REGULAR ARTICLE

Community traitscape of foliar nitrogen isotopes reveals N availability patterns in a tallgrass prairie

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Abstract

Background and aims Nutrients are important determinants of community assembly, yet the roles they play in structuring plant communities are still poorly understood. One inferential approach to understanding how environmental factors structure plant communities is examining the distribution of key functional traits among species of a community—a community *traitscape*.

Methods To better understand how nitrogen (N) and water availability structure grasslands, we measured N concentrations and isotope ratios for 366 herbaceous species in a mesic N-limited temperate grassland, Konza Prairie. We also compared foliar N concentrations and N isotopes between Konza species and a global dataset.

Results Species that had either high foliar N concentrations or high $\delta^{15}N_L$ were not necessarily more or less abundant on the landscape nor more or less likely to be found in uplands, grazed areas, or burned areas. Apparently there are unique hot spots of high N

availability at Konza and the typical non-Fabaceae Konza species occupies sites with greater N availability than found globally.

Conclusions Although nascent, the Konza traitscapes suggest that plant diversity in nutrient-limited communities might be strongly dependent on high-nutrient availability sites that enable high-fertility species to persist in a matrix of low nutrient availability.

Abbreviations

MAT   Mean annual precipitation
[N_L]   Foliar nitrogen concentrations

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Introduction

Nutrients are important determinants of community assembly (Chalcraft et al. 2008; Gough et al. 2000; Suding et al. 2005), yet we are still learning about the roles they play in structuring plant communities. Questions regarding how resources structure a broad community, if not an entire flora, can be inferred from the distribution of functional traits across species (Craine et al. 2001). Characterizing multi-dimensional relationships among traits of a broad cross-section of a community or flora, which we refer to here as a

traitscape, provides the opportunity to characterize the functional characteristics of a community and infer how environmental factors structure it independent of current abundances (Grime 2002). Characterizing community traitscapes holds the potential for better predictions of how communities will respond to changes in environmental conditions, comparing current environmental conditions among communities, and inferring conditions that structured the community in the past.

The need to quantify community traitscapes comes into focus when trying to understand the role of N in structuring a species-rich mesic North American grassland, Konza Prairie. Konza Prairie is considered to be strongly limited by N (Gough et al. 2000; Knapp et al. 1998). At Konza, fertilization with N increases aboveground productivity and alters the abundance of plant species (Collins et al. 1998; Knapp et al. 2001; Suding et al. 2005). Yet, these experiments are limited to a single location that might not be representative of the full diversity of environmental conditions at Konza. They also show little change in abundance for the majority of the small number of species present in the plots and, as such, shed little light on what factors might be causing their rarity.

One approach to examining the resource availability experienced by plants is to measure the N isotopes in their tissues. Although many distinct processes contribute to the ultimate nitrogen isotope signature ($^{15}N{:}^{14}N$ or $\delta^{15}N$ when standardized) of a leaf, the most parsimonious interpretations suggest that plants that have high leaf $\delta^{15}N$ ($\delta^{15}N_L$) and leaf N concentrations ($[N_L]$) most likely come from areas of high N availability (Craine et al. 2009; Hietz et al. 2011). Additional variation in $\delta^{15}N_L$ among species has been associated with differences in the form of N that plants prefer. Yet, results have been mixed as to whether plants that are relatively enriched in $\delta^{15}N$ are more reliant on NO_3^- or NH_4^+ (Kahmen et al. 2008; Miller and Bowman 2002), likely in part because plants that are more reliant on NO_3^- are more likely to occupy sites with higher N availability where NO_3^- is relatively enriched as a result of gaseous N loss pathways.

In order to understand the role of N availability in structuring a grassland plant community, we measured leaf traits and N isotopes at the point of first flowering for 366 herbaceous species collected from throughout the whole of Konza Prairie. We examined the relationships among different traits to determine the degree to which aspects of plant N economies matched up with other leaf traits and the degree to which they might be associated with differences in abundance. For example, if species that typically experience high N availability are relatively rare at Konza, then there should be a negative relationship between $\delta^{15}N_L$ and abundance. We then compare the Konza traitscape of foliar nitrogen concentrations and $\delta^{15}N_L$ to a global dataset. If the typical Konza species occupies areas of lower N availability than found globally, Konza species should have lower $\delta^{15}N_L$ and/or $[N_L]$ than observed globally.

