Structural and compositional heterogeneity influences the thermal environment across multiple scales

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Abstract. Heterogeneity has a critical influence on biodiversity and ecosystem processes. While the influence of heterogeneity on species diversity and abundance is well documented, how heterogeneity influences the distribution and arrangement of necessary resources across a landscape is still unclear. Heterogeneity in vegetation structure and composition is often cited as an important factor in the near-ground thermal environment; however, because of a paucity of comparative studies across landscapes that differ in their degree of vegetation heterogeneity, researchers lack knowledge of the underlying mechanisms that influence variation in the thermal environment. Particularly, we do not have a clear understanding of the relative contribution of structural and compositional vegetation heterogeneity to thermal patterns. Therefore, we assessed the thermal environment in nine grassland landscapes that differed in their degree of structural and compositional heterogeneity. At the landscape level, we used a variance partitioning approach with linear mixed models to measure the link between four metrics of vegetation heterogeneity and temperature variability. At the microsite level, we used piecewise structural equation models to assess the fine-scale drivers of temperature in these landscapes and develop a causal model describing the relationship between vegetation variables and temperature. We found that temperature variance at the landscape scale was strongly related to the diversity of plant functional groups, heterogeneity in plant species composition, and variation in vegetation height. At finer scales, species richness, vegetation height, and overhead obstruction were the best predictors of temperature once weather was accounted for. Vegetation composition variables indirectly influenced fine-scale temperature variation through their effects on vegetation structure. These results suggest that scale has a strong influence on the observed relationship between temperature variance and different metrics of vegetation heterogeneity. Our results provide support for the role of landscape heterogeneity in shaping the thermal landscape and offer insights into the possible impacts of habitat homogenization on the thermal environment.

Key words: grasslands; heterogeneity; landscape homogenization; temperature; thermal heterogeneity; thermal variance.

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**INTRODUCTION**

A foundational concept in ecology is that landscape heterogeneity is a primary determinant of biodiversity (McArthur and McArthur 1961, Lack 1969, Tews et al. 2004). Heterogeneity is defined as the variation in biotic and abiotic conditions across space and through time (Wiens 1997). Heterogeneous landscapes offer organisms a greater variety and abundance of critical resources (Gould and Walker 1997, Halaj et al. 2000), and physical refugia from adverse abiotic conditions (Suggett et al. 2011) or predators (Huffacker et al. 1963). As a result, heterogeneity is recognized as a critical component of conservation efforts (Christensen 1997). A relatively unexplored mechanism that potentially underpins biodiversity in highly variable systems is the link between vegetation heterogeneity and the thermal environment. The recognition of temperature as a critical component of ecosystems and the fundamental niche for many species suggests that developing a clearer understanding of how landscape heterogeneity shapes the thermal environment may be an important step toward effective conservation of biodiversity.

Temperature is among the most important environmental conditions that shape ecological patterns and processes (Begon et al. 2006). The thermal environment influences a variety of ecosystem processes such as nutrient cycling by regulating microbial activity in soils (Mielnick and Dugas 2000, Tscherko et al. 2001), and water cycles by altering rates of evaporation or transpiration (Gates 1968, Schlesinger and Jasechko 2014). Temperature also shapes the distribution and abundance of many plant and animal species (Magnuson et al. 1979, Woodward 1988), as well as growth and survival rates of these species (Berry and Bjorkman 1980, Cunningham et al. 2013). For these reasons, variation in thermal conditions across a landscape may have profound impacts on the spatial structure of populations and ecosystem processes (Rosenberg et al. 1983). This has led researchers to posit that more thermally heterogeneous systems may have higher biodiversity because these areas provide wider ranges of temperatures offering a greater diversity of thermal niches (Elmore et al. 2017).

Many organisms require a specific range of temperatures at which physiological and metabolic processes are able to operate optimally (Angilletta and Angilletta 2009). Ambient weather conditions frequently exceed these tolerance ranges for many species, so behavioral modifications or access to sites with thermally buffered microclimates are important strategies for minimizing exposure to deleterious thermal conditions (Carroll et al. 2015, Tanner et al. 2017, Rakowski et al. 2019). Vegetation structure and composition are particularly important for shaping the near-ground thermal environment in many landscapes, which in turn influences what temperatures are available for many organisms (Saunders et al. 1998, Jenerette et al. 2007, Carroll et al. 2016). Selection for certain vegetation patches or structure by a number of animals has been linked to differences in temperature among vegetation patches (Hovick et al. 2014, Carroll et al. 2015, Rakowski et al. 2019). Further, the use of cooler areas has been linked to improved survival or fitness outcomes in several species (Warner and Andrews 2002, Hovick et al. 2014, Grisham et al. 2016, Raynor et al. 2018). Given the importance of the thermal environment to survival and habitat selection for many species, understanding the factors that influence temperature variability across the landscape may be essential for managing and conserving biodiversity.

