.42	<0.01	0.159	-1.73	10.080	10.080	1.690	1.690
			OUMA	**3.13**	**0.99**	0.158	-1.70	1.186	1.306	0.154	0.154
			OUMV	16.75	<0.01	0.065	-1.70	5.794	5.794	0.992	1.250
Awn length	0.06*	0	BM	33.54	<0.01	-	-	-	-	0.139	0.139
			BMS	8.38	0.28	-	-	38.006	38.006	7.868	7.686
			OU	23.38	<0.01	0.914	0.425	-	-	0.039	0.361
			OUM	10.99	0.08	0.720	0.074	16.709	16.709	5.695	5.695
			OUMA	**6.80**	**0.62**	0.760	0.133	0.841	0.892	0.171	0.171
			OUMV	13.71	0.02	0.727	0.089	6.802	6.802	1.426	1.557

Parameter estimations (θ, α, and σ) from the best evolutionary model determined by the lowest value of Akaike's Information Criterion with a correction for a small design (AICc) and AICc weight value among six candidate models (BM, BMS, OU, OUM, OUMA, and OUMV). The best models are marked by bold letters; asterisks above the values of phylogenetic signal indicate that they are significantly different from zero. AICc, Akaike's Information Criterion with a correction.
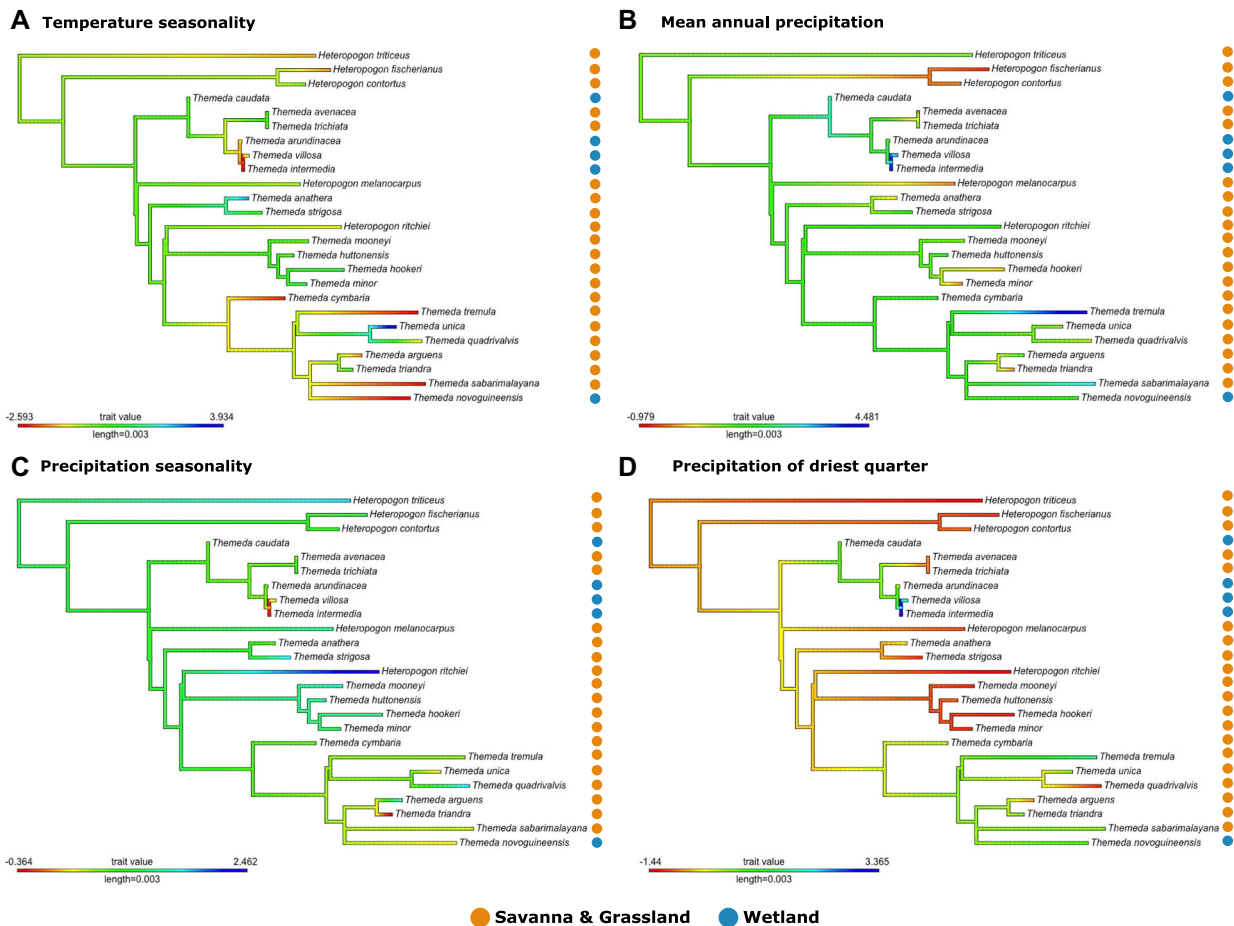
Fig. 4. Phylogenetic visualization of ancestral state reconstructions of four bioclimatic niche evolution, temperature seasonality (**A**), mean annual precipitation (**B**), precipitation seasonality (**C**), and precipitation of the driest quarter (**D**).

