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Research Article

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 overparameterization, 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 "FactoMineR" 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 nonparametric 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

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)	✓

Continued

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 (σ^2) 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 $R = h^2S$ 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," "waterlogged 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

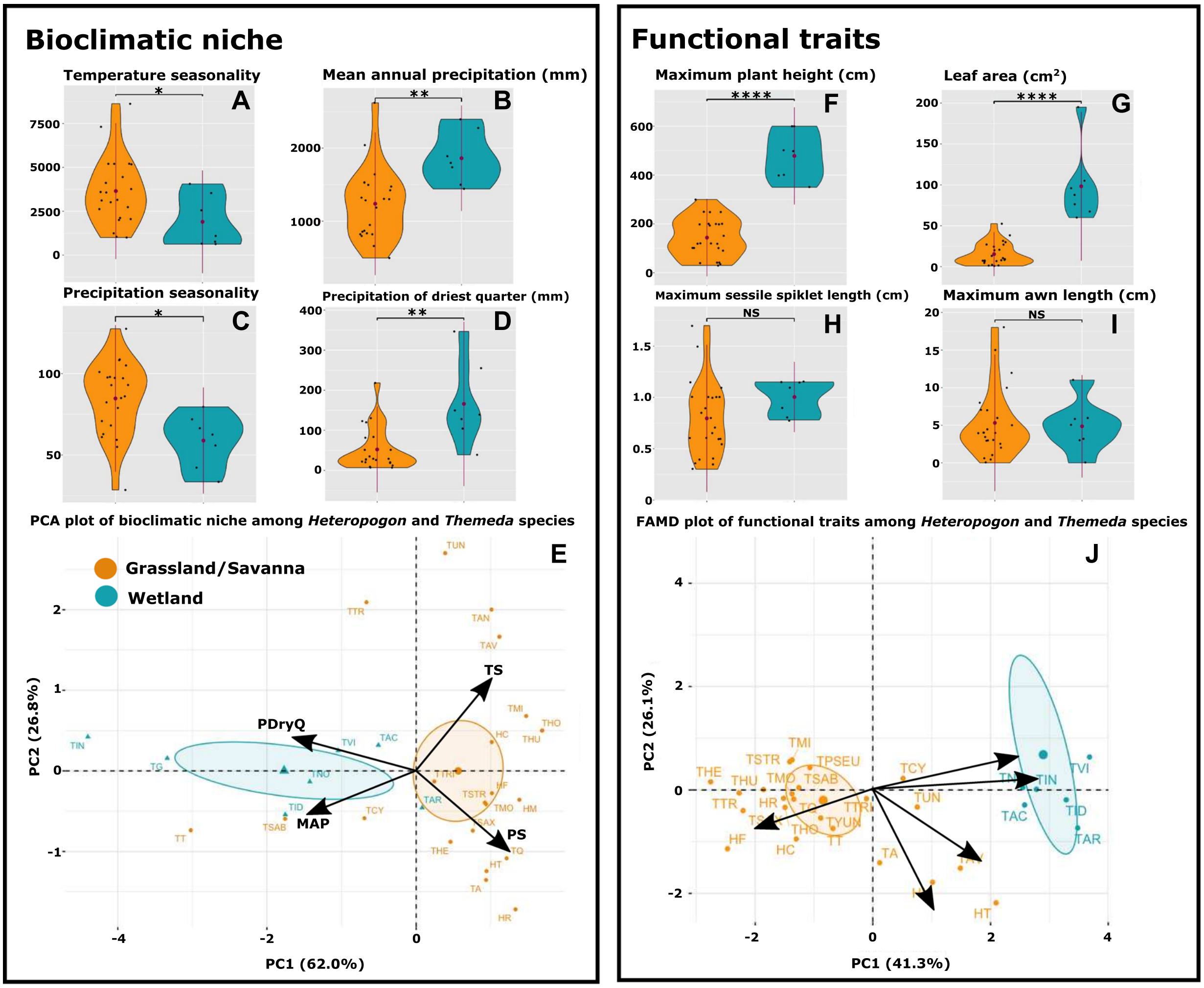

Fig. 1. Box plots representing bioclimatic ranges (**A**–**D**) and functional traits (**F**–**I**) between grassland/savanna (orange) and wetland (blue) and principal component analysis (PCA) of bioclimatic variables (**E**) and functional traits (**J**) of *Heteropogon* and *Themeda* species distinguishing 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 cm^2) than the grassland/savanna species (15.3 ± 2.75 cm^2) ($P < 0.05$; 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 (cm^2)	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).