Methods

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) (Knapp et al. 1998). Mean annual temperature is 13°C, with average monthly temperatures ranging from −3°C in January to 27°C in July. Annual precipitation for Konza Prairie averaged 844 mm from 1983 to 2009, with approximately 75% falling in the April through September growing season and peak precipitation occurring in June. The flora of Konza Prairie is comprised of 597 known species, of which 536 are herbaceous species.123 of the herbaceous species are graminoids and 407 are dicotyledonous species with a mix of C_3 and C_4 species in both groups. At Konza, grazing, burning, and landscape position are the main ecological contrasts, other than climate, that affect plant communities (Knapp et al. 1998).

Plants for the study were collected from March to October in 2009 and 2010. Generally, weekly during 2009 and almost daily during 2010, areas throughout Konza, exclusive of areas receiving resource manipulations, were surveyed for herbaceous species that had recently begun flowering (Craine and Towne 2010). For each species, we collected one to several plants from a single location, depending on their size, with all plants from the location aggregated to a single bulked sample (see below). The first plants found flowering on Konza were collected with environments ranging from forest understory to intermittent wetlands to upland grasslands. We then determined leaf thickness and leaf tissue density (Craine and Towne 2010) on leaves that represented the entire canopy and therefore N that had been acquired throughout the growing season for that species. Dried leaf matter

was ground and analyzed on a Delta Plus mass spectrometer (Thermo Electron Corporation, Bremen, Germany) in combination with a CE 1110 elemental analyzer (Carlo Erba Instruments, Milan, Italy) for N concentrations as well as N isotope ratios. Leaf N isotopes are reported as the difference in ratios relative to an atmospheric N_2 standard (Högberg 1997) and referred to here as $\delta^{15}N_L$. The within-run variability (estimated as the standard deviation of working standards) was 0.2‰ for $\delta^{15}N$. The between-run variability was estimated by comparing the measured value of a working standard to its calibrated value and was <0.22‰ for $\delta^{15}N$. For each plant, in addition to measuring $\delta^{15}N_L$, we also measured $\delta^{13}C_L$, an index of water use efficiency. Across species, traits associated with N and $\delta^{13}C_L$ were largely independent of one another—species experiencing high N availability are not more or less likely to use water more efficiently (Online Resource 1).

The 366 species collected represent 94.7% of the herbaceous cover averaged across 20 watersheds (see below). Due to complexity in identifying species in the field, 42 species were collected and measured twice. Differences in N concentrations and $\delta15N_L$ between the two samples averaged 6.5 mg/g for $[N_L]$ and 1.9‰ for $\delta^{15}N_L$. Since we did not necessarily want to average out extreme values in determining the range of environmental conditions at Konza, foliar metrics were not averaged for replicates of the same species.

Relationships among foliar leaf traits and isotope values were determined with standardized major axis regression. We also tested for differences in isotope values among select functional groups: monocots vs. eudicots (forbs), plants with C_3 vs. C_4 photosynthetic pathways, species native to North America vs. those that are not native, and those that differ in life history characteristics (annuals, biennials, and perennials). In addition, we tested for relationships between foliar N metrics and 10 abundance metrics across 20 watersheds from 1993 to 2009 (Craine and Towne 2010). These include the abundance of species in each of two landscape positions (upland and lowland), in areas that differ in grazing by bison (grazed and ungrazed), and areas that differ in their burning history (frequent [annual] and infrequent [~every 20 years]). We also include the difference in abundance between each of the three contrasts and the overall abundance averaged across all contrasts. Two statistical outlier samples that had $\delta^{15}N_L > 10‰$ were removed

from these analyses of relationships between leaf N metrics and abundance.