and the other in *Themeda novoguineensis* (Figs. 4C, 4D). A possible reversal from mesic habitats to a drier savanna environment was also observed in the clade of *Themeda avenacea* and *Themeda trichiata*.

Plant height, leaf length, leaf width, leaf area, and awn length showed low phylogenetic signals (0.06–0.18; Table 6). The analyses suggested OUMA best-fit models are selected for culm height, leaf length, leaf area, leaf width to length ratio, and awn length. The OUMA model suggested that the wetland functional traits diverged toward significantly higher trait values than the grassland/savanna ones as indicated by higher ϑ values. Nonzero α values indicated that selective pressure was put on trait adaptation in the grassland/savanna and wetland groups (Fig. 5A; Table 6).

The most likely ancestral state of the *Heteropogon-Themeda* clade was the geniculate awn with a probability of 0.62 (Fig. 5B; Table 7). Character mapping made it clear that straight awns are mostly present in wetland species, while the awns of the grassland/savanna species were mostly geniculate (Fig. 5B). The best model of awn evolution showed unequal and reversible states between geniculate and straight types, and between geniculate and awnless ones, but not between straight and awnless (Fig. 5C; Table S7). Transition rates between states were obtained from median values and presented in the state transition diagram (Fig. 5C). The rates

of changes from the derived states back to the geniculate state were much higher than those of changes from geniculate towards the derived states, 3.75 versus 12.07 (geniculate⇌straight) and 1.67 versus 17.55 (geniculate⇌awnless) (Fig. 5C; Table 7). Furthermore, transitions from geniculate to straight were faster than the transition to awnless (3.75 vs. 1.67; Fig. 5C; Table 7). The reversible rates between straight and awnless states were equal to zero.