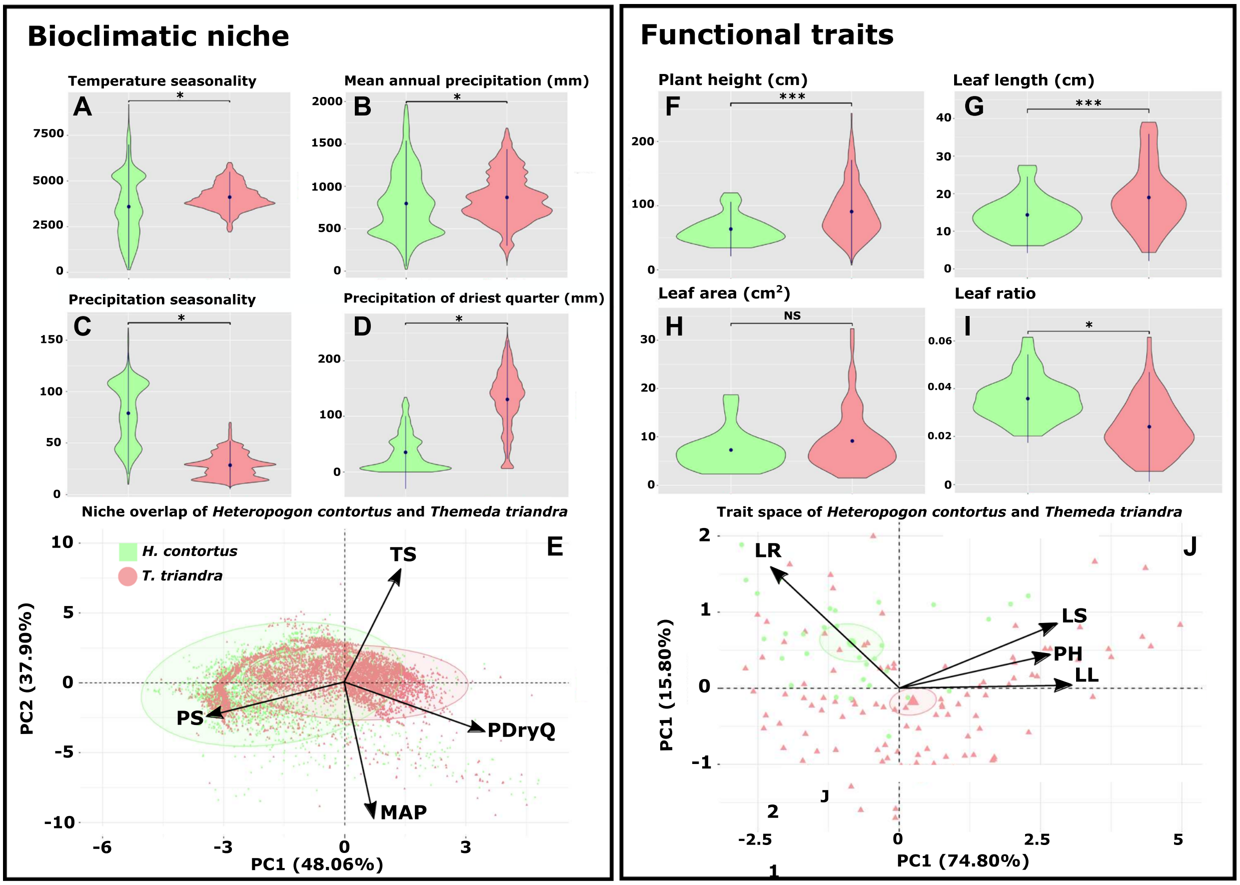

Fig. 2. Box plots showing significant differences in bioclimatic factors (**A**–**D**) and height- and size-related leaf traits, except leaf area (**F**–**I**) of two widespread species *Heteropogon contortus* and *Themeda triandra*. Bioclimatic niche space (**E**) and trait space (**J**) of two species 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 (cm^2)	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	□	□	□	□	▨	▨	▨	■	▨	▨	▨	▨	▨	▨	□	▨	▨	□	▨	▨	▨
TAN	□	▨	□	□	▨	▨	▨	▨	■	▨	▨	▨	▨	▨	□	□	▨	▨	▨	▨	▨
TCY	▨	□	▨	□	▨	▨	▨	▨	▨	■	▨	▨	▨	▨	▨	□	□	□	▨	▨	▨
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*.

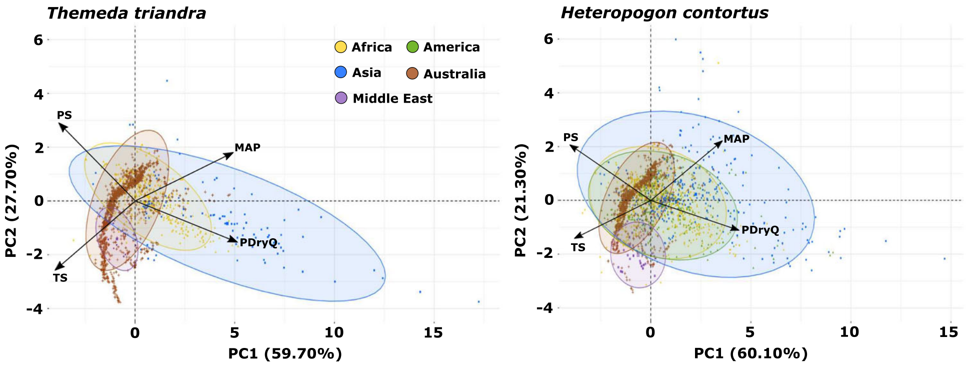

Fig. 3. Principal component analyses of climatic niche space using the four bioclimatic variables between *Heteropogon contortus* and *Themeda triandra* populations from Africa, America, Asia, Australia, and the Middle east. MAP = mean annual precipitation, PDryQ = precipitation of driest quarter, PS = 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		Best model	AICc	AIcc weight	θ_1 (grassland/savanna)	θ_2 (wetland)	α_1 (grassland/savanna)	α_2 (wetland)	σ_1^2 (grassland/savanna)	σ_2^2 (wetland)
	K	λ									
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	26.56	<0.01	0.683	1.591	-	-	0.142	0.634
			OUM	**5.10**	**0.50**	0.103	1.344	27.121	27.121	9.634	9.634
			OUMA	9.02	0.07	0.153	1.353	1.332	1.320	0.534	0.534
			OUMV	5.46	0.42	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.

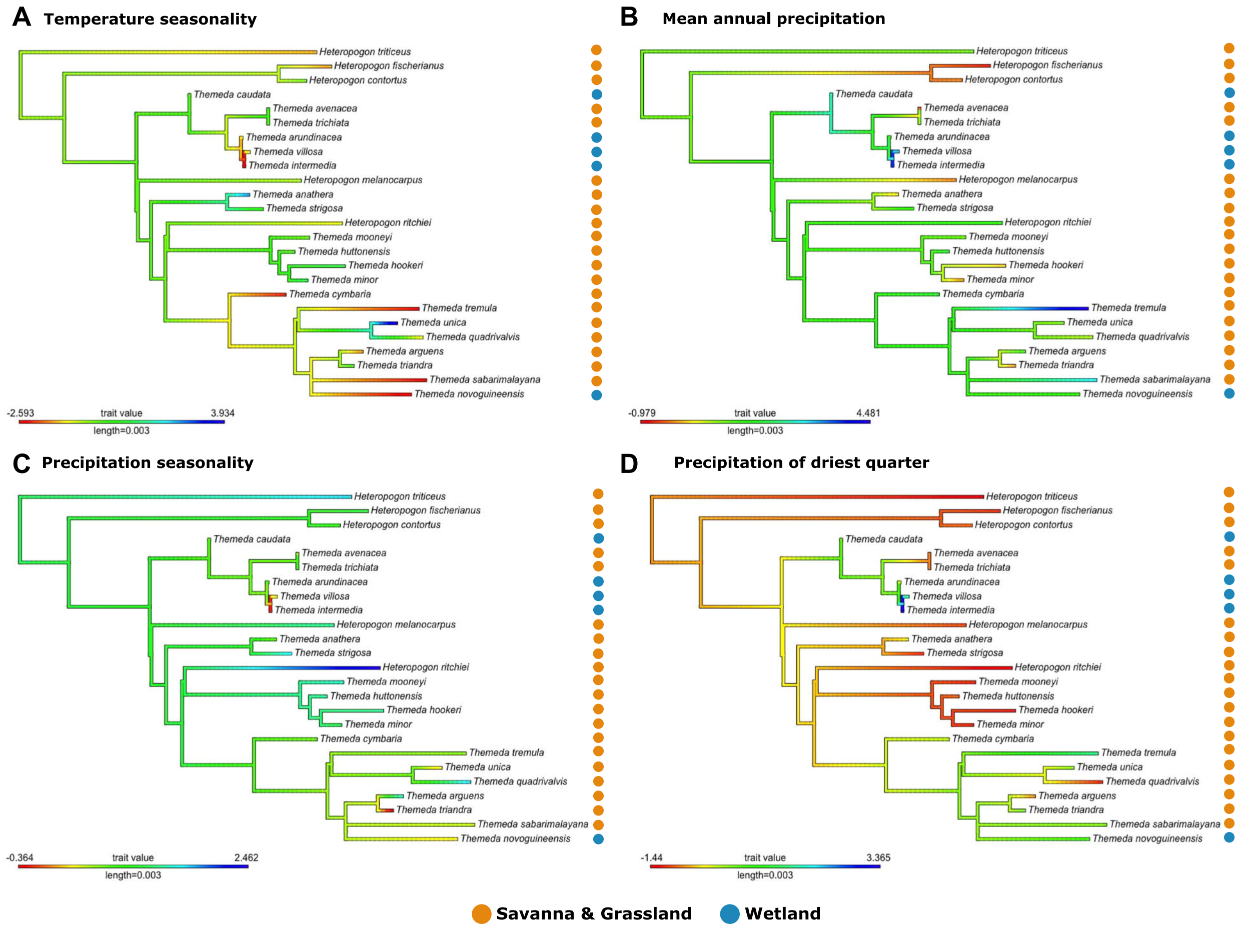

Fig. 4. Phylogenetic visualization of ancestral state reconstructions of four bioclimatic niche evolution, temperature seasonality (**A**), mean annual precipitation (**B**), precipitation seasonality (**C**), and precipitation of the driest quarter (**D**).