In order to contextualize the patterns of $\delta^{15}N_L$ and $[N_L]$ at Konza, we used a global dataset of $[N_L]$ and $\delta^{15}N_L$ from wild-grown, unfertilized plants from around the world with good bioclimatic coverage (Craine et al. 2009). Original data can be found at http://knb.ecoinformatics.org. We compared foliar N metrics of Konza plants and the global dataset first without any numerical adjustment to the global values. $\delta^{15}N_L$ from the global dataset were then adjusted using global relationships (Craine et al. 2009) to Konza's mean annual temperature and precipitation, geometric mean $[N_L]$, and the average value of plants that utilize arbuscular mycorrhizal fungi to determine if Konza values were higher than expected given these factors (Online Resource 2). For example, at the global scale, there is a positive relationship between mean annual temperature and foliar $\delta^{15}N$. In order to compare Konza values to the global dataset having removed variation in foliar $\delta^{15}N$ that could be ascribed to sites having higher mean annual temperature (MAT), sites warmer than Konza had their $\delta^{15}N_L$ lowered proportional to the difference in MAT between the site and Konza and the slope of the global relationship between MAT and $\delta^{15}N_L$. A similar regression was run for $[N_L]$ of the global data for just climate parameters and mycorrhizal type to compare Konza's $[N_L]$ with the global dataset having removed variation in $[N_L]$ from the global dataset that could be ascribed to climate and mycorrhizal type. Each model was run for non-N_2-fixing species, Poaceae species, and Fabaceae (N_2-fixing) species only. All statistics were computed with JMP 8.0.2 (SAS Corporation, Cary, NC, USA).

Results

Foliar nitrogen concentrations and isotopes

Across all 368 non-Fabaceae samples encompassing 330 species, $[N_L]$ averaged 23.7 mg/g and ranged from 8.8 mg/g in *Gentiana puberulenta* to 61.3 mg/g in *Datura stramomium*. Across the 330 species, $\delta^{15}N_L$ averaged 0.8‰ and ranged from −5.29‰ for *Aristida purpurea* to 21.4‰ for one of the two *Callirhoe involucrata* we sampled. Among the 42 Fabaceae samples encompassing

36 species, $[N_L]$ averaged 33.2 mg/g and ranged from 11.8 mg/g for *Desmodium canescens* to 54.6 mg/g for *Trifolium repens*, while $\delta^{15}N_L$ averaged −2.1‰ and ranged from −4.2‰ for *Psoralidium tenuiflorum* to 1.4‰ for *Senna marilandica*, the only Fabaceae plant sampled with $\delta^{15}N_L > 0$.

There were no significant differences among grasses and non-leguminous forbs in $[N_L]$ (*P*=0.38) or $\delta^{15}N_L$ (*P*=0.53), even after accounting for photosynthetic pathway (data not shown). Among non-Fabaceae species, annuals had higher $[N_L]$ on average (26.4±1.0 mg/g) than perennials (22.7±0.06 mg/g; *P*=0.004) with biennials (26.2±2.2 mg/g) more similar to annuals than perennials. Annuals had higher $\delta^{15}N_L$ than perennials (2.3±0.4‰ vs. 0.3±0.2‰; *P*< 0.001) with biennials (0.4±0.8‰) similar to perennials. Results were similar with Fabaceae included (data not shown). Non-native non-Fabaceae species were more enriched in ^{15}N than native species after controlling for differences in life history (2.5±0.5‰ vs. 0.5± 0.2‰, respectively; *P*<0.001) and also had higher $[N_L]$ (30.5±1.3 mg/g vs. 22.7±0.05 mg/g; *P*<0.001). For Fabaceae species, non-native species had higher $\delta^{15}N_L$ than native species (−1.5±0.4‰ vs. -2.3± 0.2‰, respectively; *P*=0.04) and higher $[N_L]$ (41.8± 3.2 mg/g vs. 30.9±1.7 mg/g; *P*=0.005).

Examining relationships between pairs of leaf traits, for non-Fabaceae species, plants with high $[N_L]$ had higher $\delta^{15}N_L$ ($\delta^{15}N_L$=−8.2+0.377*$[N_L]$; *r*=0.55, *P*< 0.001; Fig. 1). For Fabaceae species, plants with high $[N_L]$ also had higher $\delta^{15}N_L$, though $\delta^{15}N_L$ increased less with increasing $[N_L]$ for Fabaceae than non-Fabaceae species ($\delta^{15}N_L$=−5.7+0.106*$[N_L]$; *r*=0.48, *P*=0.001; Fig. 1).

