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GLOBAL CHANGE ECOLOGY - ORIGINAL PAPER

Functional consequences of climate change-induced plant species loss in a tallgrass prairie

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Abstract Future climate change is likely to reduce the floristic diversity of grasslands. Yet the potential consequences of climate-induced plant species losses for the functioning of these ecosystems are poorly understood. We investigated how climate change might alter the functional composition of grasslands for Konza Prairie, a diverse tallgrass prairie in central North America. With speciesspecific climate envelopes, we show that a reduction in mean annual precipitation would preferentially remove species that are more abundant in the more productive lowland positions at Konza. As such, decreases in precipitation could reduce productivity not only by reducing water availability but by also removing species that inhabit the most productive areas and respond the most to climate variability. In support of this prediction, data on species abundance at Konza over 16 years show that species that are more abundant in lowlands than uplands are preferentially reduced in years with low precipitation. Climate change is likely to also preferentially remove species from particular functional groups and clades. For example, warming is forecast to preferentially remove perennials

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K. K. McLauchlan Department of Geography, Kansas State University, Manhattan, KS 66506, USA over annuals as well as Cyperaceae species. Despite these predictions, climate change is unlikely to unilaterally alter the functional composition of the tallgrass prairie flora, as many functional traits such as physiological drought tolerance and maximum photosynthetic rates showed little relationship with climate envelope parameters. In all, although climatic drying would indirectly alter grassland productivity through species loss patterns, the insurance afforded by biodiversity to ecosystem function is likely to be sustained in the face of climate change.

Keywords Climate change · Grasslands · Functional traits · Konza Prairie · Biogeography

Introduction

The interactions between plant species and their environment are determined by plant "functional traits", which range from photosynthetic rates to rooting depth to the timing of flowering. Not only do the functional traits of species determine species success in a given environment but they also control the flows of materials and energy through the ecosystem. As such, it is the functional trait composition of a flora that determines such ecosystem services such as carbon fixation, nutrient retention, biomass production, and the ability to support herbivores (Cadotte et al. 2009; De Deyn et al. 2008; Diaz et al. 2007; Hodgson et al. 2005; Luck et al. 2009; Wedin and Tilman 1996).

Climate change is likely to locally extirpate plant species (Sala et al. 2000; Thomas et al. 2004) or entire clades of plants (Willis et al. 2008), and consequently alter the functional trait composition of ecosystems. Although recent advances in species distribution models and climate change experiments have increased our predictive capacity Author's personal copy

to understand range shifts and potential biodiversity loss with climate change (Fay et al. 2002; Peterson et al. 2008), the functional consequences of these losses are poorly understood. We have little knowledge about whether climate change will preferentially remove species with certain sets of traits, species from particular clades, or species that are consistently rare or dominant in given environments. Certain clades may be disproportionately extirpated in response to climate change (Willis et al. 2008), and this could lead to shifts in phylogenetic composition and function of ecosystems if there is phylogenetic signal in the traits and functions of species (Cavender-Bares et al. 2009). Without understanding the functional traits that are likely to be lost with climate change, predicting future ecosystem functioning is greatly diminished. Characterizing key plant traits across a diverse set of species is integral for relating community and ecosystem responses to climate changes (Fischlin et al. 2007; Kahmen et al. 2005; Parmesan and Yohe 2003; Walther et al. 2002).

The North American tallgrass region is likely to be significantly altered by climate change, but we have little specific information about how climate change will alter the functional composition of tallgrass prairies. The region is characterized by strong gradients in precipitation and temperature (Borchert 1950), while its flora is comprised of species with varied climatic distributions and little endemism (Axelrod 1985; Williams and Jackson 2007). Air temperatures for central North America are forecast to increase approximately 3.5°C by 2100 (Christensen et al. 2007). Predictions of the magnitude and scope of future changes in precipitation for the tallgrass region vary among climate models rendering increases in precipitation as likely as decreases (Christensen et al. 2007). Responses to historic variability suggest these grassland ecosystems are likely to be highly sensitive to climate change (Knapp et al. 1998; Weaver 1968; Wells 1970). In tallgrass prairie, experimental warming reduces soil moisture and increases leaf temperature, altering gene transcriptional profiles (Travers et al. 2010), leaf physiology (Nippert et al. 2009), phenology (Sherry et al. 2007), and productivity (Sherry et al. 2008). Similarly, experimental alteration of precipitation affects soil moisture, which impacts plant physiology (Fay et al. 2002; Nippert et al. 2009), community productivity (Sherry et al. 2008), and community composition (Knapp et al. 2002; Sherry et al. 2008).