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

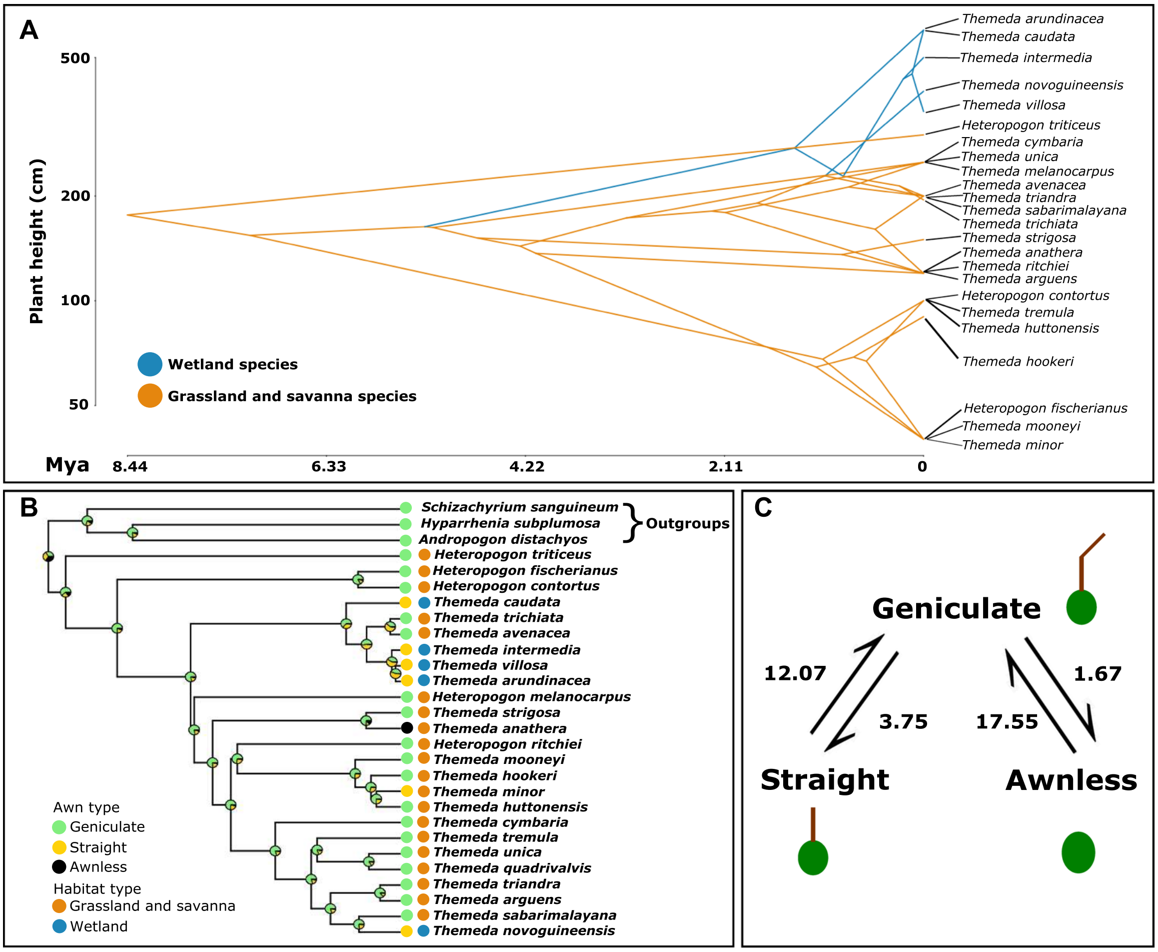

Fig. 5. Phylogenetic comparative analysis of two morphological traits, maximum plant height (**A**) evolved through the Ornstein–Uhlenbeck (OU) model towards different trait optima, ancestral state reconstruction of awn type (**B**), and transition diagram between states (**C**).

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 preexisting 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 intraspecific 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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References

Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164: S165–S184.

Ahrens CW, James EA, Miller AD, Scott F, Aitken NC, Jones AW, Lu-Irving P, Borevitz JO, Cantrill DJ, Rymer PD. 2020. Spatial, climate and ploidy factors drive genomic diversity and resilience in the widespread grass *Themeda triandra*. *Molecular Ecology* 29(20): 3872–3888.

Amarasinghe L, Pemadasa MA. 1982. The ecology of a montane grassland in Sri Lanka. II. The pattern of four major grasses. *Journal of Ecology* 70: 17–23.

Amjad MS, Arshad M, Sadaf HM, Shahwar D, Akrim F, Arshad A. 2016. Floristic composition, biological spectrum and conservation status of the vegetation in Nikyal valley, Azad Jammu and Kashmir. *Asian Pacific Journal of Tropical Disease* 6: 63–69.

Arthan W, Dunning LT, Besnard G, Manzi S, Kellogg EA, Hackel J, Lehmann CER, Mitchley J, Vorontsova MS. 2021. Complex evolutionary history of two ecologically significant grass genera *Themeda* and *Heteropogon* (Poaceae: Panicoideae: Andropogoneae). *Botanical Journal of the Linnean Society* 196(4): 437–455.

Aubin I, Munson AD, Cardou F, Burton PJ, Isabel N, Pedlar JH, Paquette A, Taylor AR, Delagrange S, Kebli H, Messier C, Shipley B, Valladares F, Kattge J, Boisvert-Marsh L, McKenney D. 2016. Trait to stay, traits to move: A review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environmental Reviews* 24: 1–23.

Barkworth ME, Capels KM, Long S, Piep MB eds. 2003. *Flora of North America north of Mexico, Vol. 25. Magnoliophyta: Commelinidae (in part): Poaceae, Part 1*. New York: Oxford University Press.

Barrow CJ. 1994. *Wetlands*. New York: Land Degradation & Development.

Bazzaz FA. 1991. Habitat selection in plants. *The American Naturalist* 137: S116–S130.

Beaulieu JM, Jhwueng DC, Boettiger C, O'Meara BC. 2012. Modeling stabilizing selection: Expanding the Ornstein–Uhlenbeck model of adaptive evolution. *Evolution* 66(8): 2369–2383.

Bertassello LE, Bertuzzo E, Botter G, Jawitz JW, Aubeneau AF, Hoverman JT, Rinaldo A, Rao PSC. 2021. Dynamic spatio-temporal patterns of metapopulation occupancy in patchy habitats. *Royal Society Open Science* 8: 201309.

Bhatia KK. 1958. A mixed teak forest of central India. *Journal of Ecology* 46: 43–63.

