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Abstract Explaining relationships between species richness and biogeographical patterns over a broad geographic scale is a central issue of biogeography and macroecology. We document the realized climate niches for grasses in China's nature reserves and discuss its formation mechanism using grass richness data combined with climatic, physiological, and phylogenetic data. Our results suggest that climate niche structure of grasses is phylogenetically conservative for BEP (Bambusoideae, Ehrhartoideae, and Pooideae) and PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae) clades along temperature gradients and for Chloridoideae and Panicoideae along precipitation gradients. At the national scale, the divergence patterns of climate niches between two major clades are more distinguishable than between C_3 and C_4 grasses. High rates of climate niche evolution are found in C_4 clades in the subtropical forest region. There appears to be a strong association between elevation gradients and grass diversity: the specific environmental conditions (e.g. energy) and the rapid shifts of climate conditions drive high grass diversification. Evolutionary conservatism of climate niches may be influenced by the specific adaptive ability to changing environmental conditions within NAD-ME/NADP-ME clades. Our results indicate that adaptations to major climate changes may be accomplished by C_4 grass nodes of high climate niche evolutionary rates in China's nature reserves.

Keywords BEP and PACCMAD clades · C_4 node · Niche evolution · Phylogeny · Poaceae · Species distribution model

Introduction

Among the Poaceae (grass family) there are two main photosynthetic types, C_3 and C_4. In C_3 photosynthesis, CO_2 is directly fixed by the oxygen sensitive ribulose-bis-phosphate carboxylase/oxygenase (Rubisco) and the first stable fixation product is the C_3 compound phosphoglyceric acid (PGA). In C_4 photosynthesis, CO_2 is initially fixed by the oxygen-insensitive phosphoenolpyruvate carboxylase (PEPC) and the first stable fixation product is the C_4

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compound, malic acid (Sage 2004). C_4 photosynthesis is a major evolutionary success and about ½ of the species in the grass family utilize this pathway. The grass family is economically and ecologically important, accounting for about 25% of global gross primary productivity (Sage 2004; Edwards et al. 2010) and about 23% of global grain production (Monfreda et al. 2008). Grasses utilizing the C_4 photosynthetic pathway dominate nearly all grasslands in tropical, subtropical, and warm temperate zones, and rank among the world's most important crops, weed plants, and potential biofuels such as corn, sugarcane, and sorghum (Sage et al. 1999a).

C_4 grasses are dominant in warm-climate regions; they rarely occur in cold-climate regions of the world. C_4 grasses possess the biochemical characteristics allowing them to concentrate CO_2 and minimize photorespiration; therefore, giving an advantage to individuals that occupy regions of high temperatures and high light intensities (Ehleringer et al. 1997; Still et al. 2003). Many studies addressing climatic effects on C_4 grass distribution (Teeri and Stowe 1976; Chazdon 1978; Vogel and Fuls 1978; Rundel 1980; Hattersley 1983; Collins and Jones 1985; Klink and Joly 1989; Paruelo and Lauenroth 1996; P'yankov et al. 2000) reported the positive correlation between growing season temperature and C_4 grass abundance. Whereas precipitation gradients seemed to have less impact on C_3 and C_4 grass distribution globally (Sage 2004).

Explaining relationships between species richness and biogeographical patterns over a broad geographic scale is a central issue of biogeography and macroecology. Traditionally, only climate factors were considered as potential determinants (Hattersley 1983; Epstein et al. 1997; P'yankov et al. 2000). Since the last decade, an increasing number of phylogenetic frameworks have been reconstructed for many groups of organisms, and these have been integrated into studies of plant diversity (Tofts and Silvertown 2000; Webb et al. 2002; Edwards and Still 2008; Edwards et al. 2010). Recent studies have found that the conservation of characters occurred during the evolutionary history, e.g. the autumn leaf coloration of forests (e.g. Archetti 2009). For grasses, some authors have found evidence for climate niche conservatism among C_4 species using phylogenetic methods (Edwards and Still 2008; Webb et al. 2002), whereas others have shown evidence for niche divergence of C_4 grasses (Tofts and Silvertown 2000; Edwards and Smith 2010). The contrasting hypotheses suggest that rates of climate niche evolution might be rapid in some C_4 grass clades and slow in others. Moreover, variation among C_4 grass clades is poorly documented and the concomitant causes poorly understood.

There are three predominant C_4 subtypes: nicotinamide adenine dinucleotide malic enzyme (NAD-ME), nicotinamide adenine dinucleotide phosphate malic enzyme (NADP-ME), and phosphoenolpyruvate carboxy-kinase (PCK) (Hattersley 1992; Hattersley and Watson 1992). Some studies indicate that the range expansion of different C_4 variants depend on physiological tolerance to different climate conditions (Taub 2000; Carmo-Silva et al. 2009). However, diversity patterns of different C_4 variants may depend on their adaptation abilities (Taylor et al. 2010). There is a strong association between C_4 variants and their subordinate subfamilies. Almost all C_4 species of Chloridoideae are NAD-ME or PCK subtype, while the vast majority of C_4 species of Aristidoideae, Arundinoideae, and Panicoideae are NADP-ME subtype (Prendergast et al. 1987; Kellogg 1999; Taub 2000; Peterson et al. 2010). The presence of NADP-ME panicoid species in one climatic type might limit other NADP-ME panicoid species from dispersing into that space, e.g. two sympatric species occupying different elevation ranges (Sage et al. 1999b; Taub 2000). Thus, geographic overlap among phylogenetically related species in different clades may limit evolutionary rates of climate niches, and geographic isolation among unrelated species may accelerate these rates. Yet, the effects of geographic isolation among clades of different C_4 variants on the rates of climatic-niche evolution have never been explicitly tested (Webb et al. 2002).

The currently accepted phylogeny of Poaceae shows two well-supported clades: Bambusoideae, Ehrhartoideae, and Pooideae (BEP) and Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae (PACMAD) (Sánchez-Ken et al. 2007; Bouchenak-Khelladi et al. 2008; Soreng et al. 2009; Peterson et al. 2010; Sánchez-Ken and Clark 2010). Modern phylogenetic analyses show that grass diversity is regulated by a complex set of factors indirectly related to the photosynthetic pathway at different spatial scales (Crisp et al. 2009; Edwards and Smith 2010). On Hawaiian Islands, water-use efficiency conferred by the C_4 pathway determines C_4 grass distribution along a precipitation gradient within PACMAD clade (Edwards and Still 2008; Price 2004). On the continental (eastern Asia) scale, China represents a large climate window with variable climatic regions ranging from the subtropical forest region to the cold temperate region within the latitude range of 18°35′–48°36′N and longitude range of 80°18′–133°42′E. Significant relationships exist between energy (temperature variants) and grasses at the national scale and between elevation gradients and C_4 grasses in the subtropical forest region (Liu et al. 2009). Except for floristic surveys and statistical analyses of grass diversity (Yin and Li 1997; Sun 2004), little is known about the climate niche structure and its formation mechanism for Chinese grasses.

The software Phylocom (Webb et al. 2008), which measures phylogenetic signals and evolution of ecological traits using the standard deviation of descendant clades (including polytomies), has provided an easy way to integrate phylogenetic information into the study of climate niches (Swenson 2009; Yan et al. 2010). The evolutionary rates have changed during the evolutionary history, and testing the rate shifts is a critical step in constructing causal hypotheses. The program Brownie (O'Meara et al. 2006) can help resolve rate shifts by using maximum likelihood ratio estimation and likelihood ratio tests to measure the lability of temperature and precipitation niches in different nodes within the phylogeny.

