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Research

Effects of contemporary environment and Quaternary climate change on drylands plant diversity differ between growth forms

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Previous studies on large-scale patterns in plant richness and underlying mechanisms have mostly focused on forests and mountains, while drylands covering most of the world's grasslands and deserts are more poorly investigated for lack of data. Here, we aim to 1) evaluate the plant richness patterns in Inner Asian drylands; 2) compare the relative importance of contemporary environment, historical climate, vegetation changes, and mid-domain effect (MDE); and 3) explore whether the dominant drivers of species richness differ across growth forms (woody vs herbaceous) and range sizes (common vs rare). Distribution data and growth forms of 13 248 seed plants were compiled from literature and species range sizes were estimated. Generalized linear models and hierarchical partitioning were used to evaluate the relative contribution of different factors. We found that habitat heterogeneity strongly affected both woody and herbaceous species. Precipitation, climate change since the mid-Holocene and climate seasonality dominated herbaceous richness patterns, while climate change since the Last Glacial Maximum dominated woody richness patterns. Rare species richness was strongly correlated with precipitation, habitat heterogeneity and historical climatic changes, while common species richness was strongly correlated with MDE (woody) or climate seasonality (herbaceous). Temperature had little effects on the species richness patterns of all groups. This study represents the first evaluation of the large-scale patterns of plant species richness in the Inner Asian drylands. Our results suggest that increasing water deficit due to anthropogenic activities combined with future global warming may increase the extinction risk of many grassland species. Rare species (both herbaceous and woody) may face severe challenges in the future due to increased habitat destruction caused by urbanization and resource exploitation. Overall, our findings indicate that the hypotheses on species richness patterns based on woody plants alone can be insufficient to explain the richness patterns of herbaceous species.

Keywords: drylands, herbaceous diversity, plant richness patterns



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Introduction

Large-scale patterns of species richness and their determinants are central yet controversial in macroecology (Araújo and Rahbek 2008). Among different factors that have been proposed to explain species richness patterns, present climate (Currie and Paquin 1987), long-term climate change (Sandel et al. 2011), habitat heterogeneity (Stein et al. 2014) and geometric constraints (Colwell and Lees 2000) have been widely explored. The contemporary temperature and precipitation can significantly affect the species richness patterns, which have been well examined for many taxa at various spatial scales (Currie 1991, Svenning and Skov 2007). Habitat heterogeneity can affect species richness by providing more niche space and more opportunities for species' diversification (Stein et al. 2014, 2015). Conversely, habitat fragmentation caused by human disturbance may have stronger effects on species loss than global warming (Hof et al. 2011, Li and Yang 2014). Long-term climate fluctuations across the Quaternary can also influence species richness. For example, species with low dispersal ability tend to be constrained to refugia with stable climates during the glacial periods (Loarie et al. 2009, Sandel et al. 2011). Geometric constraints on neutrally, but cohesively expanding species distributions could lead to high species richness in the center of a bounded study area regardless of ecological factors, which has been termed as the 'mid-domain effect' (MDE; Colwell et al. 2004, Grytnes et al. 2008, Mezajoya and Torres 2016). Although the effects of these factors have been evaluated in previous studies, how their relative effects vary among taxa with different range sizes (i.e. common vs rare species; Jetz and Rahbek 2002, Lennon et al. 2010) and growth forms (i.e. woody vs herbaceous species; Crous et al. 2013) remains controversial.

Species with different range sizes may respond differently to climate and habitat changes. Studies have shown that rare species adapted to small-scale environments (Rabinowitz 1981) or formed by historical climate change (Svenning and Skov 2007) may not easily shift their ranges to timely track the long-term climate changes due to dispersal limitation (Jansson 2003). In contrast, common species can cope up with the drastic climatic changes better than rare species (Svenning and Skov 2007) and thus their richness patterns may be more in equilibrium with the present climate (Liu et al. 2016). Therefore, the same extent of long-term climate change may generate different effects on common and rare species richness (Dynesius and Jansson 2000, Normand and Svenning 2011, Sandel et al. 2011), which indicates that the range sizes should be well considered when studying the richness patterns at large scales.

Woody and herbaceous plants have different morphologies and generation time, thus could respond differently to environmental changes. Global herbaceous floras show an accelerated speciation within a relatively recent history due to their shorter generation time than woody species (Linder 2008, Smith and Donoghue 2008, Hughes and Atchison 2015). Most previous studies on plant richness patterns

are focused on woody species (Svenning and Skov 2007, Wang et al. 2012b, Xu et al. 2013). Many studies focusing on herb-dominated vegetation types (e.g. grasslands, tundra, etc.) have explored the relationship between plant richness and climate and soil condition using community-level data (Chytrý et al. 2003, 2007, 2012). However, it remains controversial whether the richness patterns of woody and herbaceous species respond differently to climate, habitat and historical factors at large-spatial scale (Antonelli et al. 2009, Albuquerque et al. 2011). Furthermore, the effects of the interaction between range sizes and growth forms on plant richness patterns have not been adequately explored.

Global drylands cover ca 38–41% of the terrestrial area and are considered to be highly sensitive to climate change and human activities (Reynolds et al. 2007, Maestre et al. 2015). However, studies on large-scale richness patterns have mostly focused on species-rich regions such as tropical mountains and rainforests, while drylands remain more poorly investigated. The climatic drivers of species distributions in large scales remain controversial. For example, although water availability has been suggested to be the major limitation for the survival and dispersal of dryland plants (Hoekstra et al. 2005, Tietjen et al. 2009, Li et al. 2013), a recent study suggests that climate variability drives the spatial turnover in plant species composition in dryland ecosystems (Ulrich et al. 2014). Therefore, further studies are needed to reveal the primary determinants of species richness in drylands. The drylands in Inner Asia (35–55°N, 45–120°E, following Mohammat et al. 2013) are characterized by diverse flora and vegetation (Eyre 1971), including steppe, shrublands, tugai forests (poplar forests), and islands of mountain forest surrounded by broad grasslands (Miehe et al. 2007). The Inner Asian drylands are experiencing enhanced climate change (Reynolds et al. 2007, Wang et al. 2008) and mountain forest fragmentation due to intense human pressure (Miehe et al. 2007). Understanding plant richness patterns and the underlying mechanisms would be helpful for improving the conservation of plant diversity and vegetation under climate changes in this region. However, few studies have focused on the large-scale species richness patterns in this area due to lack of species distribution data.