4 Discussion

We present evidence for repeated biome shifts between savannas and wetlands related to functional traits that have adaptive significance. Within the *Heteropogon-Themeda* clade, climatic niche shifts between grasslands/savannas and wetlands are labile evolutionary processes that have occurred multiple times in a relatively short period (~10 million years). The evolutionary lability that we observe might be related to three different processes. First, grassland/savanna-wetland mosaics represent habitat proximity and facilitate species movements from grasslands/savannas to wetlands and vice versa (Donoghue & Edwards, 2014). Second, wetlands could have left some functional niche roles vacant due to being a relatively low biodiversity
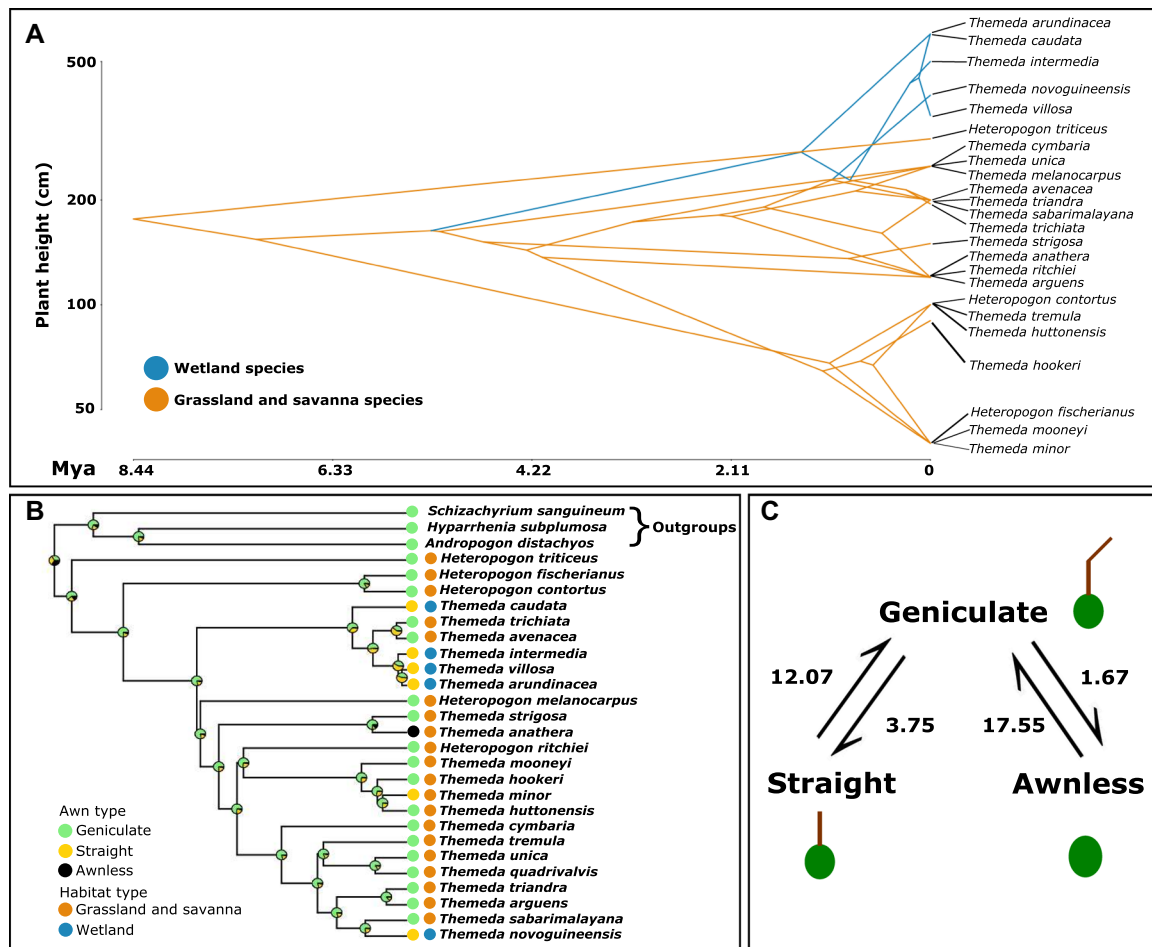
Fig. 5. Phylogenetic comparative analysis of two morphological traits, maximum plant height (**A**) evolved through the Ornstein–Uhlenbeck (OU) model towards different trait optima, ancestral state reconstruction of awn type (**B**), and transition diagram between states (**C**).

Table 7 Awn-type evolution analysis showing transition rates with a 95% confidence interval (CI) and mean between three states (geniculate [0], straight [1], and awnless [2]), probabilities at the ancestral node of the *Heteropogon-Themeda* clade, and the total time spent in each state

	Geniculate (95% CI [mean])	Straight (95% CI [mean])	Awnless (95% CI [mean])	Probability at the ancestral node	Mean total time spent in each state
Geniculate	-	3.72–3.77 (3.75)	1.66−1.68 (1.67)	0.62	0.79
Straight	12.01−12.13 (12.07)	-	0 (0)	0.23	0.17
Awnless	17.47−17.63 (17.55)	0 (0)	-	0.15	0.04

Note that there are 48.63 changes between states on average.

habitat (Hector, 2011; Deane et al., 2016). Wetlands could also have imposed functional constraints, as reflected in the small number of grass lineages found within them (Du et al., 2016) and costly specialized functional adaptations to flooding stress (Moor et al., 2017; VanWallendael et al., 2019). Lastly, natural grass invasiveness (e.g., tall stature) permits grasses to compete and replace other species (Linder et al., 2018; Canavan et al., 2019).

