Grasslands in an Era of Climate Change: The Ecology of Microclimates and Implications for Grassland Climate Adaptation

By

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Land Acknowledgment

The fieldwork associated with this dissertation was conducted on the ancestral homelands of the Ho-Chunk, Myaamia, Očhéthi Šakówiŋ, Sauk, Fox, Kickapoo, and Peoria Nations. Indigenous peoples were the first human stewards of North American grasslands. They used fire to maintain grassland habitats for hunting and nomadic agriculture, and they were likely very knowledgeable about the ecology of many grassland species. The arrival of European settlers led to the violent and cruel removal of indigenous people from these lands and ushered in an era of unprecedented habitat destruction and degradation for the continent's grasslands. For both of those things, I am terribly sorry. The stewardship of what remains now falls to us, and it is my hope that future generations can do far better than we have thus far.

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Dissertation Abstract

Climate change will increasingly become a major focus of conservation and wildlife management efforts in the coming decades as ecosystems and species are exposed to greater variability and extremes of climate. However, climate change is a heterogenous process and these changes, and the impacts associated with them, will be mediated by habitat characteristics and the scales at which these are evaluated. North American grasslands are endangered from over a century of agricultural conversion and degradation, and these grassland ecosystems are likely to be highly vulnerable to climate change due to their low-elevation occurrence, open canopy structure, and fragmented states. This dissertation is primarily concerned with exploring how climate interacts with grassland habitats and the species that inhabit them, and what implications these relationships have for developing climate adaptation strategies. **Chapter 1** examines the occurrence of grassland microclimate heterogeneity by leveraging a novel remote-sensing dataset to quantify what microclimate variation occurs in these open systems and what features of the environment drive it. These findings are then considered in the context of climate change with implications for understanding grassland climate microrefugia. **Chapter 2** is an application of the microclimate product developed in Chapter 1 and explores how sensitive grassland-nesting bird species may or may not be able to access thermal microrefugia based on their life-histories and degree of habitat specialization. Finally, **Chapter 3** broadly synthesizes the state of knowledge regarding climate adaption practices in North American grasslands through a systematic review. These data are then combined with input solicited from management professionals to create a structured Grassland Climate Adaptation Menu as a tool to facilitate translation of adaptation concepts to specific practices in grasslands.

Dissertation Introduction

Under current climate trajectories, the world's grasslands will experience a suite of climate-driven environmental changes including extreme summer maximum-temperatures, more frequent and intense drought, increased surface water loss, extended growing seasons, and elevated concentrations of CO_2 (Gibson and Newman 2019). Grassland biomes may be poorly equipped to buffer these changes relative to other ecosystems for several reasons. First, grasslands often occur at lower elevations where the velocity of climate change is relatively high compared to other ecosystems meaning that climatic changes may be realized more rapidly than species can respond (Loarie *et al* 2009, Dobrowski *et al* 2013). Second, by their very nature, grasslands lack the closed-canopy structure of forests, and thus the near-surface environment in grasslands tends to experience greater temperature and humidity extremes (Suggitt *et al* 2011). Third, in North America, grasslands have suffered extreme habitat loss due to agricultural conversion that began during European settlement of the Great Plains and continues today (WWF 2024, Samson *et al* 2004). As a result, remaining grasslands comprise a landscape that is both highly degraded and highly fragmented (Scholtz *et al* 2018, Augustine *et al* 2021, Bardgett *et al* 2021), and likely will have low resilience to increasing climate extremes (Martin and Watson 2016). While there can be little doubt that active management and climate adaptation will be required to protect grassland species and ecosystem services under climate change (Miller Hesed *et al* 2023, Holechek *et al* 2020), grasslands have often been neglected in conservation planning (Hoekstra *et al* 2005), policy and international climate treaties (Gibson and Newman 2019, Bardgett *et al* 2021), and climate adaption research (Cady *et al* 2023).

At an organismal level, one approach to better inform the management of grassland species in the era of climate change is to increase our understanding of which species will be most vulnerable, and why. Vulnerability is typically partitioned into two components, exposure (extrinsic) and sensitivity (intrinsic) (Williams *et al* 2008, Pacifici *et al* 2015). For example, North American grassland birds are thought to have a high vulnerability to climate change because their ranges will be exposed to large climate shifts, and because their demographics are responsive to climate variability (Wilsey *et al* 2019, McCauley *et al* 2017, Maresh Nelson *et al* 2023). However, there is increasing recognition that a realistic understanding of species exposure may require more than the coarse-scale macroclimate data that have typically been employed in vulnerability assessments (Maclean and Early 2023, Pincebourde and Woods 2020).

Ecologists are coming to understand that climate, like vegetation cover or structure, is a critical aspect of habitat and one that can be explicitly measured (Elmore *et al* 2017, Garcia *et al* 2019). Habitat is a potentially strong mediator of how climate forcings affect species (Kim *et al* 2022, Lauck *et al* 2023), and importantly, many species select habitat at scales that are orders of magnitude finer than the resolutions at which climate has been often modeled (Potter *et al* 2013, Hannah *et al* 2014, Nadeau *et al* 2017). Growing awareness of this fact, coupled with rapidly improving remote sensing technologies (Bramer *et al* 2018, Zellweger *et al* 2019), has initiated a microclimate revolution in ecology over the past decade. An increasing number of published studies now provide compelling examples of how microclimates may affect the habitat selection, demographics, and climate resilience of species across taxa (Wattles *et al* 2018, McGinn *et al* 2023, Suggitt *et al* 2018, Rytteri *et al* 2021, Brigham and N. Suding 2023). However, understandably perhaps, these advances have disproportionately focused on forested ecosystems and the temperature buffering provided by extensive vegetation canopy (McGinn *et al* 2023, Kim *et al* 2022, Frey *et al* 2016, De Frenne *et al* 2021, Scheffers *et al* 2014), while the ecological importance of grassland microclimates remains less explored (though not entirely, see Bennie *et al* 2008, Grisham *et al* 2016, Stuhldreher and Fartmann 2018).

The first two chapters of this dissertation are concerned with advancing the understanding of microclimates in temperate grasslands to inform management and climate adaptation in these systems. **Chapter 1** (Bernath-Plaisted *et al* 2023b) is both methodological and exploratory in nature and leverages a unique dataset consisting of systematic climate logger (iButtons) measurements, fine-resolution multispectral imagery, and LiDAR (light detection and ranging) collected by UAS (unpiloted aircraft systems) to predict grassland microclimates at centimeter-resolution, and model what environmental features drive variation. This analysis revealed spatially complex variation in near-surface temperature and vapor pressure anomalies in Wisconsin grasslands at magnitudes that are likely ecologically meaningful. Consistent with biophysical expectations (Geiger *et al* 2009, Bramer *et al* 2018), this work also demonstrates that vegetation height and density, as well as microtopography, can strongly influence grassland microclimate conditions. Managers are therefore encouraged to consider how management activities that can homogenize vegetation conditions (at least in the short term), such as mowing and burning (Londe *et al* 2020, Gardiner and Hassall 2009), may affect the presence of climate microrefugia for different grassland species.

Chapter 2 (in review) is a theoretical and practical application of the microclimate product developed in chapter 1 to the ecology of a declining and climate-vulnerable assemblage, grassland nesting birds (Maresh Nelson *et al* 2023, Bernath-Plaisted *et al* 2023a, Zuckerberg *et al* 2018). This chapter shows that despite the availability of potential microrefugia found in taller grassland vegetation clumps and shrubs, ground-nesting grassland obligate species appear constrained by their evolved preferences for sparser cover, while more generalist and shrub-nesting species gain thermal benefits by selecting more buffered nest sites. These findings illustrate how microclimate exposure and species life histories can interact to inform vulnerability, and suggest that the widely recommended adaptation strategy of fostering habitat heterogeneity to increase climate resilience in grasslands (Londe *et al* 2020, Hovick *et al* 2014, Carroll *et al* 2016) may not benefit more specialized species.

Yet, the microclimate applications discussed above are only one example of climate adaptation thinking in grassland systems. In reality, a great diversity of practices will likely be needed to address climate threats to various management objectives, species, and ecosystem services (Miller Hesed *et al* 2023, Lyons *et al* 2023, Briske *et al* 2015, Galatowitsch *et al* 2009). Unfortunately, several recent reviews of climate adaptation literature across ecosystems suggest that guidance and recommendations for actionable practices are often lacking (LeDee *et al* 2021, Cady *et al* 2023). **Chapter 3** (prepared manuscript) seeks to address this knowledge gap—specifically in North American grassland ecosystems—by combining information from a systematic review of grassland climate adaption topics, and input on recommended practices from management professionals to create a Grassland Climate Adaptation Menu. This menu follows a similar format to climate adaptation menus produced for other ecosystems by the Northern Institute of Applied Climate Science (NIACS) (Swanston *et al* 2016, Handler *et al* 2022), and it consists of a hierarchical list of increasingly specific adaptation *strategies*, *approaches*, and *tactics*. The results of this chapter revealed that while the number of studies addressing climate change in grasslands is growing, only a small proportion of these make specific management recommendations. This chapter discusses some of the most widely promoted adaptation practices in grasslands—such as landscape planning, adjustments to fire and grazing, seed-sourcing and restoration practices, assisted migration, and many others—and presents a resulting menu that contains dozens of specific, referenced example adaptation tactics in a structured format intended to provide guidance for managers.

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Chapter 1: Microclimate complexity in temperate grasslands: implications for conservation and management under climate change

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Abstract

As climate change advances, there is a need to examine climate conditions at scales that are ecologically relevant to species. While microclimates in forested systems have been extensively studied, microclimates in grasslands have received little attention despite the climate vulnerability of this endangered biome. We employed a novel combination of iButton temperature and humidity measurements, fine-scale spatial observations of vegetation and topography collected by UAS, and gridded mesoclimate products to model microclimate anomalies in temperate grasslands. We found that grasslands harbored diverse microclimates and that primary productivity (as represented by NDVI), canopy height, and topography were strong spatial drivers of these anomalies. Microclimate heterogeneity is likely of ecological importance to grassland organisms seeking out climate change refugia, and thus there is a need to consider microclimate complexity in the management and conservation of grassland biodiversity.

Introduction

Climate and climate change are heterogeneous across multiple spatial scales (Loarie *et al* 2009, Ackerly *et al* 2010). At fine spatial scales (typically < 100 m), microclimates may occur where variation in the surface environment creates decoupling from broader conditions (Geiger *et al* 2009, Bramer *et al* 2018). Microclimates are ecologically significant because they may best reflect the conditions experienced by species in their habitats (Potter *et al* 2013, Hannah *et al* 2014). Such microclimate variation can have significant ecological consequences influencing the behavior, habitat use, and demographics of species (Frey *et al* 2016a, Grisham *et al* 2016). Further, microclimates may potentially act as microrefugia, buffering species from rapid climate change by allowing them to exploit environmental heterogeneity to remain within their climatic niche (Suggitt *et al* 2018, Kim *et al* 2022).

Measuring the influence of climate at ecologically relevant scales is a critical step towards understanding the climate vulnerability (or resiliency) of species, but this task is complicated by a mismatch between available climate products and the scale of environmental heterogeneity experienced by organisms (Potter *et al* 2013, Nadeau *et al* 2017, Lembrechts *et al* 2019). This mismatch can be multidimensional, as microclimate conditions may vary both vertically (due to differing biophysical processes near the Earth's surface) and horizontally (due to fine-scale variation in vegetation and surface topography) (Geiger *et al* 2009, Bramer *et al* 2018).

An increasing number of microclimate studies have been conducted in forests revealing the ecological importance of temperature buffering provided by horizontal canopy structure (Frey *et al* 2016b, Zellweger *et al* 2020). In contrast, few detailed studies of microclimate variation have been conducted in open grasslands (but see Bennie *et al 2008*). This may be because grasslands are perceived as homogenous and topographically simple systems or because grasslands appear to have limited capacity to buffer climate relative to forests (Loarie *et al* 2009, Suggitt *et al* 2011). Yet this limited buffering capacity suggests that grassland-dependent species may be more vulnerable to climate change (Jarzyna *et al* 2016), emphasizing the importance of understanding microclimate variation within grassland systems.

Grasslands are among the most threatened and least protected ecosystems on earth (Scholtz and Twidwell 2022) and provide habitat for a diversity of climate-sensitive species, including pollinators (Hanberry *et al* 2021) and declining grassland birds (Rosenberg *et al* 2019). Grassland ecosystems are projected to experience a high velocity of climate change relative to other habitats because of their open structure and low elevation occurrence (Loarie *et al* 2009, Dobrowski *et al* 2013). Yet, despite lacking a canopy structure or large elevational gradients, spatial variation in grassland microclimate conditions may occur for several reasons.

First, the near-surface environment experiences greater climate variability because of heat storage in the ground, reduced wind velocity, and less efficient heat-transfer and mixing processes (Bramer *et al* 2018, Maclean *et al* 2021, Geiger *et al* 2009). Second, variation in microtopography may impart differences in microclimate by influencing topographic shading and the drainage of cold air and surface run-off (Bennie *et al* 2008, Pastore *et al* 2022). Finally, variation in vegetation structure may also affect temperature and humidity conditions. For example, although grassland vegetation is narrow-leafed and primarily vertically oriented, this foliage may provide shading at lower solar angles throughout the day (Duffy *et al* 2021), and importantly, dense vegetation also influences temperature and humidity conditions via evapotranspiration (Bramer *et al* 2018). Wooded edges can also shade adjacent grasslands—

reflecting incoming shortwave radiation during the day and trapping outgoing thermal emittance at night—potentially creating a temperature gradient with proximity to these edges (Latimer and Zuckerberg 2017).

Such variation in grassland microclimate may affect the ecology of grassland-dependent species. For example, there is evidence that microclimates may influence grassland bird species distributions (Jähnig *et al* 2020), adult survival (Pérez-Ordoñez *et al* 2022), and nest success and productivity (Carroll *et al* 2018, Lloyd and Martin 2004). Similarly, grassland insects, such as butterflies, also appear sensitive to microclimate and may select habitat and oviposition in response to these conditions (Scherer and Fartmann 2022). Both temperature and humidity can impose physiological limits on organisms mediating processes like desiccation, heat stress mortality, egg unviablity, and behavioral trade-offs (Hoffmann *et al* 2021, van de Ven *et al* 2019, McKechnie and Wolf 2010). Thus, microclimates could be of particular importance to species living in exposed environments where they may often operate near tolerance limits (Carroll *et al* 2016).

However, an obstacle to quantifying grassland microclimates is a lack of fine-scale remote sensing data to characterize such environmental variation. Most widely available satellite sources of land cover and habitat data provide imagery at resolutions of 30 m or much greater (Bramer *et al* 2018), and 1-m data available from some commercial systems may not be sufficient to capture relevant variation in space or time. In open grasslands, environmental heterogeneity may be more fine-grained relative to forested and montane environments (Zellweger *et al* 2019). Unpiloted Aircraft Systems (UAS) have recently emerged as a powerful tool to address such challenges. Specifically, UAS are capable of collecting imagery at sub-meter resolutions describing environmental characteristics relevant to microclimates, such as elevation, microtopography, primary productivity, and canopy height (Duffy *et al* 2021).

Our study had three objectives: 1) assess variation and magnitude of near-surface anomalies in temperature and vapor pressure in temperate grasslands, 2) understand the drivers of this microclimate variation, and 3) create spatially explicit models of grassland microclimates suitable for use in future ecological studies. We modeled microclimate using anomalies in near-surface iButton measurements of temperature and vapor pressure as responses predicted by a combination of fine-scale UAS environmental variables and gridded climate products (to characterize background conditions). Our approach provides what, to our knowledge, are the first fine-resolution, spatiotemporal models of microclimate variation in temperate grasslands.

Methods

Experimental design and study area

We collected fine-scale, near-surface climate data, and environmental covariates from 15 May to 30 July 2021, at four grasslands located in Dane and Iowa counties in southern Wisconsin, USA (42° 55' 11.45”, -89° 50' 5.91"). We focused on microclimate during the summer months because this period encompasses the critical reproductive phase for many grassland-dependent organisms. Our study sites ranged in size from 8.7–11.0 ha and were situated at similar mean elevations of 296–320 m, though the total elevational range between the highest and lowest points among all sites was 43 m. Our study sites were in Wisconsin’s historically unglaciated Driftless area (Figure S1) and characterized by rolling topography and a mosaic of agricultural land, forest edge, drainages, riparian zones, planted grasslands, and prairie remnant. The four sites were on a mixture of public, private, and non-governmental organization-owned lands. All sites were considered planted grasslands, but two were non-native, cool-season monocultures, and two diverse warm-season sites that resembled native Tallgrass prairie (Figure S2). Cool-season sites were dominated primarily by Smooth Brome (*Bromus inermis*) while warm-season sites were dominated by Big Bluestem (*Andropogon gerardi*), Indian Grass (*Sorghastrum nutans*), and a diversity of native forbs. The sites varied with respect to topographic complexity and level of shrub encroachment. We deliberately chose sites that would capture a range of conditions in midwestern grasslands.

iButton data collection

We systematically deployed iButtons (DS1923, Maxim Integrated, San Jose CA, USA) at a 5-cm height and at a 55-m grid resolution across each of four sites to capture the range of environmental variation within grassland sites; the number of iButtons per site ranged from 23 to 30 for a total of 109 iButtons (Figures S3-S6). Five units across all sites failed to collect data, leaving a total sample size of 104. It has been demonstrated that unshielded iButtons in high irradiance, low-wind conditions may be biased toward warmer temperatures by as much as 15°C (Maclean *et al* 2021). To help mitigate this potential bias, we housed iButtons in ventilated PVC capsules coated with reflective foil tape (Figure S7). PVC capsules have been shown to reduce error by approximately 50% (Maclean *et al* 2021), and the addition of foil tape to deflect direct solar irradiance likely further reduced this rate. We programmed iButtons to log hourly temperature and relative humidity measurements for the duration of the study period. Upon retrieving data from iButtons, we converted relative humidity to absolute vapor pressure (i.e., partial pressure of water vapor) using Teton’s formula (Norman and Campbell 1998). Because the primary objective of our study was to identify relative variation in grassland microclimates (e.g., “hot spots” and “cool spots”, “humid spots” and “dry spots”) rather than attempt to model exact temperature or humidity mechanistically, we calculated anomaly by subtracting hourly measurements for each unit from the mean of all other iButtons at the same site for each logging interval. We then summarized hourly anomaly by day for each iButton by averaging all hourly anomalies for a given day, thus producing daily mean anomalies of temperature and vapor pressure for each measurement location.