Here, we compiled the first database of seed plant distributions in the Inner Asian drylands and estimated the species richness patterns for different growth forms (woody vs herbaceous) and range sizes (common vs rare). Then we evaluated the relative importance of contemporary environment, habitat heterogeneity, historical climatic and vegetation changes, and mid-domain effect (MDE) dynamics on plant species richness.

Material and methods

Study area

Our study focused on the drylands located in the central part of the Eurasian continent (35–55°N, 45–120°E). This area was once named as central Asia (Okur 2014),

but is usually referred to Inner Asia in more recent literature (Mohammad et al. 2013), which is the term used here. The aridity index (AI), defined as the ratio of mean annual precipitation to mean annual potential evaporation, has been widely used to define drylands (Jansen et al. 2007), and is also used here. Early studies normally used $AI < 0.65$ as the threshold to identify drylands (Middleton and Thomas 1997), while recent studies have suggested $AI < 0.7$ as a better choice (Jansen et al. 2007). In our study, we used both thresholds in preliminary analyses, but chose the latter because the boundary of drylands under this definition is more close to the boundary of steppe and forests. In order to maintain a continuous region of the study area, a small number of grid cells with $AI > 0.7$ surrounded by drylands were also kept in our analysis, which covered 10% of the entire study area. Finally, the Inner Asian drylands included the continuous region covering Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan, Mongolia and western China (Fig. 1a).

Species distribution data

We constructed the ‘Database of plant species distribution in the Inner Asian drylands’ using a great number of published regional and local floras for China, the five central Asian

countries (the former Union of Soviet Socialist Republics, USSR), and Mongolia (see Supplementary material Appendix 3 for a complete list of data sources). Data sources for the species distribution in China included all published provincial floras of the six western provinces, including Ningxia (2 volumes), Gansu (2 volumes), Xinjiang (6 volumes), Xizang (5 volumes), Qinghai (4 volumes) and Inner Mongolia (5 volumes and 3 other regional floras covering entire Inner Mongolia). We also compiled the available information from ‘Flora of China’ and other regional atlases and floras of these provinces, e.g. ‘Atlas of woody plants in China’ (2 volumes), ‘The vascular plants and their eco-geographical distribution of the Qinghai-Tibetan Plateau’ (1 volume), ‘Desert plants in China’ (1 volume), ‘Index florae Karakorum-Kunlunensis’ (1 volume) and ‘Atlas of tree in Gannan’ (1 volume). The data in these provincial and regional floras are all county level (ca 10 000 km² in average).

The species distribution data in Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan are from ‘Atlas of trees and shrubs in U.S.S.R.’ (3 volumes, in Russian) and ‘Flora of U.S.S.R.’ (50 volumes). The atlases and floras of U.S.S.R. cover all these five countries and provide detailed maps or descriptions of plant distributions. The distribution data in Mongolia are from ‘Rangeland plants of Mongolia’ (1 volume) and ‘Conspectus of the vascular plants of