Much of our understanding of how vegetation heterogeneity shapes the thermal environment has come from studies in heterogeneous landscapes that have focused on the role of specific patch types in shaping the thermal environment (Saunders et al. 1998, van Beest et al. 2012, Krause et al. 2013, Carroll et al. 2015, Rakowski et al. 2019). At present, there are relatively few comparative studies evaluating the thermal environment across multiple landscapes that differ in their degree of structural and compositional heterogeneity (Elmore et al. 2017), and this lack of comparative data limits our ability to understand the underlying mechanisms that shape temperature variation in a landscape. Though it is often helpful to understand variation in temperature according to broad patch types in the context of specific organisms, this approach can also obscure the drivers of temperature variation or the scales at which variation occurs. This is because broadly classifying areas by vegetation patches or plant type may hide small-scale variation in vegetation structure and composition.
within patches that can influence temperature indirectly by changing exposure to solar radiation or altering airflow, or directly through physiological processes such as transpiration or reflective heating (Cook et al. 1964, Stuntz et al. 2002). By considering how temperature varies within and between patches, ecologists can potentially gain a better understanding of the factors that shape ecosystem processes and the distribution of organisms across landscapes.

While the influence of temperature on organisms and ecosystem processes is well established in the literature, the precise mechanisms that determine temperature variation across a landscape are not well understood. In this study, our primary objective was to develop a clearer understanding of how vegetation heterogeneity influences the thermal environment at multiple scales. In particular, we focused on how variation in plant communities shaped the thermal environment by comparing thermal patterns from nine landscapes that varied in their overall structural and compositional complexity. As part of our investigation, we assessed the thermal environment at two scales. At the landscape scale, we tested for a relationship between landscape-level measures of vegetation heterogeneity and variance in temperature to assess the relative importance of vegetation structure versus composition of vegetation patches in shaping broad-scale patterns of thermal variation. At the microsite scale, we developed a causal model describing the relative contribution of various vegetation composition and structure measures to fine-scale temperature variation within and between patches.

**SITE SELECTION AND STUDY SITE**

We choose grasslands of the Southern Great Plains of North America as a case study to explore how vegetation heterogeneity influences temperature. Historically, grasslands in this region were highly dynamic systems with diverse plant communities and variable disturbance regimes. Similar to grasslands across the globe, grasslands in the Southern Great Plains have undergone widespread homogenization, primarily as a result of intensive agronomic practices (Hoekstra et al. 2005, Fuhlendorf et al. 2012). Intensive use of herbicides or highly altered fire and grazing patterns have greatly simplified vegetation communities and reduced structural diversity in many grasslands (New 1997, Fuhlendorf et al. 2012). In extreme cases, entire vegetation communities have been replaced by introduced forage species to promote production of domestic grazers (*Bos taurus*; Franklin et al. 2006, Gabbard and Fowler 2007). As a result, grasslands in this region form a gradient from heavily altered and simplified landscapes often dominated by few introduced grass species to areas where the vegetation community is still relatively intact and diverse with both monocots and dicots. This gradient of structural and compositional heterogeneity creates a natural opportunity for investigating the effects of vegetation heterogeneity on the thermal environment.

We sampled the thermal environment and vegetation data from nine grassland landscapes chosen from three grassland heterogeneity types (three grassland landscapes in each type). We ranked grassland landscapes from low to high heterogeneity based on their broadly defined plant communities to represent a gradient of structural and compositional vegetation complexity (Fig. 1, Table 1). In the subsequent analysis, we refer to the nine grassland sites as separate landscapes for clarity purposes. For low heterogeneity grassland landscapes, we used areas that were dominated by a non-native grass species that was introduced as a forage species (Bermuda grass; *Cynodon dactylon*; Table 1). These sites are representative of highly modified grasslands that have been converted from their historical plant community and have relatively low species richness and uniform vegetation structure. This type of dramatic conversion is typical of many grassland systems globally (Hoekstra et al. 2005). For the medium heterogeneity landscapes, we used grasslands dominated by native graminoids (monocots), but with limited broad-leaved (dicots) plant composition which could represent moderate levels of human grassland modification (Table 1) where long-term management practices such as herbicide or grazing may have simplified the plant community. Finally, for the grassland landscapes with the highest levels of heterogeneity, we selected areas where the broad-leaved plant component of the community was still intact with limited agronomic modification (Table 1). This grassland type would have a
variety of monocots and dicots (both herbaceous and low growing woody).

We selected our study sites from research properties managed by Oklahoma State University (OSU) in Payne County, Oklahoma, USA. We collected data for the moderate and high heterogeneity sites (native grass and grass/shrub communities) on the OSU Research Range and the Cross Timbers Experimental Range Station located approximately 20 kilometers southwest of Stillwater, Oklahoma, USA. Vegetation was composed primarily of tallgrass prairie species such as big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), and a variety of broad-leaved herbaceous plants including western ragweed (*Ambrosia psilostachya*), various asters including white heath aster (*Symphyotrichum ericoides*), and the invasive legume sericea lespedeza (*Lespedeza cuneata*). The high heterogeneity sites differed from the moderate heterogeneity sites as these areas were also interspersed with patches of native shrubs, including Oklahoma blackberry (*Rubus oklahomus*), Chickasaw Plum (*Prunus angustifolia*), winged sumac (*Rhus copallinum*), and smooth sumac (*Rhus glabra*). The low heterogeneity sites (introduced grass pastures) were located on the OSU Cimarron River Valley Research Station located north of Perkins, Oklahoma, USA. Vegetation in these grasslands was dominated by Bermuda grass. To control for confounding effects, we choose to focus on heterogeneity in species composition and structure and thus attempted to control for the immediate effects of disturbance processes such as fire and grazing. For these reasons, we selected grasslands that received only moderate and similar grazing pressure, and that had been unburned for at least two years as previous research in this region indicates that biomass accumulation drastically declines after two growing seasons (Fuhlendorf et al. 2006). Landscapes ranged in size from 2.5 to 8.5 hectares (mean 6.8 ha).