Some studies argued that few grass lineages have successfully diversified outside the tropics (Edwards and Still 2008; Edwards and Smith 2010; Edwards et al. 2010), leaving open questions to debate reasons for the dominant distribution of C_4 grasses in subtropical and temperate regions, and the high evolutionary rates of climate niches in subtropical lineages over a broad geographic scale. The present study aims to: (1) ascertain climate niche structure at the national scale by reconstructing the phylogeny for grasses in China's nature reserves and (2) assess the evolutionary lability of climate niches among nodes of C_4 grass variants. We also compare differences in climate niche structure and evolution between continental (Chinese) and insular (Hawaiian) grass floras, and suggest a mechanism underlying subtropical and tropical C_4 grass distribution.

Methods

Data collection

We used the diversity database for 145 grass species collected from 115 nature reserves in China (Liu et al. 2009). Even though there are taxonomic inconsistancies (i.e., misidentifications) with the species determinations in the original database (29 out of 145 are not reported in the Flora of China; Chen et al. 2006), the ecological signal is not diminished or compromised. These nature reserves cover a total area of 1,312,445 km^2, which accounts for 13.6% of the country's area (Yin and Li 1997). Distribution range of the 115 nature reserves covers the major biomes and floristic phyla in China. In our analysis, we excluded those nature reserves smaller than 5 km^2 or larger than 500,000 km^2 to avoid spatial overlap (Palmer and White 1994).

Mean annual temperature (°C) and mean annual precipitation (mm) for each nature reserve were obtained from the China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn/shuju/), and these were based on polygons of each reserve boundary, compiled from the 1961–1999 database with a resolution of 0.1° × 0.1° from 480 meteorological stations in China (Fig. 1a). The temperature and precipitation data of each taxon were obtained by averaging parameter values from those nature reserves where each taxon was distributed. The fundamental climate niches would be the range of climatic variables where a species could potentially exist (Austin et al. 1990), and estimates of fundamental climate niches for large numbers of species are difficult to obtain. For practical reasons, we had to rely on surrogates estimated by the combination of mean climatic variables that best described a species' geographical range and realized climate niches (Roe and Baker 2007; Hof et al. 2010).

Reserves occupied by species are listed in Fig. 1b. Native or alien status for each species was determined by consulting Chen et al. (2006) and many other floristic treatments. Literature sources for the photosynthetic types (Hattersley 1986; Renvoize 1987; Sage et al. 1999b; Ueno et al. 2005; Ueno and Sentoku 2006; P'yankov et al. 2010) are listed in Appendix 1 (supplementary material). Probabilities for climatic variables of six categories (C_3, C_4, BEP, PACMAD, Chloridoideae, and Panicoideae) were

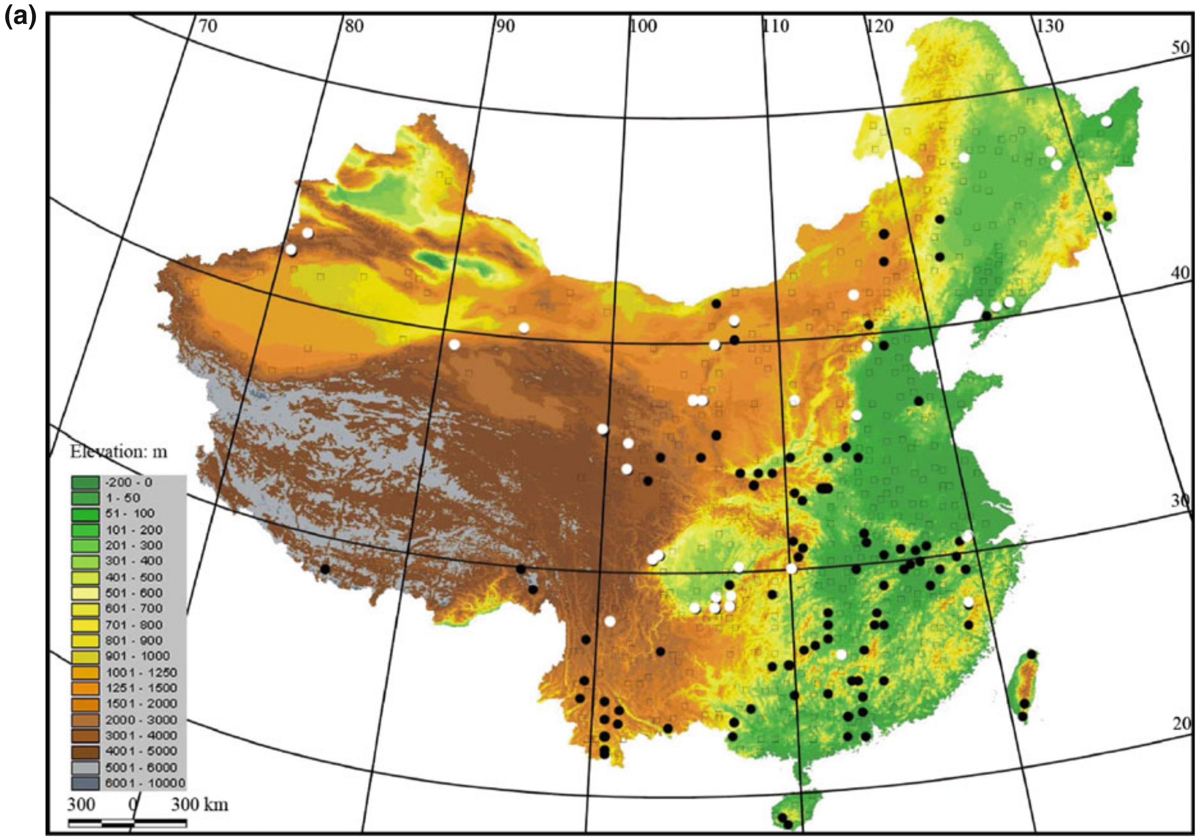

Fig. 1 Data collection of **a** the locations of 115 nature reserves and 480 meterological stations and **b** nature reserves containing each grass species in China (Liu et al. 2009). *Black circle* the percentage of C_4 grass species higher than 50%; *White circle* the percentage of C_3 grass species higher than 50%; *Gray square* meterological station; *Green bar* C_3 grass; *Red bar* C_4 grass. (Color figure online)

analyzed by cumulative distribution function in SPSS version 17.0 (Norušis 2009).

Phylogenetic analysis

Plastid DNA sequences (*ndhF*, *rbcL*, and *matK*) of 145 grass species and two outgroup species were downloaded from the National Center for Biotechnology Information (NCBI; http://wwwncbinlmnihgov/) and used to reconstruct phylogeny of grasses in China's nature reserves (see Appendix 2 in supplementary material). *Flagellaria indica* (Flagellariaceae) and *Joinvillea ascendens* (Joinvilleaceae) were chosen as outgroups (Bouchenak-Khelladi et al. 2008). We purged duplicate sequences using SCaFoS (Roure et al. 2007) by selecting the longest sequence for the same taxon. Alignments of each plastid gene sequence matrix were performed with the online MAFFT version 6 (http://alignbmrkyushu-uacjp/mafft/software/), then three aligned matrixes of plastid genes were combined with WinClada version 1.00.08 (Nixon 2002). The final matrix consisted of 4,969 characters of 147 taxa (see Appendix 3 in supplementary material).