Biswas O, Ghosh R, Paruya DK, Mukherjee B, Thapa KK, Bera S. 2016. Can grass phytoliths and indices be relied on during vegetation and climate interpretations in the eastern Himalayas? Studies from Darjeeling and Arunachal Pradesh, India. *Quaternary Science Reviews* 134: 114–132.

Blomberg SP, Garland T, Jr., Ives AR. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* 57: 717–745.

Bocksberger G, Schnitzler J, Chatelain C, Daget P, Janssen T, Schmidt M, Thiombiano A, Zizka G. 2016. Climate and the distribution of grasses in West Africa. *Journal of Vegetation Science* 27(2): 306–317.

Bor NL. 1951. Some new Indian grasses. *Kew Bulletin* 6(3): 445–453.

Bor NL. 1960. *The grasses of Burma, Ceylon, India and Pakistan (excluding Bambuseae)*. Oxford: Pergamon Press.

Bortherton SJ, Joyce CB. 2015. Extreme climate events and wet grasslands: Plant traits for ecological resilience. *Hydrobiologia* 750: 229–243.

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014. BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 10: e1003537.

Broennimann O, Fitzpatrick M, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin MJ, Randin C, Zimmermann NE, Graham CH, Guisan A. 2011. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* 21(4): 481–497.

Brummit RK. 2001. World Geographical Scheme for Recording Plant Distributions. Edition 2. Biodiversity Information Standards (TDWG). Available from http://www.tdwg.org/standards/109 [accessed March 2021].

Butler MA, King AA. 2004. Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *The American Naturalist* 164(6): 683–695.

Canavan S, Meyerson LA, Packer JG, Pyšek P, Maurel N, Lozano V, Richardson DM, Brundu G, Canavan K, Cicatelli A, Čuda J, Dawson W, Essl F, Guarino F, Guo WY, van Kleunen M, Kreft H, Lambertini C, Pergl J, Skálová H, Soreng RJ, Visser V, Vorontsova MS, Weigelt P, Winter M, Wilson JRU. 2019. Tall-statured grasses: A useful functional group for invasion science. *Biological Invasions* 21: 37–58.

Caruso CM, Mason CM, Medeiros JS. 2020. The evolution of functional traits in plants: Is the giant still sleeping? *International Journal of Plant Sciences* 181: 1–8.

Cavanagh AM, Godfree RC, Morgan JW. 2019. An awn typology for Australian native grasses (Poaceae). *Australian Journal of Botany* 67(4): 309–334.

Cayssials V, Rodríguez C. 2013. Functional traits of grasses growing in open and shaded habitats. *Ecology and Evolution* 27: 393–407.

Chamberlain S, Barve V, Mcglinn D, Oldoni D, Desmet P, Geffert L, Ram K. 2020. rgbif: Interface to the global biodiversity information facility API. R package version 3.5.2. Available from https://CRAN.R-project.org/package=rgbif [accessed July 2020].

Chao L. 2009. Effects of *Eupatorium Adenophorum* Sprengel invasion on soil substrate-induced respiration. *Bulletin of Botanical Research* 27(6): 729–735.

Chen-feng L, Zheng-ning W, Kang-ning HE, Jing Y, Wei-qiang Z, Jing-hui T. 2004. Change of soil water content and light of several plantations at loess plateau semi-arid area and its effect on forest stand. *Journal of West China Forestry Science* 33: 34.

Clayton WD, Vorontsova MS, Harman KT, Williamson H. 2006. GrassBase—The Online World Grass Flora. Kew: Royal Botanic Gardens, Kew. Available from http://www.kew.org/data/grasses-db.html [accessed November 2020].

Colmer TD, Voesenak LACJ. 2009. Flooding tolerance: Suites of plant traits in variable environments. *Functional Plant Biology* 36(8): 665–681.

Cooper N, Thomas GH, Venditti C, Meade A, Freckleton RP. 2016. A cautionary note on the use of Ornstein-Uhlenbeck models in macroevolutionary studies. *Biological Journal of the Linnean Society* 118: 64–77.

Craine JM, Dybzinski R. 2013. Mechanisms of plant competition of nutrients, water and light. *Functional Ecology* 27(4): 833–840.

Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, Weston PH, Westoby M, Wilf P, Linder HP. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458: 754–756.

Crisp MD, Cook LG. 2012. Phylogenetic niche conservatism: What are the underlying evolutionary and ecological causes? *New Phytologist* 196(3): 681–694.

Daehler CC, Carino DA. 1998. Recent replacement of native pili grass (*Heteropogon contortus*) by invasive African grasses in the Hawaiian Islands. *Pacific Science* 52(3): 220–227.

Dangol DR, Maharjan KL. 2012. Spatial and temporal dynamics of flora in forest, grassland and common land ecosystems of Western Chitwan, Nepal. *Kokusai Kyoryoku Kenkyushi* 18(4): 77–92.

Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772.

Deane DC, Fordham DA, He F, Bradshaw CJA. 2016. Diversity patterns of seasonal wetland plant communities mainly driven by rare terrestrial species. *Biodiversity and Conservation* 25: 1569–1585.

Dell'Acqua M, Fricano A, Gomarasca S, Caccianiga M, Piffanelli P, Bocchi S, Gianfranceschi L. 2014. Genome scan of Kenyan *Themeda triandra* populations by ALFP markers reveals a complex genetic structure and hints for ongoing environmental selection. *South African Journal of Botany* 92: 28–38.

Deshpande UR. 1988. The genus *Heteropogon* Pers. (Poaceae) in India. *Bulletin of the Botanical Survey of India* 30: 120–125.

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A. 2016. Ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography* 40(6): 774–787.

Djufri D, Wardiah W. 2017. The diversity of undergrowth plants on *Acacia nilotica* stands as food resources of banteng (*Bos jabanicus*) in Baluran National Park, East Java, Indonesia. *Biodiversitas* 18: 288–294.

Donoghue MJ, Edwards EJ. 2014. Biome shifts and niche evolution in plants. *Annual Review of Ecology, Evolution, and Systematics* 45: 547–572.

Du ZY, Wang QF, China Phylogeny Consortium. 2016. Phylogenetic tree of vascular plants reveal the origins of aquatic angiosperms. *Journal of Systematics and Evolution* 54(4): 342–348.

Dunning LT, Liabot AL, Olofsson JK, Smith EK, Vorontsova MS, Besnard G, Simpson KJ, Lundgren MR, Addicott E, Gallagher RV, Chu Y, Pennington RT, Christin PA, Lehmann CER. 2017. The recent and rapid spread of *Themeda triandra*. *Botany Letters* 164: 327–337.

Dutta R, Sarma SK. 2018. Growth forms, phenology, composition and uses of the aquatic macrophytes found in the downstream of the Subansiri river ecosystem, Assam. *International Journal of Basic and Applied Research* 8(8): 408–420.

Eden MJ. 1974. The origin and status of savanna and grassland in Southern Papua. *Transactions of the Institute of British Geographers* 63: 97–110.

Ens E, Hutley LB, Rossiter-Rachor NA, Douglas MM, Setterfield SA. 2015. Resource-use efficiency explains grassy weed invasion in a low-resource savanna in north Australia. *Frontiers in Plant Science* 6: 560.