Although biome shifts were documented to drive evolution to form distinct habitat groups of the *Heteropogon-Themeda*

clade, discordance between habitat occupancy and distribution patterns leaves some questions unanswered. Currently, wetland species are confined to Southeast Asia and parts of India (POWO, 2019), and a high proportion of tropical wetlands exist in Southeast Asia (Greb et al., 2006; Finlayson et al., 2018; Toochi et al., 2019). Within the *Heteropogon-Themeda* lineage, the observation of fewer species in wetlands than in grasslands/savannas (7 vs. 24 species) may reflect the limitations of the wetland species in dispersal and/or establishment. The dispersal limitations could be due to (1) habitat

unavailability, (2) insufficient time to diversify, and (3) failure to diversify (Sexton et al., 2017; Sheath et al., 2020). Habitat unavailability is an unlikely cause since savanna-wetland mosaics are prevalent (Bertassello et al., 2021), but African wetlands have not been colonized by *Heteropogon-Themeda* wetlands species despite some wetland species sharing bioclimatic preferences with other species (e.g., *Themeda arundinacea*; Table 5). The patchy nature of wetlands across the tropics could also slow the rate of dispersal. Insufficient time might not be the case as the speciation events of the clade occurred in a relatively short timescale. Failure to diversify is likely, but largely understudied. One possibility is that the wetland species might not possess enough diverse subpopulations to migrate and adapt to new local conditions (Sexton et al., 2017).

Within the *Heteropogon-Themeda* clade, we documented clearly distinct trait syndromes related to growth and dispersal between the grassland/savanna and wetland species. Greater culm height, leaf length, and leaf area in the wetland species indicated that they use different growth strategies from the grassland/savanna species. The tall stature of wetland species could simply be a result of high water availability that promotes plant growth (Moles et al., 2009), and facilitates light capture in a competitive environment (Craine & Dybzinski, 2013). In contrast, the overall shorter stature of savanna species is likely related to water availability and seasonal dryness (Fig. 1; Colmer & Voesenak, 2009; Olson et al., 2018), although within savannas, positive relationships between plant height and flammability have also been observed (Simpson et al., 2016), just as positive correlations have also been found between plant height and range size in the Andropogoneae (Mashau et al., 2021). Within the wetland species, greater leaf area is thought to have parallel adaptation with plant height to accommodate plant production, where the smaller leaves of grassland/savanna species could help mitigate drought effects by reducing transpiration (Farooq et al., 2012). Under inundating conditions, wetland species should benefit from nonhygroscopic straight awns through vertical diaspore burial rather than the twisting activities produced by geniculate awns (Peart, 1981). Alternatively, there could be a reduction in awn function that results in a dispersal mode relying on hydrochory (Nilsson et al., 2010). Active twisting functions in hygroscopic awns of the grassland/savanna species should bury diaspores well in humid accessible soil or cracking surface, enabling avoidance of fire (Peart, 1979, 1981). Peart & Clifford (1987) showed that moisture and soil types show the composite effects in awn functions. However, the exact selective pressures between these two awn types and their associations with dispersal and burial efficiency remain unknown. Apart from the moisture, Garnier & Dajoz (2001) found that fire characteristics positively correlate with awn length, where significantly different awn lengths in the grassland/savanna and wetland species could indicate the different fire regimes in these systems. Fine-grained fire, community composition, and awn length data would be required to test the effect of fire on dispersal traits.