Microclimate predictors

We used a combination of UAS-collected LiDAR (Light Detection and Ranging) and multispectral imagery to derive 7 spatially explicit layers of vegetation and topography for each site summarized at 60-cm resolution (Figures S3-S6). We collected imagery using a Matrice M210 V2 RTK drone (DJI, Shenzhen, China) equipped with two sensors: 1) Sentera 6x (Sentera, Minneapolis MN, USA) 5-band multispectral camera with 5.4 cm resolution, and 2) VLP–16 LiDAR sensor (Velodyne Lidar, San Jose CA, USA) with a point density of 190-300/m^2. The multispectral camera had an additional downwelling incident light sensor that measured incoming radiation and was used to radiometrically correct images to account for changing illumination conditions throughout the flights. To further reduce the bias of illumination conditions on collected imagery, we conducted flights during the hours of 1000-1500 CST in clear and calm conditions and flew at an altitude of 120 m (AGL). However, we conducted LiDAR flights at a lower altitude of 80-m AGL to increase point density. We collected all imagery at a speed of 8-10 m/s with 80% photo overlap for the multispectral camera and with cameras in a nadir position. We conducted 3 flights at each site throughout the season—once in May, June, and July—to capture seasonal variation in vegetation predictors.

We processed multispectral imagery using structure from motion techniques with Metashape Pro (Version 1.6.5, Agisoft LLC, St. Petersburg, Russia) to produce orthorectified rasters. We processed LiDAR point clouds in R (Version 4.2.1; R Core Team, 2022) using the *LidR* package (Roussel *et al* 2020). We used a Digital Terrain Model (DTM; Zellweger *et al* 2019, Duffy *et al* 2021) created from LiDAR point clouds to characterize bare earth elevation at each of our sites, and we then used these data to derive layers for topographic positioning index (TPI)—where high index values are associated with higher elevation relative to the neighborhood—slope, aspect, and hill shade with the *terra* package in R (Hijman 2022). TPI was created using a moving window of ~ 20 m in each cardinal direction within which the elevation of each 60-cm focal cell was subtracted from the neighborhood mean. Thus, our TPI product was calculated at a 20-m scale but ultimately yielded a 60-cm resolution layer. There is no commonly accepted standard for the most appropriate window size for TPI in microclimate studies, therefore we selected our neighborhood size based on how well it appeared to capture the microtopography of the site according to our field observations. We found that, at our sites, larger neighborhoods tended to overlook smaller depressions and created a variable that was more similar to simple elevation. Hill shade was calculated using values for solar noon at the mid-point of the study period to best represent the potential influence of terrain-adjusted solar irradiance. Photogrammetry terrain models can increase error when bare ground is heavily obstructed because imagery cannot penetrate canopy cover (Klápště *et al* 2020). To address this issue, we used a hybrid approach to create a canopy height model (CHM) by differencing the multispectral-derived digital surface models (DSMs) of the canopy from the LiDAR-collected DTM representing bare earth, thus creating a raster layer representing vegetation height (Zellweger *et al* 2019). Finally, we calculated Normalized Difference Vegetation Index (NDVI) using the Sentera red (670 nm) and near-infrared (NIR; 870 nm) channels *[NIR – red] / [NIR + red]* as an index of primary productivity (e.g., Duffy *et al* 2021). NDVI is generally considered a proxy for greenness identifying areas of live, photosynthetically active vegetation. In our study area, greening of cool-season plant species may begin in March or April following snowmelt, while warm-season species often begin in late May or June. During our study season, NDVI at cool-season monoculture sites appeared to reach a peak in June, while diverse warm-season sites showed a more diffuse pattern of greening (Figures S8-9). For NDVI and CHM (e.g., vegetation height)—which were somewhat dynamic throughout the season—we associated iButton measurements with the spectral capture from the appropriate month (e.g., iButton measurements from May were associated with NDVI and CHM values from the May imagery collection) to make our models as realistic as possible (Figures S8-S11).

In addition to UAS spatial predictors, we created rasters of distance to nearest wooded edge by manual digitization in ArcGIS (Version 10.5.1; ESRI, Redlands CA, USA). We also included a site-level variable, ecotype, to account for potential differences between warm and cool-season sites. Finally, to account for the influence of broader climate context on microclimate anomalies (Wolf *et al* 2021), we included mesoclimate predictors (horizontal scale of 1–300 km; Bramer *et al* 2018) in our models. This also allowed us to examine how microclimate dynamics behaved under different climate conditions, such as hot and sunny relative to cool and cloudy days.

We sourced mesoclimate predictors from Daymet, a daily, 1-km resolution gridded climate product available continent-wide across North America (Thornton *et al* 2021). Daymet uses daily weather station data, and data describing terrain, large bodies of water, winds, and storms to interpolate local climate conditions; these predictions are then cross-validated

(Thornton *et al* 2021). Table 1 summarizes all predictor variables included in our microclimate models including UAS-collected predictors, site-level variables, and Daymet mesoclimate variables.

Random Forests models

We used Random Forests to model microclimate at grassland sites using iButton collected temperature and vapor pressure anomalies as response variables predicted by a set of spatially explicit vegetation and topographic features, as well as gridded mesoclimate variables (Table 1). Although we included mesoclimate predictors in our models, our approach was not intended as a downscaling, but rather to model our iButton response variables under varying external conditions. Random Forests are a decision tree-based, machine learning algorithm capable of achieving high predictive accuracy without overfitting through ensemble modeling and a bootstrapping technique known as bagging (Breiman 2001, James *et al* 2013). Random Forests have several additional advantages including the ability to handle high-dimensional data, model complex interactions, and a lack of restrictive assumptions. We calculated Pearson's correlation coefficient (r) among all pairs of spatial predictors and found $r < 0.7$ in all cases (Figure S12). We implemented Random Forests in R with the *ranger* package (Wright and Ziegler 2017) and performed k-fold cross-validation with 10 partitions, in which ground-collected iButton measurements were withheld for testing. These control data were then compared with predictions from the trained model to calculate root-mean-squared errors (RMSE) as a metric of model performance. We performed cross-validation and model tuning using the *caret* package (Kuhn 2022). We tuned our Random Forest models across a range of *mtry* values, as well as two different split rules, using 1501 trees for each iteration (Table S1). The *mtry value* determines how many predictors are included in each bagging and thus represents a balance between good prediction and overfitting. We provided a range of low and high *mtry* values relative to the number of predictors in our models and selected the optimal value from the tuning grid models.

We extracted variable importance, Individual Conditional Expectations (ICE), and partial dependence for each model using the *flashlight* package (Mayer 2021). Variable importance is calculated by assessing the drop in model performance when a feature is randomly permuted, thus a low variable importance score indicates a lack of influence on model performance (Breiman 2001). In our results, we present variable importance as a percentage of total drop in performance from all features combined. This allows variable importance to be compared across models with different units in the response variable. Partial dependence is a global metric that examines the average effect of a feature on the response variable when all other predictors are held constant (Friedman 2001) and can be interpreted analogously to a marginal effects plot. ICE plots represent the local observations from which partial dependence is produced, and they are suitable for identifying interactions, non-linearity, and other complex effects that may be obscured when observations are averaged as in partial dependence (Molnar 2022). We assessed interaction between features in our models using Friedman's H, also implemented in the *flashlight* package (Mayer 2021). Friedman's H is calculated from the decomposition of partial dependence for a given feature and can be interpreted as the proportion of variance explained by that feature that is attributed to covariance with another feature (Molnar 2022). Finally, we tested our models for spatial autocorrelation, and those procedures are described in Supplementary Materials, Appendix S1.

Spatial prediction of grassland microclimates

We produced spatially explicit, 60-cm resolution, microclimate predictions for both temperature and vapor pressure anomalies at our four grassland study sites by using Random Forests models to predict across raster stacks containing each spatial predictor. For NDVI and CHM, we used mean layers for prediction to represent typical grassland conditions. To examine how microclimates changed under different climate conditions, we produced three sets of spatial predictions for each study site representing cool and cloudy days, mean conditions for the season, and hot and sunny days. We characterized these conditions, respectively, by setting Daymet temperature and solar irradiance variables to their lower 5th percentile (5%), mean, and upper 95th percentile (95%) values.

Results

Hourly iButton summaries revealed similar microclimate profiles among study sites, suggesting few broad differences in climate dynamics between warm- and cool-season grasslands (Figure S13). Across all sites, daily mean temperatures and vapor pressures ranged from 5.4–30.7°C and 781.1–3168.3 Pa, respectively (Figure S14). Hourly profiles of temperature and vapor pressure anomalies exhibited deviations from mean conditions of up to 10°C and 3000 Pa, respectively, during daytime hours (Figures S15-S16). Daily summaries of raw iButton data revealed that, on average, grassland microclimates at our sites tracked mesoclimate conditions described by Daymet variables (Figure 2a), but experienced lower minima (Figure 2b), notably higher maxima (Figure 2c), and ultimately were subject to larger diurnal temperature ranges—particularly on warmer days (Figure 2d).

Random Forests models of daily mean temperature ($R^2 = 0.71$) and vapor pressure anomalies ($R^2 = 0.52$) had predictive accuracies of 0.38 °C and 55.2 Pa, respectively (Table S3).

The top spatial predictors in both models included primary productivity, as represented by NDVI, canopy height (CHM), elevation, and relative topographic positioning (TPI); aspect also informed vapor pressure anomaly (Figure 3). In addition to spatial UAS predictors, Daymet daily mean temperature and solar irradiance were also modestly informative in our models (Figure 3), suggesting that background climate conditions affected grassland microclimate dynamics.

Analysis of partial dependence showed that areas of high primary productivity (NDVI), and to a lesser extent taller vegetation (CHM), supported cooler anomalies (Figure 4a-b). By contrast, higher elevation, as well as higher index values for relative topographic positioning (TPI), were moderately associated with warmer temperature anomalies (Figure 4c-d). Similarly, areas of more productive and taller vegetation were associated with higher vapor pressure anomalies (more humid; Figure 4a-b), while higher elevation positions were much drier (Figure 4c-d). Partial dependence plots for all variables modeled can be found in the Supplementary Materials, Figures S17-S18. Daily mean temperature and solar irradiance from Daymet characterizing broader mesoclimate conditions had non-unidirectional effects (Figure 5a-5b). Specifically, warm mesoclimate temperatures and high irradiance appeared to increase both negative and positive anomalies in temperature and vapor pressure, effectively increasing the magnitude of microclimates produced by variation in the spatial predictors discussed above. This relationship was confirmed by plots of absolute iButton anomalies against Daymet mesoclimate conditions throughout the season (Figure S19). We also assessed pairwise interactions between all predictors in both of our models and found that only the interaction between elevation and vegetation height (CHM) in the temperature anomaly model appeared to be substantive (Figure S20).

Finally, spatially explicit predictions of microclimate revealed heterogeneous conditions at grassland sites reflecting underlying variation in vegetation and topography (Figure 6; spatial predictions of microclimate for all sites can be viewed in Supplementary Materials, Figures S21-S22). However, the magnitude of anomalies became more pronounced under hot and sunny conditions (Figure 6; 95th percentile). Under these conditions, the range of daily temperature anomalies between the coolest and warmest areas was as much as 3.5°C at some sites (Figure S23). Similarly, differences in daily vapor pressure anomalies between the most humid and dry areas at some sites were as much as 250 Pa (Figure S24). Model error structures showed little directional bias in prediction and were broadly similar among sites although differences in distribution tails suggested some differences in predictive accuracy (Figures S25-S26). Additionally, at several sites, there was evidence that extreme values were predicted with greater uncertainty (Figures S27-S28).

Discussion

Grasslands are a globally endangered ecosystem (Scholtz and Twidwell 2022) that is likely to experience rapid climate change (Loarie *et al* 2009). Consequently, many grassland-dependent species are vulnerable to climate conditions (González-Varo *et al* 2013, Wilsey *et al* 2019), and microclimates may play an important role in buffering these species from future changes (e.g., Suggitt *et al.* 2018). However, a lack of studies examining the magnitude and drivers of grassland microclimate has limited understanding of this potential. We found that grasslands support substantial variation in microclimate anomalies, and in some cases, the magnitude of temperature variation (3.5°C mean; 10°C hourly) may be of a similar order to projected climate change for the central United States (Pörtner *et al* 2022; 3 and 6°C warmer under 2 and 4°C average global warming scenarios, respectively). The spatial distribution of grassland microclimates was driven largely by vegetation conditions, including primary productivity and vegetation height, as well as elevation and topographic positioning. Microclimate differences also became more pronounced in hot and sunny conditions, suggesting that microclimates could play an important ecological role as microrefugia during extreme events (e.g., heat waves).

Broadly, microclimate temperatures recorded by iButtons in our study documented greater climate variability near the surface in grasslands, as well as substantially greater maxima, and to a lesser extent, lower minima relative to regional conditions described by Daymet. This was expected given that there is greater climate variability near the surface. In addition, our model residuals indicated that in some cases, the most extreme anomalies were predicted with greater uncertainty and thus these estimates should be interpreted cautiously. Much higher maximum temperatures recorded in grasslands could also reflect bias associated with iButton use in the absence of canopy (Maclean *et al* 2021), or a lack of temperature buffering in grasslands relative to other cover types (Suggit *et al* 2011). It is likely that both mechanisms were at play suggesting that while some maxima we observed may have been exaggerated, grasslands do experience greater exposure to temperature extremes as reported elsewhere (Loarie *et al* 2009, Suggit *et al* 2011).

Temperature anomalies in our study were most influenced by primary productivity, and productive areas were correlated with cooler microclimates suggesting that dense vegetation may buffer heat extremes in grassland habitats. This effect was likely driven by evaporative cooling through plant stomatal conductance associated with photosynthetic capacity (Bramer *et al* 2018, Duffy *et al* 2021). Vegetation height also had a moderate cooling effect—likely from shading during lower solar angles. The importance of vegetation productivity and structure suggests that microclimate buffering of temperature in grassland systems may be threatened by extreme droughts and changes to precipitation patterns associated with future climate change (Cook *et al* 2022); prolonged drought conditions may cause browning of vegetation and an associated reduction in evapotranspiration, as well as diminished plant structure. However, an important limitation of our study is that climate observations were made at a 5-cm height, typically below the grass canopy. Therefore, microclimate dynamics above or near the top of vegetation could operate differently.

Both elevation and topographic position also influenced microclimate, and low-lying areas relative to neighborhoods, as well as lower elevations in general, were associated with cooler and more humid anomalies—an effect possibly driven by the pooling of cold air and surface water run-off, as well as nighttime humidity inversion (Geiger *et al* 2009, Bramer *et al* 2018, Pastore *et al* 2022). Although cold air drainage is more often associated with mesoclimatic processes in mountainous systems (Ashcroft and Gollan 2012, Dobrowski 2011), even depressions with depths as little as 2-m may be sufficient to influence temperature conditions and cold air movement (Mahrt 2022). Another possibility is that lower and less exposed positions tend to receive more terrain shading and reduced wind speeds, thus preserving moisture and leading to greater evaporative cooling; this might explain the interaction of elevation and vegetation height observed in our temperature model. Regardless, our findings suggest that although grassland ecosystems are characterized as low-lying and lacking in topographic complexity (e.g., compared to montane forests), small microtopographic differences can support strong microclimate variability (Mahrt 2006, 2022).

Given that vegetation played an important role in mediating grassland microclimates, lack of differences between cool- and warm-season grassland sites was surprising and suggests that site productivity and vegetation structure, and not species composition or functional traits (Zellweger *et al* 2019), have a greater influence on microclimate conditions. However, we did not collect primary productivity data at a fine temporal grain (e.g., daily measurements), and it is conceivable that differences in C3 and C4 carbon pathways in cool and warm-season plants (Wang *et al* 2013) may influence microclimate differently throughout the season depending on the timing of greening. Plant functional diversity may also play an important role in supporting the resiliency of grasslands to extreme climate events (Craine *et al* 2013), thus further study on the subject could be of value.

The magnitude of temperature and vapor pressure anomalies was also influenced by daily temperature and solar irradiance, which drove increasing anomalies in both positive and negative directions (e.g., warmer and cooler, more and less humid). Hot and sunny days supported greater microclimate anomalies, suggesting heat extremes impart greater contrast across grassland landscapes. This effect is likely driven by diurnal temperature and vapor cycles in which extremes occur at the surface where heat stored in the ground is transferred to the near-surface air layer via convection (Geiger *et al* 2009). On hot and sunny days where there is high energy input into the system, these extremes are likely to be greater, thus creating high anomalies in exposed areas and low anomalies where conditions are buffered by other factors. The ultimate result of these biophysical processes is greater microclimate deviation from mean conditions with heat and irradiance extremes—a phenomenon that is of high ecological importance to grassland species seeking refugia to avoid exposure to conditions beyond their thermal and moisture tolerance limits (Grisham *et al* 2016, Ruth *et al* 2020, Scherer and Fartmann 2022).