**METHODS**

Throughout this study, we define three levels of organization, the landscape, patch, and microsite levels. We defined landscapes as areas

![Fig. 1. Example grasslands representing landscapes characterized by (A) low, (B) medium, and (C) high vegetation heterogeneity in Payne County, Oklahoma, USA, in 2019. Low heterogeneity landscapes were characterized by low species richness and uniform vegetation. Medium heterogeneity landscapes were characterized by high species diversity with variable structure. High heterogeneity landscapes had similar vegetation communities to medium heterogeneity landscapes but also contained a number of woody plant species.](image-url)
composed of one or more patch types, with patches being areas within a landscape composed of distinct vegetation from the surrounding area (Turner et al. 2001). We defined microsites throughout the study as specific locations within patches that may differ in their microclimates due to fine-scale variation in vegetation structure or composition (Rosenberg et al. 1983). We acknowledge there is considerable overlap between these levels that are dependent on the scale of observation; however, we choose these definitions to represent what may be perceived by a small ground-dwelling animal that would be influenced by the near-ground temperature in our study landscape. We do not attempt to compare the specific thermal conditions among specific patch types (ex. shrubs versus herbaceous), as our focus was on how differences in number and variation of patches influences thermal variability at the landscape level and to assess how specific structural and compositional characteristics at the microsite level influences thermal variability within and between patches.

**Data collection**

We sampled the thermal environment and vegetation in September of 2019. This month was selected for sampling as September is characterized by stable weather, high temperatures (15-yr average 22°C; average minimum and maximum temperatures: 16°–33°C) and dry conditions (15-yr average rainfall: 7.1 cm), meaning patterns of thermal heterogeneity would likely be the most pronounced and easily detected during this period if they existed. Additionally, September is at the peak of annual biomass accumulation, and most perennial plants are identifiable and available to sample during this time. To sample thermal conditions, we generated 30 random locations (hereafter referred to as microsites) within each of the nine grassland landscapes. We constrained sample locations so that each point had to be greater than 50 meters from woodland borders to minimize the effect of shading, and at least 10 meters from the next closest sample point. We used Maxim Integrated Thermochron i-Button data loggers (Model Number: DS1921G; Maxim Integrates Products, Sunnyvale, California, USA; hereafter, I-button) to collect thermal data. We secured each I-button to a steel spike using double-sided mounting tape, and we drove the spikes into the ground such that each I-button was approximately 5–10 centimeters above the ground surface. We did this to avoid insulation of the I-buttons by grass litter at ground level, which allowed us to better characterize the effects of surrounding vegetation structure. Field tests were performed before data collection to ensure that the steel spikes had minimal effect on I-button temperature readings. Each I-button was programmed to record temperature every 15 min. We selected days that had minimal to low cloud cover, no precipitation, and near average ambient temperatures to collect thermal data. Each thermal sample period was 48 h in length so that we could capture a

| Measurement                        | Low heterogeneity (n = 90) | Medium heterogeneity (n = 84) | High heterogeneity (n = 87) |
|-----------------------------------|---------------------------|-------------------------------|-----------------------------|
| % Grass                           | 94.7 (8.5)                | 45.8 (19.5)                   | 47.5 (26.8)                 |
| % Forb                            | 1 (4.6)                   | 17 (11.5)                     | 14.3 (12.5)                 |
| % Litter                          | 2.9 (2.2)                 | 18.1 (13.0)                   | 15.2 (16.8)                 |
| % Shrub                           | 0.1 (0.5)                 | 0.8 (3.3)                     | 22.9 (31.3)                 |
| % Bare ground                     | 3.4 (4.0)                 | 12.1 (14.0)                   | 12.1 (14.5)                 |
| Vegetation height (cm)            | 43.1 (12.8)               | 58.4 (23.1)                   | 81.5 (46.9)                 |
| Overhead obstruction              | 0.5 (1.6)                 | 10.7 (7.1)                    | 9 (7.6)                     |
| Species richness                  | 1.6                       | 6.5                           | 6.1                         |

Note: Measurements include the percent cover of plant functional groups, vegetation height in centimeters, overhead obstruction (average angle of obstruction), and microsite-level species richness.