Enquist BJ, Condit R, Peet RK, Schildhauer M, Thiers BM. 2016. Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. *PeerJ Preprints* 4: e2615v2.

Erwin KL. 2009. Wetlands and global climate change: The role of wetland restoration in a changing world. *Wetlands Ecology and Management* 17: 71–84.

Falster DS, Westoby M. 2003. Plant height and evolutionary games. *Trends in Ecology and Evolution* 18(7): 337–343.

Farooq M, Hussain M, Wahid A, Siddique KHM. 2012. Drought stress in plants: An overview. In: Aroca R ed. *Plant responses to drought stress, from morphological to molecular features*. Heidelberg: Springer. 37–61.

Fensham RJ, Wang J, Kilgour C. 2015. The relative impacts of grazing, fire, and invasion by buffel grass (*Cenchrus ciliaris*) on the floristic composition of a rangeland savanna ecosystem. *The Rangeland Journal* 38(3): 227–237.

Finlayson CM. 2005. Plant ecology of Australia's tropical floodplain wetlands: A review. *Annals of Botany* 96: 541–555.

Finlayson CM, Everard M, Irvine K, McInnes R, Middleton B, van Dam A, Davidson NC. 2018. *The wetland book. I: Structure and function, management, and methods*. Springer Netherlands: Dordrecht.

Forrestel EJ, Ackerly DD, Emery NC. 2015. The joint evolution of traits and habitat: Ontogenetic shifts in leaf morphology and wetland specialization in *Lasthenia*. *New Phytologist* 208: 949–959.

Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J. 2017. Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews* 92: 1156–1173.

Gallaher TJ, Adams DC, Attigala L, Burke SV, Craine JM, Duvall MR, Klahs PC, Sherratt E, Wysocki WP, Clark LG. 2019. Leaf shape and size track habitat transitions across forest–grassland boundaries in the grass family (Poaceae). *Evolution* 73(5): 927–946.

Garnier LKM, Dajoz I. 2001. Evolutionary significance of awn length variation in a clonal grass of fire-prone savannas. *Ecology* 82(6): 1720–1733.

Gavrilets S, Losos JB. 2009. Adaptive radiation: Contrasting theory with data. *Science* 323: 732–737.

GBIF. 2020. Global Biodiversity Information Facility. Available from https://www.gbif.org [accessed 20 July 2020].

Ghosh SB. 2012. Biodiversity and wild fodder of Gorumara National Park in West Bengal, India. *Journal of Environment and Ecology* 3: 18–35.

Gillison AN. 1983. Tropical savannas of Australia and the Southwest Pacific. In: Bourliére F, Goodall DW eds. *Tropical savannas. Ecosystems of the world*. Amsterdam: Elsevier. 183–243.

Goergen E, Daehler CC. 2001. Reproductive ecology of a native Hawaiian grass (*Heteropogon contortus*; Poaceae) versus its invasive alien competitor (*Pennisetum setaceum*; Poaceae). *International Journal of Plant Sciences* 162: 317–326.

Gopal B. 2013. Future of wetlands in tropical and subtropical Asia, especially in the face of climate change. *Aquatic Science* 75: 39–61.

Greb SF, DiMichele WA, Gastaldo RA. 2006. Evolution and importance of wetlands in earth history. In: Greb SF, DiMichele WA eds. *Wetlands through time*. Colorado: Geological Society of America. 1–40.

Gressitt JL. 1982. *Biogeography and ecology of New Guinea*. Cham: Springer.

Grice AC, McIntyre S. 1995. Spear grass (*Heteropogon contortus*) in Australia: Dynamics of species and community. *The Rangeland Journal* 17: 3–25.

Hector A. 2011. Diversity favours productivity. *Nature* 472: 45–46.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

Hijmans RJ, van Etten J. 2012. raster: Geographic analysis and modeling with raster data. R package version 2.0-12. Available from http://CRAN.R-project.org/package=raster [accessed September 2020].

Huang B, Wu W, Hong Z. 2021. Genetic loci underlying awn morphology in Barley. *Genes* 12(10): 1613.

Humphreys AM, Antonelli A, Pirie MD, Linder HP. 2010. Ecology and evolution of the diaspore "burial syndrome". *Evolution* 65(4): 1163–1180.

Jardine EC, Thomas GH, Forrestel EJ, Lehmann CER, Osborne CP. 2020. The global distribution of grass functional traits within grassy biomes. *Journal of Biogeography* 47: 553–565.

Josse J, Husson F. 2016. missDNA: A package for handling missing values in multivariate data analysis. *Journal of Statistical Software* 70: 1–31.

Joyce CB, Simpson M, Casanova M. 2016. Future wet grasslands: Ecological implications of climate change. *Ecosystem Health and Sustainability* 2(9): e01240.

Joyce CB, Wade PM. 1998. Wet grasslands: A European perspective. In: Joyce CB, Wade PM eds. *European wet grasslands: Biodiversity, management and restoration*. Chichester: John Wiley and Sons. 1–11.

Karthikeyan S, Jain SK, Nayar NP, Sanjappa M. 1989. *Florae indicae enumeratio: Monocotyledonae*. Calcutta: Botanical Survey of India.

Keir AF, Vogler WD. 2006. A review of current knowledge of the weedy species *Themeda quadrivalvis* (grader grass). *Tropical Grasslands* 40: 193–201.

Kellogg EA. 2015. *The families and genera of vascular plants vol. XIII. Flowering plants. Monocots. Poaceae*. Cham: Springer.

Kelly R, Healy K, Anand M, Baudraz MEA, Bahn M, Cerabolini BEL, Corneilssen JHC, Dwyer JM, Jackson AL, Kattge J, Niinemets Ü, Penuelas J, Pierce S, Salguero-Gómez R, Buckley YM. 2021. Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale. *Ecology Letters* 24(5): 970–983.

Kennedy A, Gillen J, Keetch B, Creaser C, the Mutitjulu Community. 2001. Gully erosion control at Kantju Gorge, Uluru-Kata Tjuta National Park, central Australia. *Ecological Management & Restoration* 2: 17–27.

Kirkpatrick JB, Bowman DMJS, Wilson BA, Dickinson KJM. 1987. A transect study of the Eucalyptus forests and woodlands of a dissected sandstone and laterite plateau near Darwin, Northern Territory. *Australian Journal of Ecology* 12: 339–359.

Kirkpatrick JB, Fensham RJ, Nunez M, Bowman DMJS. 1988. Vegetation-radiation relationships in the wet-dry tropics: Granite hills in northern Australia. *Vegetatio* 76: 103–112.

Kothandaraman S, Dar JA, Sundarapandian S, Dayanandan S, Khan ML. 2020. Ecosystem-level carbon storage and its link to diversity, structural and environment drivers in tropical forests of Western Ghats, India. *Scientific Reports* 10: 13444.

Kumar MA, Sreenath A, Anjaneyulu P, Saravanan S, Rao BRP. 2018. *Themeda helferi* (Panicoideae: Poaceae): A new record for India. *Rheedea* 28: 57–61.

Lang RD. 2008. Defining the original extent and floristic composition of the naturally treeless grasslands of the Liverpool Plains, Northwestern Slopes, New South Wales. *Cunninghamia* 10(3): 407–421.