Bayesian analyses were conducted using BEAST version 1.5.3 (Drummond and Rambautx 2007), the software employed a Bayesian Markov chain Monte Carlo (MCMC) to co-estimate topology, and branch lengths were proportional to the relative divergence time among nodes. The analysis was performed using the GTR + G + I model with a fixed substitution rate of 1.0, a gamma distribution, and four rate categories. Tree prior model was implemented as Yule process with rate variation across branches assumed to be uncorrelated with lognormal distribution (Drummond et al. 2006). Posterior distributions of parameters were estimated using two independent MCMC analyses of 20,000,000 generations with

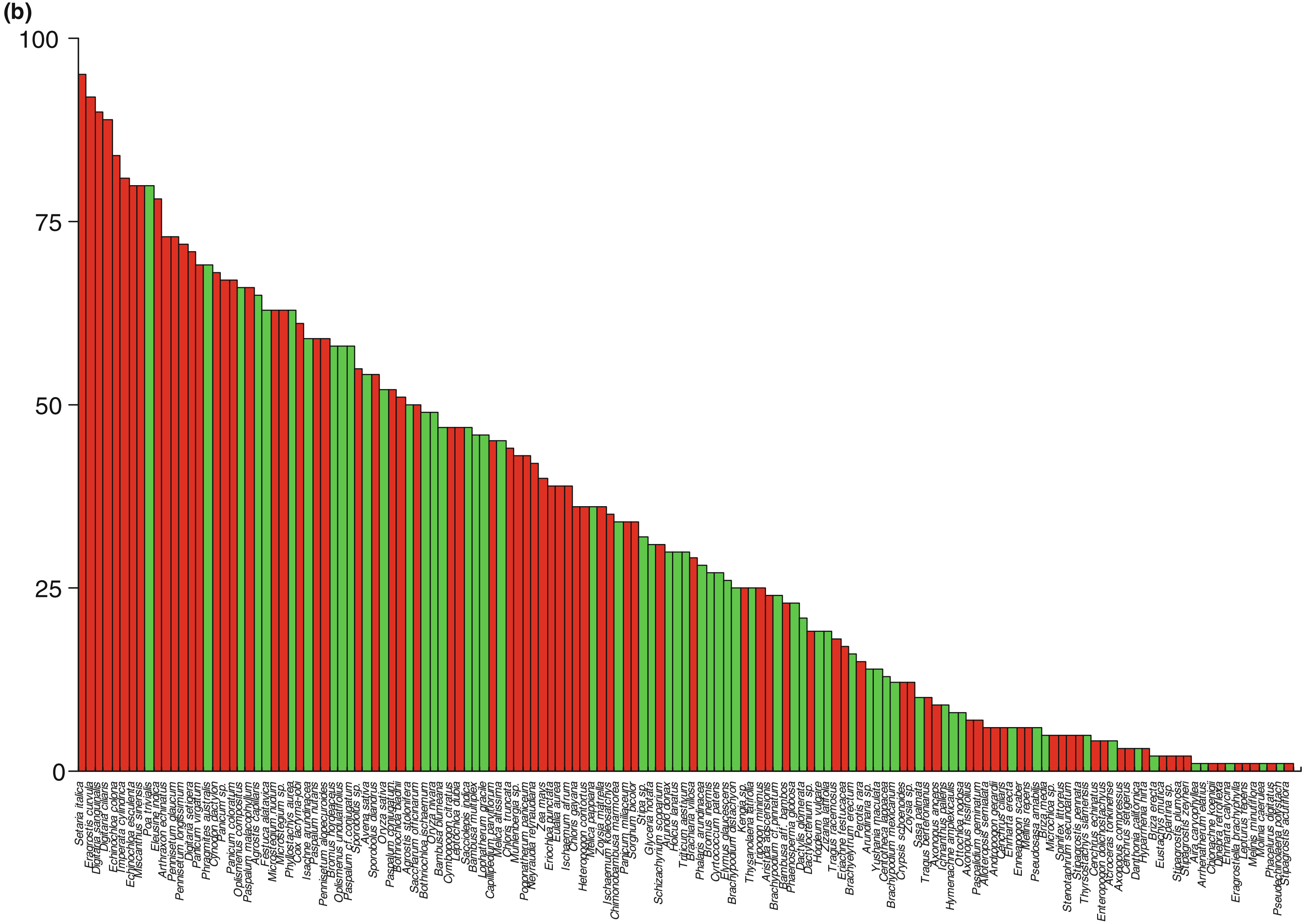

Fig. 1 continued

sampling every 1,000 generations. Statistics of each run were checked by Tracer version 1.5 (http://beastbioedacuk/Tracer). A majority rule consensus tree was generated (c. 36,000) after removing 10% burn-in samples.

Climate niche divergence

The AOT (analysis of traits) module was used to calculate the divergence of mean annual temperature and mean annual precipitation among nodes in Phylocom version 4.1 (Webb et al. 2008). Based on the photosynthetic traits of terminal taxa, 103 nodes include: 35 C_3 nodes, 55 C_4 nodes, and 13 C_3/C_4 nodes. The C_4 photosynthesis subtypes of terminal taxa were manually mapped on the majority rule consensus tree. The independent-samples *T* test in SPSS version 17.0 (Norušis 2009) was used to analyze differences in root mean square deviation of climatic traits derived from node *i* (D_i) of C_3 and C_4 nodes, BEP and PACMAD nodes, and Chloridoideae and Panicoideae nodes.

Rates of climatic-niche evolution were analyzed using Brownie version 2.0b7 (O'Meara et al. 2006). We rejected the null model if both an Akaike Information Criterion (AIC) difference larger than 7.00 and a chi-squared *P* value smaller than 0.05 were encountered (http://www.brianomeara.info/brownie). The node divergence widths of climate parameters within different photosynthetic types and C_4 photosynthetic subtypes were analyzed using box plot graphs in SPSS version 17.0. The bottom and top lines in the box were the first and the third quartiles, and the horizontal line was the mean value.

Results

Climate niches of Chinese grasses

Eighty-six percent of the nature reserves (54/63) south of 30° N latitude and 65% of the nature reserves (28/43) between 30° N and 40° N latitude contained 50% or more C_4 grasses, whereas 55% of the nature reserves (11/20) north of 40° N latitude contained 50% or more C_3 grasses (Fig. 1a). The total number of nature reserves for each species is given in Fig. 1b. The most widespread grass, *Setaria italica* was found in 95 nature reserves. The following 12 species (singletons), *Aira caryophyllea*, *Arrhenatherum elatius*, *Chionachne koenigii*, *Dinebra retroflexa*, *Ehrharta calycina*, *Eragrostiella brachyphylla*, *Lepturus repens*, *Melinis repens*, *Molinia caerulea*, *Phacelurus digitatus*, *Pseudechinolaena polystachya*, and *Stipagrostis acutiflora*, were found in a single nature reserve. Five species (doubletons), *Briza erecta*, *Eustachys mutica*, *Spartina* sp., *Stipagrostis plumosa*, and *Stipagrostis zeyheri*, were found in only two nature reserves. Phylocom analysis was initially conducted excluding singletons and doubletons; the result (available from authors) showed that the niche characterizations were roughly concordant with the findings involving all species. Therefore, they are included in our study without systematic bias.