| Measurement                        | Mean | Range          | Mean | Range          | Mean | Range          |
|-----------------------------------|------|----------------|------|----------------|------|----------------|
| % Grass                           | 94.7 | 38–98          | 45.8 | 3–85.5         | 47.5 | 0–85.5         |
| % Forb                            | 1    | 0–38           | 17   | 3–38           | 14.3 | 0–63           |
| % Litter                          | 2.9  | 0–15.5         | 18.1 | 3–63           | 15.2 | 3–98           |
| % Shrub                           | 0.1  | 0–3            | 0.8  | 0–15.5         | 22.9 | 0–98           |
| % Bare ground                     | 3.4  | 0–15.5         | 12.1 | 0–63           | 12.1 | 0–63           |
| Vegetation height (cm)            | 43.1 | 22–79          | 58.4 | 3–110          | 81.5 | 24–300         |
| Overhead obstruction              | 0.5  | 0–7.75         | 10.7 | 0–45           | 9    | 0–36.75        |
| Species richness                  | 1.6  | 1–4            | 6.5  | 3–12           | 6.1  | 1–11           |
range of weather conditions within and between sample days at a microsite. We randomly assigned one landscape from each grassland type (one landscape with low, moderate, and high heterogeneity) to one of three sample groups, and we collected thermal data at all three landscapes in each sample group simultaneously. We did this to minimize variation in weather conditions among the three grassland heterogeneity types. We used onsite weather stations that recorded weather conditions every 5 min at both the Stillwater and Perkins sites to compare the ambient temperature to the I-button temperatures (Oklahoma Mesonet Stations; Brock et al. 1995).

After collection of the temperature data was complete, we revisited each site to collect vegetation structure, species composition, and functional group composition measurements. At each microsite, we centered a standard 20 × 50 cm Daubenmire frame over the I-button location and recorded the percent cover of plant functional group (grass, litter, forb, and shrub) and bare ground (Daubenmire 1959). Forbs are defined as herbaceous (non-woody) broad-leaved plants. We then identified and recorded every plant species observed within the frame. To measure vegetation structure, we recorded plant height directly over the I-button site and four angles of obstruction measurements. Angle of obstruction provides an index of the amount of cover directly above a point, which would influence the amount of solar radiation and airflow at a site (Kopp et al. 1998). We measured the angle of obstruction by attaching a digital level to a meter stick and tilting the digital level at an angle until it came into contact with the vegetation layer (Carroll et al. 2016). We recorded an angle of obstruction measurement in each of four cardinal directions at each site, and we averaged the four obstruction measurements to obtain a single overhead obstruction metric per site (Carroll et al. 2016). We did not consider height thresholds for the angle of obstruction measurements as the majority of vegetation encountered was <2 m tall, and we placed I-buttons 50 m away from forested areas.

Data analysis

Landscape-level vegetation and thermal heterogeneity.— We used four metrics to characterize vegetation heterogeneity at the landscape level based on the vegetation data collected at microsites. Below, we describe how each landscape-level heterogeneity metrics were calculated prior to final data analyses.

To estimate structural heterogeneity for each landscape, we calculated the standard deviation of vegetation height and overhead obstruction across all sites within each of the nine grasslands. To estimate compositional heterogeneity based on the percent cover of plant functional groups, we used an ordination-based approach similar to McGranahan et al. (2016). Specifically, we used a polar coordinate analysis to plot each site in ordination space based on its composition of functional group cover estimates. We then estimated the centroid (weighted mean value of the cover data in a group) for each grassland landscape. To assess functional group heterogeneity, we then calculated the mean distance from each site in a landscape to the centroid from that landscape using Gower distance values (Anderson et al. 2006). This measure assumes that grasslands with higher functional group diversity will have more points that are farther from the average conditions (centroid) in a landscape resulting in a higher mean distance for more heterogeneous landscapes (Anderson et al. 2006, McGranahan et al. 2016). We used the function vegdist and betadisper in the R package vegan for this analysis (Oksanen et al. 2019). To estimate heterogeneity of species composition at the landscape level, we calculated the average Bray-Curtis dissimilarity values between all sites in a grassland. Landscapes with greater variation in species across microsites should have, on average, higher dissimilarity values than grasslands where species composition is similar across sites. We used different distance measures for the functional group and species-level data as the Gower distances allowed us to use the percent cover data for functional groups while the Bray-Curtis distances are better suited for our presence/absence species-level data (Anderson et al. 2006).

To estimate the amount of thermal variability that could be attributed to site-level differences in each grassland landscape, we used a variance partitioning approach with mixed-effects models (McGranahan et al. 2016, 2018). Using the lme4 package in program R (Bates et al. 2019), we calculated separate mixed-effect model for each
grassland landscape with I-button temperatures as the response variable and a random effect variable for I-button site in a grassland landscape. We assigned each I-button temperature reading to the closest air temperature and solar radiation reading from the onsite weather stations and included ambient temperature and solar radiation as well as the time of day as fixed effects in the model to account for known sources of temperature variation. We used the variance estimate ($\sigma^2$) for the I-button site random effect in each landscape as an index of thermal variance resulting from site-level differences after accounting for weather and time of day. These variance estimates were used in the subsequent analysis to link thermal variance to vegetation heterogeneity.