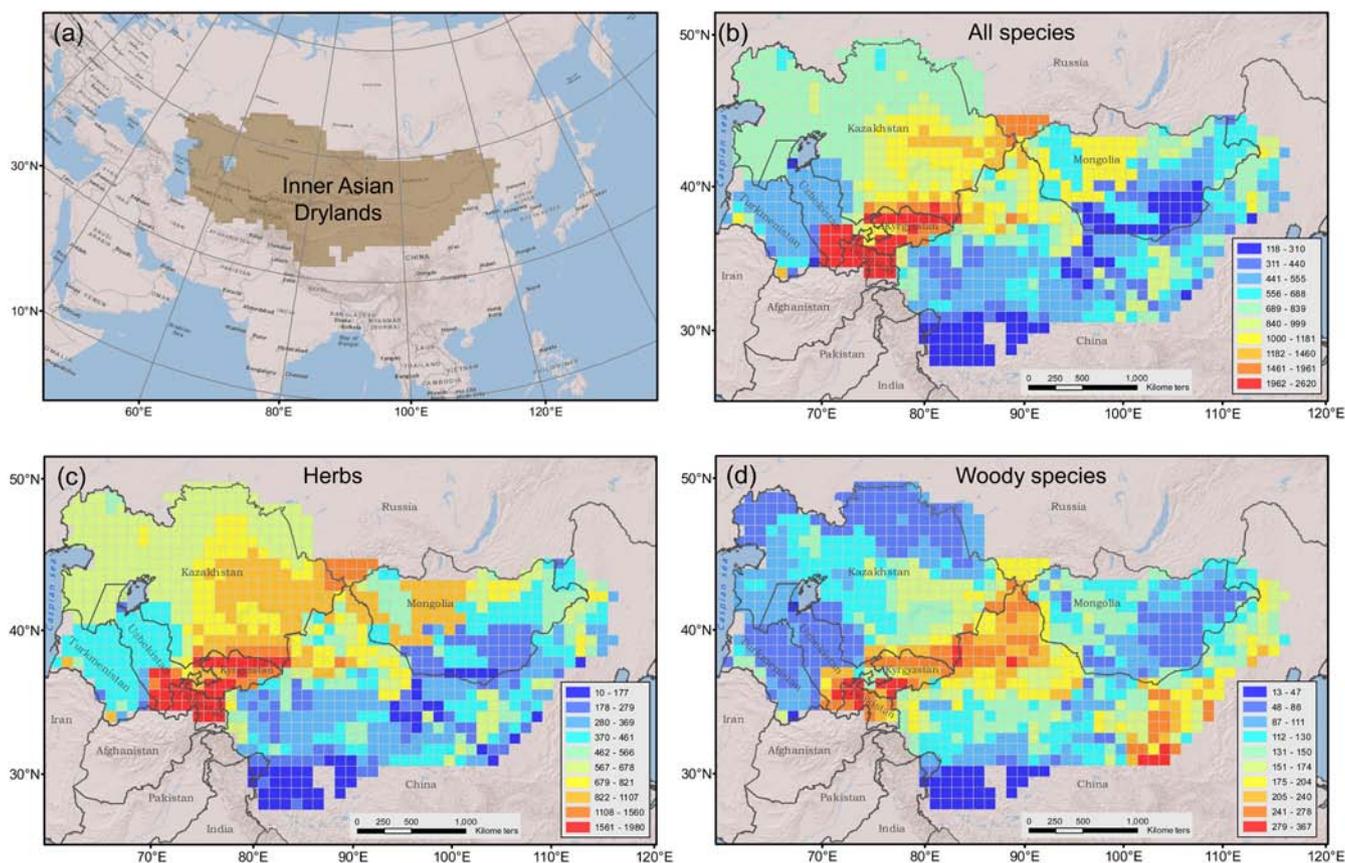


Figure 1. Patterns of species richness in the Inner Asian drylands. (a) The location of the study area (brown region). See Material and methods for the definition of drylands. Patterns of species richness for all species (b), herbaceous species (c) and woody species (d).

Mongolia' (1 volume). We further collected occurrence data from online databases that provide specimen records in these countries, including the 'National specimen information infrastructure' (NSII, <www.nsii.org.cn> accessed in July 2015), the 'Virtual guide to the flora of Mongolia, and the global biodiversity information facility' (GBIF). The nomenclature of species names from different sources were merged following 'The plant list database' (<www.theplantlist.org/> accessed at 12 March 2014). After finishing the general database, the distribution map of each species was generated and examined carefully to further improve the quality of the distribution data. The records of cultivation were removed and infraspecific units (i.e. subspecies and varieties) were merged to species.

The distribution maps were then transformed into gridded distributions with Albers cubic equal area projection at a spatial resolution of 100 × 100 km in ArcGIS 10.0 (ESRI, Redlands, CA) to eliminate the potential influence of area on the estimation of species richness. The median size of original geographical units from regional and local publications mentioned above is 7246.6 km², which is close to the size of a 100 × 100 km² grid cell. However, most geographical units in Mongolia and the regions in the west of the Tianshan–Altai divide are much larger than the size of a 100 × 100 km² grid cell. The species richness in the regions with large geographical units tends to be overestimated when the species distributions were transformed into a 100 × 100 km² grid. To improve the spatial resolution of species distributions in the west of the Tianshan–Altai division and to eliminate the spatial bias in species richness estimation, species distribution was further refined by its elevational range. Specifically, for each species, the grid cells whose elevation is 100 m lower or higher than the lower or upper limits of species elevation range were eliminated. This method has been used in previous studies on species distributions in different regions (Li et al. 2013, Yan et al. 2013). The elevation ranges of species were collected from published national and provincial floras of China, the former Union of Soviet Socialist Republics (USSR), and online databases including 'eFloras.org' (<www.efloras.org/project_list.aspx>), 'Scientific database of China plant species' (<http://db.kib.ac.cn/eflora/Default.aspx>) and 'Chinese plant subject databases' (<www.plant.csdb.cn/>). In total, 747 735 grid occurrences data for 13 248 seed plant species were used in the subsequent analyses. Grid cells along the border of the study area were removed when less than half of their area (< 5000 km²) was inside the study area. Finally, we compared the generated species richness patterns with previous studies on global plant species richness and found that our results are consistent with previous estimations for this region (Mutke et al. 2005, Krefl and Jetz 2007).

Classification of growth forms and range sizes

The collected plant species were categorized into two growth forms: woody (incl. tree, shrub, dwarf shrub and woody liana) and herbaceous (incl. herb and herbaceous liana).

Growth form information was collected from the published floras mentioned above and online databases including 'The Tropicos' (<www.tropicos.org/Home.aspx>), 'eFloras.org' (<www.efloras.org/project_list.aspx>), 'Scientific database of China plant species' (<http://db.kib.ac.cn/eflora/Default.aspx>) and 'Chinese plant subject databases' (<www.plant.csdb.cn/>). In total, 9776 species were recorded as herbaceous and 2231 species as woody. In the whole database, the proportion of species with missing growth form information was 9.37%.

The range size of a species is defined as the number of grid cells occupied by the species. Histograms of range sizes were strongly right-skewed and were similar between the two growth forms (Supplementary material Appendix 2 Fig. A2.1). The number of grid cells occupied by herbaceous species ranged from 1 to 839 and those by woody species ranged from 1 to 877. Following previous classification methods (Araújo and Rahbek 2008, Liu et al. 2016), we ranked the species of each growth form in descending order of range size and then categorized the upper 25% species as common species and the lower 75% as rare species. However, some species may have large distribution ranges outside our study area, but only small ranges inside, leading to pseudo-rare species, which may bias our estimation of rare species richness, and hence was removed from our analysis. Here, a species was identified as a pseudo-rare species if its global distribution range (see Supplementary material Appendix 3 for the list of data sources) was larger than 25% of our study area, but only less than 50% of its distribution was within our study area. The distribution ranges of these species were large enough to be defined as common species, but could be identified as rare species by mistake if the main distribution range was not in our study area. Finally, after removing the pseudo-rare species, 5719 rare and 2441 common herbaceous species and 972 rare and 656 common woody species were used in further analyses.

Environmental data

We divided the environmental factors into seven categories as following. 1) Temperature variables (Temp.), including mean annual temperature (MAT) and potential evapotranspiration (PET), mean temperature of summer (MTS, summer is defined as period from June to August) and mean temperature of winter and spring (MTW, winter and spring are defined as period from December through January to May). MAT and PET have been widely used in previous studies to represent environment energy (Currie 1991). MTS and MTW were used to compare the effects of temperature between dry and wet seasons. 2) Precipitation variables (Precip.), including mean annual precipitation (MAP), precipitation of summer (MPS), precipitation in winter and spring (MPW) and rainfall (RAIN, the total precipitation of the months with mean monthly temperature > 0°C). 3) Contemporary climate variation (Clim.-var.), including mean diurnal temperature range (DRT) and precipitation season seasonality (PSN). 4) Habitat heterogeneity (Habit-heter.), including spatial precipitation