To begin to predict the functional consequences of climate change in grasslands, we first determined mean annual precipitation (MAP) and mean annual temperature (MAT) envelopes for 440 herbaceous non-wetland vascular plant species that are present at Konza Prairie, a tallgrass prairie in Kansas, USA. We then test relationships between climate envelope parameters and a set of 12 functional traits as well as abundance of the species at Konza across topography, burning, and grazing contrasts. In testing for relationships with the lower bounds of MAP (MAP_L) and the upper bounds of both MAP (MAP_U) and MAT (MAT_{U}) , we test whether climate change is likely to disproportionately cause the loss of species with certain functional characteristics or from particular clades, which can serve as a better proxy for function than common functional groups (Edwards et al. 2007). For example, if species that are restricted to high precipitation regions tend to flower late in the growing season, a decline in mean annual precipitation would preferentially remove late-season flowering species, which then could impact pollinator communities or seasonal carbon uptake. In determining the relationships between climate envelopes and abundance of species at Konza, we can then test whether a 3°C increase in temperature or a 150-mm increases or decrease in precipitation would likely alter the general pattern of species abundance at Konza by preferentially removing species that are rare or abundant under certain environmental conditions.

Materials and methods

Site and flora description

The study was conducted at Konza Prairie Biological Station, a 3,487-ha native tallgrass prairie located in northeastern Kansas, USA (39.08°N, 96.56°W). Mean annual temperature from the Konza weather station 1983–2009 is 13°C. Annual precipitation for Konza Prairie averaged 844 mm from 1983 to 2009, with approximately 75% falling in the April through September growing season. The Konza flora contains 593 vascular plant species derived from 98 families (Towne 2002; Towne, unpublished). Of these, the 455 species that are not more prominent in wetlands, and/or are not woody, were the focus of this study, which allows us to center predictions for the herbaceous grassland flora.

Generating climate envelopes and predicted losses

For each species, climate envelopes were generated from occurrence data acquired from the Global Biodiversity Information Facility (http://www.gbif.org) in January 2010. Occurrence data were restricted to the conterminous United States in an attempt to standardize sampling effort among species and differences in inter-continental spread. In addition, species can have different climate envelopes on different continents (Beaumont et al. 2009), and our exclusive focus was on ranges centered around Konza. Due to Konza's central location in the conterminous US, the effects on climate envelope parameters caused by Author's personal copy

excluding adjacent countries should be minimized. Only occurrence data that were geo-referenced were included in the dataset. Species for which there were less than 50 occurrence data points were excluded from our dataset, which produced a final set of 440 species with climate envelopes.

For each species occurrence, we extracted 50-year mean annual temperature and mean annual precipitation (1950–2000) from WorldClim (http://www.worldclim.org). For each species, we then determined the 10 and 90% quantiles of MAT and MAP to describe the species' climate envelope. We had also acquired for each occurrence annual temperature range and diurnal temperature range from WorldClim and potential evapotranspiration and an aridity index (MAP/PET) from the CGIAR-CSI Global-Aridity and Global-PET Geospatial Database (Trabucco and Zomer 2009), but found little to no additional explanatory power for those variables over MAT and MAP (data not shown). The 10% quantile was used as the index of the upper bounds for MAT and MAP for each species.

Phylogenetic relationships and functional traits

To test whether there was a phylogenetic signal in climate envelope parameters, and therefore whether climate change would preferentially remove species from given clades, the *K* statistic and associated randomization test (Blomberg et al. 2003) were used. Treating predicted species loss under a particular climate scenario as a binary trait, the *nodesig* function in Phylocom (Webb et al. 2008) was used to compare the number of lost descendants from each node to the number expected if species loss was random with respect to phylogeny, i.e. observed numbers compared to 1,000 random shufflings of the taxa labels on the phylogeny. Those nodes in the top 5% of the random distribution were considered to be significantly more likely to lose descendents than expected.