We used simple linear regression to describe the relationship between our four measures of heterogeneity and the temperature variance estimates from the mixed-effects models. For each regression, we used the variance estimates from the linear mixed-effects models as the response variable, and a single measure of heterogeneity as a predictor variable resulting in four regression models. We deemed a vegetation heterogeneity variable as influencing thermal variance if the $P$-value associated with the slope parameter was $\leq 0.05$, and we further measured the strength of the relationship using the $R^2$ value from each of the regression models.

**Microsite-level path analysis.**—To describe the relationships between vegetation variables and infer the relative contribution of vegetation composition, vegetation structure, species richness, and weather on I-button temperature at the microsite level, we fit a piecewise Structural Equation Model (piecewise SEM) to the data. This analysis allowed us to evaluate multivariate relationships as well as describe causal pathways in a system by allowing explanatory variables to influence a response variable directly or indirectly through other predictor variables. Standard SEMs assume independence of observations, but piecewise SEMs allow for the modeling of hierarchal relationships in separate generalized linear mixed models, which are then combined into a single causal network. Shipley (2009) provides a simple metric to assess the completeness of a causal network developed with piecewise SEMs using directional separation (d-separation) tests and Fisher’s C statistic. As this is primarily an exploratory analysis meant to improve our understanding of the relationships between our variables, we constructed a single piecewise SEM. We built our model based on previous research on drivers of the thermal environment in grasslands, and to test whether vegetation composition and richness directly or indirectly (through their effects on structure variables such as overhead obstruction and vegetation height) influenced I-button temperature. We constructed the components of the SEM using separate linear mixed models with a random effect for the I-button site nested in grassland. The separate linear mixed models were combined into a single causal network, and we assessed model fit using d-separation tests and Fisher’s C using the R package piecewiseSEM (Lefcheck 2016).

**RESULTS**

We observed a wide range of I-button temperatures relative to ambient temperatures throughout the study in all three landscape types (Fig. 2A). However, the three landscape types differed in their range and average temperatures throughout the study. Low heterogeneity grassland landscapes had a narrower range of temperatures during midday hours, which corresponded to the hottest part of the day (11:00–17:00; Fig. 2B), and were on average cooler throughout the day compared to the medium and high heterogeneity landscapes (Fig. 3A). The medium and high heterogeneity grassland landscapes showed similar ranges in midday temperatures and similar average hourly temperatures throughout the study. Low heterogeneity grassland landscapes had a narrower range of temperatures during midday hours, which corresponded to the hottest part of the day (11:00–17:00; Fig. 2B), and were on average cooler throughout the day compared to the medium and high heterogeneity landscapes (Fig. 3A). The medium and high heterogeneity grassland landscapes showed similar ranges in midday temperatures and similar average hourly temperatures (Figs. 2B, 3A). Despite the similarity in the mean and range of I-button temperatures, the medium and high heterogeneity landscapes showed distinct differences in hourly temperature variability as measured by the standard deviation of temperatures, especially during the midday (Fig. 3B). Specifically, the high heterogeneity landscapes had the largest standard deviations in temperature during the midday period. The low heterogeneity landscapes showed the least temperature variability throughout the day (Fig. 3B).
Landscape-level temperature variance

Variance in the thermal environment at the landscape level as estimated by the linear mixed-effects models showed a general trend toward higher variance estimates for the landscapes that were predicted to have greater heterogeneity (Fig. 4). The three landscape types also differed in their degree of between landscape variability, with low heterogeneity landscapes having a small range for their variance estimates and high heterogeneity sites showing the greatest range in landscape-level variance estimates. When we considered specific measures of vegetation heterogeneity, we found temperature variability was strongly related to both functional group composition and diversity of plant species at the landscape level (Fig. 4A, B). Landscapes with greater diversity in species composition, as measured by the average Bray-Curtis dissimilarity among sites, had a strong positive relationship with estimates of temperature variability ($\beta = 1.45$, $P = 0.005$, $R^2 = 0.69$; Fig. 4A). We observed a similar pattern for functional group composition, where grassland landscapes that had greater heterogeneity in functional groups showed greater level temperature variability ($\beta = 4.64$, $P = 0.037$, $R^2 = 0.49$; Fig. 4B). Temperature variability at the landscape level was significantly related to only one of the two structure variables we considered. Temperature variability

Fig. 2. (A) Scatter plots showing the distribution of I-button temperatures over the range of observed ambient temperatures for the three landscape types (low, medium, and high heterogeneity) and (B) plots showing range and distribution of midday I-button temperatures in landscapes grouped landscape heterogeneity types in Payne County, Oklahoma, USA, in 2019. The red dashed line in panel (A) shows where I-button temperature equals ambient temperature and each curve in panel (B) represents a separate landscape.
in a landscape was positively related to the standard deviation of vegetation height ($\beta = 0.016$, $P = 0.04$, $R^2 = 0.46$; Fig. 4C), but standard deviation in overhead obstruction was not significantly related to temperature variance at the $\alpha = 0.05$ level ($\beta = 0.07$, $P = 0.09$, $R^2 = 0.35$; Fig. 4D). However, the $R^2$ value and $P$-value for the relationship between variability in overhead obstruction and thermal variability still suggest moderate support for a positive relationship between these variables.