(MAPR) and elevational range (ELER) within a grid cell. Spatial temperature range was highly correlated with ELER ($r > 0.85$) and was hence not included in our analysis. 5) Past climate change (Past-clim.), including temperature anomaly (the absolute values of the difference in MAT between the past and the present) and velocity (the spatial distance that species must migrate to track climate change) since the mid-Holocene (MH, ca 6000 yr BP; MHano and MHvl, respectively) and the Last Glacial Maximum (LGM, ca 22 000 yr BP; LGMano and LGMvl, respectively). 6) Past vegetation change (Past-veg.), including the relative grassland area variation calculated as the difference between modern and past grassland proportions (for the mid-Holocene: GrassVar.MH; for the LGM: GrassVar.LGM). 7) Mid-domain effect (MDE) variable, which was calculated for overall, herbaceous and woody species and for common and rare species separately. MDE describes geometric constraints on species distributions that could lead to a central-aggregated pattern in the study area regardless of ecological factors. This variable was calculated using dye diffusion algorithm and were conducted using the R function developed by Wang et al. (2012b).

Both modern and past temperature and precipitation data were retrieved from the WorldClim website (<www.worldclim.org>) at a spatial resolutions of 1 arc minute (past climate data are reconstructed by MPI-ESM-P model (Watanabe et al. 2011). Elevation data was calculated from GTOPO30 digital elevation model (resolution: 3", resampled to 100 × 100 km²; available at <http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info>). Data used to calculate PET are from the Global Aridity and PET Database (available at <www.cgiar-csi.org/data/global-aridity-and-pet-database>). The definition of grassland followed the Global land cover characteristics database ver. 2.0 (available at <http://edc2.usgs.gov/glcc/globdoc2_0.php>). The grassland distribution in the present, mid-Holocene and LGM were reconstructed (Supplementary material Appendix 2 Fig. A2.5) following the method of Wang et al. (2017). The calculation of all variables is provided in Supplementary material Appendix 1 Table A1.2.

Models and statistical analyses

Species richness was estimated as the total number of species in each grid cell. To compare the explanatory power of each environmental variable on species richness, we developed univariate generalized linear models (GLMs) with quasi-Poisson residuals between species richness and environmental variables among the seven groups (i.e. overall, woody, herbaceous and common and rare species within growth forms). The explanatory power of each environmental variable was estimated as the adjusted R^2_{adj} (%) of the GLM model. Modified t-test were used in significance test to eliminate the influence of spatial autocorrelation on p values (Clifford et al. 1989). The R^2_{adj} (%) of the GLM model was significant only when $p < 0.1$.

To differentiate independent and joint effects of each variable on species richness, hierarchical partitioning analysis

(Nally 2000) was applied as a comparison with univariate GLMs results. We first conducted a principal component analysis (PCA) within each of the environmental groups and then extracted the first axis to represent each group. We standardized the mid-domain effect variable instead because PCA cannot be applied to a group containing only one variable. Then, we conducted hierarchical partitioning (HP) analyses for all species and species groups with different life forms and range sizes. Specifically, these PCA scores were used as predictors and the richness of each species group were used as response variables.

To further evaluate if the same combination of environmental factors has different effects on richness patterns between different species groups, we conducted multiple GLMs with different combination of environmental factors as predictors. Specifically, for each model, we chose one factor from each of the seven environmental factor categories (the anomaly and velocity represent different aspects of past climate change and they are not strongly correlated ($R < 0.5$), thus we chose either of the anomaly and velocity or both) and combined the chosen factors in the GLMs. Finally, 576 models with different combinations of environmental factors were generated and AIC and the R^2_{adj} for each model was calculated. Models were ordered by descending order of the R^2_{adj} (%) for overall species group, and then AIC and the R^2_{adj} of each species group were compared to evaluate the performance of different models.

Data deposition

All environmental data are available from the WorldClim website (<www.worldclim.org>) and the data of species distribution are available upon request.

Results

Pattern of species richness

Plant species in drylands peak in the mountainous regions such as Tianshan and Altai Mountains, and Pamirs (Fig. 1b). Species richness centers differ between growth forms (Fig. 1c, d) and between common and rare species (Fig. 2). Specifically, the northern part of the Inner Asian drylands (i.e. Eastern Kazakh Steppe and western Mongolian Plateau) harbors more herbaceous than woody species, while the southeastern part (i.e. northwestern China) harbors more woody than herbaceous species (Fig. 1). Most of the rare species concentrate in the mountainous parts of the Inner Asian drylands. Common herbaceous species peak in Eastern Kazakh Steppe, while common woody species peak in the central part of the entire study area (Fig. 2).

Determinants of overall species richness

Univariate GLMs showed that the dominant factors for overall species richness were mean annual precipitation, precipitation in winter and spring, spatial precipitation