Lehmann CER, Archibald SA, Hoffmann WA, Bond WJ. 2011. Deciphering the distribution of the savanna biome. *New Phytologist* 191: 197–209.

Lehmann CER, Parr CL. 2016. Tropical grassy biomes: Linking ecology, human use and conservation. *Philosophical Transaction Royal Society B* 371: 20160329.

Lehmkuhl JF. 1994. A classification of subtropical riverine grassland and forest in Chitwan National Park, Nepal. *Vegetatio* 111: 29–43.

Lekhak MM, Yadav SR. 2012. Herbaceous vegetation of threatened high altitude lateritic plateau ecosystems of Western Ghats, southwestern Maharashtra, India. *Rheedea* 22: 39–61.

Lewis T, Clarke PJ, Reid N, Whalley RDB. 2008. Perennial grassland dynamics on fertile plains—Is coexistence mediated by disturbance? *Austral Ecology* 33: 128–139.

Li X, Fang X, Wu F, Miao Y. 2011. Pollen evidence from Baode of the northern Loess Plateau of China and strong East Asian summer monsoons during the Early Pliocene. *Chinese Science Bulletin* 56: 64–69.

Li Y, Du F, Wang J, Li R, Liu Y. 2016. Desert vegetation in dry valleys of the upstream of Jinsha River. *Biodiversity Science* 24(4): 489–494.

Li Y, Zou D, Shrestha N, Xu X, Wang Q, Jia W, Wang Z. 2020. Spatiotemporal variation in leaf size and shape in response to climate. *Journal of Plant Ecology* 13: 87–96.

Linder HP, Lehmann CER, Archibald S, Osborne CP, Richardson DM. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* 93(2): 1125–1144.

Liu CF, Yin J, He KN. 2004. Indicatory function of soil moisture of undergrowth vegetation in the *Robinia pseudacacia* forests with different densities in semi-arid region on the loess plateaus. *Science of Soil and Water Conservation* 2(2): 62–67.

Liu H, Edwards EJ, Fleckleton RP, Osborne CP. 2012. Phylogenetic niche conservatism in C_4 grasses. *Oecologia* 170: 835–845.

Liu H, Osborne CP. 2014. Water relations traits of C_4 grasses depend on phylogenetic lineage, photosynthetic pathway, and habitat water availability. *Journal of Experimental Botany* 66(3): 761–773.

Liu J, Shen YX, Zhu X, Zhao GJ, Zhao ZM, Li ZJ. 2019. Spatial distribution patterns of rock fragments and their underlying mechanism of migration on steep hillslopes in a karst region of Yunnan Province, China. *Environmental Science and Pollution Research* 26: 24840–24849.

Lunt ID. 1995. Seed longevity of six native forbs in a closed *Themeda triandra* grassland. *Australian Journal of Botany* 43: 439–449.

Lê S, Josse J, Husson F. 2008. FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software* 25: 1–18.

Mahata A, Jena SK, Palita SK. 2019. First record in 129 years of the Tree brown *Lethe drypetis* todara Moore, 1881 (Lepidoptera: Nymphalidae: Satyrinae) from Odisha, India by fruit-baiting. *Journal of Threathened Taxa* 11(15): 15047–15052.

Manner H, Lang H. 2006. A quantitative analysis of the induced grasslands of the Bismarck Mountains, Papua New Guinea. *Singapore Journal of Tropical Geography* 2: 40–48.

Mantlana KB, Arneth A, Veenendaal EM, Wohland P, Wolski P, Kolle O, Wagner M, Lloyd J. 2008. Photosynthetic properties of C4 plants growing in an African savanna/wetland mosaic. *Journal of Experimental Botany* 59(14): 3941–3952.

Marler TE, Ferreras UF. 2017. Current status, threats and conservation needs of the endemic *Cycas wadei* Merrill. *Journal of Biodiversity & Endangered Species* 5: 3.

Mashau AC, Hempson GP, Lehmann CER, Vorontsova MS, Visser V, Archibald S. 2021. Plant height and lifespan predict range size in southern African grasses. *Journal of Biogeography* 48(12): 3047–3059.

Melack JM, Hess LL. 2010. Remote sensing of the distribution and extent of wetlands in the Amazon basin. In: Junk W, Piedade M, Wittmann F, Schöngart J, Parolin P eds. *Amazonian floodplain forests. Ecological studies (analysis and synthesis)*. Springer Netherlands: Dordrecht. 210: 43–59.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, 1–8.

Moles AT, Warton DI, Warman L, Swenson NG, Laffan SW, Zanne AE, Pitman A, Hemmings FA, Leishman MR. 2009. Global patterns in plant heights. *Journal of Ecology* 97(5): 923–932.

Mondal N, Sukumar R. 2015. Regeneration of juvenile woody plants after fire in a seasonally dry tropical forest of Southern India. *Biotropica* 47(3): 330–338.

Moor H, Rydin H, Hylander K, Nilsson MB, Lindborg R, Norberg J. 2017. Towards a trait-based ecology of wetland vegetation. *Journal of Ecology* 105(6): 1623–1635.

Morales-Fierro V. 2014. *Taxonomy, distribution and functional traits in Themeda Forssk.* (*Poaceae*). M.Sc. Thesis. Edinburgh: University of Edinburgh.

Morgan JW, Lunt ID. 1999. Effects of time-since-fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. *Biological Conservation* 88(3): 379–386.

Mott JJ, Ludlow MM, Richards JH, Parsons AD. 1992. Effects of moisture supply in the dry season and subsequent defoliation on persistence of the savanna grasses *Themeda triandra*, *Heteropogon contortus* and *Panicum maximum*. *Australian Journal of Agricultural Research* 43: 241–260.

Mott JJ, Tothill JC. 1984. Tropical and subtropical woodlands. In: Harrington GN, Wilson AD, Young MD eds. *Management of Australia's rangeland*. East Melbourne: CSIRO. 255–269.

Muhammad SA, Malik ZH, Malik NZ, Sadia MA. 2012. The position of *Pinus roxburghii* in the forests of Kolti hills, Azad Jammu and Kashmir. *African Journal of Plant Science* 6(3): 106–112.

Murthy MLK. 2003. *Pre- and protohistoric Andhra Pradesh up to 500 B.C.* Chennai: Orient Blackswan.

Mylliemngap W, Barik SK. 2019. Plant diversity, net primary productivity and soil nutrient contents of a humid subtropical grassland remained low even after 50 years of post-disturbance recovery from coal mining. *Environmental Monitoring and Assessment* 191: 697.

Nanjarisoa O, Besnard G, Ralimanana H, Jeannoda VH, Vorontsova MS. 2017. Grass survey of the Itremo Massif records endemic central highland grasses. *Madagascar Conservation & Development* 12: 34–40.

Naskar M, Bera S. 2018. Taxonomic assessment of opal phytoliths from grasses of deltaic West Bengal, India. *Nordic Journal of Botany* 36(4): e01695.

Neldner VJ, Fensham RJ, Clarkson JR, Stanton JP. 1997. The natural grasslands of Cape York Peninsula, Australia. Description, distribution and conservation status. *Biological Conservation* 81: 121–136.