The 12 functional traits examined in this study were derived from multiple sources. Data on first flowering was derived from a combination of field collection in 2009 and observations as part of the Konza Environmental Education Program over 8 years (http://keep.konza.ksu.edu/). Earliest flowering dates were averaged across all years. A series of leaf, root, and whole-plant traits were derived from plants grown under standardized conditions from seed or vegetative reproductive parts (Tucker et al. 2011). Leaf functional traits included maximum mass-based photosynthetic rate, stomatal conductance, the angle at which leaves are held relative to the ground, leaf tissue density and leaf thickness as well as their compose, specific leaf area. Root functional traits included the average root diameter for the fine roots (<2 mm), root tissue density, and specific root

length, which is composed from the two previous traits. Also included were the fraction of biomass in roots of 3-month-old plants and the water potential at which plant leaves ceased stomatal conductance once watering ceased, which we consider an index of physiological drought tolerance. Data on SLA, leaf tissue density, leaf thickness, and leaf angle were also collected on plants at Konza for a number of species (Craine and Towne 2011). Functional trait data were averaged when species were measured in both campaigns.

Species abundance

Species abundance was determined on 16 watersheds from 1994 to 2009. The watersheds, which average 40.7 ha, differ in the timing of fire, the frequency of fire, and whether native grazers (bison) are present. Grazing on three watersheds began in October 1987 and expanded to another three watersheds in 1992. Stocking rate increased over time so that grazing intensity removes approximately 25% of the grass production. The fire treatments for most watersheds have been in place since 1983, except for four watersheds that had their fire treatments (annually burned and unburned) reversed in 2001. In each watershed, 40 plots for determining species abundance are divided evenly between shallow xeric upland soils (cherty, silty clay loams overlying limestone and shale layers; Udic Argiustolls, Florence series), and mesic lowland soils (deeper colluvial and alluvial deposits; Pachic Argiustolls, Tully series). The total elevational range for Konza is only 120 m and upland and lowland plots only differ on average by 30 m.

For each topographic position (uplands and lowlands) in a watershed, species composition was determined in 20 permanently marked 10-m² circular plots evenly spaced along four randomly located 50-m-long transects. At each plot, the canopy cover of vascular plants was visually estimated using a modified Daubenmire cover scale (Bailey and Poulton 1968) twice a year (late May-June; mid-August-September). The cover of each species was recorded as the maximum abundance at the plot level between the two time points after converting each Daubenmire scale value to the midpoint of the cover range and then averaging across the 20 plots for a watershed's topographic position. A total of 224 herbaceous non-wetland species were observed among all sampled plots over the 16 years. Of these, 166 species were found in both uplands and lowlands and used to determine the relative abundance of species between the two topographic positions. Similar subsets of the flora were used to determine the relative abundance of species between grazed and ungrazed watersheds (163 species) and frequently and infrequently burned watersheds (185 species).

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Species loss patterns

To estimate the relative susceptibility of the Konza flora to changes in climate, we assessed the number of species for which Konza would be out of their climatic range with three specific climate changes: a 3°C increase in temperature and 150-mm increases and decreases in precipitation. All are possible for Konza by the end of the current century (Christensen et al. 2007). Patterns of species loss with climate change are based on the assumption that plants with the highest lower bounds will be first to be removed with a decrease in a given climate variable and vice versa. Assuming that the first species to be lost would be the one with the most extreme climate envelope parameter (MAT_{U} , MAP_L, and MAP_U), we then assessed how many species would then have climatic bounds that were exceeded by the new climate. In estimating the number of species that would be lost with climate change, the species with the most extreme climate envelope parameter was considered to be lost first and used to anchor the patterns of loss. For example, Potentilla arguta had an upper bound of MAT of 11.1°C, i.e. 90% of its range was in places with MAT $< 11.1^{\circ}$ C. Based on its MAT_U, the number of species with $11.1 \leq MAT < 14.1$ was considered as the estimate of species loss due to a 3°C increase in temperature. Similar calculations served to estimate the relative susceptibility of the Konza flora to the other climate change scenarios. The patterns of range shifts and eventual extirpation will certainly be more complex than this and would involve biotic factors, interannual variability in climate, and climate synergies, but this was a simple and transparent index to compare loss patterns with different climate change scenarios.

Associations with climate envelope parameters

Differences among functional groups in climate envelope parameters were tested with ANOVA and Tukey's HSD. In assessing differences in climate envelope parameters for functional classifications or bivariate relationships between traits/abundance and climate envelope parameters, we use an α for significance of 0.01 to account for the multiple comparisons and to focus only on more ecologically significant relationships. Those with $0.01 < \alpha < 0.05$ are reported but not discussed. To calculate changes in average traits for the flora with a given climate change scenario, we predicted trait values across all 440 species to compile a flora-wide average under current climate conditions. We then removed the species predicted to be lost under the climate change scenario and recalculated the flora-wide average. Assessing the responses of upland and lowland species cover to interannual variation in precipitation relied on calculations of critical climate periods (Craine et al. 2009, 2010). In short, the periods for which total precipitation best explained abundance were identified by varying the start and end dates of the precipitation periods to maximize explained variation. Total precipitation was determined for 820 periods including all possible periods from day 150 to 276 (May 30 to October 3) with a minimum period length of 12 days. Precipitation data at Konza were taken from a weather station located adjacent to headquarters.