**Microsite-level temperature**

Our structural equation model describing the direct and indirect relationships between vegetation variables and I-button temperature at the microsite level fit the data well (Fisher’s $C = 4.354$, $P = 0.824$; high $P$-values indicate that the proposed model likely did not occur by chance and that it is unlikely that paths that were not included contained important information). The standardized coefficients for air temperature and solar radiation indicate these variables had the strongest influence on I-button temperature at the microsite, with I-button temperature increasing as both variables increased (air temperature $\beta = 0.71$, standardized $\beta = 0.46$, $P < 0.001$; solar radiation $\beta = 0.01$, standardized $\beta = 0.55$, $P < 0.001$; Table 2, Fig. 5). Vegetation structure and species richness had the next greatest influence on I-button microsite temperature. At microsites with greater overhead obstruction and

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**Fig. 3.** Mean (A) and standard deviation (B) of hourly I-button temperatures in grassland landscapes characterized by their degree of structural and compositional vegetation heterogeneity in Payne County Oklahoma, USA, in 2019.
vegetation height, I-button temperatures were on average cooler compared to microsites with lower values for these variables (overhead obstruction $\beta = -0.04$, standardized $\beta = -0.04$, $P < 0.001$; vegetation height $\beta = -0.01$, standardized $\beta = -0.04$, $P = 0.003$; Table 2, Fig. 5). I-button temperature was positively related to species richness, resulting in higher average temperatures at sites with greater species richness ($\beta = 0.89$, standardized $\beta = 0.032$, $P = 0.0075$). Percent cover of bare ground at a microsite was the only composition variable that directly influenced temperature, resulting in warmer temperatures at sites with greater amounts of bare ground ($\beta = 0.02$, standardized $\beta = 0.04$, $P < 0.001$). Percent cover of grass, forbs, shrubs, or litter did not have a significant direct influence on I-button temperature at the microsite level (Table 2, Fig. 5).

While vegetation structure (height and overhead obstruction) had the strongest direct

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**Fig. 4.** Linear regression results showing the relationship between temperature variability at the landscape level and four metrics of vegetation heterogeneity. The data were collected from nine grassland landscapes classified by their predicted level of heterogeneity (low, medium, high) in Payne County, Oklahoma, USA, 2019. Thermal variance estimates were regressed on (A) variation in plant species composition among sites measured using Bray-Curtis dissimilarity, (B) variation in the composition of plant functional groups across sites, (C) variation in vegetation height, and (D) variation in overhead obstruction.
influence on I-button temperature, vegetation composition variables indirectly influenced I-button temperatures through their interactions with the structure variables (Table 2, Fig. 5). As bare ground at a site increased, overhead obstruction decreased ($\beta = -0.12$, standardized $\beta = -0.19$, $P < 0.001$) and vegetation was on average shorter ($\beta = -0.4$, standardized $\beta = -0.14$, $P = 0.007$). Sites with greater shrub cover tended to have greater overhead obstruction ($\beta = 0.15$, standardized $\beta = 0.41$, $P < 0.001$), and greater vegetation height ($\beta = 1.06$, standardized $\beta = 0.64$, $P < 0.001$). In addition to its direct effect on I-button temperature, species richness also influenced temperature indirectly through its negative effect on overhead obstruction ($\beta = -0.73$, standardized $\beta = -0.27$, $P = 0.0004$). Species richness did not influence vegetation height. Percent cover of grass, forbs, and litter had minimal influence on vegetation structure (Table 2, Fig. 5).

**DISCUSSION**

Heterogeneity is considered the foundation of biodiversity and a critical for shaping spatial patterns of ecosystem processes (McArthur and McArthur 1961, Lack 1969, Tews et al. 2004). Our results provide support for variation in the thermal environment as being a potential mechanism for increased biodiversity in heterogeneous landscapes, as landscapes with more variable vegetation structure and composition likely contain a broader array of thermal niches for organisms to select from (Elmore et al. 2017). However, the relative importance of vegetation composition versus structure in influencing the thermal environment differed depending on the scale of observation. For example, landscapes that were more compositionally diverse, at both the plant functional group and species levels, had higher variation in temperature at broad scales compared to grasslands that were compositionally more dominated by a single species or functional group.