The difference between BEP and PACMAD clade was the most pronounced along temperature gradients (Fig. 2a), and the difference between Chloridoideae and Panicoideae was the most pronounced along precipitation gradients (Fig. 2b). Distinct differences in average temperature ranges were observed between BEP and PACMAD clades (12.7°C vs. 17.5–18.6°C) and were more distinguishable than the ranges between C_3 and C_4 species (12.7–17.5°C vs. 18.6°C) and between Chloridoideae and Panicoideae (15.6 vs. 17.0°C). Differences in average precipitation ranges between Chloridoideae and Panicoideae (956.9 vs. 1175.6 mm) were more distinct than ranges between C_3 and C_4 species (956.9–1318.9 mm vs. 1279.7 mm) and between BEP and PACMAD clade (969.0 mm vs. 1318.9–1279.7 mm) (Table 1). Our database of grass diversity yielded the same ecological pattern reported in previous publications (Chazdon 1978; Rundel 1980; Epstein et al. 1997). Therefore, any potential biases of sampling inherent in data collection seem not to have affected the assessment of climate niche divergence between C_3 and C_4 species, BEP and PACMAD clades, and Chloridoideae and Panicoideae, respectively.

Climate niche divergence

The ten nodes having the largest divergences of climate niches across the phylogenetic tree were identified using Phylocom (Table 2). Nine nodes of PACMAD clade and one node of BEP clade were marked by temperature niche divergence; the largest temperature niche divergence was found in a single C_3/C_4 PACMAD node AZ. Seven nodes of

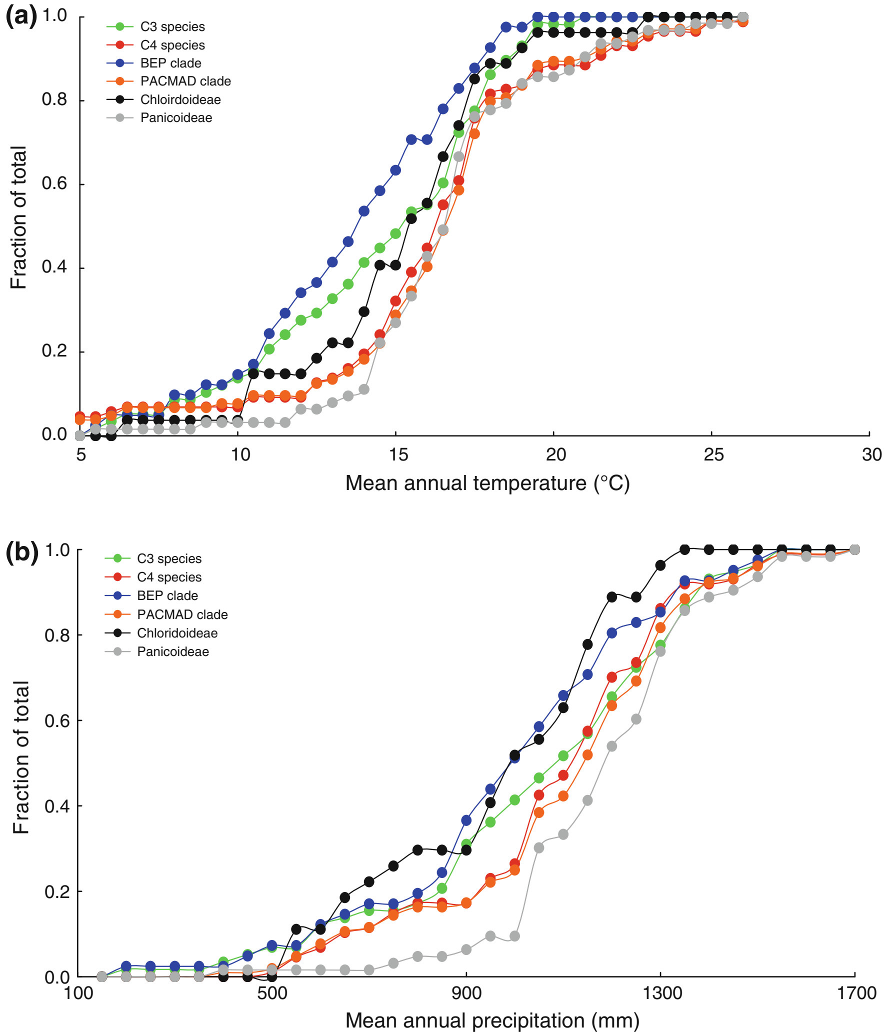

Fig. 2 Cumulative distribution curves of **a** mean annual temperature and **b** mean annual precipitation of investigated grass species

PACMAD clade and three nodes of BEP clade were marked by precipitation niche divergence; the largest precipitation niche divergence was found in a single C_3 PACMAD node AM (Fig. 3). The divergence patterns of temperature niche between BEP and PACMAD clades ($P < 0.001$) and between C_3 and C_4 species ($P = 0.039$) were significant. The divergence patterns of precipitation niche between BEP and PACMAD clade ($P < 0.001$) were significant, while precipitation niche divergence patterns between C_3 and C_4 species were insignificant ($P = 0.054$) (Table 3).

Among box plots of mean annual temperature (Fig. 4a), the divergence widths in C_3 nodes were the widest, the divergence widths in C_4 nodes were the narrowest, and differences of divergence widths within each kind (C_3, C_4, or C_3/C_4) of nodes were significant (Table 3). Among box plots of mean annual precipitation (Fig. 4b), the divergence widths in C_3 nodes were the widest, the divergence widths in C_4 nodes were the narrowest, whereas divergence widths within C_3 or C_4 nodes were significantly different except for C_3/C_4 nodes (Table 3). The significant rate changes of climate niche evolution were determined by AIC difference and chi-square test in Brownie (Fig. 3). The significant increase of temperature niche evolution was marked in node AP, which represents the C_3/C_4 node in Panicoideae. The significant increase of precipitation niche evolution was marked in node AX, which represents the C_3/C_4 node of all investigated species in Panicoideae. We reject the null model when it applies to multiple rates

Table 1 Descriptive statistics of photosynthetic pathways and phylogenetic compositions along climatic gradients in Chinese grass flora

Node category	No. of total species	No. of native species	Mean annual temperature (±SD)	Mean annual precipitation (±SD)
C_3 BEP	41	34	12.7 (±5.3)	969.0 (±415.3)
C_3 PACMAD	16	16	17.5 (±3.1)	1318.9 (±229.2)
C_4 PACMAD	88	74	18.6 (±2.4)	1279.7 (±240.5)
Chloridoideae	27	9	15.6 (±3.7)	956.9 (±247.1)
Panicoideae	63	29	17.0 (±3.3)	1175.6 (±212.2)

SD Standard deviation

Fig. 3 Majority rule consensus tree of three chloroplast genes ▶ of Poaceae with the constraint of a strict molecular clock in BEAST. *Scale bar* mean substitutions per site; *Number above branches* posterior probabilities; *Blue line* C_3 grass; *Red line* C_4 grass; *Yellow circle* reversal nodes from C_4 to C_3 species; *Green circles* 10 largest divergences in precipitation niches; *Red circles* 10 largest divergences in temperature niches; *Letters* "A–CY": nodes for climatic-niche evolution test; *Red node* multiple rates of temperature niche evolution; *Green node* multiple rates of precipitation niche evolution; *Black triangle* NAD-ME subtype including PCK subtype; *Black rhombus* NADP-ME subtype; BEP (*Bam* Bambusoideae; *Ehr* Ehrhartoideae; *Poo* ooideae) and PACMAD (*Pan* Panicoideae; *Aru* Arundinoideae; *Chl* Chloridoideae; *Mic* Micrairoideae; *Ari* Aristidoideae; *Dan* Danthonioideae). (Color figure online)

for these two nodes (see Appendix 4, in supplementary material).