Relationships between foliar N metrics and leaf tissue density support the interpretation that plants that occupied sites with high N availability are plants that are experiencing high N availability, if not being better adapted to success under high N availability. Plants with low-density leaves had higher $\delta^{15}N_L$ (*r*=−0.24, *P*<0.001), but this was largely due to the negative relationship between leaf tissue density and $[N_L]$ (*r*=−0.40, *P*<0.001) and not significant after accounting for the relationship (partial *r*=−0.09). The observed relationships between $[N_L]$ and $\delta^{15}N_L$ were not phenological. Species that began flowering later in the year had lower $[N_L]$ ($[N_L]$=35.1–0.060*DOY; r^2=0.05, *P*<0.001), but did not have consistently higher or lower $\delta^{15}N_L$ (*P*=0.86). Plants with thick
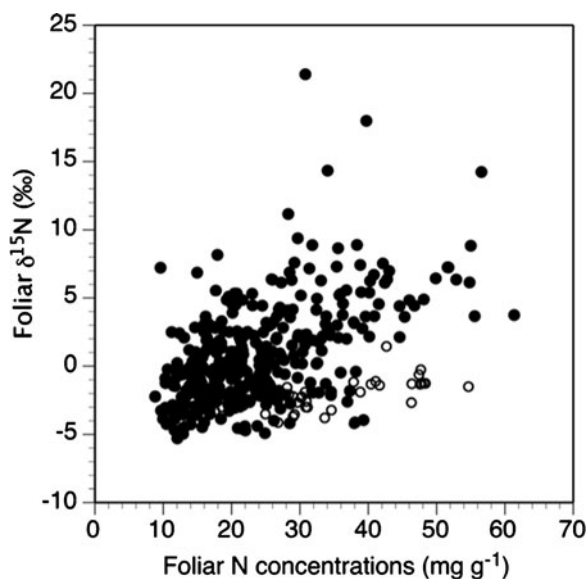

Fig. 1 Relationships between foliar N concentrations $[N_L]$ and foliar $\delta^{15}N$ for 366 Konza herbaceous species from Fabaceae family (*open circles*) or other families (*closed circles*)

leaves did not differ consistently in $\delta^{15}N_L$ (*P*=0.37) or $[N_L]$ (*P*=0.70) compared to plants with thin leaves.

Species that had either high foliar N concentrations or $\delta^{15}N_L$ were not necessarily more or less abundant on Konza (Fig. 2) nor more or less likely to be found
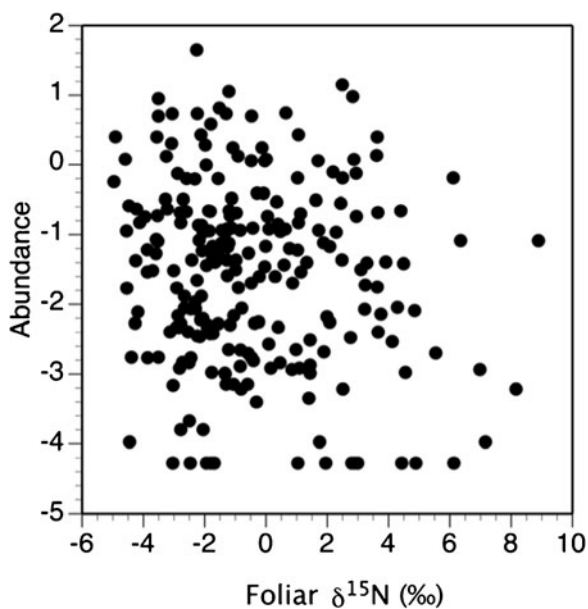

Fig. 2 Relationship between foliar $\delta^{15}N$ and log-transformed abundance quantified as % cover and averaged across 20 watersheds from 1993 to 2009

in uplands, grazed areas, or burned areas. There were no ecologically significant relationships between either $\delta^{15}N_L$ or $[N_L]$ and any of the 10 abundance metrics ($r^2 < 0.02$, $P > 0.01$ for all contrasts; Online Resource 3). That said, species too rare to be found in the long-term abundance plots but present at Konza had higher $[N_L]$ (26.9 vs 23.2 mg g^{-1}, respectively) and higher $\delta15N_L$ (1.6 vs. −0.3‰, respectively).