**Table 2.** Structural equation model coefficients describing the relationships among vegetation composition (percent cover), species richness, vegetation structure, air temperature, solar radiation, and I-button temperature in grassland landscapes that form a gradient of structural and compositional heterogeneity located in Payne County, Oklahoma, USA, in 2019.

| Response variable | Predictor variable | Estimate | Standard error | $p$ | Standardized coefficients |
|-------------------|--------------------|----------|----------------|-----|---------------------------|
| I-button temperature | Air temperature     | 0.71     | 0.01           | 0.00| 0.46                      |
| I-button temperature | Solar radiation    | 0.01     | 0.00           | 0.00| 0.55                      |
| I-button temperature | % Grass            | 0.00     | 0.00           | 0.87| 0.00                      |
| I-button temperature | % Forb             | 0.00     | 0.01           | 0.92| 0.00                      |
| I-button temperature | % Bare             | 0.02     | 0.01           | 0.00| 0.04                      |
| I-button temperature | % Litter           | 0.01     | 0.01           | 0.16| 0.02                      |
| I-button temperature | Height             | -0.01    | 0.00           | 0.21| -0.02                     |
| I-button temperature | Overhead obstruction | -0.04 | 0.01           | 0.00| -0.05                     |
| I-button temperature | Species richness   | 0.09     | 0.03           | 0.01| 0.04                      |
| Vegetation height   | % Grass            | -0.09    | 0.11           | 0.38| -0.08                     |
| Vegetation height   | % Forb             | 0.03     | 0.17           | 0.83| 0.01                      |
| Vegetation height   | % Bare             | -0.39    | 0.15           | 0.01| -0.14                     |
| Vegetation height   | % Litter           | 0.10     | 0.15           | 0.51| 0.04                      |
| Vegetation height   | % Shrub            | 1.06     | 0.10           | 0.00| 0.64                      |
| Vegetation height   | Species richness   | -0.27    | 0.82           | 0.74| -0.02                     |
| Overhead obstruction | % Grass            | 0.00     | 0.02           | 0.89| 0.01                      |
| Overhead obstruction | % Forb             | 0.02     | 0.04           | 0.54| 0.04                      |
| Overhead obstruction | % Bare             | -0.12    | 0.03           | 0.00| -0.19                     |
| Overhead obstruction | % Litter           | -0.05    | 0.03           | 0.12| -0.10                     |
| Overhead obstruction | % Shrub            | 0.15     | 0.03           | 0.00| 0.41                      |
| Overhead obstruction | Species richness   | -0.73    | 0.20           | 0.00| -0.27                     |
| Overhead obstruction | Vegetation height  | -0.01    | 0.01           | 0.52| -0.04                     |
homogeneous. Alternatively, at the microsite level, we found that vegetation structure was a better predictor of fine-scale temperature than vegetation composition. As our study is among the first to compare the thermal environment across multiple landscapes that vary in their degree of heterogeneity, our findings provide insights into the factors that influence thermal patterns across diverse landscapes. Further, this study indicates that the simplification of ecosystems resulting from human activity can have important implications for the thermal environment, which could in turn affect ecological processes and landscape biodiversity.

Vegetation composition and structure are inherently linked, yet their relative influence on the thermal environment varied depending on the scale of observation. Our findings at the landscape level are similar to previous studies that attributed thermal patterns to specific patch or vegetation types in different landscapes (van Beest et al. 2012, Carroll et al. 2016, Rakowski et al. 2019). However, when we assessed causal relationships at the microsite level, vegetation composition had minimal direct effects on variability in microsite temperatures. At the microsite level, temperature was more strongly associated with variation in overhead obstruction and vegetation height than vegetation composition variables. Despite this, vegetation composition variables still indirectly influenced temperature at the microsite level through their direct effects on vegetation structure. Specifically, bare ground was associated with shorter vegetation and lower overhead cover, resulting in warmer I-button temperatures at the microsite. In contrast, increased shrub cover was related to increased vegetation height and overhead cover.

Fig. 5. Path diagram describing the relationships between vegetation composition (green box), vegetation structure (yellow box), vegetation diversity (blue box), and I-button temperature at the microsite. Significant paths \((P < 0.05)\) are represented by solid arrows, and non-significant paths are represented by dashed arrows. Red and blue arrows are used to describe negative and positive relationships, respectively. Standardized coefficients and p-values are given for significant paths only. Widths of the significant paths are scaled to the size of the standardized coefficients.
resulting in cooler I-button temperatures. Based on these results and results of previous studies, careful consideration of scale is imperative when conducting studies of the thermal environment, as the scale of observation affects the relative importance of vegetation structure and composition on temperature patterns (Saunders et al. 1998, Sears et al. 2011, Elmore et al. 2017). Though there is likely no single appropriate scale for all studies of ecological processes (Wiens 1997), a clear understanding of how scale influences the observed relationship between vegetation and temperature is needed for accurately predicting availability of different microclimate temperature and how this can in turn influence different organism’s spatial distribution in a landscape. Further, it is important to consider that the relationship between scale, vegetation, and thermal patterns may differ among landscapes with different vegetation communities. Therefore, an important area for future research will be to test how transferable the relationships described in our study are to other systems that differ in their vegetation communities and their sources of heterogeneity.