Among box plots of mean annual temperature (Fig. 4c), the divergence widths in NAD-ME nodes were wider than those in NADP-ME nodes; the widest divergence width was found in node BL (from *Enteropogon dolichostachyus* to *Kengia songorica* in Fig. 3). Divergence widths within nodes of C_4 photosynthesis subtypes were significantly different ($P < 0.001$). Among box plots of mean annual precipitation (Fig. 4d), the divergence widths in NADP-ME nodes were wider than NAD-ME nodes with the widest divergence width exhibited in node H (*Sorghum bicolor* and *Phacelurus digitatus* in Fig. 3). Divergence widths within nodes of each C_4 subtype were also significantly different ($P < 0.001$) (Table 3).

Discussion

Climatic-niche structure

The realized climate niches of Chinese grasses is characterized by the following four points: (1) the temperature niche is phylogenetically conservative for BEP and PACMAD clades, and the precipitation niche is phylogenetically conservative for Chloridoideae

Table 2 Ten nodes of the largest divergences of climatic niches from phylogeny of Poaceae in China's nature reserves

Mean annual temperature					Mean annual precipitation				
Node name	Photosynthesis clade	V_i	A_i	D_i	Node name	Photosynthesis clade	V_i	A_i	D_i
AZ	C_3/C_4 PACMAD	3	7.005	8.603	AM	C_3 PACMAD	7	391.188	723.864
BV	C_4 PACMAD	5	4.496	7.409	AZ	C_3/C_4PACMAD	3	459.988	556.282
U	C_4 PACMAD	4	4.826	7.258	BY	C_3 BEP	2	524.616	524.617
AM	C_3 PACMAD	7	3.456	6.469	CN	C_3 BEP	25	271.009	486.698
D	C_4 PACMAD	3	5.736	5.736	X	C_4 PACMAD	7	183.453	376.853
CN	C_3 BEP	25	3.400	5.568	AH	C_3 PACMAD	2	368.388	368.388
X	C_4 PACMAD	7	5.487	5.562	CA	C_3 BEP	5	358.341	358.341
Z	C_4 PACMAD	3	4.099	5.12	H	C_4 PACMAD	2	351.926	351.927
BA	C_3/C_4 PACMAD	69	3.396	4.785	BS	C_4 PACMAD	27	247.731	343.041
M	C_4 PACMAD	23	3.188	4.613	BQ	C_4 PACMAD	6	216.342	321.928

V_i Number of species descended from parent node i; A_i climatic trait value at node i; D_i Root mean square deviation of climatic trait values of species descended from node i

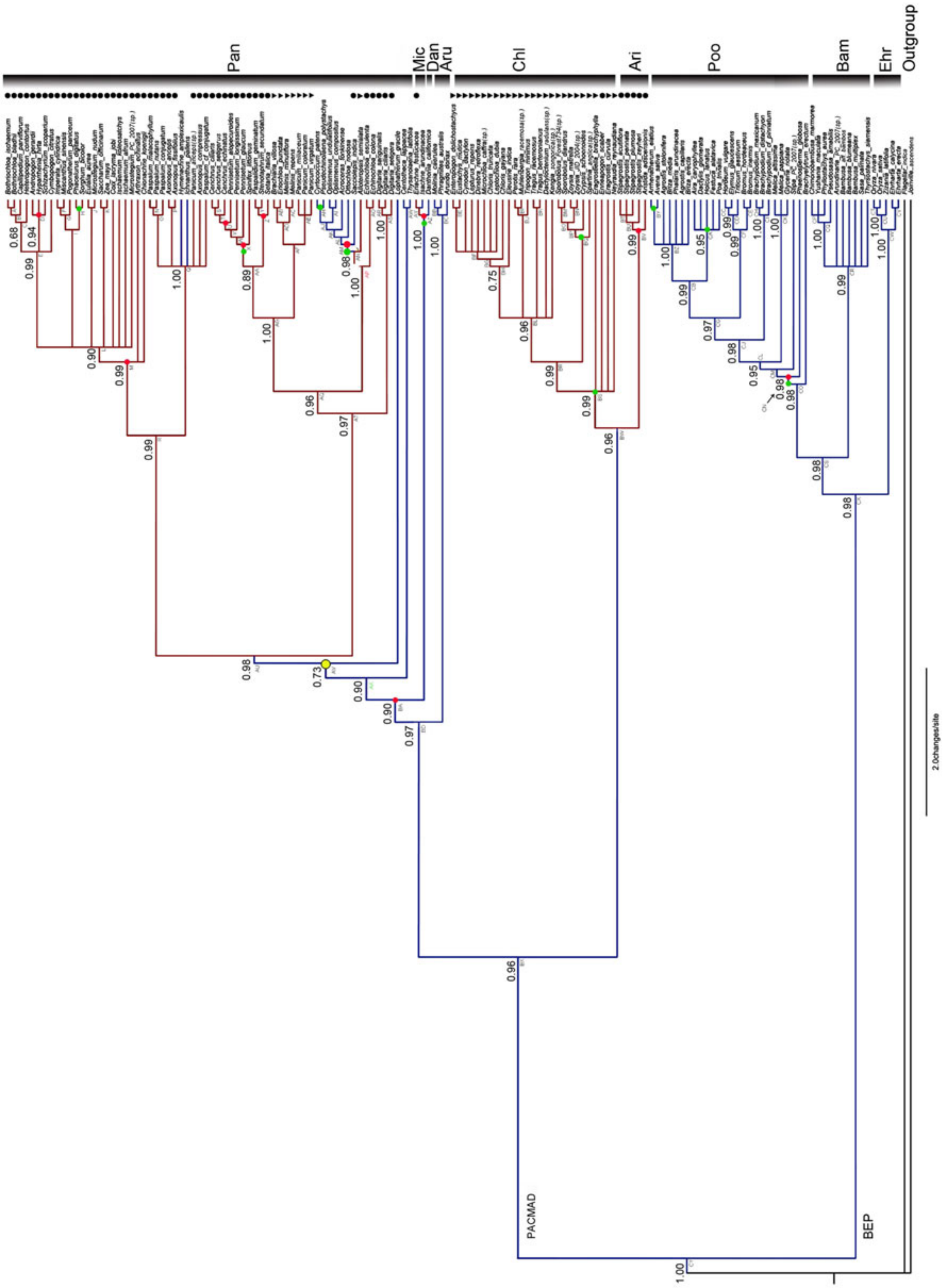
Pan
Mic
Dan
Aru
Chl
Ari
Poo
Bam
Ehr
Outgroup
PACMAD
BEP
2.0changes/site
1.00
0.96
0.97
0.90
0.90
0.73
0.98
0.99
0.96
0.98

Table 3 Independent-samples *T* test of root mean square deviation of climatic trait values (D_i) of species descended from node *i*

Climatic factor	D_i divergence value	
	Nodes	*P* value
Mean annual temperature	C_3	0.011*
	C_4	0.000*
	C_3/C_4	0.039*
	BEP	0.000*
	PACMAD	0.000*
	NAD-ME	0.000*
	NADP-ME	0.000*
Mean annual precipitation	C_3	0.000*
	C_4	0.000*
	C_3/C_4	0.054
	BEP	0.000*
	PACMAD	0.000*
	NAD-ME	0.000*
	NADP-ME	0.000*

* *P* value < 0.05 considered to be statistically significant

and Panicoideae owing to the tendency of climate niches to be more similar for these two pairs of phylogenetic groups (Table 1; Fig. 2); (2) the divergence patterns of temperature niche between BEP and PACMAD clades and between C_3 and C_4 species are distinguishable (Table 3); (3) the temperature niche evolutionary pattern for multiple rates is found in the C_3/C_4 node AP (Panicoideae) and the precipitation niche evolutionary pattern for multiple rates is found in the C_3/C_4 node AX (Panicoideae); and (4) the widest divergence width of climate niches is among C_3 nodes, while the narrowest divergence width of climate niches is among C_4 nodes.