Many grassland-dependent species are experiencing widespread declines and are vulnerable to climate change (González-Varo *et al* 2013, Wilsey *et al* 2019). Fine-scale temperature and humidity conditions are important to many of these grassland organisms and can influence their reproductive success, and use of habitat across landscapes. For example, grassland birds may select nest sites that buffer eggs and nestlings from lethal thermal extremes and desiccation (e.g., Grisham et al. 2016, Carroll et al. 2018). Landscape-level thermal conditions, and the presence of refugia, can also influence the habitat use and survival of these species (Hovick *et al* 2014, Carroll *et al* 2016, Ruth *et al* 2020). Similarly, oviposition and habitat use in grassland insects and pollinators is also influenced by microclimates (Gardiner and Hassall 2009, Scherer and Fartmann 2022). Consequently, microclimates may become an increasingly important aspect of managing and conserving grassland biodiversity under climate change.

Grasslands are often subject to intensive management actions such as prescribed fire, grazing, and mowing. Understanding how these tools influence microclimates is of critical importance. For example, given the role of primary productivity in fostering cooler microclimates, managers may wish to consider activities that could enhance productivity such as sustainable grazing regimes (to avoid overgrazing) or irrigation to improve primary productivity during extreme droughts (Greenwood *et al* 2016). By contrast, intensive activities such as frequent mowing may be less desirable for creating microrefugia during the breeding season as they reduce primary productivity and homogenize structure. In some cases, these activities have even been implicated in disrupting microclimates required by insect species (Gardiner and Hassall 2009, Thomas *et al* 2009). Finally, the importance of topography in creating grassland microclimate complexity suggests that prioritizing the acquisition and conservation of grassland areas of high topographic complexity will likely increase the prevalence of microrefugia for climate-vulnerable grassland species (Bennie *et al* 2008, Suggitt *et al* 2018).

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Table 1. Predictors used in Random Forests models of mean daily temperature and vapor pressure microclimate anomalies at grassland study sites.

Predictor	Notation	Type	Source	Resolution
Canopy height model	CHM	Vegetation	UAS	60-cm
Normalized difference vegetation index	NDVI	Vegetation	UAS	60-cm
Distance to wooded edge	Wood edge	Vegetation	GIS	60-cm
Grassland type	Ecotype	Vegetation	Site level	NA
Digital terrain model	Elevation	Topography	UAS	60-cm
Topographic positioning index	TPI	Topography	UAS	60-cm
Slope	Slope	Topography	UAS	60-cm
Aspect	Aspect	Topography	UAS	60-cm
Hill shade	Hillshade	Topography	UAS	60-cm
Mean temperature	Mean temp.	Mesoclimate	Daymet	1-km
Mean vapor pressure	Mean vapor	Mesoclimate	Daymet	1-km
Cumulative precipitation	Daily precip.	Mesoclimate	Daymet	1-km
Short-wave solar irradiance	Solar	Mescoclimate	Daymet	1-km

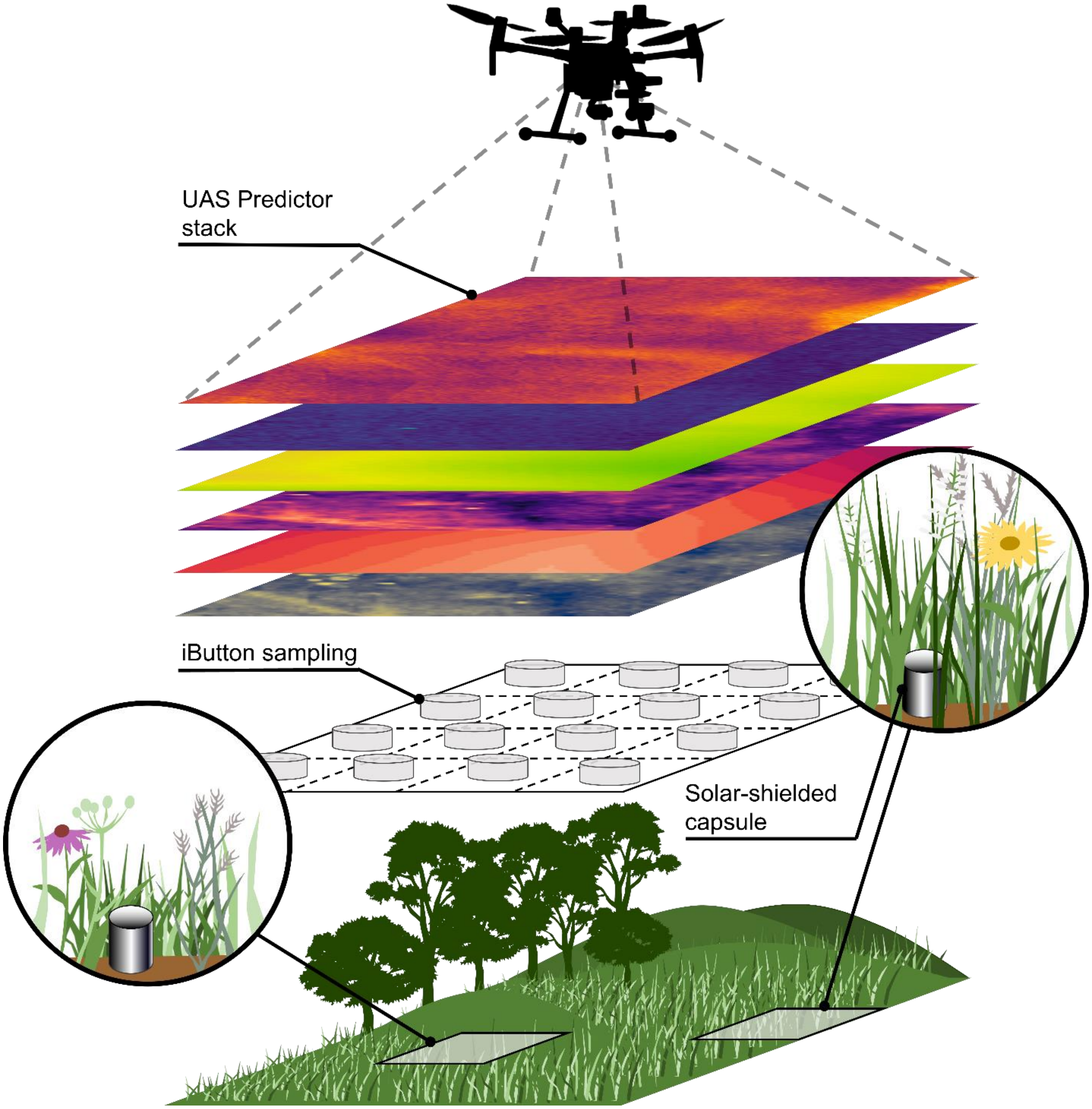


Figure 1. Conceptual illustration of microclimate study design showing iButton and UAS imagery sampling across a range of vegetation and topographic conditions at grassland study sites.

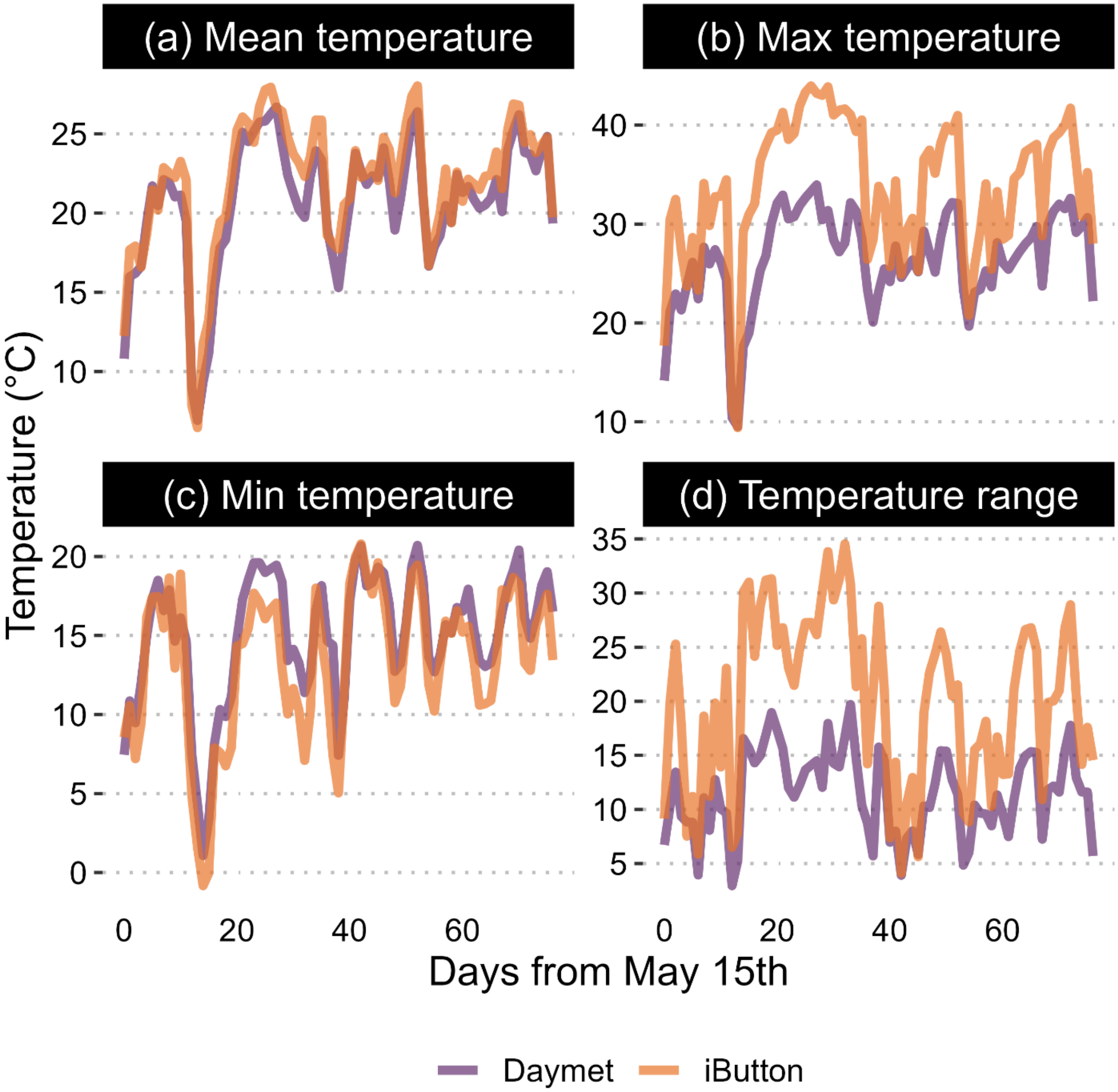


Figure 2. Raw iButton microclimate measurements summarized by day of season and averaged across all sites plotted alongside Daymet observations for the same period. While mean microclimate temperatures closely tracked regional conditions, maxima and minima exceeded Daymet estimates suggesting that grassland microclimates experience a larger range of temperature conditions than regional climate.

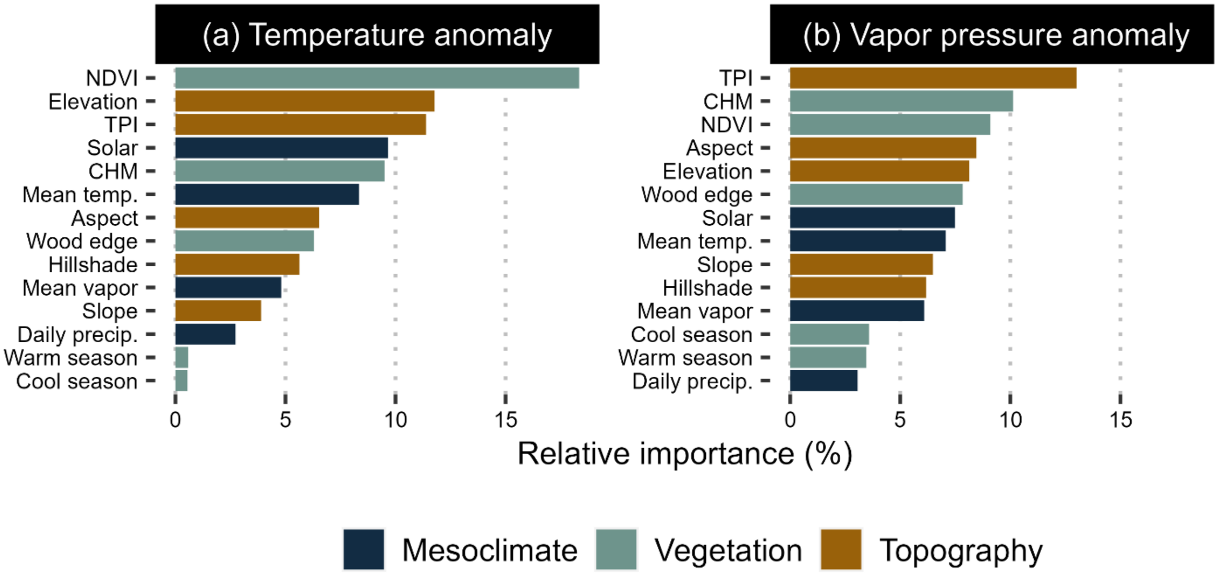


Figure 3. Relative importance of predictor variables expressed as a percentage for Random Forests models of temperature **(a)** and vapor pressure **(b)** microclimate anomalies. Anomalies of both temperature and vapor pressure were most strongly influenced by vegetation characteristics including productivity (NDVI) and vegetation height (CHM), as well as topographic conditions (elevation and TPI). Additional variation was explained by broader mesoclimate conditions including mean temperatures and solar irradiance; site type, (cool vs warm season) had little independent influence.

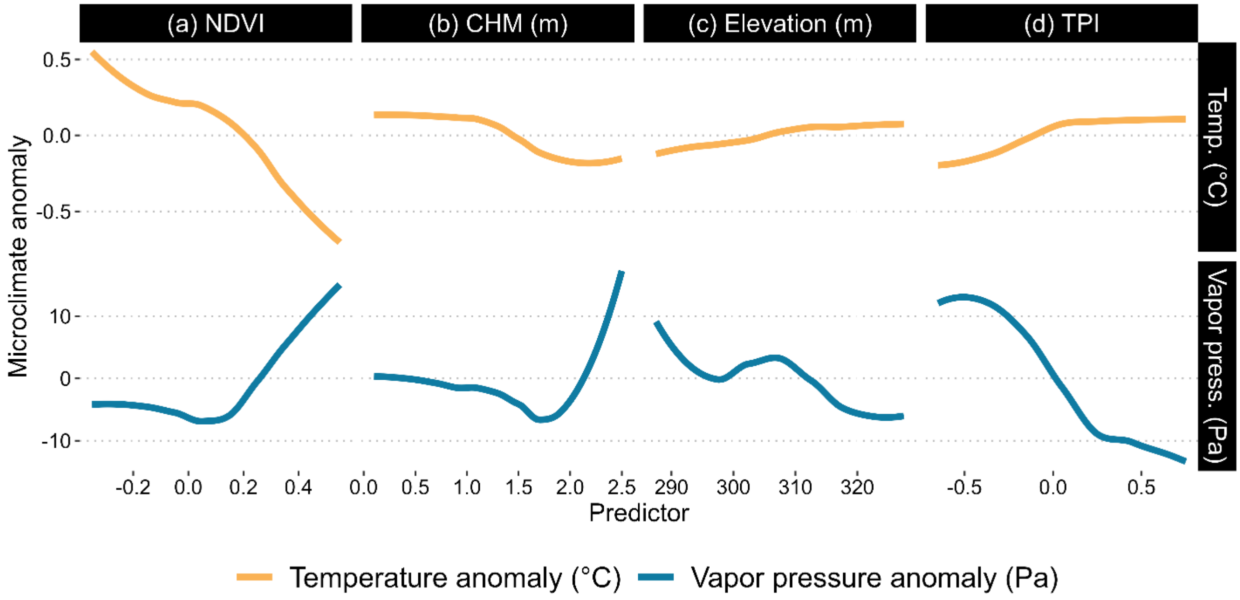


Figure 4. Smoothed partial dependence of mean daily temperature and vapor pressure anomalies for top spatial predictors in Random Forests models of grassland microclimate. Primary productivity **(a)** and vegetation height **(b)** had cooling effects on temperature anomaly, while higher elevations **(c)** and relative topographic positions **(d)** (TPI) tended to be warmer. Similarly, vapor pressures (e.g., humidity) were higher in productive areas with taller vegetation, and lower (e.g., dryer) at higher elevations and topographic positions.