Results

Konza grassland species exhibited a wide range of climate envelopes that represented the transitional nature of the tallgrass flora (Fig. 1). Based on their climate envelopes, species loss from Konza would be more sensitive to warming than changes in precipitation. For example, a 3°C



Fig. 1 Distribution of 440 Konza Prairie non-wetland herbaceous species with respect to the upper bound of MAT (MAT_U) and **a** the lower bound of precipitation (MAP_L) and the upper bound of temperature (MAP_U) . For **b**, the orthogonal (reduced major axis) regression is displayed

increase in MAT would remove 16.3% of the herbaceous flora. In contrast, a 150-mm decline in MAP would cause the loss of 9.1% of the herbaceous flora. A MAP increase of 150 mm would cause the loss of just 1.3% of the herbaceous flora as the Konza climate approached the upper bound of precipitation envelopes for relatively few species.

Changes in temperature or precipitation would alter the plant functional type and phylogenetic composition of the Konza flora in contrasting ways. Increases in temperature would remove perennials at a rate 2.4 times higher than annuals. A 3°C increase in temperature would remove 19.8% of the perennials, but only 8.4% of the annuals. Decreases in precipitation would preferentially remove species native to North America at a relative rate that was 2.0 times higher than non-native species (Table 1). In contrast, warming would differentially remove non-native species at rate that was 29% higher than native species. Climate change would also preferentially remove species from particular clades. There is phylogenetic signal in both the lower bounds of precipitation and upper bounds of temperature for species (K = 0.27, P = 0.008; K = 0.26, P < 0.001, respectively). With a 150-mm decline in mean annual precipitation, species from the Verbenaceae/ Acanthaceae clade would be lost at a rate that was 5 times higher than expected (4 of 8 species lost). A 3°C warming would preferentially remove Brassicaceae species 2 times more than expected (7 of 21 species lost), while Cyperaceae and Boraginaceae species would be removed at a rate 3 times more than expected (9 of 18 and 3 of 6 species lost, respectively).

Climate change appears unlikely to alter many aspects of the functional trait composition of the flora. Examining relationships between climate envelope parameters and functional traits, climate change is unlikely to cause the preferential loss of species with flowering phenology at a certain time in the growing season (P > 0.05). Most leaf and root traits did not relate to temperature or precipitation

 Table 1 Differences among plant functional types in climate envelope parameters

	n	MAPL	MAP _U	MAT _U
Annual	119	520 ± 21	1,236 ± 16	17.1 ± 0.2 a
Biennial	28	561 ± 42	$1,\!286\pm27$	16.5 ± 0.4 ab
Perennial	293	557 ± 13	$1,\!212\pm11$	16.4 ± 0.1 a
Introduced	82	449 ± 24 a	$1,\!261\pm14$ a	15.9 ± 0.2 a
Native	358	570 ± 11 b	$1,\!215\pm11$ b	16.7 ± 0.1 b
Forb	347	561 ± 12 a	$1,\!224\pm10$	16.5 ± 0.1
Grass	93	$498 \pm 21 \ b$	$1,\!221\pm19$	16.7 ± 0.3

MAP mean annual precipitation, *MAT* mean annual temperature, *L* and *U* lower bounds and upper bounds designated with subscripts Differences at P < 0.05 among categorical contrasts denoted with different letters; those contrasts where P < 0.01 shown in bold

 Table 2
 Relationships between climate envelope parameters and 12 functional traits

	п	MAP_L	$\operatorname{MAP}_{\mathrm{U}}$	MAT _U
Flowering (DOY)	212			
Thick _L (mm)	117			
$\rho_{\rm L} ~({\rm g~cm^{-3}})$	117			
SLA (cm ² g ^{-1})	123		0.055 (0.05)	
Angle _L (°)	118			
Diam _R (mm)	101	0.22 (0.05)		
$\rho_{\rm R} \ ({\rm g \ cm^{-3}})$	101	$1.1e^{-4}$ (0.06)		
SRL (m g^{-1})	101			
$A_{max} \ (\mu mol \ m^{-2} \ s^{-1})$	101	-0.005 (0.06)		
$g_{s} \pmod{m^{-2} s^{-1}}$	101			
Ψ _{crit} (MPa)	95	0.027 (0.07)		
f _R	96			