A clear difference of average temperature range is found between BEP and PACMAD clades. The difference in mean annual temperature between C_3 BEP and C_3 PACMAD are greater in China (12.7 vs. 17.5°C) than in Hawaii (17.0 vs. 18.4°C; Edwards and Still 2008). Therefore, temperature gradients seem to have more impact on BEP and PACMAD clade distribution. In China, the phylogenetic pattern indicates that additional preadaptive characteristics (e.g. capacities of different species for resource acquisition) other than functional differences of photosynthesis pathways, enable the BEP clade to be dominant in cold-climate regions and the PACMAD clade to be dominant in warm-climate regions. However, the striking difference in precipitation between C_3 PACMAD and C_4 PACMAD nodes (3361 vs. 1,404 mm) in Hawaii indicates that precipitation may have more impact on the distribution of BEP and PACMAD species (Cabido et al. 2008). Higher water-use efficiency conferred by C_4 PACMAD nodes may play a critical role in C_3 and C_4 grass distribution along a precipitation gradient within the PACMAD clade in Hawaii.

Some conservative traits will determine the ability to occupy a realized climate niches for grasses (Donoghue 2008). The difference of niches may be big enough to reduce competition with other species under stable conditions. However, it is more likely that taxa experienced intermittent interactions with other taxa in different niches accompanying the environmental shifts. Hence, interspecific interactions between ecologically similar allopatric species, as opposed to the edaphic environment, promote phylogenetic clustering when many traits across the phylogeny are investigated (Kozak and Wiens 2007). The ancestors of the C_3 BEP and C_4 PACMAD lineages possessed such traits, thereby enabling their descendants to succeed in a similar type of habitat. As a result, descendants of a lineage will tend to be most successful in an appropriate climate niche due to interspecific competition, thus these ecological traits would be preserved in allopatric species within these two major clades (Lord et al. 1995; Edwards and Smith 2010).

Climate niche divergence

Our results may have some implications for explaining the strong association between elevation gradients and grass diversity in the subtropical forest region (Liu et al. 2009). First, our previous study suggested that high-energy (e.g., mean annual sunshine hours, mean annual temperature, annual potential evapotranspiration, and annual actual evapotranspiration) drives greater grass diversity in the subtropical forest region. Here, we show that multiple rates of temperature and precipitation niche evolution underlie this pattern in two grass nodes AP and AX (see Appendix 4 in supplementary material). In the field, regional species diversity of these two nodes peaks at lower elevations (e.g., 1,435 m), where energy and productivity are greater. Therefore, high grass diversification

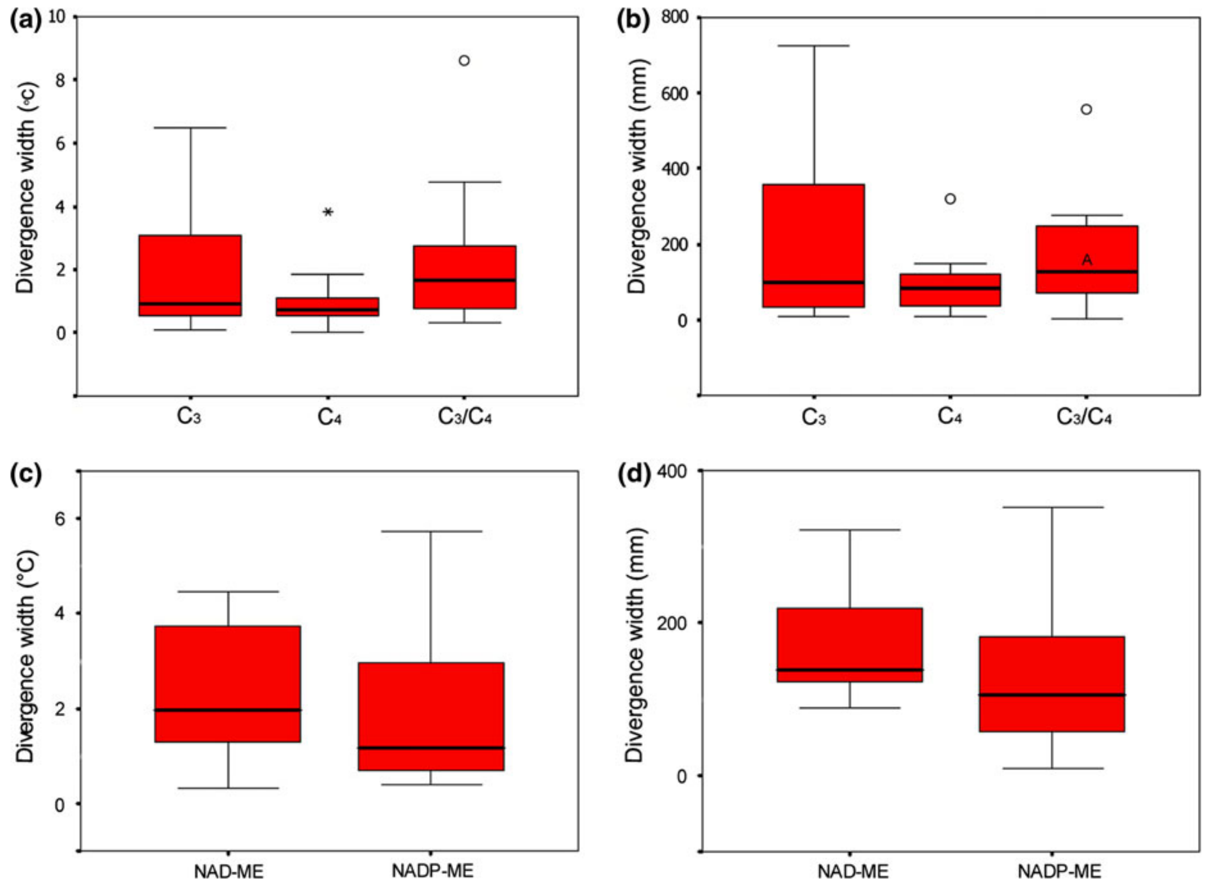

Fig. 4 Box plots of divergence width of mean annual temperature (*left y-axis*) and of mean annual precipitation (*right y-axis*): **a**, **b** among photosynthetic types; **c**, **d** among C_4 subtypes. *Horizontal line* median value; *Vertical lines* 95% confidence intervals; *Circles* outliers; *Asterisk* extreme outlier larger than [third quartile + 2 × (third quartile − first quartile)]; *Letter* "A": the insignificant difference ($P < 0.05$)

rates in the subtropical forest region seem to be associated with the greater carrying capacities of subtropical ecosystems, as predicted by previous publications (Belsky et al. 1993; O'Brien et al. 2000; Rahbek and Graves 2001). Second, stable tropical climates may promote selection for narrow ranges of climatic tolerances of tropical species, leading to greater turnover of species along elevation gradients (Janzen 1967). Our study demonstrates that shifts between climate conditions occur more rapidly in the subtropical region, where climate fluctuates (including glaciation) seasonally (Ying 2001; Shen et al. 2005).