Nilsson C, Brown R, Jansson R, Merritt DM. 2010. The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews* 85(4): 837–858.

Ntakirutimana F, Xie W. 2019. Morphological and genetic mechanisms underlying awn development in monocotyledonous grasses. *Genes* 10(8): 573.

O'Connor TG. 1997. Micro-site influence on seed longevity and seedling emergence of a bunchgrass (*Themeda triandra*) in a semi-arid savanna. *African Journal of Range & Forage Science* 14: 7–11.

Olson ME, Soriano D, Rosell JA, Anfodillo T, Donoghue MJ, Edwards EJ, León-Gómez C, Dawson T, Martínez JJC, Castorena M, Echeverría A, Espinosa CI, Fajardo A, Gazol A, Isnard S, Lima RS, Marcati CR, Méndez-Alonzo R. 2018. Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences of the United States of America* 115(29): 7551–7556.

Oviedo Prieto R, Herrera Oliver P, Caluff MG. 2012. National list of invasive and potentially invasive plants in the Republic of Cuba—2011. *Bissea: Boletín sobre Conservación de Plantas del Jardín Botánico Nacional de Cuba* 6: 22–96.

Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.

Pagel M, Meade A, Barker D. 2004. Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* 53: 673–684.

Paijmans K. 1983. The vegetation of the Purari catchment. In: Petr T ed. *The Purari—Tropical environment of a high rainfall river basin*. Dordrecht: Springer Netherlands. 227–252.

Pala NA, Negi AK, Gokhale Y, Bhat JA, Todaria NP. 2012. Diversity and regeneration status of Sarkot Van Panchyat in Gharwal Himalaya, India. *Journal of Forestry Research* 23(3): 399–404.

Pan Y, Cieraad E, Clarkson BR, Colmer TD, Pedersen O, Visser EJW, Voesenek LACJ, van Bodegom PM. 2020. Drivers of plant traits that allow survival in wetlands. *Functional Ecology* 34(5): 956–967.

Patzelt A. 2011. The *Themeda quadrivalvis* tall-grass savannah of Oman at the crossroad between Africa and Asia. *Edinburgh Journal of Botany* 68(2): 301–319.

Pearman PB, Guisan A, Broennimann O, Randin CF. 2008. Niche dynamics in space and time. *Trends in Ecology & Evolution* 23(3): 149–158.

Peart MH. 1979. Experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* 67: 843–863.

Peart MH. 1981. Further experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* 69: 425–436.

Peart MH, Clifford HT. 1987. The influence of diaspore morphology and soil-surface properties on the distribution of grasses. *Journal of Ecology* 75: 569–576.

Pemadasa MA. 1990. Tropical grasslands of Sri Lanka and India. *Journal of Biogeography* 17: 395–400.

Pemadasa MA, Mueller-Dombois D. 1979. An ordination study of montane grasslands of Sri Lanka. *Journal of Ecology* 67: 1009–1023.

POWO. 2019. Plants of the World Online. Available from http://www.plantsoftheworldonline.org [Accessed 19 December 2019].

Potdar GG, Salunkhe CB, Yadav SR. 2003. A new species of *Themeda* Forssk. (Poaceae) from India. *Kew Bulletin* 58: 243–246.

Pulla S, Riotte J, Suresh HS, Dattaraja HS, Sukumar R. 2016. Controls of soil spatial variability in a dry tropical forest. *PLoS One* 11(4): e1053212.

Puri GS, Patil RM. 1960. Dry deciduous forest of the Poona district, Deccan, India. *Nelumbo* 2: 149–167.

Pyron RA, Costa GC, Patten MA, Burbrink FT. 2015. Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. *Biological Reviews* 90(4): 1248–1262.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urceley C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC. 2016. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 64(8): 715–716.

R Core Team. 2021. R: A Language and Environment for Statistical Computing. Available from https://www.R-project.org [accessed April 2020].

Rahandale SS, Rahangdale SR. 2014. Plant species composition on two rock outcrops from the Northern Western Ghats, Maharashtra, India. *Journal of Threatened Taxa* 6(4): 5593–5612.

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.

Ratnam J, Tomlinson K, Rasquinha DN, Sankaran M. 2016. Savannahs of Asia: Antiquity, biogeography, and an uncertain future. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150305.

Rawat GS. 2005. Vegetation dynamics and management of Rhinoceros habitat in Duras of West Bengal: An ecological review. *National Academy Science Letter* 28(5): 179–186.

Revell LJ. 2012. Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217–223.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.

Sankaran M. 2009. Diversity patterns in savanna grasslands communities: Implications for conservation strategies in a biodiversity hotspot. *Biodiversity and Conservation* 18: 1099–1115.

Sankaran M, Ratnam J. 2013. African and Asian savannas. In: Levin SA ed. *Encyclopedia of biodiversity*. Second Edition. Amsterdam: Elsevier. 58–74.

Schoener TW. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408–418.

Scholes RJ, Hall Do. 1996. The carbon budget of tropical savannas, woodlands, and grasslands. In: Breymeyer AI, Hall DO, Melillo JM, Agren GI eds. *Global change: Effect on coniferous forests and grasslands*. Chichester: Wiley. 69–100.

Scott KA, Setterfield SA, Andersen AN, Douglas MM. 2009. Correlates of grass-species composition in a savanna woodland in northern Australia. *Australian Journal of Botany* 57: 10–17.

Sexton JP, Montiel J, Shay JE, Stephens MR, Slatyer RA. 2017. Evolution of ecological niche breadth. *Annual Review of Ecology, Evolution, and Systematics* 48: 183–206.

Shaheen H, Malik NM, Dar MEUI. 2015. Species composition and community structure of subtropical forest stands in western Himalayan foothills of Kashmir. *Pakistan Journal of Botany* 47(6): 2151–2160.

Sheath SN, Morueta-Holme N, Angert AL. 2020. Determinants of geographic range size in plants. *New Phytologist* 226(3): 650–665.

Shouliang C, Phillips SM. 2006a. Heteropogon. In: Wu ZY, Raven PH, Hong DY eds. *Flora of China: Poaceae*. Beijing: Science Press. 22: 637–638.

Shouliang C, Phillips SM. 2006b. Themeda. In: Wu ZY, Raven PH, Hong DY eds. *Flora of China: Poaceae*. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press. 22: 633–637.

Shukla AN, Kumar B, Srivastava SK. 2010. Floristic composition and vegetation types of Rewa district in Madhya Pradesh: An overview. *Annual Forester* 18(2): 283–296.

Silberbauer-Gottsberger I. 1984. Fruit dispersal and trypanocarpy in Brazilian cerrado grasses. *Plant Systematics and Evolution* 147: 1–27.

Simpson KJ, Ripley BS, Christin P-A, Belcher CM, Lehmann CER, Thomas GH, Osborne CP. 2016. Determinants of flammability in savanna grass species. *Journal of Ecology* 104: 138–148.

Skarpe C. 1996. Plant functional types and climate in a southern African savanna. *Journal of Vegetation Science* 7: 397–404.

Snyman HA, Ingram LJ, Kirkman KP. 2013. *Themeda triandra*: A keystone grass species. *African Journal of Range and Forage Science* 30(3): 99–125.