Temperature variability at the landscape level was positively related to three of the four measures of heterogeneity considered and showed a moderate relationship to the fourth measure. These findings provide evidence for the hypothesis that more heterogeneous landscapes provide a broader diversity of thermal niches for organisms (Elmore et al. 2017), potentially supporting the role of the thermal environment as one causal mechanism for the link between biodiversity and landscape heterogeneity (Retana and Cerdá 2000, Scheffers et al. 2013, Suggitt et al. 2018). Organisms often have a narrow range of temperatures at which metabolic performance is maximized, and energy inputs into thermoregulation are at a minimum (Gilchrist 1995, Angilletta and Angilletta 2009). Landscapes with more diverse thermal environments provide organisms greater opportunities to select sites with specific microsite conditions that allow them to maintain their body temperatures within these thermal preferences (Tieleman and Williams, 2002, Angilletta and Angilletta 2009, Gifford et al. 2012). Temperature is a foundational component of many species fundamental niches and likely influences patterns of biodiversity over large spatial scales. Our research adds to this by emphasizing that the consideration of fine-scale heterogeneity on temperature should be an important consideration when assessing patterns of biodiversity.

At the microsite level, species richness acted on temperature both directly and indirectly through its effects on overhead obstruction. Areas with low species richness had greater overhead cover and were associated with lower temperatures. In our study, these patterns were the result of patches of native shrubs or landscapes dominated by exotic Bermuda Grass, further emphasizing the importance of considering scale when evaluating the thermal environment. Despite the common features of low species diversity and high overhead obstruction, these vegetation types likely influenced the thermal environment in different ways. The dominance of one or a few species over large areas, such as in our low heterogeneity landscapes that were dominated by Bermuda grass, results in narrow or shortened environmental gradients reducing resources availability for other species (Hickman et al. 2006, McKinley et al. 2008, Ratajczak et al. 2012). In our study, these highly homogenous landscapes were characterized by relatively low thermal variability, potentially reducing the number of species able to use these areas due to limited thermal conditions (Bell et al. 1991). Alternatively, areas with low species diversity associated with shrub patches in high heterogeneity landscapes tended to be small in area, and likely represented keystone structures in our landscapes. Keystone structures are features whose structure or composition differs from the surrounding matrix, and whose features offer important “goods or services” for other species (Tews et al. 2004). Patches of shrubs embedded in a larger matrix of herbaceous vegetation at our high heterogeneity sites likely provide distinct structural conditions resulting in cooler microclimates for organisms (Manning et al. 2006, Martin et al. 2015, Carroll et al. 2016). Several gallinaceous bird species found in the Southern Great Plains are known to use shrub patches similar to the ones observed in our study for refuge during thermally stressful periods of the day (Carrol et al. 2015, Raynor et al. 2018, Rakowski et al. 2019). The presence of keystone structures may extend the thermal gradient in these landscapes allowing more species to inhabit these areas (Carroll et al. 2015).
Anthropogenic activities have resulted in widespread landscape and habitat homogenization across all parts of the globe. This homogenization has contributed to widespread declines in biodiversity and loss of ecosystem function (McKinney and Lockwood 1999, Western 2001, Thrush et al. 2006). Previous research in grassland systems, similar to the ones considered in this study, has demonstrated that agronomic practices, such as altering disturbance regimes and intensive use of herbicides, can result in a variety negative impacts to biodiversity and ecosystem function (Hickman et al. 2006, Fuhlendorf et al. 2006). The simplification of the thermal environment may be an additional and understudied consequence of these intensive agronomic activities. The low heterogeneity landscapes in our study, which were characteristic of highly modified grasslands, had the lowest overall thermal variability when compared to the medium and high heterogeneity landscapes that likely approximated vegetation communities prior to European settlement. While our study was not designed to evaluate the specific impact of different anthropogenic activities or agronomic practices on the thermal environment, our results provide a mechanistic understanding of which components of vegetation heterogeneity are most important in determining temperature variability, and offer insight into the possible outcomes of intensive agronomic practices that reduce heterogeneity. These results should provide future researchers with a foundation for making predictions and developing hypotheses about the impacts of human activities on landscapes and the thermal environment.

CONCLUSIONS

Many researchers have suggested that heterogeneity should be considered as the foundation of conservation efforts (Christenson 1997, Fuhlendorf et al. 2006). Landscape heterogeneity is an integral driver of ecosystem processes and biodiversity (Wiens 1997), and in this study, we provide evidence linking heterogeneity in vegetation structure and composition to the thermal environment. However, vegetation heterogeneity and temperature variability showed a complex relationship that was, in part, determined by the scale of observation. For this reason, conservation actions that aim to maintain the full range of potential thermal niches in a landscape will need to consider both compositional heterogeneity and structural heterogeneity and how they interact to shape the thermal environment across multiple spatial scales. Importantly, our results also suggest that the effects of compositional and structural heterogeneity are linked, as landscapes with a greater diversity of patches contained a greater diversity of structural conditions at microsites resulting in high thermal variability. As many ecosystems face threats from a wide variety of sources including homogenization from anthropogenic activities and climate change (Parmesan and Yohe 2003, Tilman et al. 2017), effective conservation will require careful consideration of the thermal environment and thermal niches of organisms as well as the factors that determine the distribution of fine-scale temperatures across landscapes (Sinervo et al. 2010, Suggitt et al. 2018).

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**Data Availability**

The data are currently available through the Dryad Data Repository and will be available upon publication at: https://doi.org/10.5061/dryad.kd51c5b2z.