The evolution rate of climate niches may depend on the evolution rate of physiological tolerances to extreme climates (e.g. heat or drought) for NAD-ME grasses. For example, the greater drought tolerances may constrain the NAD-ME nodes (rather than the NADP-ME nodes) dispersing from tropical forests to temperate desert regions (P'yankov and Mokronosov 1993; Ghannoum et al. 2002), and hence increased aridity tolerances might allow for rapid changes in NAD-ME grass distribution (Hattersley 1992). Furthermore, NAD-ME species with larger geographic distributions may exhibit wider temperature niche divergence (e.g. node BL in Fig. 3).

The correlation between two major C_4 variants (NAD-ME and NADP-ME) and two major subfamilies (Chloridoideae and Panicoideae) was confirmed (Carmo-Silva et al. 2009). Seventy-nine percent of NAD-ME grasses are members of Chloridoideae and 87% of NADP-ME grasses are members of Panicoideae. In other words, if the pattern of NAD-ME/NADP-ME abundance really reflects patterns of C_4 Chloridoideae/Panicoideae abundance, the adaptive ability of species to environmental changes appears to contribute considerably to the climate niche evolution (Hattersley and Watson 1992). For example, chloridoid node BI with widest divergence of temperature niche exhibits more geographic isolation than other chloridoid nodes, while panicoid node H with narrowest divergence of precipitation niche exhibits overlap with other panicoid nodes. The result indicates that NAD-ME/NADP-ME nodes display the phylogenetic signals in their climate niches (Prinzing et al. 2001; Roalson 2008).

China represents a larger climate window with four climatic regions and 51% (74/145) of grasses are native (Liu et al. 2009). Rapid species diversification is associated with rapid climate (especially temperature) niche evolution in the subtropical forest region where few nodes overlap geographically. These patterns are important for explaining continental (eastern Asia) scale patterns of grass richness, climate niche evolution, and conservatism. However, Hawaii represents a small climate window with a single tropical climatic type and 70% (106/152) of grasses are introduced (Edwards and Still 2008). Current Hawaiian grass distribution is interpreted as the product of climatic sorting (especially precipitation) processes in an insular scale (Juvik and Juvik 1998). At Hawaii, the climate niche evolution of a given species is the result of intrinsic ecological preferences and interspecific competitive abilities (Edwards and Still 2008). Our results indicate that adaptation to the climate changes has occurred in C_4 grass nodes of high climate niche evolutionary rates (e.g. nodes AP and AX) in China (Giambelluca and Schroeder 1998).

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References

Archetti M (2009) Phylogenetic analysis reveals a scattered distribution of autumn colours. Ann Bot 103:703–713

Austin MP, Nicholls AO, Margules CR (1990) Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. Ecol Monogr 60:161–177

Belsky AJ, Mwonga SM, Amundson RG, Duxbury JM, Ali AR (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. J Appl Ecol 30:143–155

Bouchenak-Khelladi Y, Salamin N, Savolainen V, Forest F, van der Bank M, Chase MW, Hodkinson TR (2008) Large multi-gene phylogenetic trees of the grasses (Poaceae): progress towards complete tribal and generic level sampling. Mol Phylogenet Evol 47:488–505

Cabido M, Pons E, Cantero JJ, Lewis JP, Anton A (2008) Photosynthetic pathway variation among C_4 grasses along a precipitation gradient in Argentina. J Biogeogr 35:131–140

Carmo-Silva AE, Francisco A, Powers SJ, Keys AJ, Ascensão L, Parry MAJ, Arrabaça MC (2009) Grasses of different C_4 subtypes reveal leaf traits related to drought tolerance in their natural habitats: changes in structure, water potential, and amino acid content. Am J Bot 96:1222–1235

Chazdon RL (1978) Ecological aspects of the distribution of C_4 grasses in selected habitats of Costa Rica. Biotropica 10:265–269

Chen SL, Li DZ, Zhu GH, Wu ZL, Lu SL, Wang ZP, Ammann KH et al (2006) Poaceae (Gramineae). In: Wu ZY, Raven PH, Hong DY (eds) Flora of China, vol 22. Science Press, Beijing and Missouri Botanical Garden Press, St Louis, pp 1–653

Collins RP, Jones MB (1985) The influence of climatic factors on the distribution of C_4 species in Europe. Vegetatio 64:121–129

Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, Weston PH et al (2009) Phylogenetic biome conservatism on a global scale. Nature 458:754–756

Donoghue MJ (2008) A phylogenetic perspective on the distribution of plant diversity. Proc Natl Acad Sci USA 105(Suppl. 1):11549–11555

Drummond AJ, Rambautx A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol Biol 7:214

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. PLoS Biol 4:699–710

Edwards EJ, Smith SA (2010) Phylogenetic analyses reveal the shady history of C_4 grasses. Proc Natl Acad Sci USA 107:2532–2537

Edwards EJ, Still CJ (2008) Climate, phylogeny and the ecological distribution of C_4 grasses. Ecol Lett 11:266–276

Edwards EJ, Osborne CP, Strömberg CAE, Smith SA, C_4 Grasses Consortium (2010) The origins of C_4 grasslands: integrating evolutionary and ecosystem science. Science 328:587–591

Ehleringer JR, Cerling TE, Helliker BR (1997) C_4 photosynthesis, atmospheric CO_2 and climate. Oecologia 112:285–299

Epstein HE, Lauenroth WK, Burke IC, Coffin DP (1997) Productivity patterns of C_3 and C_4 functional types in the U.S. Great Plains. Ecology 78:722–731

Ghannoum O, von Caemmerer S, Conroy JP (2002) The effect of drought on plant water use efficiency of nine NAD-ME and nine NADP-ME Australian C_4 grasses. Funct Plant Biol 29:1337–1348

Giambelluca TW, Schroeder TA (1998) Climate. In: Juvik SP, Juvik JO (eds) Atlas of Hawai'i, 3rd edn. University of Hawai'i Press, Honolulu, pp 49–59

Hattersley PW (1983) The distribution of C_3 and C_4 grasses in Australia in relation to climate. Oecologia 57:113–128

Hattersley PW (1986) Variations in photosynthetic pathways. In: Soderstrom RT, Hilu KW, Campbell CS, Barkworth ME (eds) Grass systematics and evolution. Smithsonian Institute Press, Washington, DC, pp 49–64

Hattersley PW (1992) C_4 photosynthetic pathway variation in grasses (Poaceae): its significance for arid and semi-arid lands. In: Chapman GP (ed) Grass evolution and domestication. Cambridge University Press, New York, pp 181–212

Hattersley PW, Watson L (1992) Diversification of photosynthesis. In: Chapman GP (ed) Grass evolution and domestification. Cambridge University Press, New York, pp 38–116

Hof C, Rahbek C, Araújo MB (2010) Phylogenetic signals in the climatic niches of the world's amphibians. Ecography 33:242–250

Janzen DH (1967) Why mountain passes are higher in the tropics. Am Nat 101:233–249