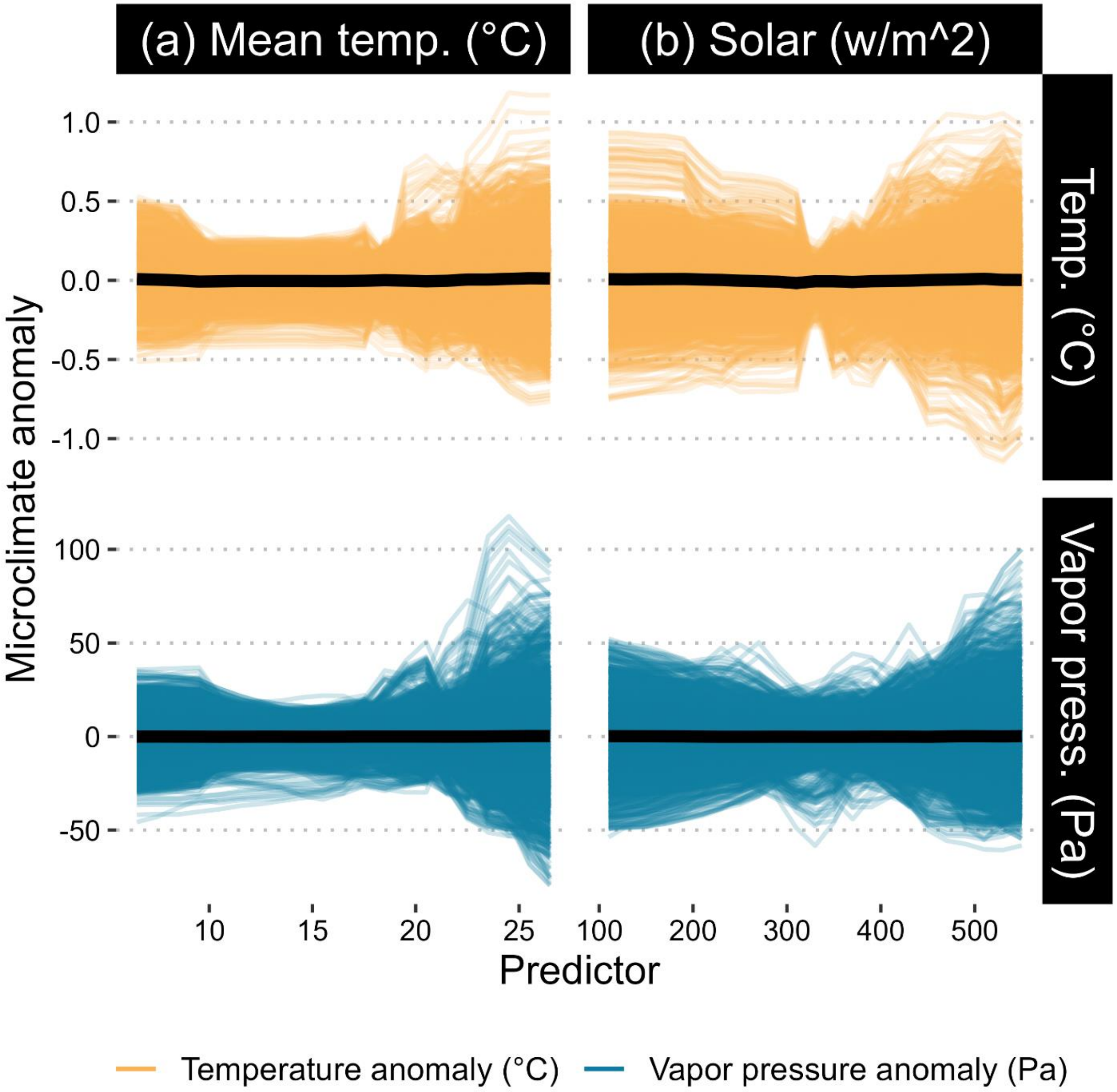


Figure 5. Partial dependence (black lines; displaying the average effect of variables) of mean daily temperature and vapor pressure anomalies overlaid with Individual Conditional Expectations (colored lines; displaying change in individual observation over variable range) for mesoclimate mean temperature **(a)** and solar irradiance **(b)** in Random Forests models of grassland microclimate. Higher daily temperatures and greater solar irradiance resulted in greater variation in anomaly for both temperature and vapor pressure.

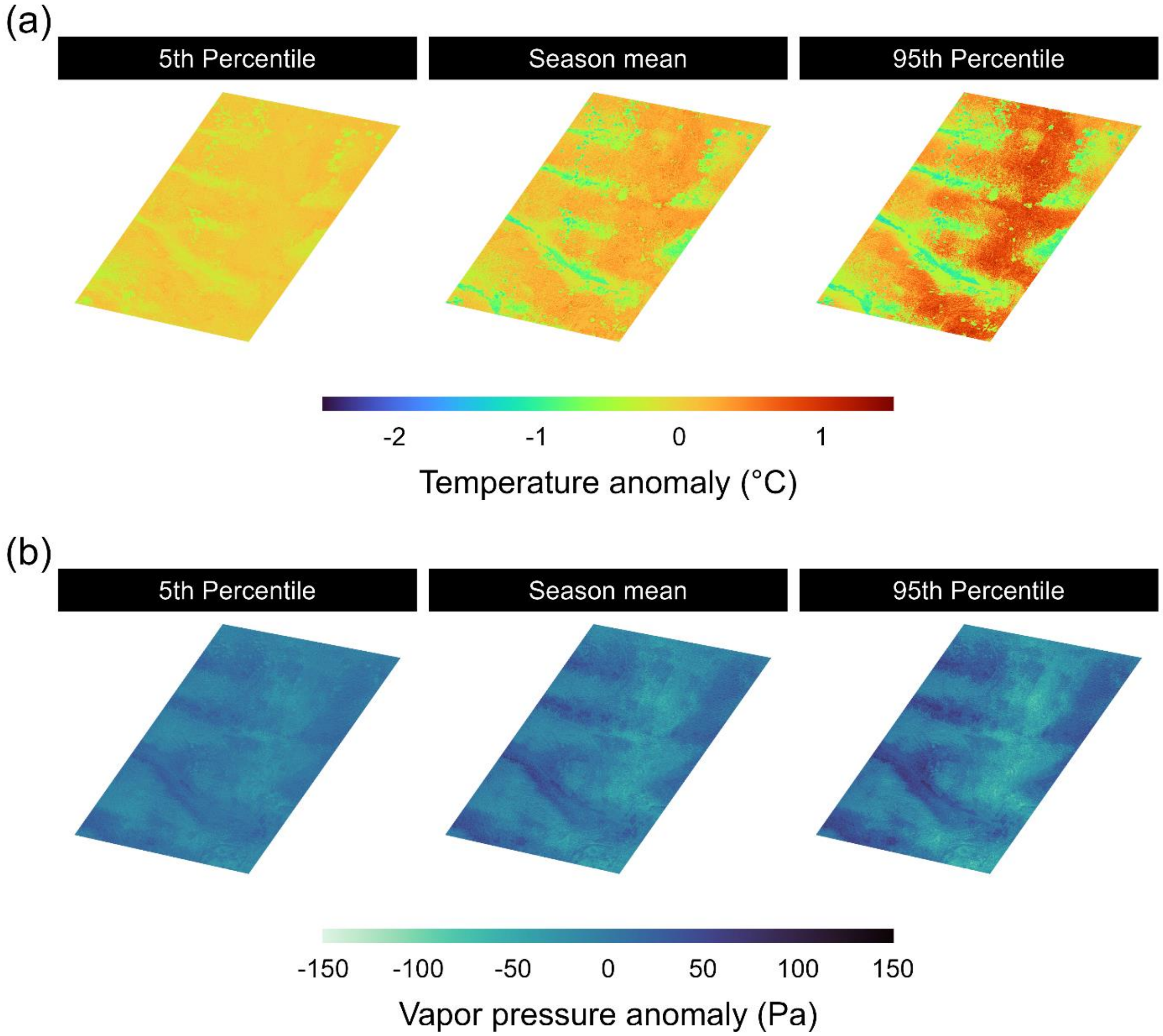


Figure 6. Variation in magnitude of microclimate anomalies with mesoclimate conditions at a grassland site using spatially explicit, 60-cm resolution, Random Forests predictions of temperature **(a)** and vapor pressure **(b)** anomalies under low (5th percentile), seasonal mean, and high (95th percentile) temperature and solar irradiance conditions.

Chapter 1: Supplemental Materials

Appendix S1: Spatial autocorrelation testing

To test our Random Forests models of daily mean temperature and vapor pressure anomalies for spatial autocorrelation, we implemented calculation of Moran's I and associated tests of significance using the *ape* package (Paradis and Schliep 2019) in R. However, because our data had repeated measures for each iButton location for each day of the season, we had to assess potential autocorrelation in our model residuals by day of the season to avoid confounding our results (e.g., it is expected that each iButton would be correlated with itself if environmental characteristics influenced microclimate). Because it would have been too computationally intensive to assess autocorrelation for all 76 days of the season individually, we divided the season into early, middle, and late periods (e.g., days 1-25, 26-50 etc.) and took a random draw for each period to account for potential temporal non-stationarity of autocorrelation. We calculated Moran's I for the model residuals for each of these three days (Table S2). Because we did not find autocorrelation at any point in the season for either model, we present the average Moran's I values for each model in Table S3.

Table S1. Tuning grid and hyperparameter values used in Random Forest models of daily temperature and vapor pressure microclimate anomalies at grassland study sites in southern Wisconsin.

mtry	Split rule	Minimum node size	Number of trees
2	variance	5	1501
3	variance	5	1501
4	variance	5	1501
5	variance	5	1501
6	variance	5	1501
7	variance	5	1501
8*	variance	5	1501
2	extratrees	5	1501
3	extratrees	5	1501
4	extratrees	5	1501
5	extratrees	5	1501
6**	extratrees	5	1501
7	extratrees	5	1501
8	extratrees	5	1501

* Tuning grid values used in top temperature model

** Tuning grid values used in top vapor pressure model

Table S2. Moran's I and associated P-values for models of grassland microclimate mean daily temperature and vapor pressure anomalies for random days of the season stratified by early, middle, and late periods.

Model	Day of season	Period	Moran's I	P-Value
Temperature	8	Early	-0.02	0.71
Temperature	50	Middle	-0.03	0.79
Temperature	64	Late	-0.04	0.85
Vapor pressure	8	Early	-0.03	0.76
Vapor pressure	50	Middle	-0.03	0.73
Vapor pressure	64	Late	-0.03	0.81
Temperature	mean	mean	-0.03	0.78
Vapor pressure	mean	mean	-0.03	0.77

Table S3. Out of bag RMSE (OOB), k-fold cross-validated RMSE, R-squared, Moran's I, and P-values associated with Moran's I for models of mean daily temperature and vapor pressure microclimate anomalies at grassland study sites.

Model	OOB RMSE	K-Fold RMSE	R-Squared	Moran's I	P-Value
Temperature	0.37° C	0.38° C	0.71	-0.03	0.78
Vapor pressure	55.1 Pa	55.2 Pa	0.52	-0.03	0.76

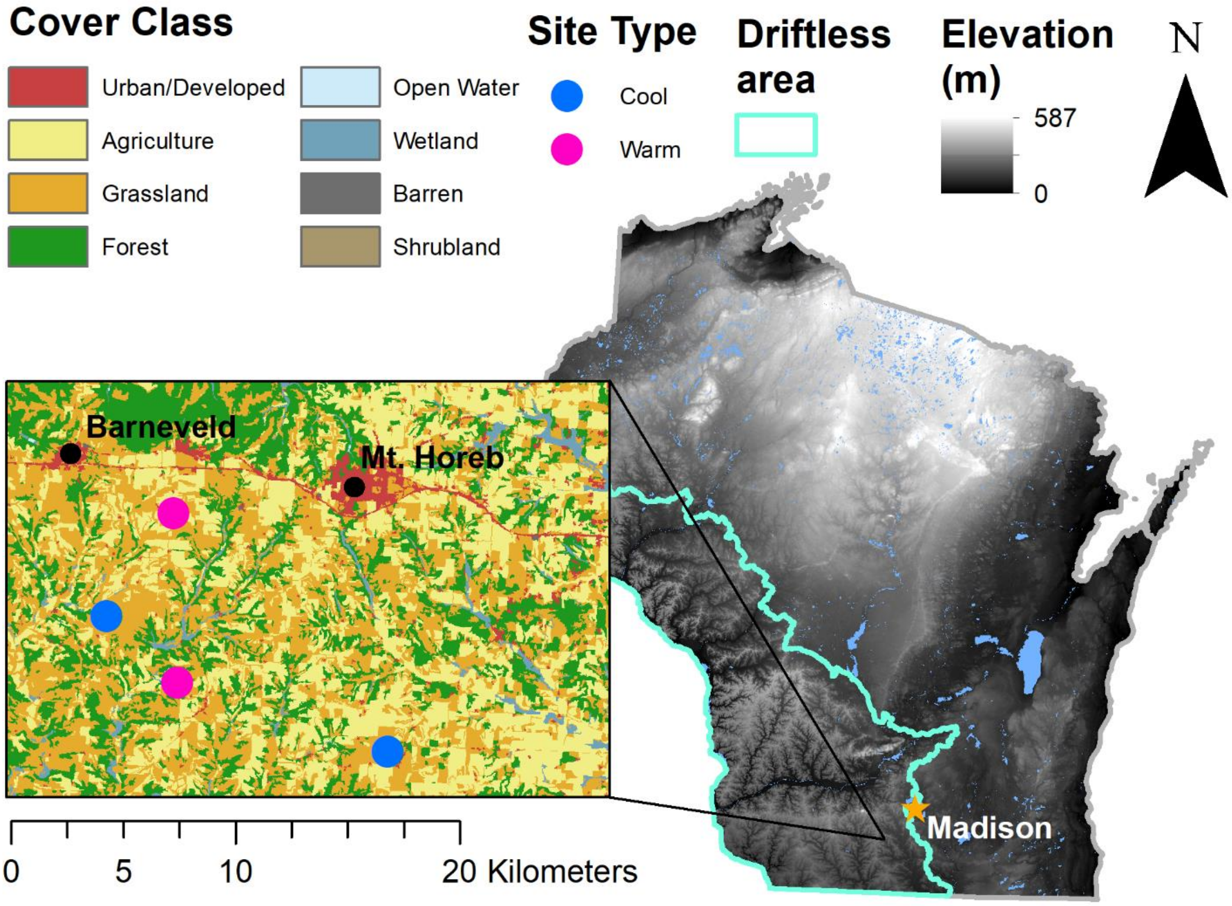


Figure S1. Locations of cool and warm-season grassland study sites used in a grassland microclimate study in southern WI, USA, 2021. Landcover data are shown for the surrounding area and sourced from https://dnr.wisconsin.gov/maps/WISCLAND. Water-masked elevation is shown for the state of Wisconsin and these data are sourced from https://www.usgs.gov/coastal-changes-and-impacts/gmted2010.

Figure S2. Cool-season **(a and b)** and warm-season **(c and d)** grassland study sites in used in a grassland microclimate study in southern Wisconsin, USA, 2021. Cool-season sites were less diverse and dominated by Smooth Brome, while warm-season sites were primarily native and similar in structure to Tallgrass prairie.