Shown are slopes of the relationship (MAP in mm; MAT in °C) with coefficients of determination in parentheses. Relationships where P < 0.01 shown in bold

Abbreviations for climate envelope parameters follow Table 1

Flowering first day of flowering, *Thick*_L leaf thickness, ρ_L leaf tissue density, *SLA* specific leaf area, *Angle*_L leaf angle, *Diam*_R root diameter, ρ_R root tissue density, *SRL* specific root length, *A*_{max} maximum photosynthetic rate, g_s stomatal conductance, Ψ_{crit} minimum water potential for conductance, f_R fraction of biomass in roots

envelope parameters (Table 2). Species that extended into drier regions had higher photosynthetic rates (y = 13.1 - 1000 $0.005 \times MAP_{I}$; $r^{2} = 0.06$, P = 0.01; Fig. 2), but not necessarily higher stomatal conductance rates. Species that extended into drier regions were more physiologically drought $(y = -6.1 + 0.0027 \times MAP_{L})$; tolerant of $r^2 = 0.07, P = 0.01$; Fig. 2), with no difference in drought tolerance between species limited to warm or cold regions. In general, even for the two traits for which there were relationships with climate envelope parameters, the most extreme climate change scenarios would scarcely change the functional composition of the Konza flora. For example, with a 150-mm decrease in precipitation, the average maximum photosynthetic rate of the herbaceous flora (averaged across species) would increase by 0.7% and the minimum water potentials would decline by 0.8%.

Changes in climate would not preferentially remove abundant or rare species, but decreases in precipitation would preferentially remove species that occupy more productive topographic positions. Climate envelope parameters did not explain any variation in average abundance at Konza when averaged across topographic, grazing, and burning contrasts for 20 watersheds over 16 years. Yet, species that extended into drier regions were more likely to be abundant in uplands than species from wetter regions. For 166 species found in both uplands and lowlands, the difference in species' abundance between uplands and lowlands decreased with increasing MAP_L



Fig. 2 Relationships between the lower bound of mean annual precipitation (MAP_L) for Konza Prairie species and **a** maximum photosynthetic rates ($y = 13.1 - 0.005 \times \text{MAP}_{\text{L}}$; $r^2 = 0.06$, P = 0.01) and **b** minimum water potentials for which plants still transpire, which is an index of physiological drought tolerance ($y = -6.1 + 0.0027 \times \text{MAP}_{\text{L}}$; $r^2 = 0.07$, P = 0.01)

 $(r^2 = 0.13, P < 0.001;$ Fig. 3). As such, decreases in mean annual precipitation at Konza would preferentially remove lowland species over upland species. There were no relationships between MAT_U and the relative abundance of species between uplands and lowlands. Unlike topography, climate envelope parameters did not explain the abundance of species across grazing or burning contrasts nor their response to grazing or burning (P > 0.05).

Analyses of changes in abundance in response to interannual variation in precipitation support the predictions that a decrease in MAP would preferentially remove lowland species. We determined the abundance of species from 1994 to 2009 across the same 20 watersheds as used above. Subsequently dividing the flora into those species that are more abundant in uplands and those that are more abundant in lowlands, the abundances of "upland" and "lowland" species were calculated for the topographic



Fig. 3 Relationships between the difference in the log abundance $(\text{cm}^2 \text{ cm}^{-2})$ between upland and lowland species and **a** the lower bound of mean annual precipitation for species. A difference in abundance of 1 indicates a species is 10 times more abundant in uplands than lowlands, while a difference of -1 indicates a species is 10 times more abundant in lowlands than uplands. Also shown are relationships between abundance of upland (*open circles*) and lowland (*closed circles*) species for **b** uplands and **c** lowlands over 16 years at Konza relative to precipitation during critical climate periods. Each *point* represents the log-transformed total abundance ($\text{cm}^2 \text{ cm}^{-2}$) of upland and lowland species averaged across 20 watersheds for a given year. The differences in log-transformed abundance for upland and lowland species for each year versus critical climate period precipitation are shown for the **d** uplands and **e** lowlands