Trait adaptability aligns well with the concept of pre-existing traits, or preadaptation facilitating biome shifts (Donoghue & Edwards, 2014). Tall stature is a conserved trait of the Andropogoneae (including the *Heteropogon-Themeda* clade) that has increased since the emergence of the ancestor of Andropogoneae (Liu et al., 2012). The ancestor of the *Heteropogon-Themeda* clade had a relatively high stature of approximately two meters, taller than most other C$_4$ grasses (Fig. 5A). The grassland/savanna and wetland species evolved towards different optimal heights to survive in different environmental conditions and competitive environments. Selection acting on leaf length and area by precipitation was estimated in this study (different α values; Table 6) and supported by Gallaher et al. (2019). Evolution towards higher trait optima in wetlands is more constrained (higher α values) than in grassland/savanna environments. Taller height and greater size-related leaf traits among the wetland species imply adaptive phenotypes as they invest and maintain growth in the presence of inter- and intra-specific competition under high availability of water (van Kleunen & Fischer, 2005). In contrast, reductions in plant height or leaf length in savanna species are considered passive adaptations as the plant does not allocate sufficient resource to growth in the limited resource (Falster & Westoby, 2003). In addition, awn characteristics are not conserved within the lineage as they commonly vary within grass lineages (Humphreys et al., 2010; Teisher et al., 2017). The lability may be linked to genetic control of awn development based on multiple genes regulating the expression of multiple characteristics (e.g., length, type, awn presence; Ntakirutimana & Xie, 2019; Huang et al., 2021).

Bioclimatic factors, habitats, and functional traits partially explained broad-level distributions at the species level. Overall climatic variables of *Heteropogon contortus* and *Themeda triandra* have significantly different climatic niches (Fig. 2; Table 4). Wider windows of temperature and PS of *H. contortus* (Figs. 2A, 2C) explain success in the ecological invasion of *H. contortus* on islands (Tothill & Hacker, 1976; Oviedo Prieto et al., 2012). *H. contortus* usually colonizes dry habitats and exposed rock outcrops where *T. triandra* is absent (Wang et al., 2016; Xavier & D'Antonio, 2017, pers. obs.). This contrast aligns well with a low range of precipitation of the driest quarter that most *H. contortus* can tolerate (Fig. 2D). Shorter plant height, leaf length, and smaller leaf ratio of *H. contortus* hinted at drought avoidance in arid conditions and tolerate intense solar radiance in low shade (Wang et al., 2016). In contrast, Snyman et al. (2013) suggested that *T. triandra* grows in the areas where annual rainfall reaches higher than 750 mm, and this results in taller stature and greater leaf size of *T. triandra* than those of *H. contortus*, as also found in this study (Fig. 2F). *Themeda triandra* fails to persist through the long dry season as water shortage leads to loss of leaves more quickly than *H. contortus* under equivalent conditions (Mott et al., 1992).

At a continental scale, precipitation and seasonality regimes cannot explain the geographic separation between *H. contortus* and *T. triandra*. The climatic similarity between African *T. triandra* and South American *H. contortus* showed that climatic conditions might not limit the spread of *T. triandra* to South America (Fig. 3; Table S5), where *T. triandra* may be the most likely to colonize. Alternatively, biotic interactions may regulate population dynamics at a local scale (Wisz et al., 2013). Use of climatic variables to explain smaller-scale distribution patterns at the species level could pose some technical limitations (Jardine et al., 2020). Alternatively, underlying factors controlling

these unequal distributions of *H. contortus* and *T. triandra* (e.g., fire, edaphic properties, competition) and environment–trait correlations have not been revealed in this study. Fine-grained plot data from local community assemblages are required to address these questions.

The grassland/savanna species provide an example of a common phenomenon that widespread pantropical species, *H. contortus* and *T. triandra,* encompass bioclimatic envelopes of their relatives with more narrow ranges (Table 5). For example, *H. contortus* and *T. triandra* co-exist with *Themeda anathera* in subtropical montane savanna in the absence of other relatives. An underlying cause may be that *H. contortus* and *T. triandra* consist of ecologically distinct populations, where some populations can tolerate environmental stress at a time through local adaptations (e.g., multiple ploidy levels; Tothill & Hacker, 1976; Ahrens et al., 2020; or phenotypic/genotypic plasticity; Dell'Acqua et al., 2014). In addition, species with more narrow ranges or restricted distribution hinted at. *H. triticeus* and *Themeda arguens* being Southeast Asian natives, and Asian savannas are known to have unique climatic control (Ratnam et al., 2016). Likewise, completely dissimilar climatic preferences of *Heteropogon ritchiei* and *T. tremula* (Indian peninsula endemics) also reflect habitat diversity across savannas.