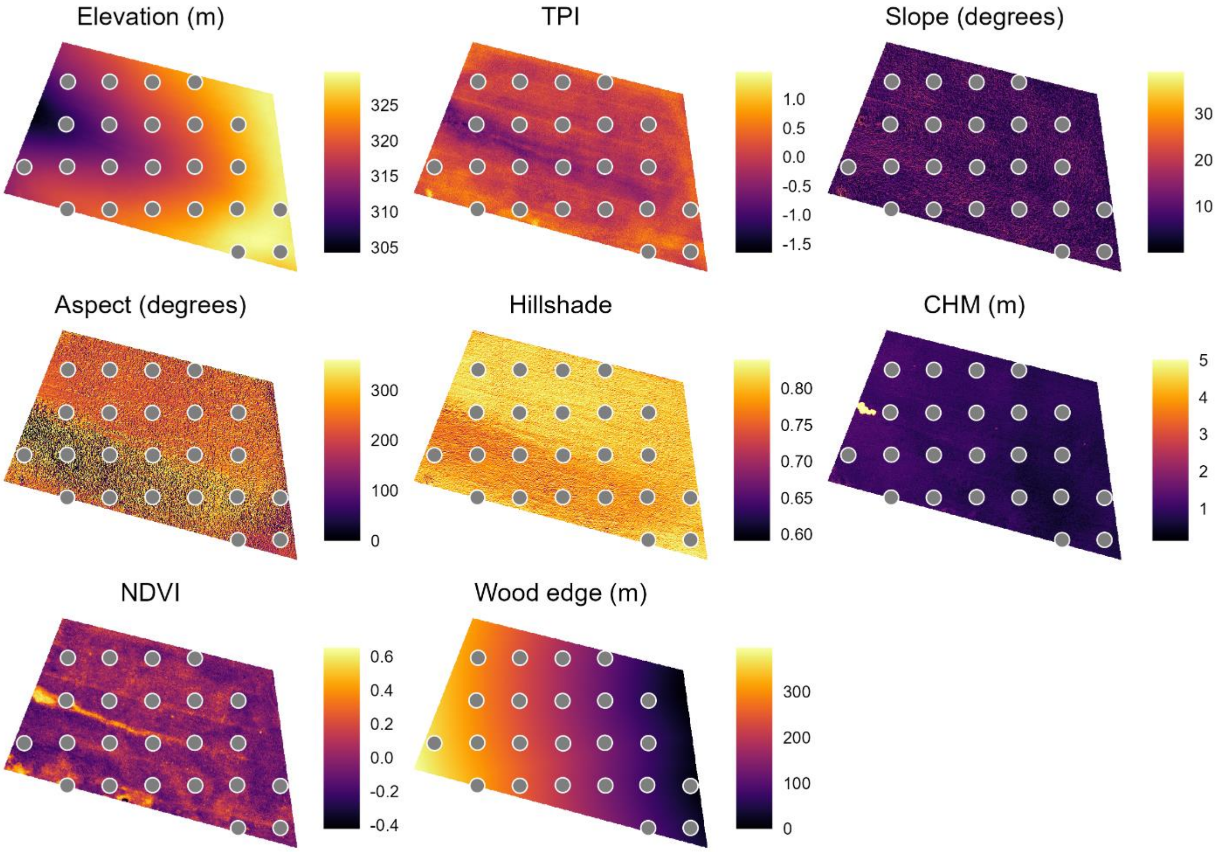
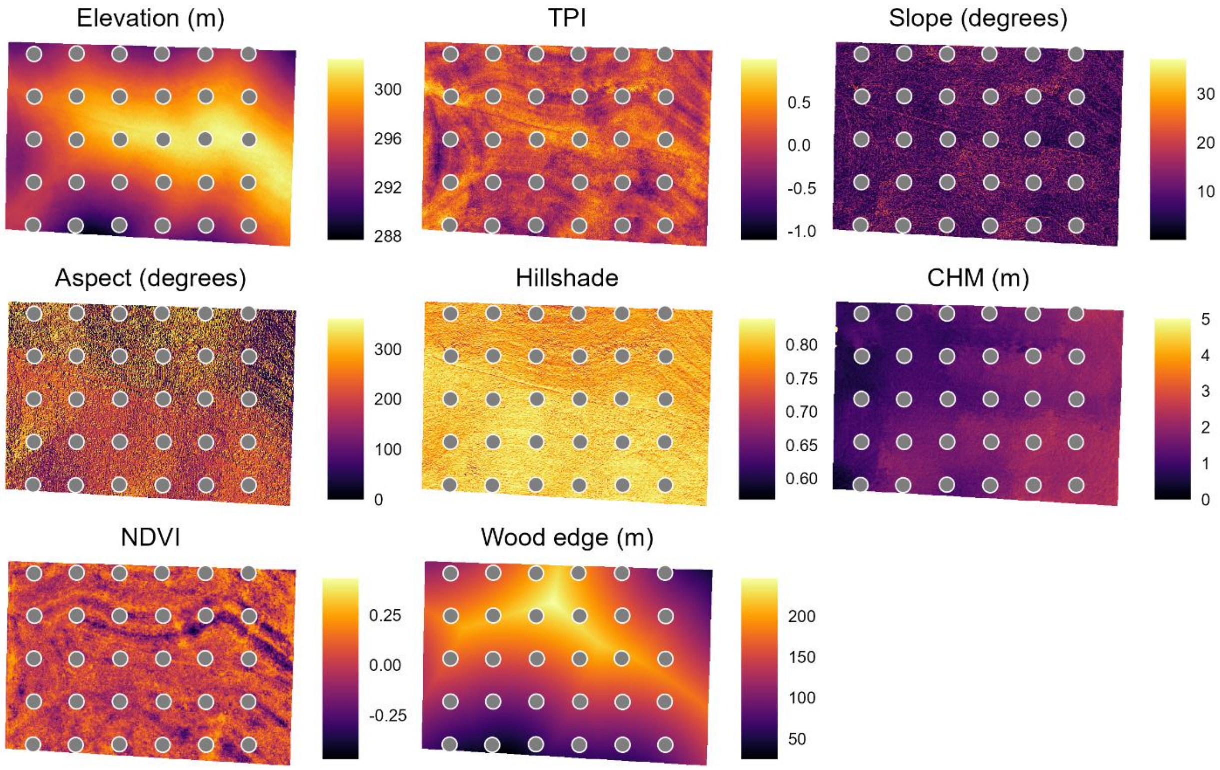


Figure S3. iButton sampling locations (gray circles) across a range of UAS-collected environmental predictors at warm season 1 grassland study site. Mean layers are shown for CHM and NDVI, which were collected in early, middle, and late season to capture changes in vegetation conditions.



Elevation (m)

TPI

Slope (degrees)

Aspect (degrees)

Hillshade

CHM (m)

NDVI

Wood edge (m)

Figure S4. iButton sampling locations (gray circles) across a range of UAS-collected environmental predictors at warm-season 2 grassland study site. Mean layers are shown for CHM and NDVI, which were collected in early, middle, and late season to capture changes in vegetation conditions.

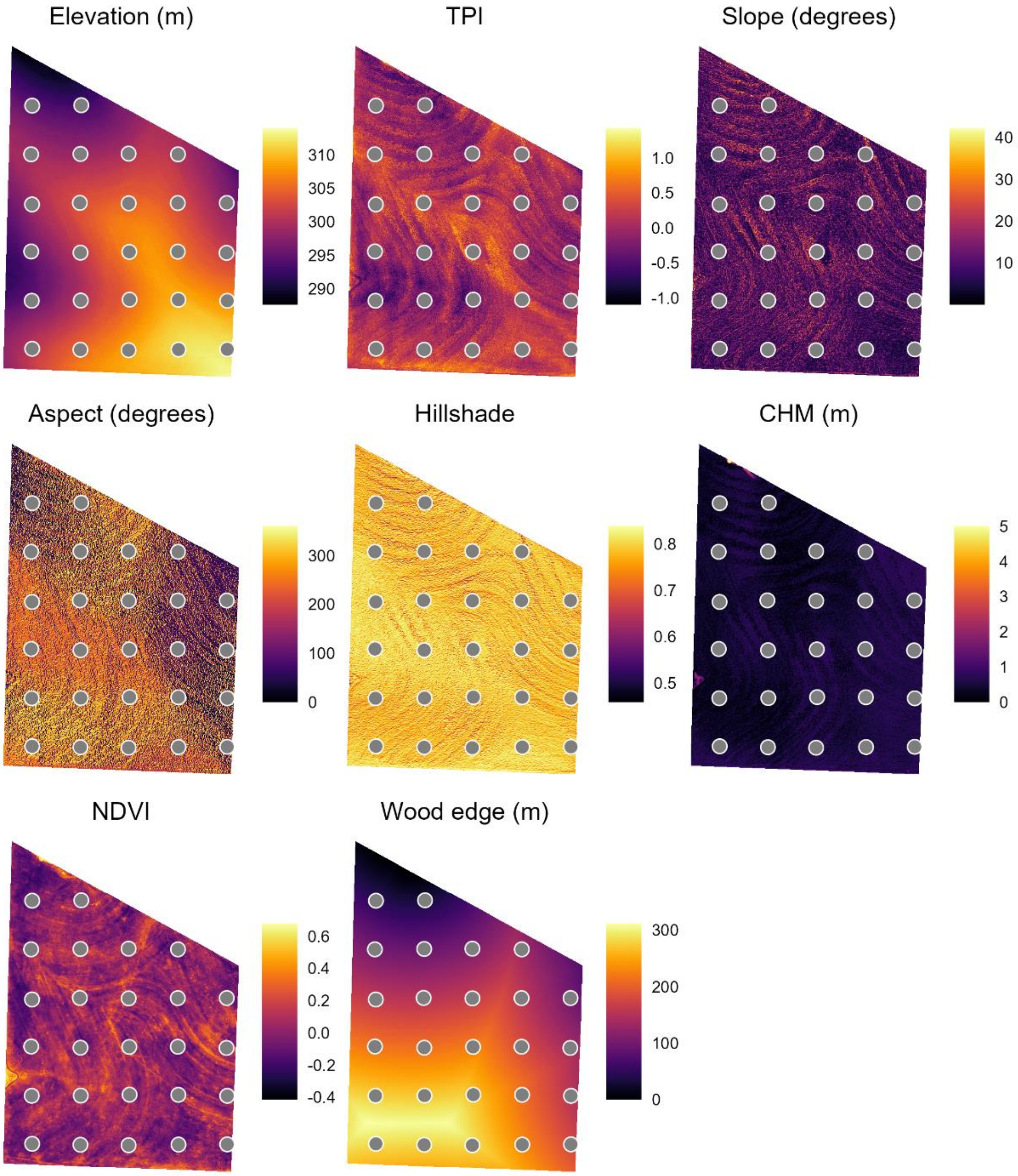


Figure S5. iButton sampling locations (gray circles) across a range of UAS-collected environmental predictors at cool-season 1 grassland study site. Mean layers are shown for CHM and NDVI, which were collected in early, middle, and late season to capture changes in vegetation conditions.

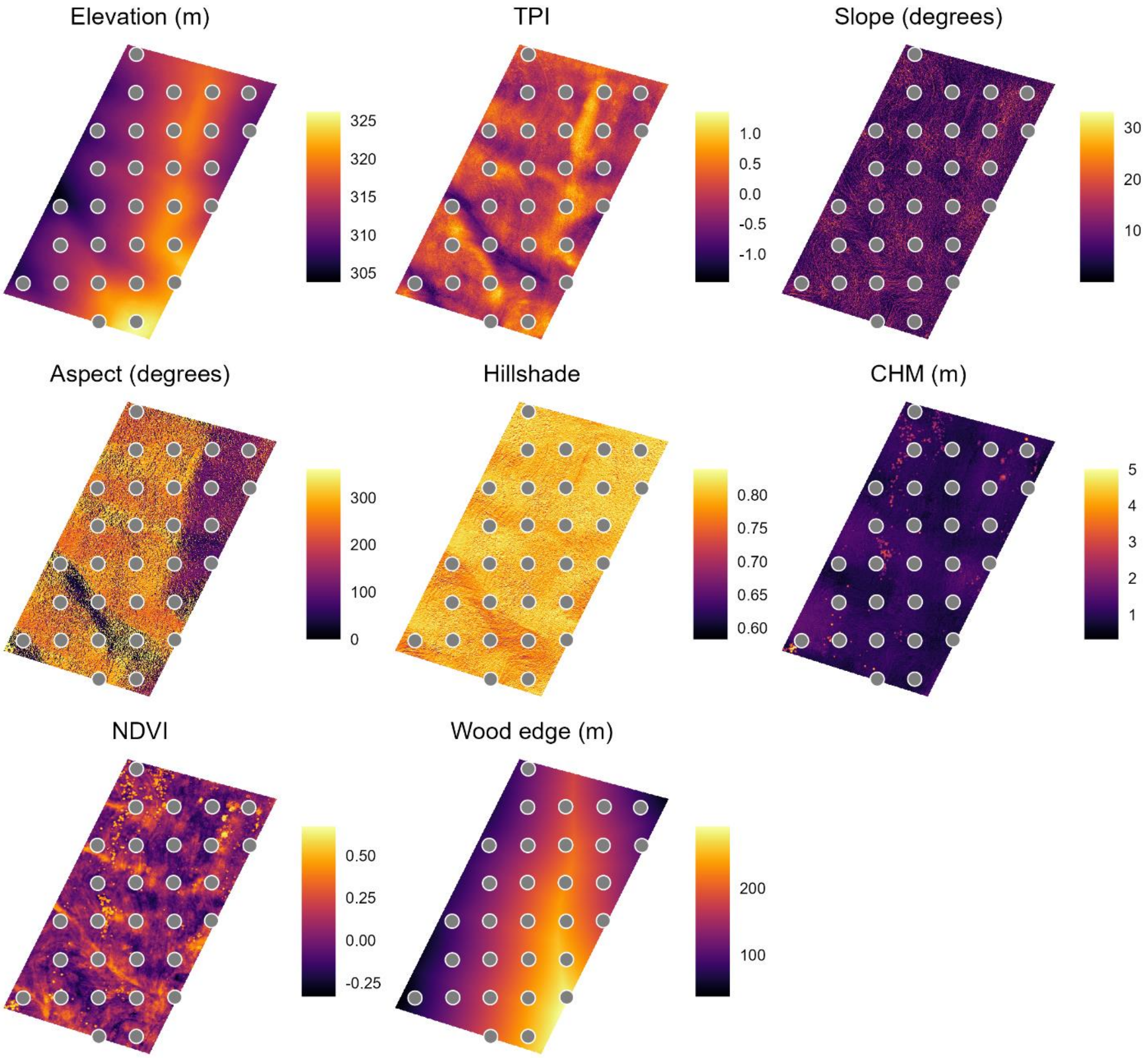


Figure S6. iButton sampling locations (gray circles) across a range of UAS-collected environmental predictors at cool-season 2 grassland study site. Mean layers are shown for CHM and NDVI, which were collected in early, middle, and late season to capture changes in vegetation conditions.

Figure S7. A reflective-foil coated PVC iButton capsule deployed at a 5-cm height in a grassland study site in southern Wisconsin, USA, 2021.

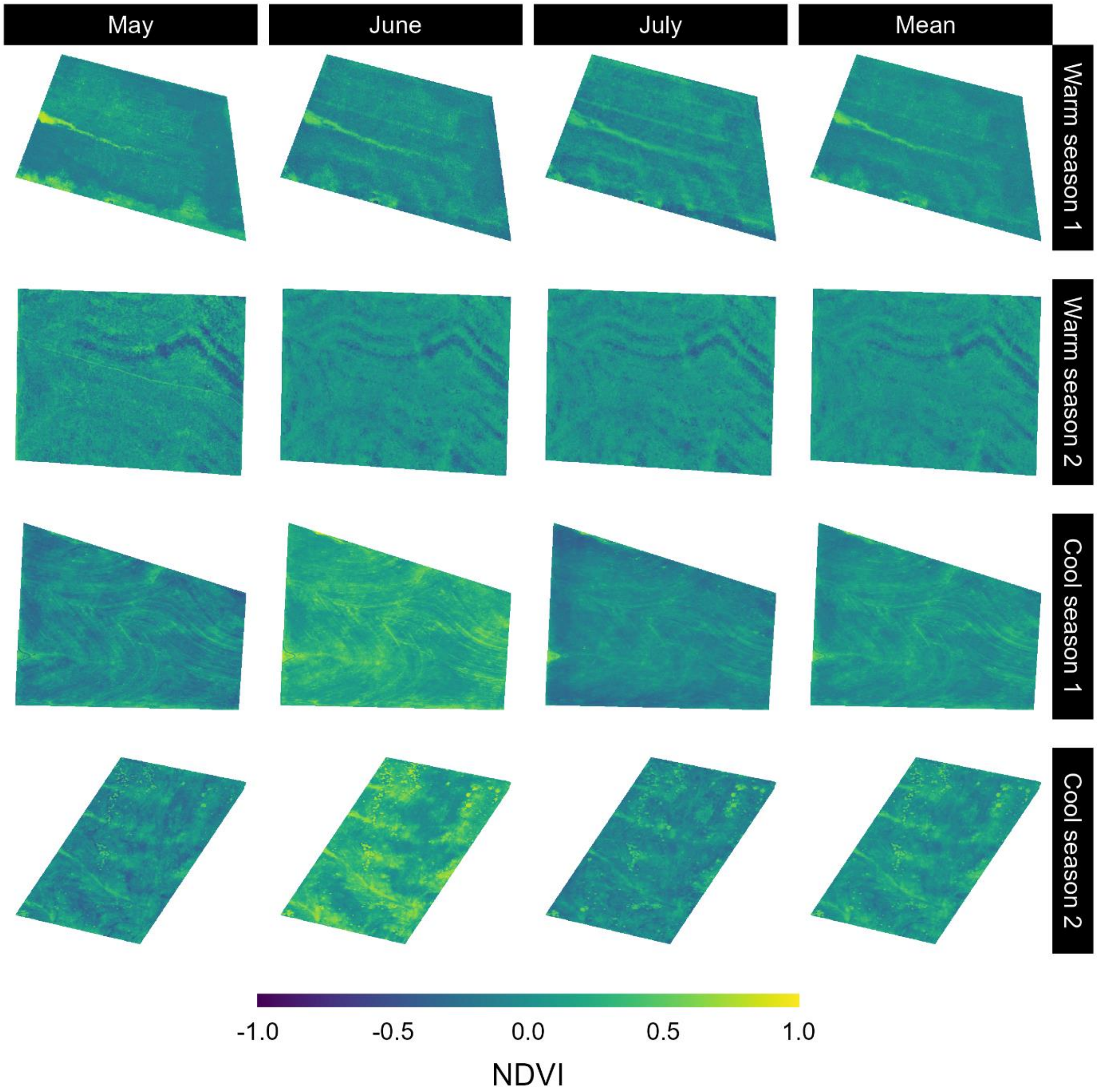


Figure S8. Time-series of NDVI from UAS spectral captures in May, June, and July, in addition to a mean of all three layers, at four grassland study sites in southern Wisconsin, USA, 2021.