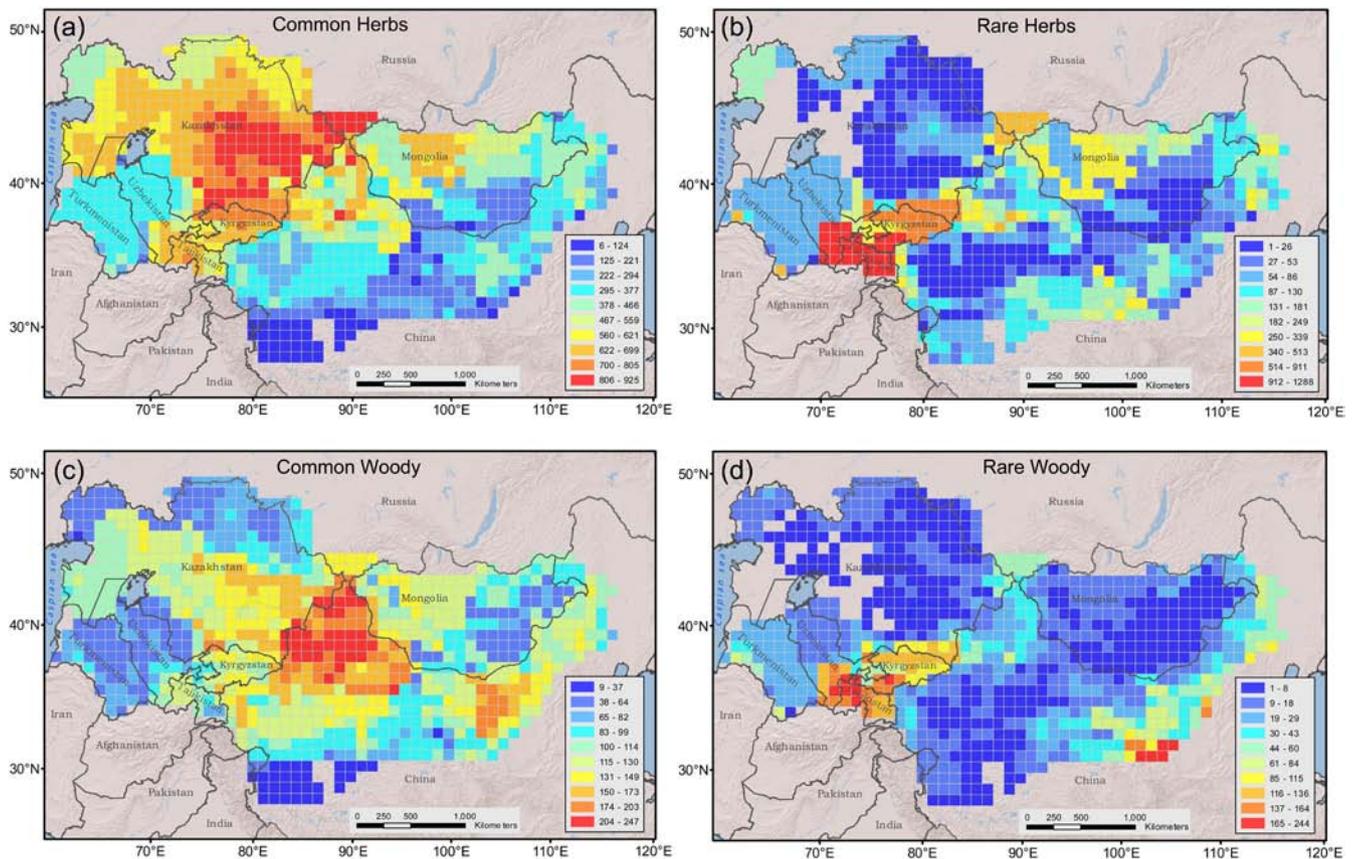


Figure 2. Patterns in species richness of the common (a) and rare (b) herbaceous species, and the common (c) and rare (d) woody species in the Inner Asian drylands.

heterogeneity, diurnal temperature range and temperature change since mid-Holocene (MHano and MHvl; Fig. 3a). Contemporary temperature did not affect species richness. Hierarchical partitioning analyses showed consistent results with those of GLMs. Precipitation had the highest total (sum of joint and independent effect) R^2 , and climate variation had the highest independent R^2 on overall species richness (Fig. 3d). The total R^2 of habitat heterogeneity on herbaceous species richness was similar to that of climate variation, but $> 50\%$ of the R^2 of habitat heterogeneity was shared with other variables.

Determinants of species richness for different growth forms and range size groups

The relative contributions of different environmental factors to richness patterns differed between woody and herbaceous species (Fig. 3, Supplementary material Appendix 1 Table A1.1) and between common and rare species (Fig. 4, Supplementary material Appendix 1 Table A1.1). The R^2 of environmental variables for herbaceous species richness was generally higher than for woody species richness. We ranked all Multi-GLMs for each growth form and very few models were good at explaining both woody and herbaceous species richness (Supplementary material Appendix 2 Fig. A2.6). The

dominant factors for herbaceous species richness were highly consistent with those for overall species richness, including present climate variation (DRT and PSN), precipitation in winter and spring, spatial precipitation heterogeneity and climate change since the mid-Holocene (MHano and MHvl). In contrast, woody species were strongly affected by habitat heterogeneity (ELER and MAPR) and climate change since the LGM (LGMano and LGMvl). Hierarchical partitioning suggested that precipitation and climate variation had the highest independent effects on herbaceous richness. In contrast, habitat heterogeneity and past climate change had the highest joint and independent effects on woody species richness (Fig. 3).

GLM results showed that the richness of rare species (both woody and herbaceous) was strongly influenced by mean annual precipitation, spatial precipitation heterogeneity and past temperature velocity at both time scales (MHvl and LGMvl; Fig. 4c, d). Common species showed a quite different pattern between woody and herb species: mid-domain effect dominated the woody richness, while climate variation (DRT and PSN) dominated the herbaceous richness (Fig. 4a, b). Hierarchical partitioning analysis showed similar pattern to that of GLMs. Past climate change, habitat heterogeneity and precipitation explained $> 20\%$ of the richness variations for both rare woody and rare herbaceous groups, while the