positions across fire and grazing contrasts. In general, lowland species varied in abundance much more among years than upland species (0.63 vs. 0.36 cm² cm⁻² for uplands, 0.98 vs. 0.10 cm² cm⁻² for lowlands). Using the critical climate period approach to identify the most relevant periods of precipitation that influenced plant cover, the abundance of lowland species relative to upland species decreased with decreasing early-summer precipitation (June 11–23; $r^2 = 0.61$, P < 0.001; Fig. 3). The greater relative abundance of upland species in dry years was due

to greater relative declines in lowland species abundance among the 16 years ($r^2 = 0.38$, P = 0.01), not increases in upland species (P = 0.67) (Fig. 3). In the lowlands, lower late summer precipitation also decreased the relative abundance of lowland species (Aug 7–Sept 9; $r^2 = 0.50$, P = 0.002; Fig. 3). Again, it was lowland species abundance that declined ($r^2 = 0.50$, P = 0.002; Fig. 3), rather than upland species. Precipitation during other critical climate periods did not explain any significant additional variation in abundance or difference in abundance with topographic position.

Discussion

Decreases in precipitation or water availability are likely to have the most consistent effects on the functional composition of the tallgrass prairie, preferentially removing native species and species that inhabit the deep-soil lowlands. Despite the clear relationships with the relative abundance of species, there were no strong correlations between MAP_L and any of our measured functional traits, which reveals our poor understanding of the functional traits that separate lowland and upland species. For example, plant species that are common in the xeric shortgrass region west of Konza typically have shallower rooting depths than tallgrass species (Weaver 1968), which might be one trait that would separate shallow-soil upland species from the deeper-soil lowland species. Yet, the broad datasets that would be required to test the role of other traits and understand which functional traits might be lost with climatic drying have yet to be assembled.

In other grasslands, the response of plant communities to drought can be complex. For example, in the Greater Yellowstone Ecosystem, drought decreased the abundance of species differentially across environments, for example decreasing the abundance of forbs in mesic meadows, but increasing them in hydric meadows (Debinski et al. 2010). It is clear from the interannual patterns of precipitation and abundance that lowland species increase more in years with high precipitation than upland species and their loss might limit the responsiveness of the grassland to interannual variability in precipitation (Craine et al. 2010). Without experiments that remove species most likely to be lost (Cross and Harte 2007) or couple species removal and environmental manipulations in experiments, it is difficult to know the exact consequences of losing lowland species in a drier environment.

In contrast to the functional consequences for precipitation declines, few species would likely be lost to increases in precipitation and there would be little functional consequence to their loss. Still, a few predominantly xeric species are found at Konza. Some of the species with low MAP_U, such as *Aristida purpurea*, occupy functionally arid microsites, but others such as *Cucurbita foetidissima* occupy wet microsites. Important future foundational research will be to understand whether the presence of more xeric species at Konza can be attributed to consistently dry microsites or periodic aridity in combination with the storage effect (Warner and Chesson 1985). In general, although we can assess which species are most likely to be lost with changes in climate, our knowledge on the mechanisms and speed of extirpation are still developing (Glenn and Collins 1992; Kelly and Goulden 2008; Lesica and McCune 2004; Morris et al. 2008).

Despite relatively high sensitivity of the flora to warming, the preferential loss of perennials and species from a few clades, and phylogenetic signal in the climate envelopes of species, warming-induced species loss would not alter the functional trait composition of the Konza flora for a large number of traits nor consistently alter the abundance of rare or common species. As such, warming would directly alter the functioning of the grassland, but not necessarily indirectly through extirpation of species or clades with consistent sets of traits. For example, warming alters the flowering phenology of individual grassland species (Sherry et al. 2007), but our results indicate that it would not preferentially remove species that flower earlier or later.

Predictions of future ecosystem functioning should consider the consequences of species loss jointly with changes in the functioning of extant species (Smith et al. 2009). Overall, our results emphasize that the insurance to ecosystem function provided by diversity shows little indication of being differentially reduced by climate change beyond any loss in richness. The functional composition of the tallgrass flora appears most sensitive to a drying climate, but in many ways functional traits are welldistributed geographically, which provides a degree of functional buffering with respect to climate change. However, each species has a unique combination of functional traits (Eviner 2004) and a more complete understanding of the functional consequences of climate change for grasslands will require broad advances in our understanding of plant species and communities. For example, the traits that generate landscape-level and geographic distributions are opaque and we do not understand how climate change affects the abundance of remaining species, no less the mechanisms by which they are extirpated. The future Konza flora will be also affected by species immigration, which requires similar work for a broader pool of grassland species, as well as elevated atmospheric CO_2 , whose effects on the functional composition of floras are unknown.

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