5 Conclusion

The *Heteropogon-Themeda* clade shows clear climatic niche shifts between grasslands/savannas and wetlands, and adaptive traits associated with these habitats. In our bioclimatic analyses, precipitation is the main correlate separating habitat types and where between habitats, there are systematic differences in plant height, leaf length, leaf area, leaf width to length ratio, awn length, and awn types in grassland/savanna and wetland species. The clear delimitation of habitat subgroups indicates that C_4 grassy biomes are diverse in their environments and functional traits. Phylogenetic investigations suggest that the *Heteropogon-Themeda* clade originated in savanna environments, with adaptive traits of the grassland/savanna and wetland species diverging into wetland-associated climatic niches under distinct selective pressures. Biogeographic and functional ecology research in other grass clades with expanded environment, trait, and molecular data will provide broader insight into the assembly of tropical grassy ecosystems. Both *Themeda* and *Heteropogon* species can be keystone species in the environments in which they are found (Snyman et al., 2013). As impacts of climate change and human activities increase, it is worth paying attention to wetlands and their endemic and overlooked grass species that occupy specific and climatically sensitive habitats. Likewise, for savannas, degradation processes impact taxonomic and functional diversity.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12846/suppinfo

Fig. S1. Principle component analysis (PCA) of 19 bioclimatic variables complied from all *Heteropogon* and *Themeda* species showing the first two axes which represent accumulated percentage of 71.60% of all variation (**A**) Pearson's coefficient matrix among 19 bioclimatic variables (**B**) Principal component analysis of 4 selected bioclimatic variables showing the first two axes explaining 88.80% of variation (**C**).

Fig. S2. Quantitative functional traits contribution plot with the first two axes explaining 67.40% of variation (**A**) Qualitative traits contribution plot with the first two axes

explaining 67.40% of variation (**B**) The positions and directions of eigenvectors in both plots indicate the relationships among bioclimatic variables.

Fig. S3. Niche overlap analysis among grassland/savanna and wetland species by PCA-env methods using four bioclimatic variables illustrating niche separation between two groups. Schoener's D and Warren's I metrices representing degree of niche overlap (D = 0.190, I = 0.410) between the two groups with statistical significance from both niche equivalency and similarity tests indicating that the two groups are not identical in occupying climatic niche spaces.

Fig. S4. Climatic niche overlap comparisons between American *H. contortus* and Asian (**A**), African (**B**), Australian (**C**), and overall tropical (**D**) *T. triandra* populations. Green and red areas represent bioclimatic envelopes of *H. contortus* and *T. triandra*, respectively. Solid and dash lines cover 100% and 50% of background or available environments.

Table S1. List of quantitative vegetative and reproductive traits of *Heteropogon* and *Themeda* species used in this study.

Table S2. List of qualitative vegetative and reproductive traits of *Heteropogon* and *Themeda* species used in this study.

Table S3. PCA and FAMD results of bioclimatic data and functional traits

Table S4. Matrix of background or similarity tests between species pairs of 21 *Heteropogon-Themeda* clade in two directions. White and grey boxes indicate that the species pairs are significantly similar ($p > 0.05$) or dissimilar ($p < 0.05$), respectively. Non-parametric tests were performed with 1000 pseudoreplicates (Warren et al, 2021). Schoener's D (upper diagonal) and Warren's I (lower diagonal) matrix from niche equivalency tests indicating how niche between species pair is identical (interchangeable).

Table S5. Schoener's D (upper diagonal) and Warren's I (lower diagonal) matrix from niche equivalency and similarity tests assessing how bioclimatic niches between *Heteropogon contortus* (HC) and *Themeda triandra* (TT) populations among continents in the Tropics are distinct.

Table S6. Schoener's D (upper diagonal) and Warren's I (lower diagonal) matrix from niche equivalency and similarity tests assessing how bioclimatic niches between *Heteropogon contortus* (HC) and *Themeda triandra* (TT) populations in tropical and temperate regions are not significantly different.

Table S7. Alternative model comparisons showing log likelihood values, probabilities at root nodes (R1, R2, R3), and transition rates among states.

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