Global nitrogen comparisons

Comparing Konza foliar N metrics with those in the global dataset without any standardizations, Konza non-Fabaceae species had higher average $[N_L]$ than non-N_2-fixing species in the rest of the world (22.7 vs. 17.6 mg/g; $P < 0.001$) and also higher geometric mean $[N_L]$ (22.0 vs. 15.8 mg/g; $P < 0.001$). There were no differences in $\delta^{15}N_L$ between Konza and the global dataset ($P = 0.88$).

The typical Konza species had higher foliar $\delta^{15}N$ compared to the global dataset, but not necessarily once the high foliar N concentrations of the Konza species were taken into account. When standardizing for climate across sites and comparing geometric means of $[N_L]$, Konza plants had higher $[N_L]$ than expected (22.0 vs. 17.5 mg/g; $P < 0.001$), which also held when restricting the comparisons to just grasses (20.6 vs. 15.7 mg/g; $P < 0.001$). After accounting for the climate of Konza and the mycorrhizal associates of plants, but not the species' foliar N concentrations, Konza species were 2.6‰ greater than expected from global relationships (1.0‰ for Konza vs. −1.6‰ for world; $P < 0.001$).

In contrast, for non-N_2-fixing plants, after accounting for the climate of Konza, the mycorrhizal associates of plants, and the foliar N concentrations of each sample, Konza species were approximately within 0.2‰ of the adjusted $\delta^{15}N_L$ of the global samples (0.78‰ for Konza vs. 0.97‰ for world, $n = 9,757$; $P = 0.29$) (Fig. 3). The same patterns were observed when restricting the datasets to just Poaceae species ($n = 2,501$; Fig. 3). Konza grasses were not consistently more or less enriched in ^{15}N than other grasses in the world after accounting for climate and leaf N (1.0‰ for Konza vs. 1.1‰ for world; $P = 0.8$).

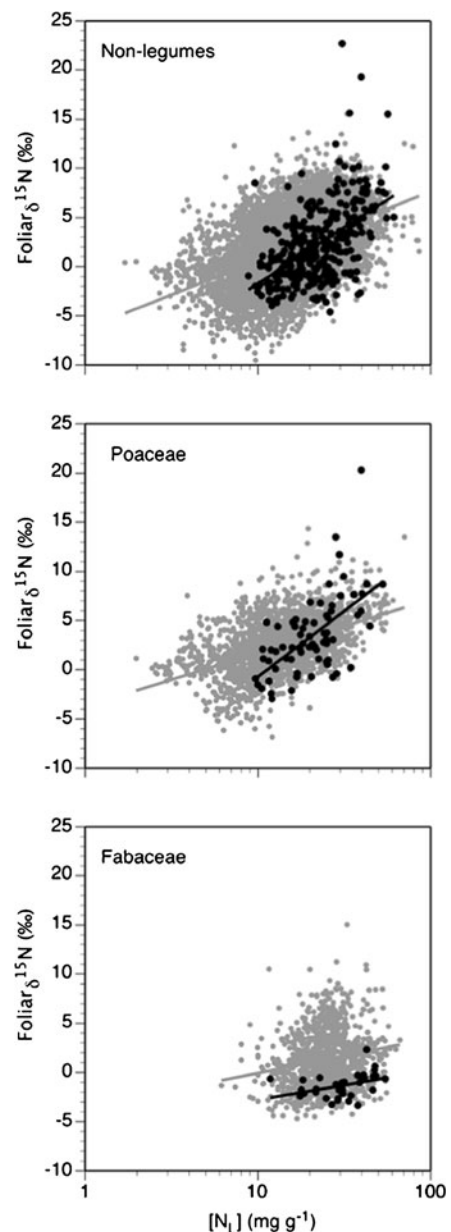While non-Fabaceae species were either similar or more enriched than leaves globally after standardization,

Fig. 3 Comparisons of relationships between $[N_L]$ and $\delta^{15}N_L$ for Konza species (*black symbols*) and the unadjusted global dataset (*gray symbols*). Shown are (a) all non-N_2-fixing species, (b) Poaceae species, and (c) Fabaceae species

for Fabaceae species, after accounting for Konza's climate and the foliar N concentrations of each sample, leaves for Konza plants were 2.2‰ lower than expected (0.1‰ vs. −2.1‰, $P < 0.001$) (Fig. 3). Konza Fabaceae species were not higher or lower in $[N_L]$ than expected based on global relationships with climate ($P = 0.68$).