Juvik SP, Juvik JO (1998) Atlas of Hawai'i, third edition edn. University of Hawai'i Press, Honolulu

Kellogg EA (1999) Phylogenetic aspects of the evolution of C_4 photosynthesis. In: Sage RF, Monson RK (eds) C_4 plant biology. Academic Press, London, pp 411–444

Klink CA, Joly CA (1989) Identification and distribution of C_3 and C_4 grasses in open and shaded habitats in São Paulo State, Brazil. Biotropica 21:30–34

Kozak KH, Wiens JJ (2007) Climatic zonation drives latitudinal variation in speciation mechanisms. Proc R Soc Lond B 274:2995–3003

Liu Q, Ge XJ, Columbus JT, Chen WL (2009) Grass (Poaceae) richness patterns across China's nature reserves. Plant Ecol 201:531–551

Lord J, Westoby M, Leishman M (1995) Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. Am Nat 146:349–364

Monfreda C, Ramankutty N, Foley JA (2008) Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. Global Biogeochem Cycles 22:1–19

Nixon KC (2002) WinClada, version 1.00.08. Computer program published by the author, Ithaca, New York, USA. http://www.cladistics.com. Accessed 1 Dec 2008

Norušis MJ (2009) SPSS 17.0 Statistical procedures companion. Prentice Hall, New Jersey, USA

O'Brien EM, Field R, Whittaker RJ (2000) Climatic gradients in woody plant (tree and shrub) diversity, water-energy dynamics, residual variation, and topography. Oikos 89:588–600

O'Meara BC, Ane C, Sanderson MJ, Wainwright PC (2006) Testing for different rates of continuous traits evolution using likelihood. Evolution 60:922–933

P'yankov VI, Mokronosov AT (1993) General trends in changes of the earth's vegetation related to global warming. Russ J Plant Physiol 40:443–458

P'yankov VI, Gunin PD, Tsoog S, Black CC (2000) C_4 plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. Oecologia 123:15–31

P'yankov VI, Ziegler H, Akhani H, Deigele C, Lüttge U (2010) European plants with C_4 photosynthesis: geographical and taxonomic distribution and relations to climate parameters. Bot J Linn Soc 163:283–304

Palmer MW, White PS (1994) Scale dependence and the species area relationship. Am Nat 144:717–740

Paruelo JM, Lauenroth WK (1996) Relative abundance of plant functional types in grasslands and shrublands of North America. Ecol Appl 6:1212–1224

Peterson PM, Romaschenko K, Johnson G (2010) A classification of the Chloridoideae (Poaceae) based on multigene phylogenetic trees. Mol Phylogenet Evol 55:580–598

Prendergast HDV, Hattersley PW, Stone NE (1987) New structure/biochemical associations in leaf blade of C_4 grasses (Poaceae). Aust J Plant Physiol 14:403–420

Price JP (2004) Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleography. J Biogeogr 31:487–500

Prinzing A, Durka W, Klotz S, Brandl R (2001) The niche of higher plants: evidence for phylogenetic conservatism. Proc R Soc Lond B 268:2383–2389

Rahbek C, Graves GR (2001) Multiscale assessment of patterns of avian species richness. Proc Natl Acad Sci USA 98:4534–4539

Renvoize SA (1987) A survey of leaf-blade anatomy in grasses XI. Paniceae. Kew Bull 42:739–768

Roalson EH (2008) C_4 Photosynthesis: differentiating causation and coincidence. Curr Biol 18:R167–R168

Roe GH, Baker MB (2007) Why is climate sensitivity so unpredictable? Science 318:629–632

Roure B, Rodriguez-Ezpeleta N, Phillipe H (2007) SCaFoS: a tool for selection, concatenation and fusion of sequences for phylogenomics. BMC Evol Biol 7:S2

Rundel PW (1980) The ecological distribution of C_4 and C_3 grasses in the Hawaiian islands. Oecologia 45:354–359

Sage RF (2004) The evolution of C_4 photosynthesis. New Phytol 161:341–370

Sage RF, Wedin DA, Li MR (1999a) The biogeography of C_4 photosynthesis: patterns and controlling factors. In: Sage RF, Monson RK (eds) C_4 plant biology. Academic Press, London, pp 313–373

Sage RF, Li MR, Monson RK (1999b) The taxonomic distribution of C_4 photosynthesis. In: Sage RF, Monson RK (eds) C_4 plant biology. Academic Press, London, pp 551–584

Sánchez-Ken JG, Clark LG (2010) Phylogeny and a new tribal classification of the Panicoideae *s.l.* (Poaceae) based on plastid and nuclear sequence data and structural data. Am J Bot 97:1732–1748

Sánchez-Ken JG, Clark LG, Kellogg EA, Kay EE (2007) Reinstatement and emendation of subfamily Micrairoideae (Poaceae). Syst Bot 32:71–80

Shen L, Chen XY, Zhang X, Li YY, Fu CX, Qiu YX (2005) Genetic variation of *Ginkgo biloba* L. (Ginkgoaceae) based on cpDNA PCR-RFLPs: inference of glacial refugia. Heredity 94:396–401

Soreng RJ, Davidse G, Peterson PM, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Morrone O (2009) Classification of New

World grasses. http://www.tropicos.org/Project/CNWG. Accessed 2 Sep 2009

Still CJ, Berry JA, Collatz GJ, Defries RS (2003) The global distribution of C_3 and C_4 vegetation: carbon cycle implications. Global Biogeochem Cycles 17:1006

Sun HQ (2004) Biodiversity analysis of Gramineae plants in Qinghai province, China. Pratacultural Sci 19:7–12

Swenson NG (2009) Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. PLoS One 4:e4390

Taub DR (2000) Climate and the US distribution of C_4 grass subfamilies and decarboxylation variants of C_4 photosynthesis. Am J Bot 87:1211–1215

Taylor SH, Hulme SP, Rees M, Ripley BS, Woodward FI, Osborne CP (2010) Ecophysiological traits in C_3 and C_4 grasses: a phylogenetically controlled screening experiment. New Phytol 185:780–791

Teeri JA, Stowe LG (1976) Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23:1–12

Tofts R, Silvertown J (2000) A phylogenetic approach to community assembly from a local species pool. Proc R Soc Lond B 267:363–369

Ueno O, Sentoku N (2006) Comparison of leaf structure and photosynthetic characteristics of C_3 and C_4 *Alloteropsis semialata* subspecies. Plant Cell Environ 29:257–268

Ueno O, Yoshimura Y, Sentoku N (2005) Variation in the activity of some enzymes of photorespiratory metabolism in C_4 grasses. Ann Bot 96:863–869

Vogel JC, Fuls EllisRP (1978) The geographical distribution of Kranz grasses in South Africa. S Afr J Sci 74:209–215

Webb CO, Ackerly DD, McPeek M, Donoghue MJ (2002) Phylogenies and community ecology. Annu Rev Ecol Evol Syst 33:475–505

Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100

Yan BG, Wen WQ, Zhang J, Yang WQ, Liu Y, Huang X, Li ZB (2010) Plant community assembly rules across a subalpine grazing gradient in western Sichuan, China. Chin J Pl Ecol 34:1294–1302

Yin LJ, Li MR (1997) A study on the geographic distribution and ecology of C_4 plants in China. I. C_4 plant distribution in China and their relation with regional climatic condition. Acta Ecol Sin 17:350–363

Ying TS (2001) Species diversity and distribution pattern of seed plants in China. Biodivers Sci 9:393–398