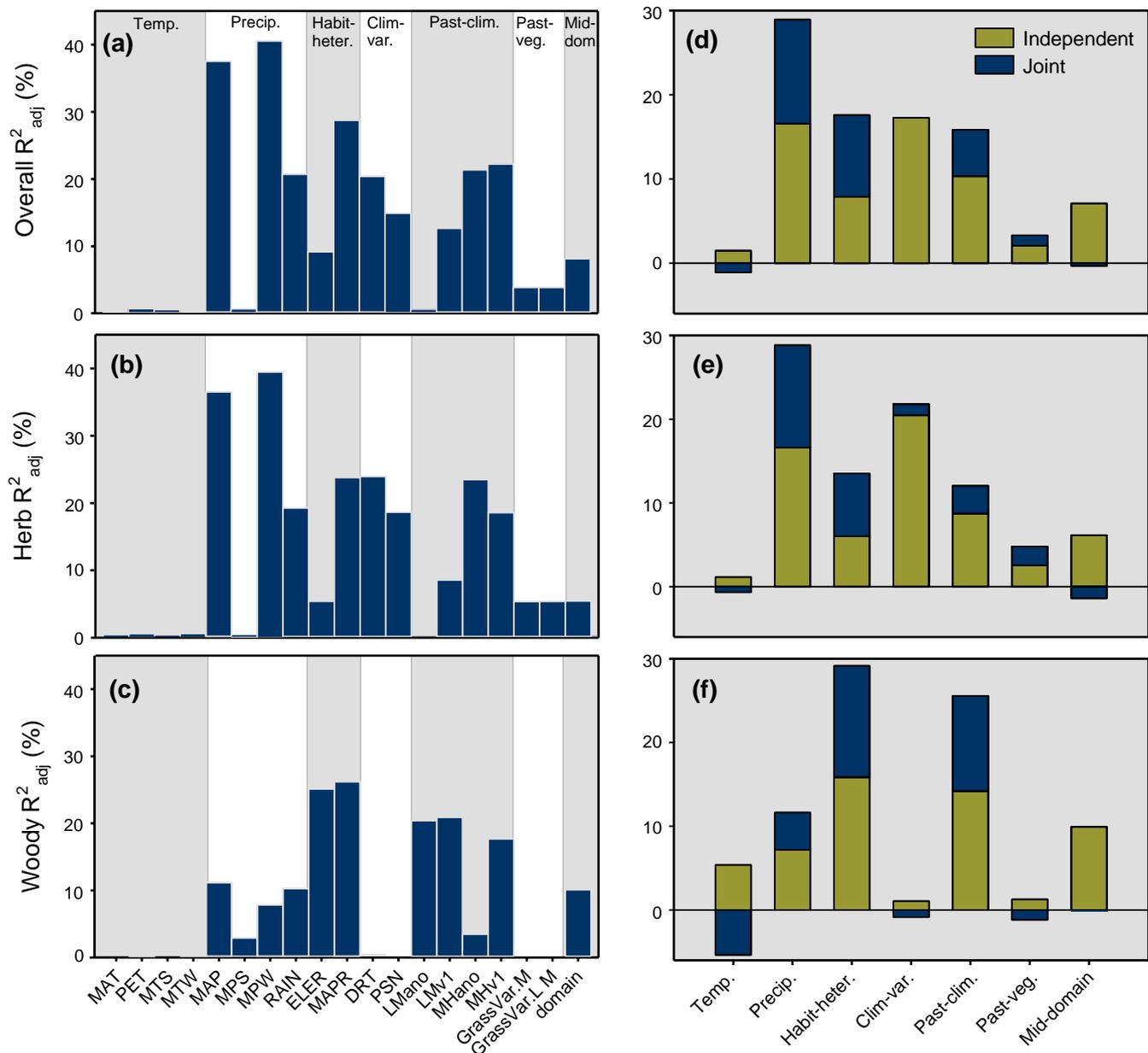


Figure 3. (a–c) The explanatory power of environmental variables (R^2_{adj} , %) on the richness patterns of all species (a), herbaceous species (b), and woody species (c) evaluated by univariate GLM models. The R^2_{adj} evaluated by univariate GLM models values of environmental variables i are shown in Supplementary material Appendix 1 Table A1.1. (d–f) Joint and independent effects of environmental variables (R^2 , %) on the richness patterns of all species (d), herbaceous species (e), and woody species (f) evaluated by hierarchical partitioning models. The first PCA axes within the seven environmental groups were extracted and then applied in the further calculation of hierarchical partitioning models. We standardized mid-domain effect because there is only one variable in this group. Abbreviations: 1) Temp. = environmental temperature (incl. MAT, PET, MTS and MTW); 2) Precip. = precipitation (incl. MAP, MPS, MPW and RAIN); 3) Habit-heter. = habitat heterogeneity (incl. ELER and MAPR); 4) Clim-var. = present climate variation (incl. DRT and PSN); 5) Past-clim. = past climate change (incl. MHano, MHvl, LGMano and LGMvl); 6) Past-veg. = past vegetation change (incl. GrassVar.LGM and GrassVar.MH); and 7) Mid-domain = mid-domain effect. MAT = mean annual temperature, PET = potential evapotranspiration, MTS = mean temperature of summer, MTW = mean temperature of winter and spring, MAP = mean annual precipitation, MPS = mean precipitation of summer, MPW = mean precipitation of winter and spring, RAIN = rainfall, logELER = range of elevation within a grid cell (log transformed), logMAPR = range of MAP within a grid cell (log transformed), DRT = mean diurnal range, PSN = precipitation seasonality, MHano = temperature anomaly since MH (the mid-Holocene, ca 6000 yr BP), logMHvl = temperature velocity since MH (log transformed), LGMano = temperature anomaly since LGM (the Last Glacial Maximum, ca 22 000 yr BP), logLGMvl = temperature anomaly since LGM (log transformed), GrassVar.MH = relative grassland area variation since MH, GrassVar.LGM = relative grassland area variation since LGM.