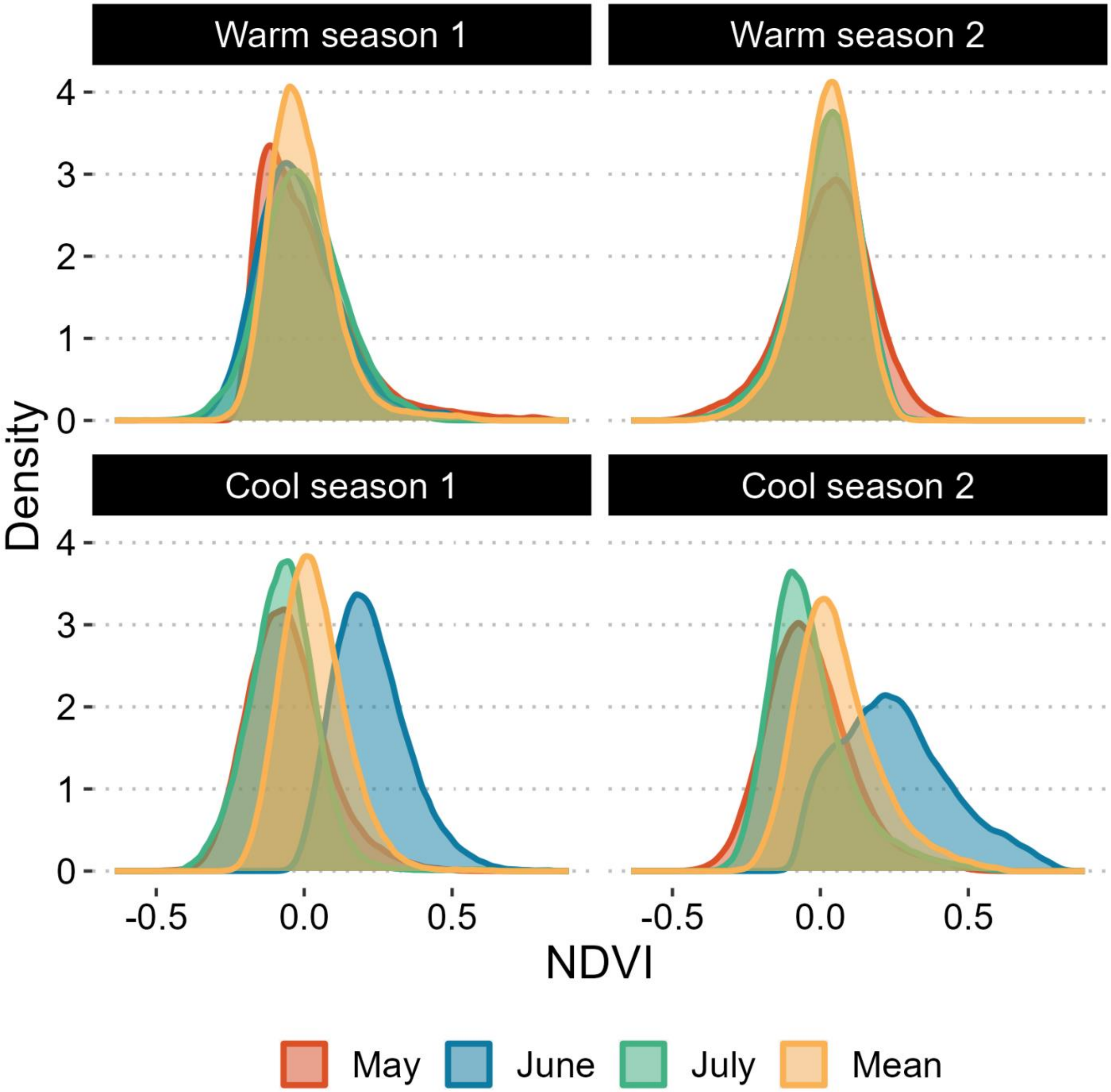


Figure S9. Density distributions of NDVI time-series from UAS spectral captures in May, June, and July, in addition to a mean of all three layers, at four grassland study sites in southern Wisconsin, USA, 2021.

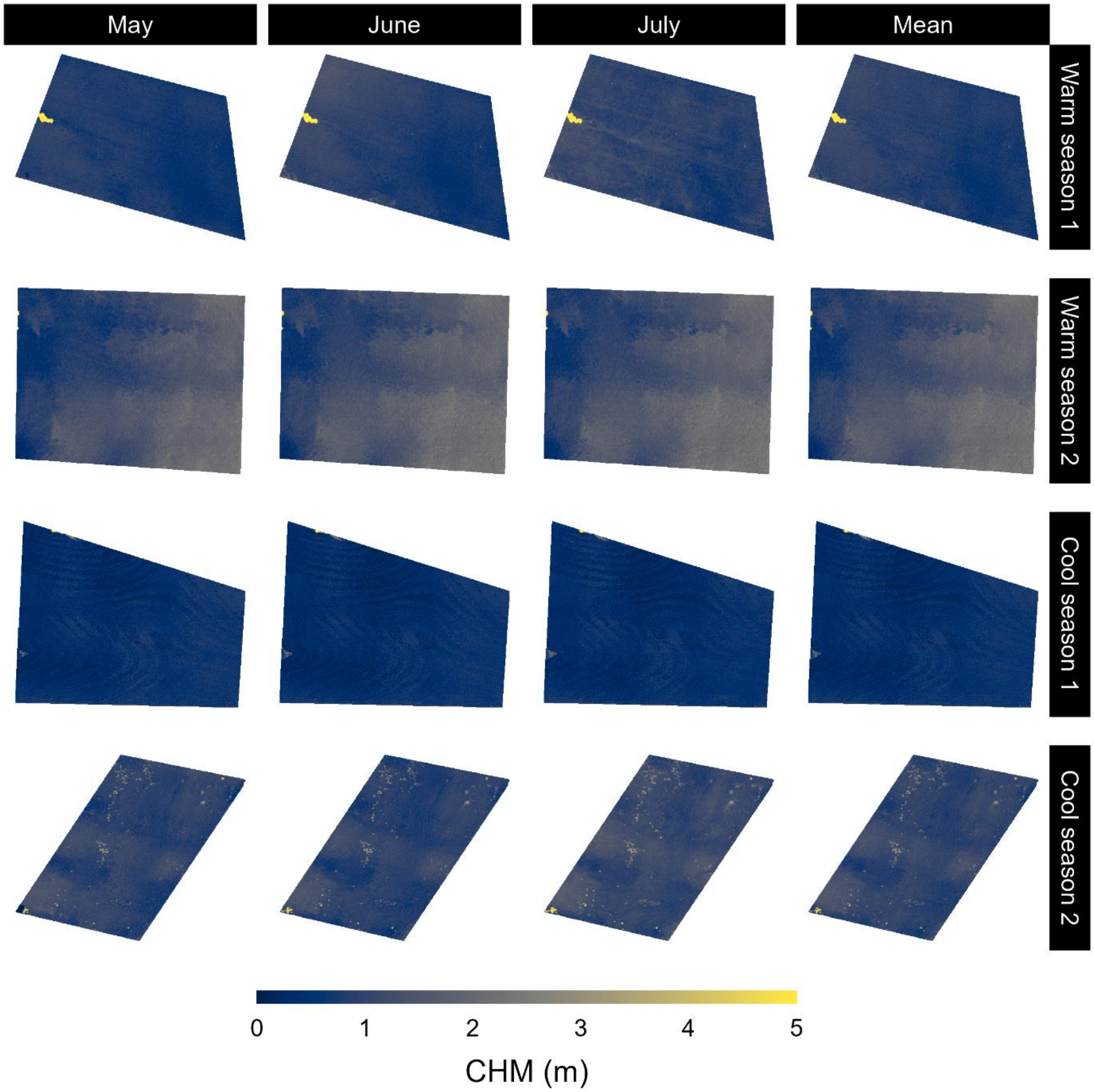


Figure S10. Time-series of canopy height models (CHM) from UAS spectral and LiDAR captures in May, June, and July, in addition to a mean of all three layers, at four grassland study sites in southern Wisconsin, USA, 2021.

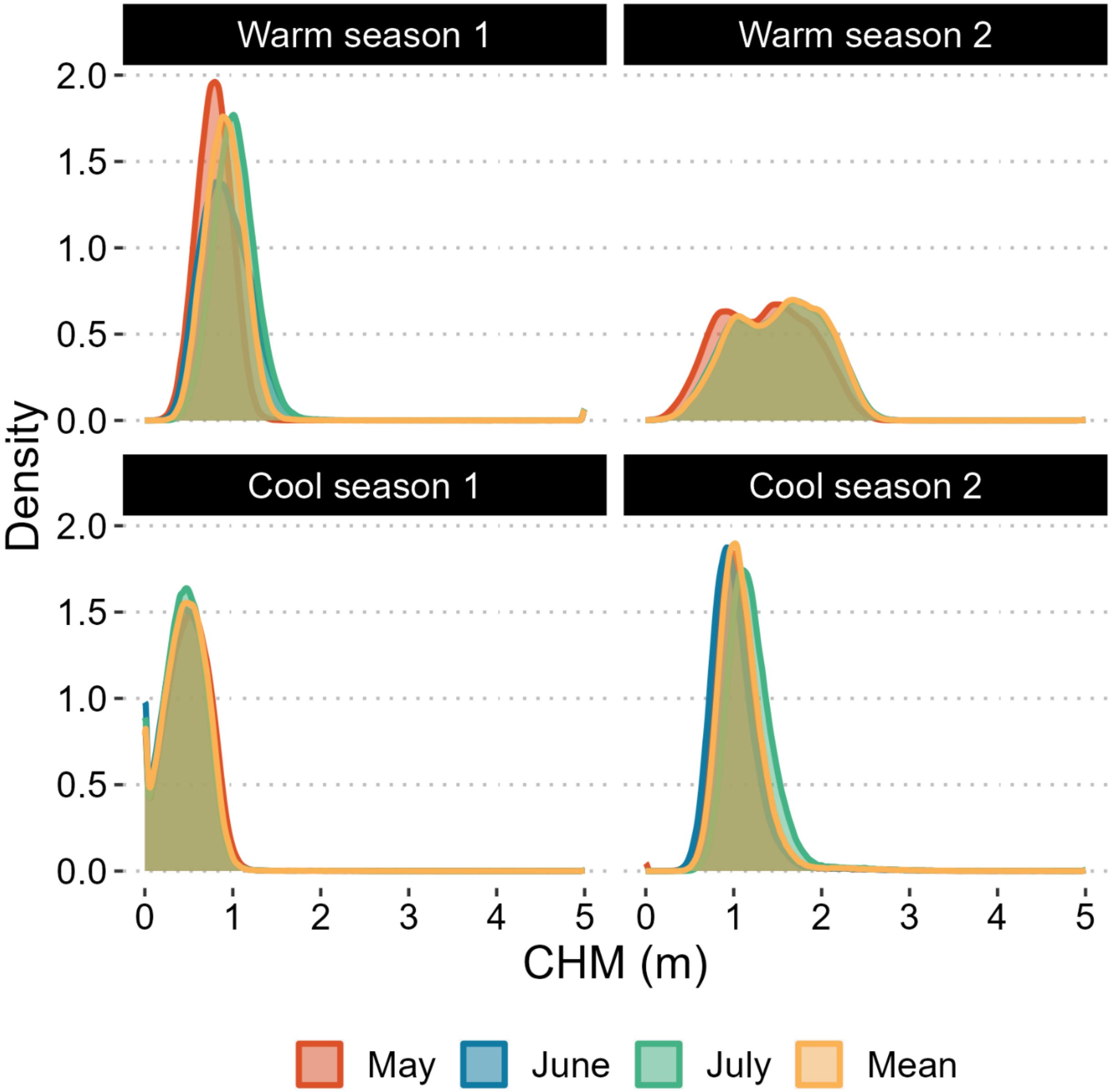


Figure S11. Density distributions of canopy height model (CHM) time-series from UAS spectral and LiDAR captures in May, June, and July, in addition to a mean of all three layers, at four grassland study sites in southern Wisconsin, USA, 2021

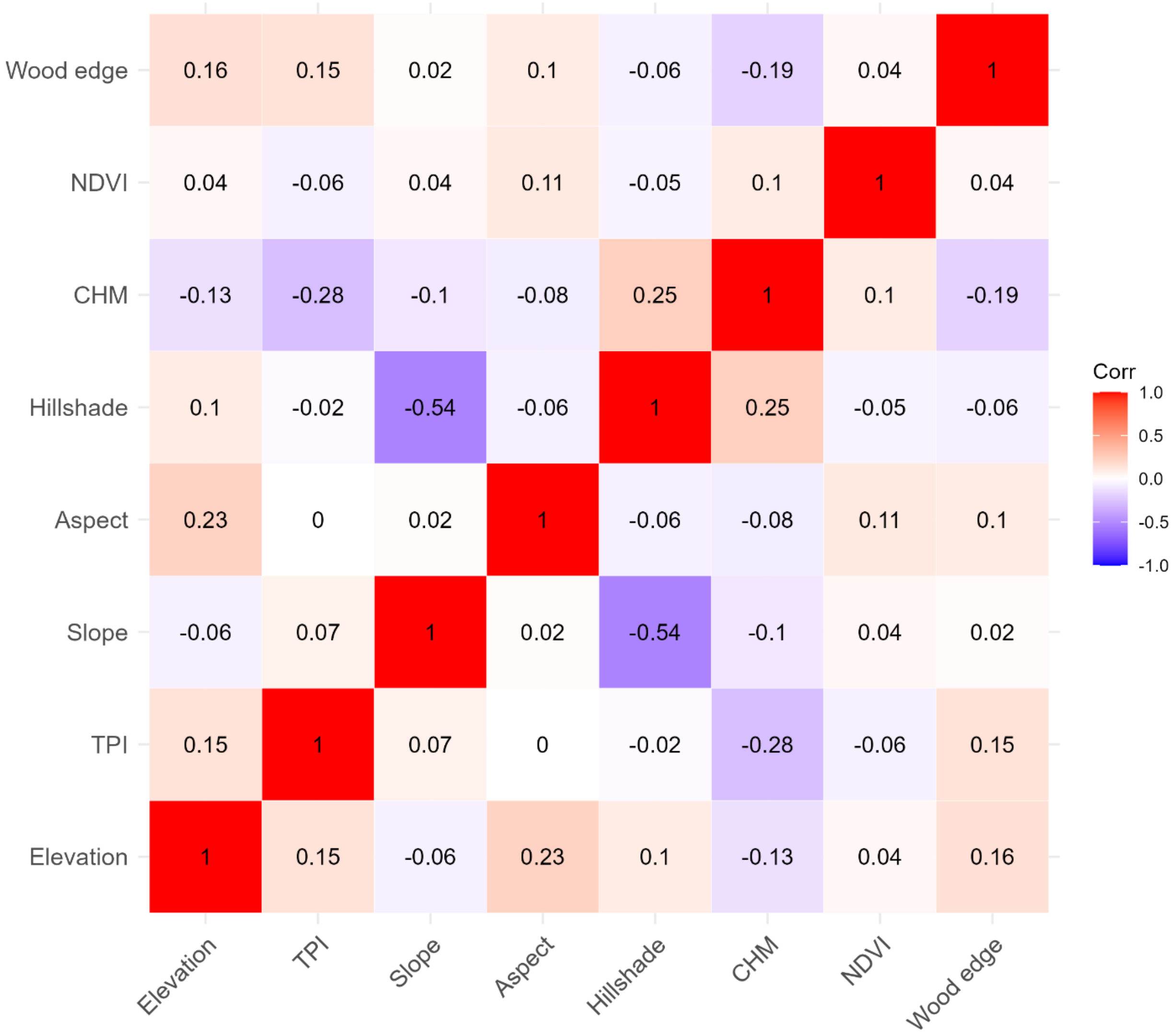


Figure S12. Pearson's correlation coefficients between eight spatial predictors used in Random Forests models of microclimate temperature and vapor pressure anomaly at grassland study sites.

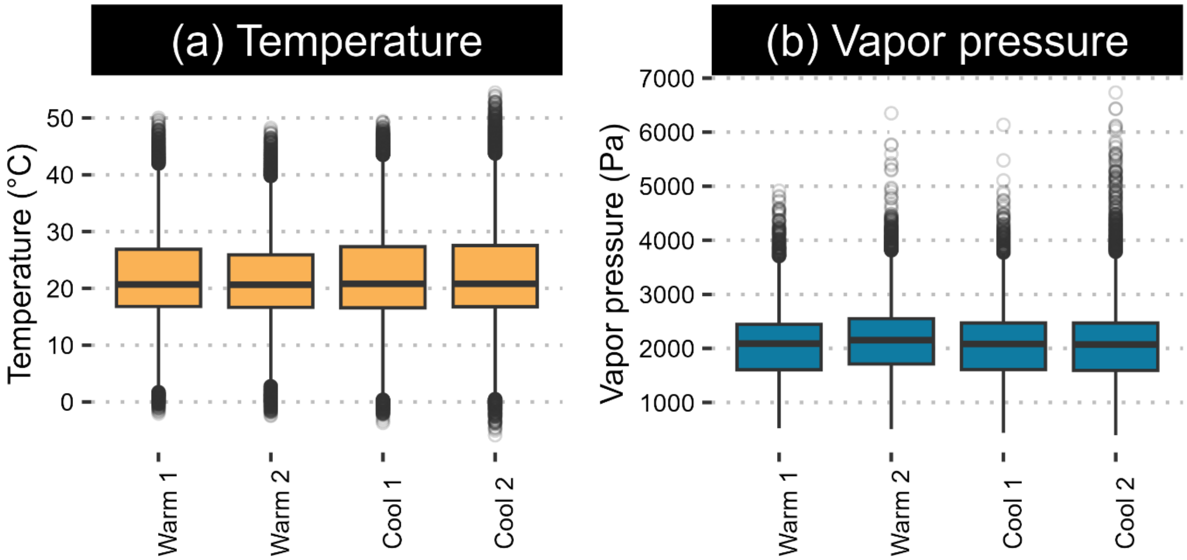


Figure S13. Box plots of hourly measurements of temperature **(a)** and vapor pressure **(b)** at four grassland study sites (2 warm-season and 2 cool-season). Measurements were collected from 104 iButtons (DS1932) distributed between the four sites (23-30 per site), in a study of grassland microclimate in southern Wisconsin, 15 May– 30 July 2021.