Sookchaloem D, Methula TS, Bhumpakphan N, Maneerat S. 2015. Species composition of understorey vegetation and large herbivore abundance in burnt and an unburnt deciduous dipterocarp forest at Huai Kha Kaeng widelife sanctuary, Thailand. *International Research Journal of Biological Sciences* 4: 7–15.

Souza-Neto AC, Cianciaruso MV, Collevatti RG. 2016. Habitat shifts shaping the diversity of a biodiversity hotspot through time: Insights from the phylogenetic structure of Caesalpinioideae in the Brazilian Cerrado. *Journal of Biogeography* 43: 340–350.

Sreekumar PV, Nair VJ. 1987. *Themeda sabarimalayana*—A new species of Poaceae from Kerala, India. *Bulletin of the Botanical Survey of India* 29: 127–128.

Srivastava SK. 2004. Floristic diversity of Bandhavgarh national park Madhya Pradesh. *Nelumbo. The Bulletin of the Botanical Survey of India* 46: 216–220.

Stinchcombe JR, Kelley JL, Conner JK. 2017. How to measure natural selection. *Methods in Ecology and Evolution* 8: 660–662.

Strohbach BJ. 2013. Vegetation of the Okavango River valley in Kavango West, Namibia. *Biodiversity & Ecology* 5: 321–339.

Subashree K, Sundarapandian S. 2017. Biomass and carbon stock assessment in two savannahs of Western Ghats, India. *Taiwania* 62(3): 272–282.

Sutomo S. 2020. Vegetation composition of savanna ecosystem as a habitat for the Komodo Dragon (*Varanus komodoensis*) on Padar and Komodo Islands, Flores East Nusa Tenggara Indonesia. *Journal of Tropical Biodiversity and Biotechnology* 5: 10–15.

Sutomo S, Darma IDP, Iryadi R. 2020. The dissimilarity in plant species composition of savanna ecosystem along the elevation gradient on Flores Island, East Nusa Tenggara, Indonesia. *Biodiversitas* 21(2): 492–496.

Tain YH, Feng YL, Liu C. 2007. Addition of activated charcoal to soil after clearing *Ageratina adenophora* stimulates growth of forbs and grasses in China. *Tropical Grasslands* 41: 285–291.

Teisher JK, McKain MR, Schaal BA, Kellogg EA. 2017. Polyphyly of Arundinoideae (Poaceae) and evolution of the twisted geniculate lemma awn. *Annals of Botany* 120(5): 725–738.

Toochi A, Jost A, Ducharne A. 2019. Multi-source global wetland maps combining surface water imagery and groundwater constraints. *Earth System Data Science* 11: 189–220.

Tothill JC, Hacker JB. 1976. Polyploidy, flowering phenology and climatic adaptation in *Heteropogon contortus* (Gramineae). *Australian Journal of Ecology* 1(4): 213–222.

Trollope WSW. 1982. Ecological effects of fire in South African savannas. In: Huntley BJ, Walker BH eds. *Ecology of tropical savannas: Ecological studies (analysis and synthesis)*. Heidelberg: Springer. 292–306.

VanWallendael A, Soltani A, Emery NC, Peixoto MM, Olsen J, Lowry DB. 2019. A molecular view of plant local adaptation: Incorporating stress-response networks. *Annual Review of Plant Biology* 70: 559–583.

van Kleunen M, Fischer M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologists* 166: 49–60.

Veldkamp JF. 2016. A revision of *Themeda* (Gramineae) in Malesia with a new species from Laos. *Blumea* 61: 29–40.

Vesey-Fitzgerald DF. 1970. The origin and distribution of valley grasslands in East Africa. *Journal of Ecology* 58: 51–75.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116(5): 882–892.

Vogler WD, Owen NA. 2008. Grader grass (*Themeda quadrivalvis*): Changing savannah ecosystems. In: van Klinken RD, Osten VA, Panetta FD, Scanlan JC eds. *Weed Management 2008: Hot Topics in the Tropics.* Sixteenth Australian Weeds Conference Proceedings, North Queensland, 18–22 May, 2008. Brisbane: Queensland Weeds Society. 213–214.

Wang XM, Zhao L, Yan BG, Shi LT, Liu GC, He YX. 2016. Morphological and physiological responses of *Heteropogon contortus* to drought stress in a dry-hot valley. *Botanical Studies* 57: 17.

Warren DL, Matzke NJ, Cardillo M, Baumgartner JB, Beaumont LJ, Turelli M, Glor RE, Huron NA, Simões M, Iglesias TL, Piquet JC, Dinnage R. 2021. ENMTools 1.0: An R package for comparative ecological biogeography. *Ecography* 44(4): 504–511.

Welker CAD, McKain MR, Estep MC, Pasquet RS, Chipabika G, Pallangyo B, Kellogg EA. 2020. Phylogenomics enables biogeographic analysis and a new subtribal classification of Andropogoneae (Poaceae–Paniocoideae). *Journal of Systematics and Evolution* 58(6): 1003–1030.

Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21(5): 261–268.

Wiens JJ, Graham CH. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 36: 519–539.

Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes JA, Guisan A, Heikkinen RK, Høye TT, Kühn I, Luoto M, Maiorano L, Nilsson MC, Normand S, Öckinger E, Schmidt NM, Termansen M, Timmermann A, Wardle DA, Aastrup P, Svenning JC. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling. *Biological Reviews* 88: 15–30.

Woodward FI, Lomas MR, Kelly CK. 2004. Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359: 1465–1476.

Woodward FI, Williams BG. 1987. Climate and plant distribution at global and local scales. *Vegetatio* 69: 189–197.

Wright IJ, Dong N, Maire V, Prentice IC, Westoby M, Diaz S, Gallagher RV, Jacobs BF, Kooyman R, Law EA, Leishman MR, Niinemets Ü, Reich PB, Sack L, Villar R, Wang H, Wilf P. 2017. Global climatic drivers of leaf size. *Science* 357(6354): 917–921.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Xavier RO, D'Antonio CM. 2017. Multiple ecological strategies explain the distribution of exotic and native C_4 grasses in heterogeneous early successional sites in Hawai'i. *Journal of Plant Ecology* 10(3): 426–439.

Xiwen L, Walker D. 1986. The plant geography of Yunnan Province, Southwest China. *Journal of Biogeography* 13(5): 367–397.

Yadava PS. 1990. Savannas of north-east India. *Journal of Biogeography* 17: 385–394.

Zhao G, Shen Y, Liu W, Tan B, Li Z, Wang Q. 2020. Quantifying the effect of shading and watering on seed germination in translocated forest topsoil at a subtropical karst of China. *Forest Ecology and Management* 459: 117811.

Zhang Y, Hu X, Liu Y, Liu Q. 2014. Caryopsis micromorphological survey of the genus *Themeda* (Poaceae) and allied spathaceous genera in the Andropogoneae. *Turkish Journal of Botany* 38(4): 665–676.

Zizka A, Silvestro D, Andermannn T, Azevedo Z, Ritter CD, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, Svantesson S, Wengström N, Zizka V, Antonelli A. 2019. CoordinateCleaner: Standard cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* 10(5): 744–751.

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.