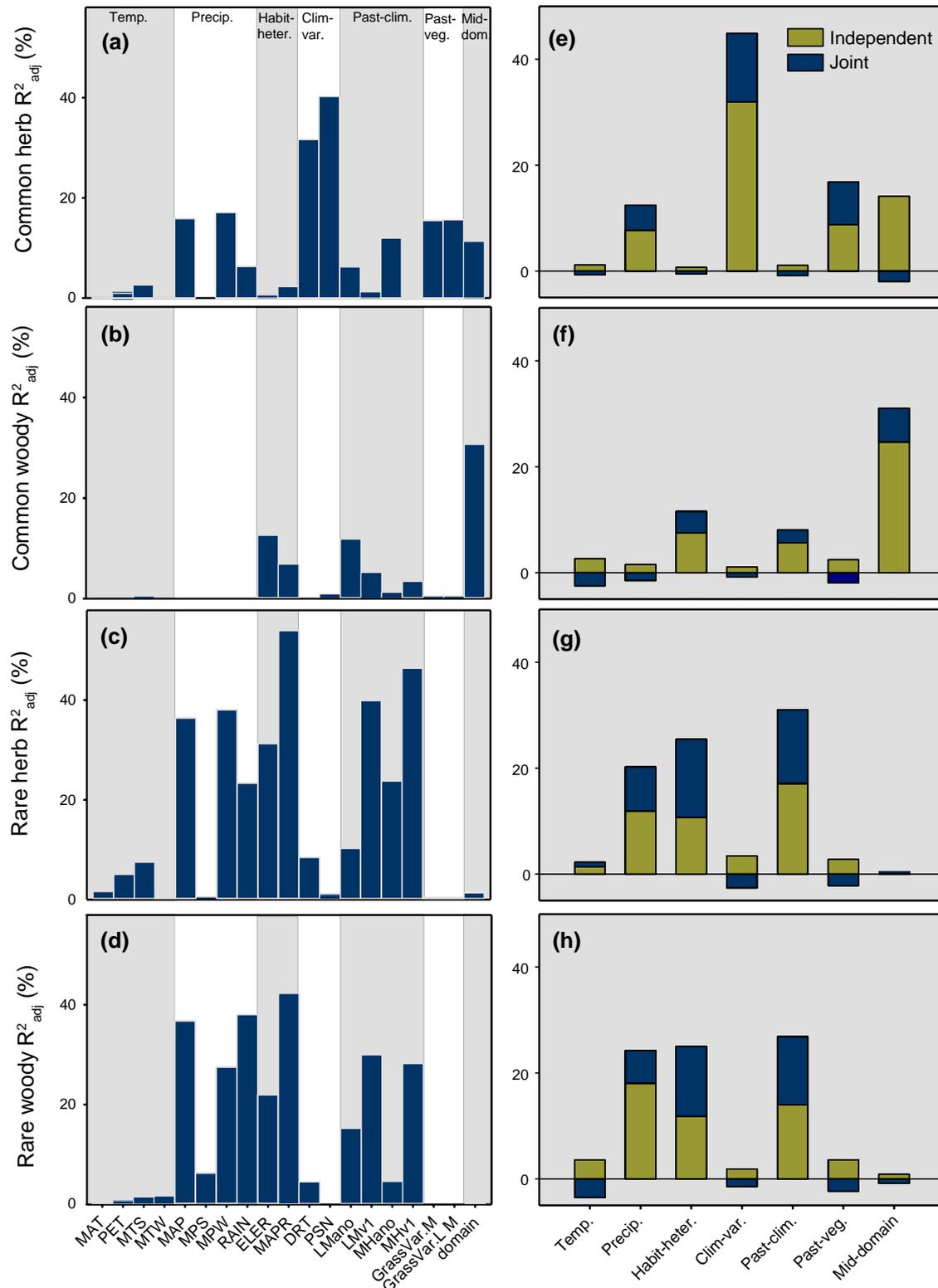


Figure 4. (a–d) The explanatory power of environmental variables (R^2_{adj} , %) on the richness patterns of common herbaceous species (a), common woody species (b), rare herbaceous species (c) and rare woody species (d) evaluated by univariate GLM models. The abbreviations of variables are the same as Fig. 3a–c. The R^2_{adj} value of environmental variables are shown in Supplementary material Appendix 1 Table A1.1. (e–h) Joint and independent effects of environmental variables (R^2 , %) on the richness patterns of common herbaceous species (e), common woody species (f), rare herbaceous species (g) and rare woody species (h) evaluated by hierarchical partitioning models. The calculation methods and abbreviations of variables are the same as Fig. 3d–f.

R^2 of other factors were close to 0 (Fig. 4g, h). In contrast, climate variation dominated the richness of common herbaceous species, while the richness of common woody species was dominated by mid-domain effects (Fig. 4e, f). Multi-GLMs models showed that environmental variables have lower R^2 or higher AIC for common species richness than for rare species richness, which was observed for both herbs and woody species (Supplementary material Appendix 2 Fig. A2.6).

Discussion

Effects of drought on species richness differ between growth forms

The species richness in drylands was more strongly limited by water availability than by temperature, which is consistent with the recent studies on soil microbes (Maestre et al. 2015), vertebrates (Li et al. 2013) and plants (Tietjen et al. 2009). However, the effects of precipitation differed between woody and herbaceous species. Precipitation, especially in winter and spring, determined herbaceous richness, but did not affect woody richness. Herbaceous richness peaked both in steppe and mountains, while hotspots of woody richness were exclusively located in mountains. Mountainous areas have steady water sources such as meltwater and headwaters. Mountains also have more snowfall than flat regions (Miehe et al. 2007). Thus, precipitation in mountains is less directly important for plants than in deserts and grasslands. There are also scattered patches of woody species occurring in semi-desert grasslands dominated by *Stipa* and *Anabasis* (Wesche et al. 2005). The dominant species in these stands usually are phreatophytes with long-lived habit (e.g. *Populus euphratica*), which have root systems with both deep and shallow roots to get groundwater (Bruehlheide et al. 2003) and thus reduce the demand for precipitation (Jensen et al. 2011, Li and Yang 2014). In contrast, herbaceous species, especially those in steppe, mainly use shallow soil water that highly depends on precipitation (Gries et al. 2003). As one of the hotspots for herbaceous species, steppes in Kazakhstan are known as winter precipitation regions (Wesche et al. 2016, also see Supplementary material Appendix 2 Fig. A2.4). Therefore, precipitation in winter and spring should be the most important period for herbs to get water, consistent with our finding that MPW was the major factor for herbaceous richness patterns.

The correlation matrix showed that the precipitation seasonality and precipitation were highly negatively correlated: climate in more arid regions tended to have high precipitation seasonality (Supplementary material Appendix 2 Fig. A2.3). Consequently, effects of these two variables on plants richness patterns were similar (Fig. 3b, c). Precipitation seasonality in drylands sets the minimum breadth of arid tolerances required by species (Carranza et al. 2008). Plants living in drylands with high precipitation seasonality may get relatively adequate water in wet season, but must tolerate the extreme drought during dry season (Morgan 2004). Therefore,

hyper-drought in dry season and high precipitation seasonality can be the major limitations for herbaceous species distribution. The increasing water deficit due to increase in urban and agricultural water usage combined with future climate change (Reynolds et al. 2007, Tietjen et al. 2009) may raise the risk of diversity loss in grasslands.