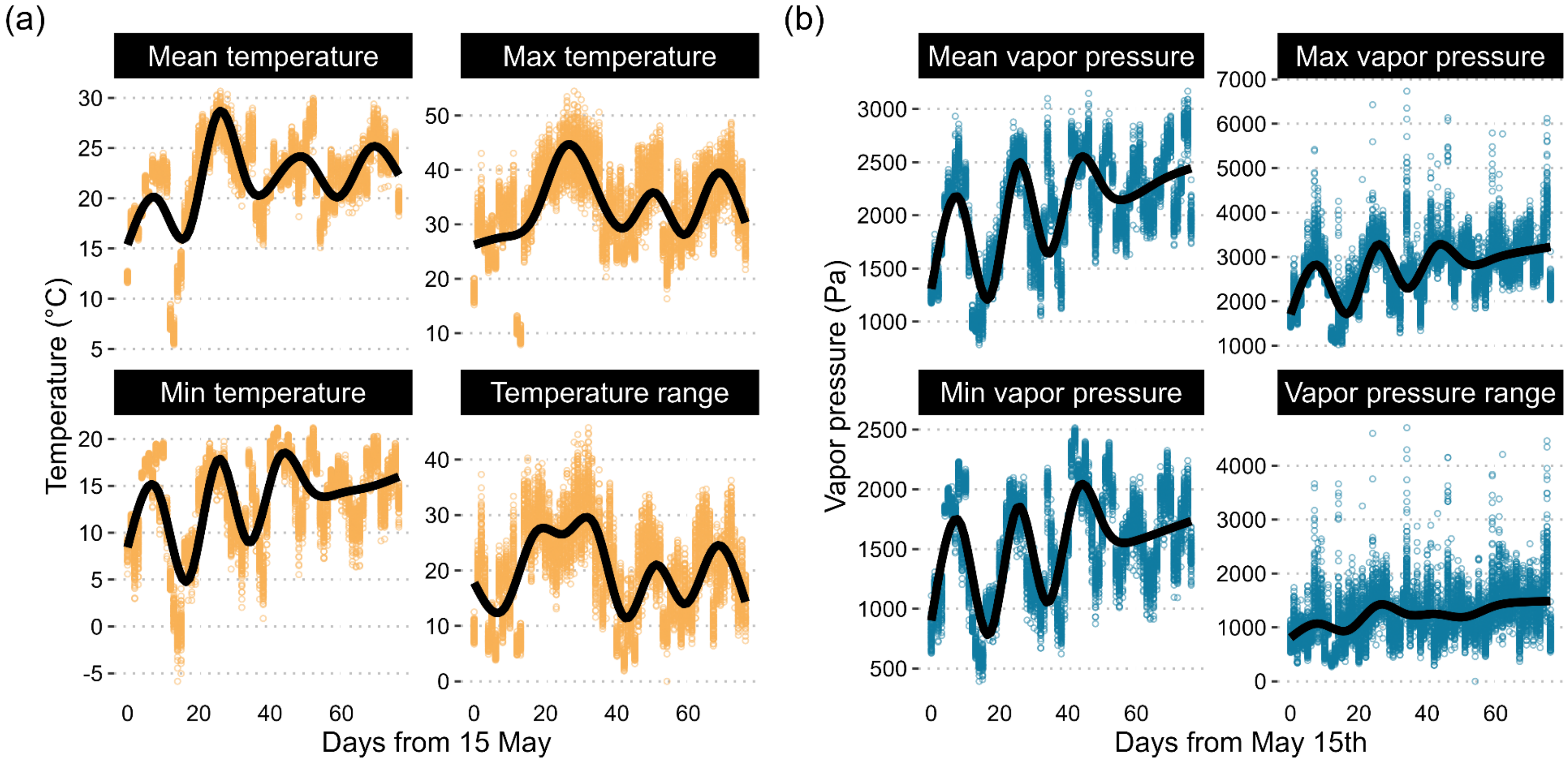


Figure S14. Daily summaries of temperature measurements **(a)** and vapor pressure measurements **(b)** by day of season for a total of 104 iButtons (DS1923) deployed across four sites (23-30 per site) in a study of grassland microclimate in southern Wisconsin, 15 May–30 July 2021. Colored circles denote individual iButton observations and black lines smoothed GAM to aid in visualizing trends.

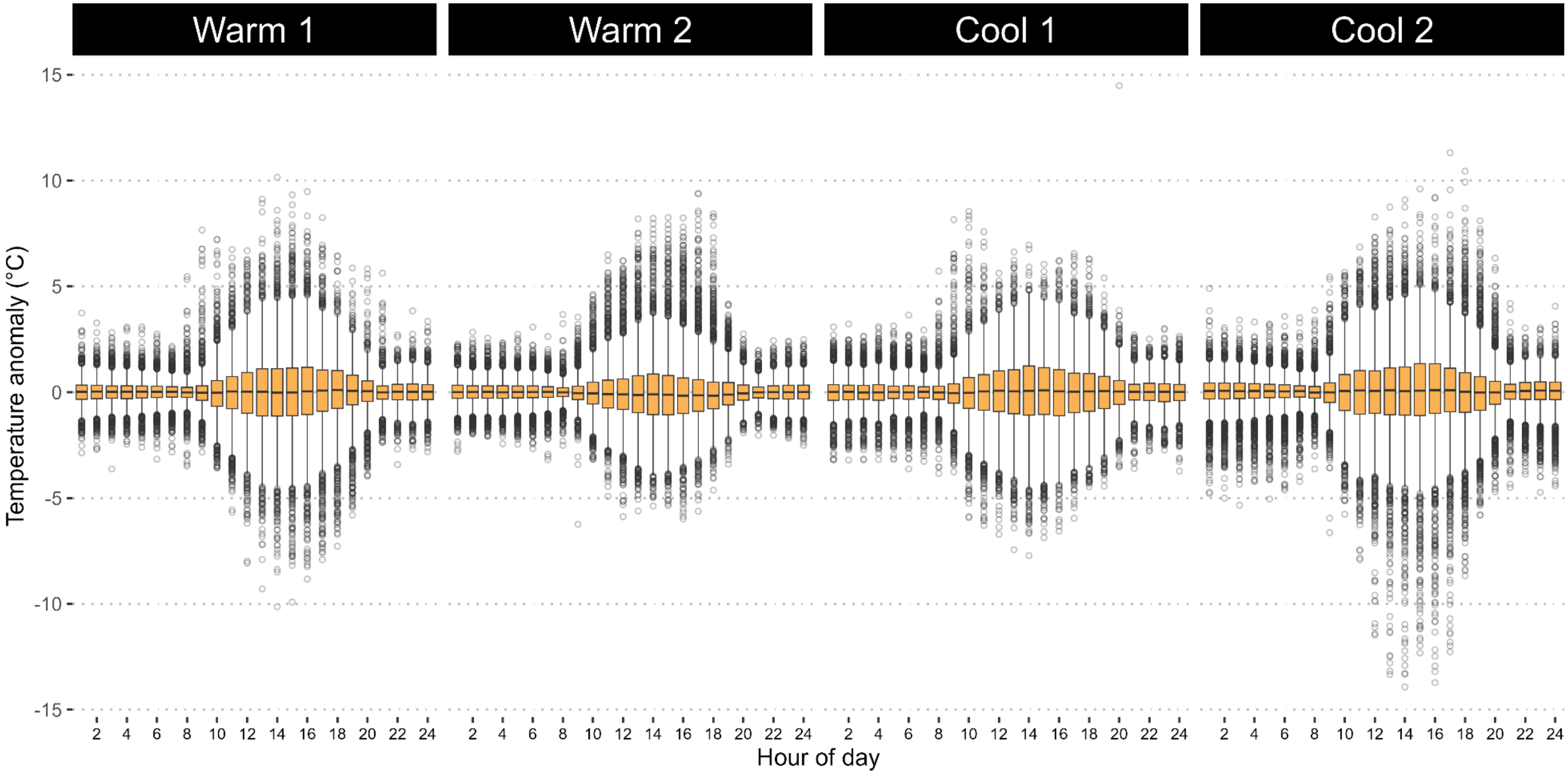


Figure S15. Hourly distributions shown as box plots of temperature anomalies for 104 iButtons (DS1923) deployed across four sites (23-30 per site) in a study of grassland microclimate in southern Wisconsin, 15 May– 30 July 2021.

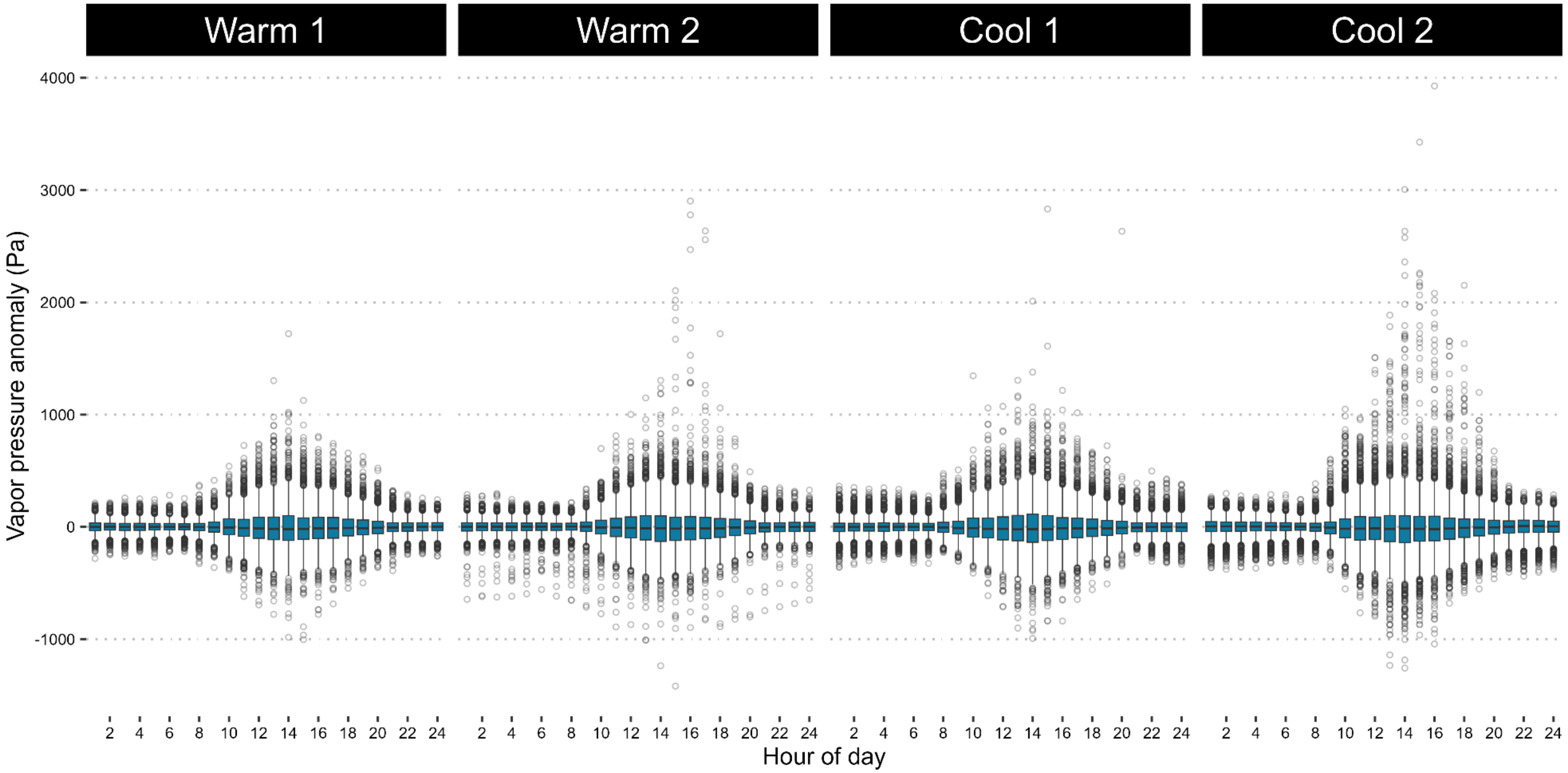


Figure S16. Hourly distributions shown as box plots of vapor pressure anomalies for 104 iButtons (DS1923) deployed across four sites (23-30 per site) in a study of grassland microclimate in southern Wisconsin, 15 May– 30 July 2021.

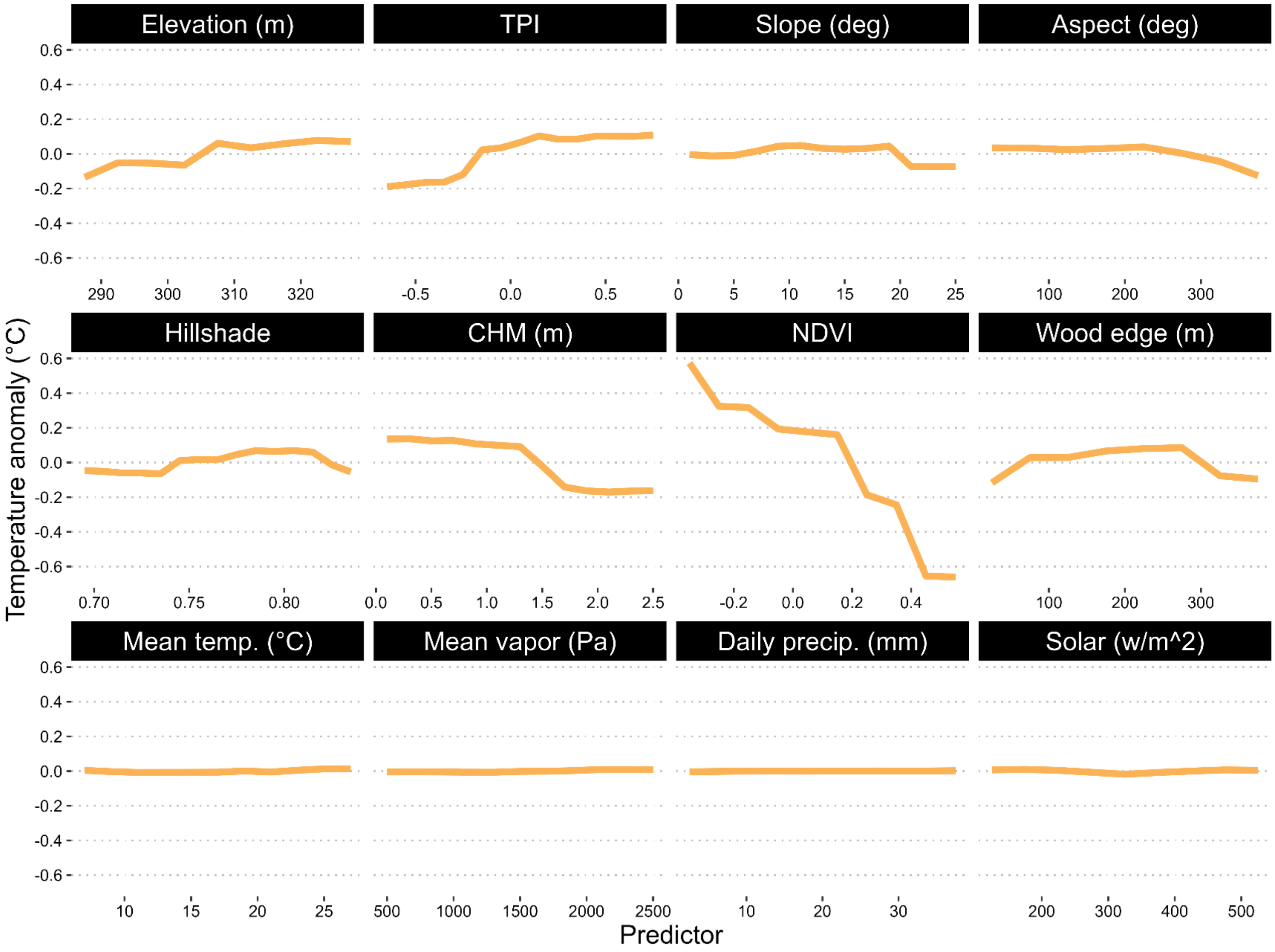


Figure S17. Raw partial dependence of mean daily temperature anomaly on environmental predictors in Random Forests models of microclimate at grassland study sites. NDVI (primary productivity) elevation, TPI (topographic position), solar irradiance, and CHM (vegetation height) were the top variables explaining temperature anomaly.