Discussion

The most significant finding associated with the Konza traitscape was that although productivity at Konza is strongly N-limited, the Konza species that we sampled experienced higher N availability than would have been expected based on its climate. Compared to the global dataset, $[N_L]$ was higher at Konza than the global average and $\delta^{15}N_L$ was higher at Konza than would be expected from its climate alone. Although foliar N concentrations in and of themselves are not necessarily diagnostic of higher N availability, across studies $\delta^{15}N_L$ is greater in sites with high N availability (Craine et al. 2009). The combination of high foliar N concentrations and $\delta^{15}N_L$ together suggests the typical species at Konza experiences relatively high N availability.

It should be mentioned that the global dataset, despite including 900 sites and covering the global terrestrial climate space, is not necessarily representative of the world's ecosystems. Yet, the grasses of many grasslands and savannas have lower $[N_L]$ and $\delta^{15}N_L$ than Konza. For example, C_3 grasses in high-altitude New Zealand grasslands or C_4 grasses in tropical *Eucalyptus* savanna typically had $[N_L]$ at or below 10 mg/g and $\delta^{15}N_L$ below −1‰, if not much lower (Craine and Lee 2003; Craine et al. 2005). The relatively high N concentrations for Konza plants are not likely an artifact of when plants were sampled during the year since plants were sampled throughout the year. Also, while any one plant could have high $[N_L]$ or $\delta^{15}N_L$ associated with the specific location sampled, the overall frequency of high (or low) values should be representative of values present in the Konza community. Sampling a representative set of leaves on the plant at the time of first flowering, if anything, would bias foliar N concentrations towards lower not higher values. Foliar N concentrations at Konza, like many grasslands, decline seasonally (Ma et al. 2011; Rao et al. 1973; Schimel et al. 1991). Although deep-soil uptake of N or preferences for NH_4^+ vs. NO_3^- could explain some variation in $\delta^{15}N_L$ for individual species at Konza, there were deep-rooted species like *Silphium laciniatum* that had low $\delta^{15}N_L$ (−3.5‰) and there are no currently-supported mechanisms that would link deep-soil N acquisition or preference for NH_4^+ over NO_3^- with elevated $[N_L]$. High $\delta^{15}N_L$ is likely generated by gaseous N loss enriching the plant-available N pool.

Denitrification rates vary spatially and temporally at Konza but can be relatively high during times and in places of high NO_3^- availability (Groffman et al. 1993). That said, denitrification rates have not been assessed in areas with bison grazing at Konza, but grazing is thought in general to promote gaseous N loss (Frank and Evans 1997).

That the typical Konza species had both high $[N_L]$ and $\delta^{15}N_L$ most likely reflects relatively high N availability for the typical species, but this does not appear to be independent of other traits of the species. That annuals, plants with low leaf tissue density, non-native species, and those associated with disturbed areas—species like *Datura stramomium*, *Xanthium strumarium*, and *Echinochloa muricata*—were more enriched in $\delta^{15}N_L$ and had higher $[N_L]$ suggests that it is plants that are adapted to high resource availability that were occupying the areas of high nutrient availability (Craine 2009; Craine et al. 2001; Grime et al. 1997; Lambers and Poorter 1992; Wright et al. 2004).

The large number of high-fertility species with high N concentrations and high $\delta^{15}N_L$ suggests that these species persist at Konza in high-fertility sites in what is thought to be a matrix of low nutrient availability. That plants earlier in the season had slightly higher $[N_L]$, but not higher $\delta^{15}N_L$, suggest that high-fertility species did not solely occupy a temporal niche. Instead it is more likely that agents of disturbance such as bison grazing, soil disturbance from small mammals, road-sides, mowed fireguards, and agriculture are partially responsible for maintaining the high fertility species at Konza (Gibson 1989; Hobbs 1996; Reichman et al. 1993). For example, bison wallows are relatively large areas mostly devoid of plant uptake, which alone would generate high N availability to plants adjacent to the wallow and high gaseous N loss (Bakker et al. 2003; Groffman et al. 1993; McMillan et al. 2011; Veen et al. 2008). Yet, bison also preferentially urinate in their wallows (Lott 2003), which would make the wallows areas of high N supply. Bison carcasses also generate islands of high fertility on the landscape that become dominated by high fertility species for years (Towne 2000).