Effects of habitat heterogeneity and MDE differ between rare and common species

The GLMs showed that rare species were significantly affected by habitat heterogeneity, while common species were not. These results were consistent among growth forms (Fig. 4a–d), suggesting that habitat heterogeneity is vital for maintaining the richness of rare species. A positive heterogeneity–richness relationship have been observed for different taxa in other regions (Stein et al. 2014, 2015). High habitat heterogeneity increases the available ecological niches to accommodate more species (Currie 1991, Jetz and Rahbek 2002) and provides refugia for ‘specialists’ and species in general to survive climate fluctuations (Kallimanis et al. 2010, Fjeldså et al. 2012). In the Inner Asian drylands, rare species occur mainly in mountainous regions, where habitat heterogeneity is the highest. Mountainous regions can provide more niches than flat areas for rare species. Specifically, plant communities in mountainous regions have a more complex layer structure and this lead to generating more types of habitats than in grasslands and deserts, e.g. shade provided by trees for ombrophytes and canopy for epiphytes. Furthermore, high mountains provide melt-water during spring and adequate summer rainfall at the windward side, while the leeward side of mountains has low rainfall and hence provide niches for drought-tolerant plants. It is noteworthy that the Inner Asian drylands are experiencing rapid land cover changes in recent years due to overgrazing and fossil fuel exploitation (Karnieli et al. 2008). Since rare species often have small populations and fragmented habitats (Sala et al. 2000), they may face severe challenges under increased habitat loss and destruction caused by urbanization and resource exploitation in the future.

Compared with rare species, the relative effects of different environmental variables on common species richness differed between woody and herbaceous species. The richness of common woody species was highest in the center and showed little spatial variation in deserts and grasslands (Fig. 2, see Supplementary material Appendix 2 Fig. A2.5 for the distribution of deserts and grasslands). Therefore, the richness of common woody species was weakly correlated with environmental variables, but strongly with the variables of mid-domain effects (Fig. 4b, e). This suggested that common woody species might experience weaker environmental constraints, and thereby relatively stronger stochastic range dynamics processes than rare woody species. This finding is consistent with previous studies on the elevational gradient of plant species diversity in southwestern China (Wang et al. 2007) and geographical pattern of bird species richness in Africa (Jetz and Rahbek 2002). Compared to common

woody species, common herbaceous species live mainly in regions with hyper-drought (Fig. 1b), and high climate fluctuations and climate seasonality dominate their species richness patterns (Fig. 3b). These results suggest that previous findings based on woody taxa could not be simply applied to herbaceous species.

Effects of long-term climate change differ between both range size and growth forms

The effects of past climate change on richness are different between woody and herbaceous species. Climate change since the mid-Holocene had stronger effects on herbaceous richness patterns than climate change since the LGM, while the opposite was true for the richness of woody species (Fig. 3b, c). Herbaceous species may respond to climate change at relatively shorter time scales than woody species, which may reflect the difference in the generation time (i.e. the time from seed germination to first blooming) between growth forms (Smith and Beaulieu 2009). A shorter generation time will lead to a higher rate of evolution (Smith and Donoghue 2008) and thus a faster micro-evolutionary adaptation (Hof et al. 2011). The micro-evolutionary adaptation occurring within few generations can increase the possibility of small adjustment in physiological, phenological or morphological traits and thus allow species to reduce the climate change adaptation lag (Nussey and Visser 2005, Hof et al. 2011). Compared with trees and shrubs that typically have long generation time (Smith and Donoghue 2008), herbaceous species often reproduce in the first or second year after germination and thus have a large possibility to track climate change timely via accommodating themselves to new emerging environments (Smith and Beaulieu 2009, Albuquerque et al. 2011). Clonal reproduction behavior may influence the age of plant species (Lavrenko and Karamysheva 1993; e.g. a 2000 yr-old *Carex curvula* in mountainous regions, Steinger et al. 1996), yet data on the longevity of clonal herbs in Inner Asian drylands are limited. Although previous studies suggest that 35–80% out of all vascular plants globally could be clonal plants, less than 5% of them reproduce mainly through clonal propagation (Dong 2011). Meanwhile, the number of species with very old ramets are relatively low in the field. For example, all of the ramets of *Leymus chinensis* (one of the dominant species in the Eurasian steppe) are less than 4 yr old, and 92% of them are less than 2 yr old (Yang and Liu 1995). Therefore, we believe that clonal reproduction need not invalidate this potential explanation for our contrasting results for woody vs herbaceous plants.

Our results also showed that climate change velocity rather than anomaly dominate the richness patterns of rare species, but not of common species, and this finding is consistent between growth forms (Fig. 4c, d, g, h). Compared with anomaly, climate change velocity is more related to the spatial migration ability of species (Stein et al. 2015). Rare species usually have genotypes controlling their adaptation to small habitat and low dispersal ability (Dynesius and Jansson 2000, Jansson 2003). These genotypes usually prefer long-term climate

stability (Jansson 2003). The accumulation of rare species in mountains can be explained by their important role as refugia due to the low climate change velocity during the Quaternary (Sandel et al. 2011). In contrast, lowlands have much higher climate change velocity (hence species have to disperse much farther to track climate change) than mountainous regions, and hence can hardly harbor rare species. These findings suggest that mountains may also provide shelters for rare species under future climate changes. Consistent with our findings, previous studies in Europe (Svenning and Skov 2004, Normand and Svenning 2011), North America (Hawkins and Porter 2003, Montoya et al. 2007) and east Asia (Wang et al. 2012a) have found that most rare species have not recolonized the northern parts of their potential distribution due to low dispersal ability or other geographic limitations. In contrast, common species tend to have strong dispersal ability and can colonize suitable habitat by long-distance dispersal. Meanwhile, common species with wide geographic ranges tend to have more possibility to cover suitable microclimates within their current distributions (Scherrer and Körner 2010).

Concluding remarks

The large-scale patterns of plant species richness in the Inner Asian drylands suggest that current precipitation and climate changes have stronger effects on the distribution of herbaceous species than woody species, which indicates that the increasing water deficit due to anthropogenic activities combined with future global warming may increase the extinction risk of many grassland species. The differences in the dominant factors affecting the patterns of woody and herbaceous species richness suggest that the findings based on one growth form alone should be cautiously interpreted when applying to the other. Compared to common species, rare species were more strongly affected by the habitat heterogeneity variables, which indicate that rare species may face more severe challenges in the future due to increased habitat destruction caused by urbanization and resource exploitation. Land cover change and decline of corridors among community patches in drylands could be a major concern in the conservation of rare species.

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Supplementary material (Appendix ECOG-03698 at <www.ecogeography.org/appendix/ecog-03698>). Appendix 1–4.