Although high local nutrient availability can reduce local plant diversity (Clark et al. 2007), landscape-level plant diversity is an aggregation of local processes (White et al. 2004). Coexistence theory predicts that spatial heterogeneity of resources promote diversity scales broader than individual plants can integrate

(Amarasekare 2003). Small-scale experimental tests of the theory at times have not supported the link between spatial resource heterogeneity and diversity (Baer et al. 2004; Reynolds et al. 2007). In addition, at Konza, across a factorial of burning and grazing treatments, the heterogeneity of soil N availability was not related to heterogeneity of community composition across 6 m^2 plots (Veen et al. 2008). Of note in that study, grazing increased the availability of N but not its variability, while 2% of the soil N availability measures had NO_3^- values 1,000 greater than average, presumably as a result of urine deposition or disturbance by mammals., Yet, other nutrient enrichment experiments have shown increases in alpha and beta diversity when nutrient enrichment is heterogeneous (Steinauer and Collins 1995) and there often are positive relationships between resource heterogeneity and diversity (Lundholm 2009). Most likely, at the landscape scale, the presence of sites with high N availability likely allow species that either require high N availability or are competitively dominant at high N availability to persist on the landscape. The presence of high N availability sites at Konza and species that are adapted to high N availability (Craine 2009) is a likely mechanism for promoting the high plant diversity of the Konza flora.

Even if N availability strongly limits production throughout Konza, the large number of relatively rare high-fertility species raises the question of whether Konza might have experienced higher fertility in the past and their rarity is a consequence of modern conditions. A number of factors would support the idea that plant available N was higher on Konza in the past. Currently, only a portion of Konza is grazed and these areas are grazed at a relatively low intensity. Fewer carcasses also are left on the landscape than would have been in the past (Towne 2000). In addition, despite elevated N deposition, foliar N concentrations in Kansas grasslands have been declining over the past 85 years, suggesting that elevated CO_2 has been lowering N availability (Gill et al. 2002; McLauchlan et al. 2010). Modern plant species composition also are likely markedly different than even a century ago. For example, *Koeleria macrantha* is the 19th most abundant species on Konza. At a nearby site, it was the second most abundant species in the uplands in 1926, which can be linked to the former prevalence of burning of grasslands during the late

winter or early spring (Towne and Owensby 1984). Preferential herbivory of high-fertility plant species could also be reducing their abundance (Howe et al. 2002; Knops et al. 2000), but this has yet to be investigated at Konza.

The uniqueness of the Konza environment and flora extended beyond species that did not fix nitrogen as Fabaceae species consistently had lower $\delta^{15}N_L$ than expected based on the climate of Konza. Regardless of expectations compared to other ecosystems, Fabaceae at Konza averaged −2.1‰, which was significantly lower than the average non-Fabaceae species (0.8‰) as well as atmospheric signature (0‰)—considered the signature of biologically fixed N (Högberg 1997). For the Fabaceae to consistently have $\delta^{15}N_L < 0$ implies that the species are likely to depend more on NO_3^- than NH_4^+, which is supported by the low root length density of Fabaceae (Craine et al. 2003). If this is the case, Konza Fabaceae, which compose about 10% of the cover, might affect non-Fabaceae species by both increasing $[N_L]$ by fixation and increasing $\delta^{15}N_L$ by preferentially acquiring NO_3^-.

Conclusions

To begin to understand the potential of traitscapes to illuminate the forces that structure plant communities, we focused on a single mesic grassland. Whether the patterns observed at Konza hold for other grasslands will require construction of similar traitscapes for other grasslands, while generating traitscapes for other traits could be used to test the relative importance of the availability of other resources as well as other stresses and disturbances in structuring communities. That said, the Konza traitscapes analyzed here suggest that communities considered to be strongly limited by nutrients might not necessarily owe their species richness to a diverse array of strategies for low nutrient availability, but instead to a diversity of sites with high-nutrient availability that enable high-fertility species to persist in a matrix of low nutrient availability.

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