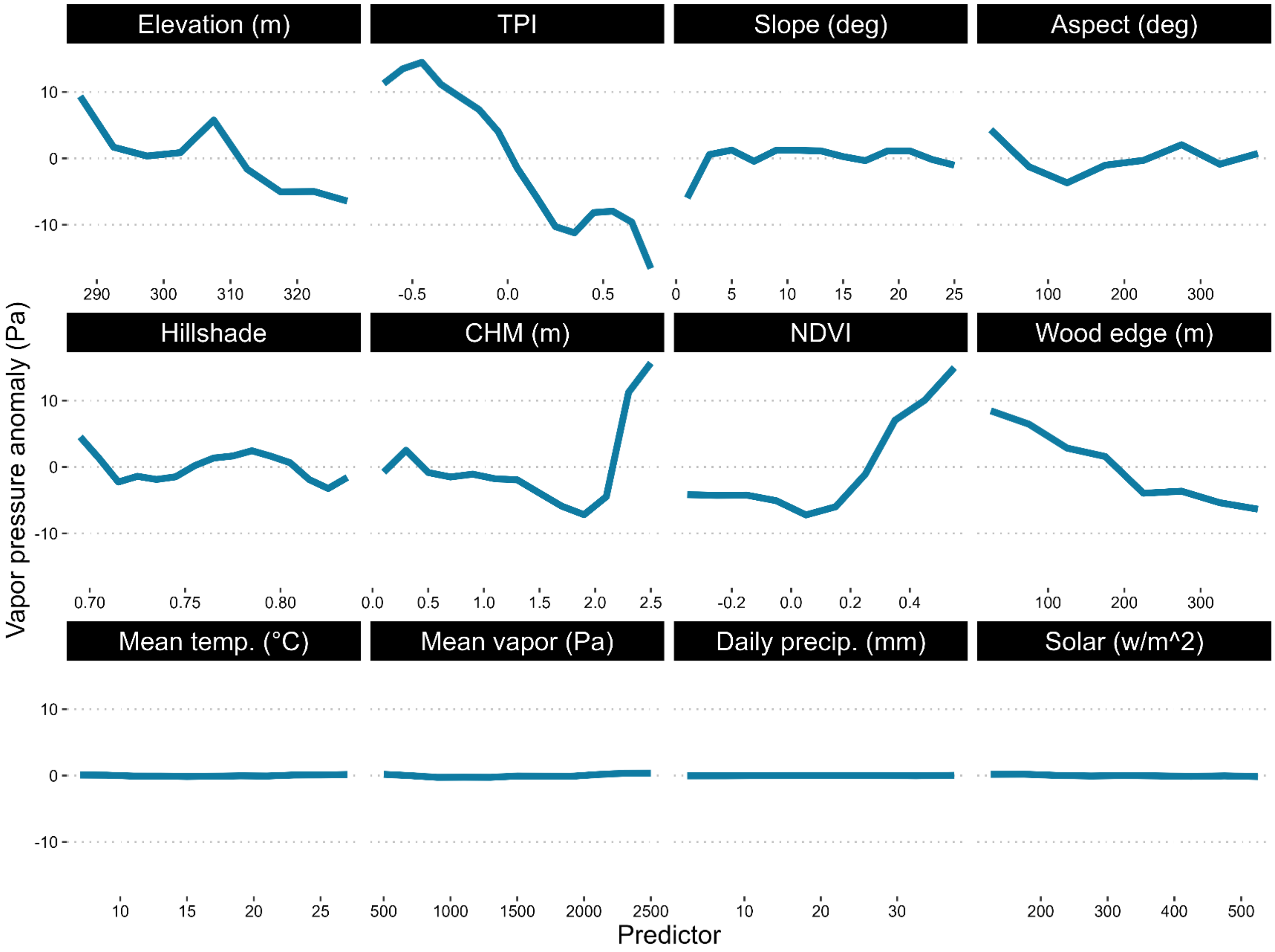


Figure S18. Raw partial dependence of mean daily vapor pressure anomaly on environmental predictors in Random Forests models of microclimate at grassland study sites. TPI (topographic position), CHM (vegetation height), NDVI (primary productivity), aspect, and elevation were the top variables explaining vapor pressure anomaly.

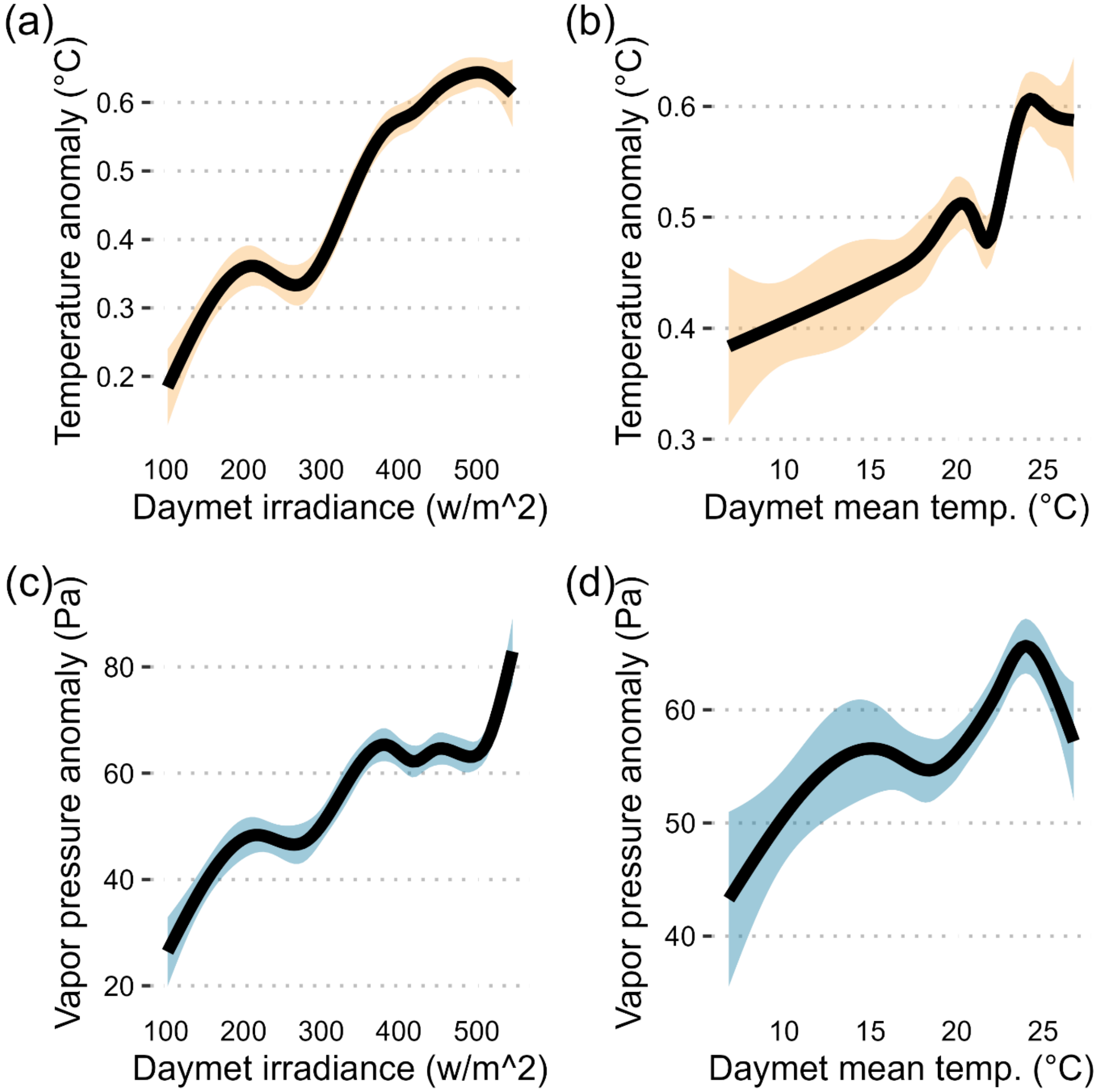


Figure S19. Absolute daily anomaly from iButton microclimate observations plotted against regional mesoclimate conditions sourced from Daymet: influence of solar irradiance on microclimate temperature anomaly **(a)**, influence of mesoclimate mean temperature on microclimate temperature anomaly **(b)**, influence of solar irradiance on microclimate vapor pressure anomaly **(c)**, and influence of mesoclimate mean temperature on microclimate vapor pressure anomaly **(d)**. The figures illustrate larger anomaly values associated with greater irradiance and higher regional temperatures. The lines are smoothed using a GAM to aid in visualizing relationships and shading denotes 95% confidence intervals.

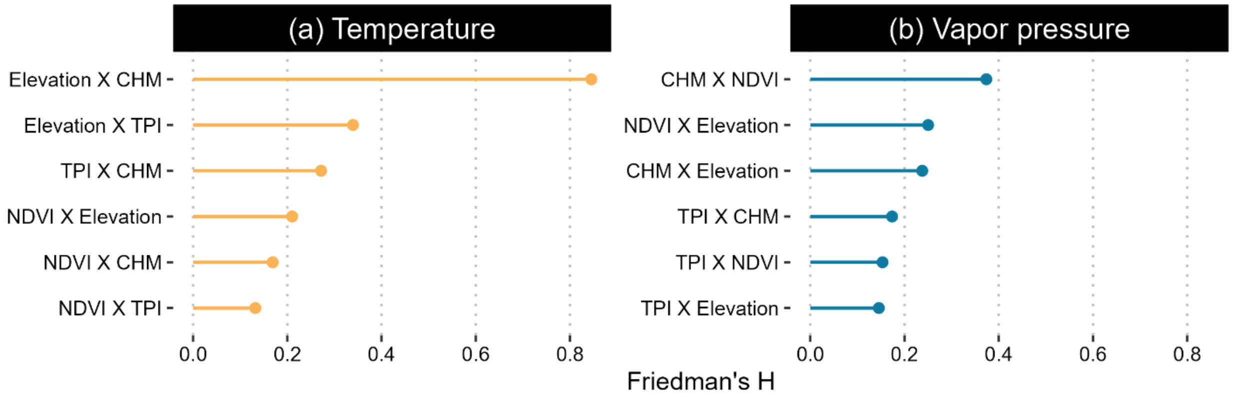


Figure S20. Pairwise interactions between top spatial and mesoclimate predictors in Random Forests models of mean daily temperature **(a)** and vapor pressure **(b)** anomalies at grassland study sites. Friedman's H is calculated from the decomposition of partial dependence for a given feature and can be interpreted as the proportion of variance explained by that feature that is attributed to covariance with another feature. There is no formal threshold for what constitutes a meaningful interaction, but generally interactions < 0.5 are considered weak.

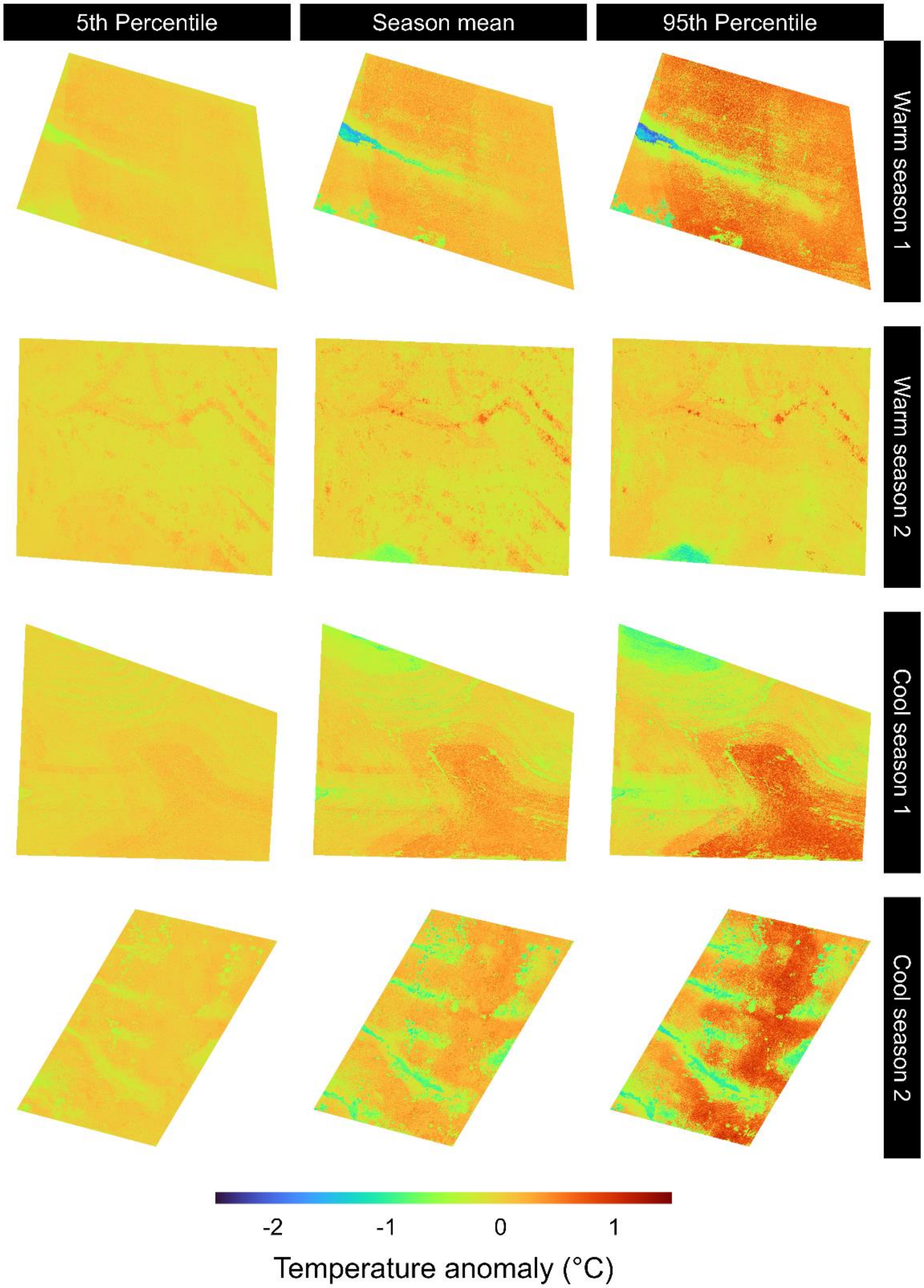


Figure S21. Spatially explicit, 60-cm resolution, Random Forests predictions of temperature microclimate anomaly at four grassland study sites. Predictions are displayed for under low (5th percentile), seasonal mean, and high (95th percentile) temperature and solar irradiance conditions to display variation in magnitude of microclimates with mesoclimate conditions.

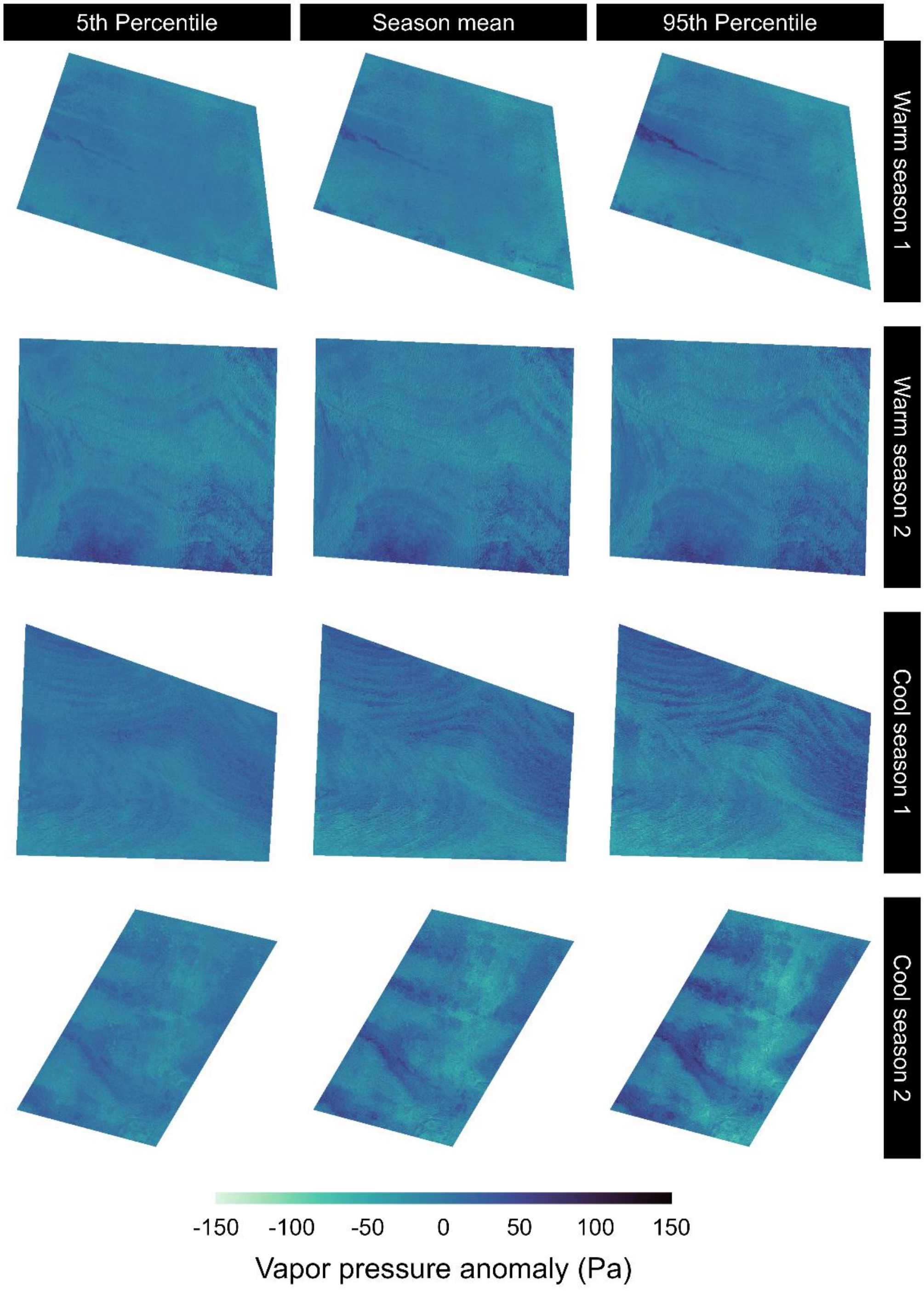


Figure S22. Spatially explicit, 60-cm resolution, Random Forests predictions of vapor pressure microclimate anomaly at four grassland study sites. Predictions are displayed for under low (5th percentile), seasonal mean, and high (95th percentile) temperature and solar irradiance conditions to display variation in magnitude of microclimates with mesoclimate conditions.

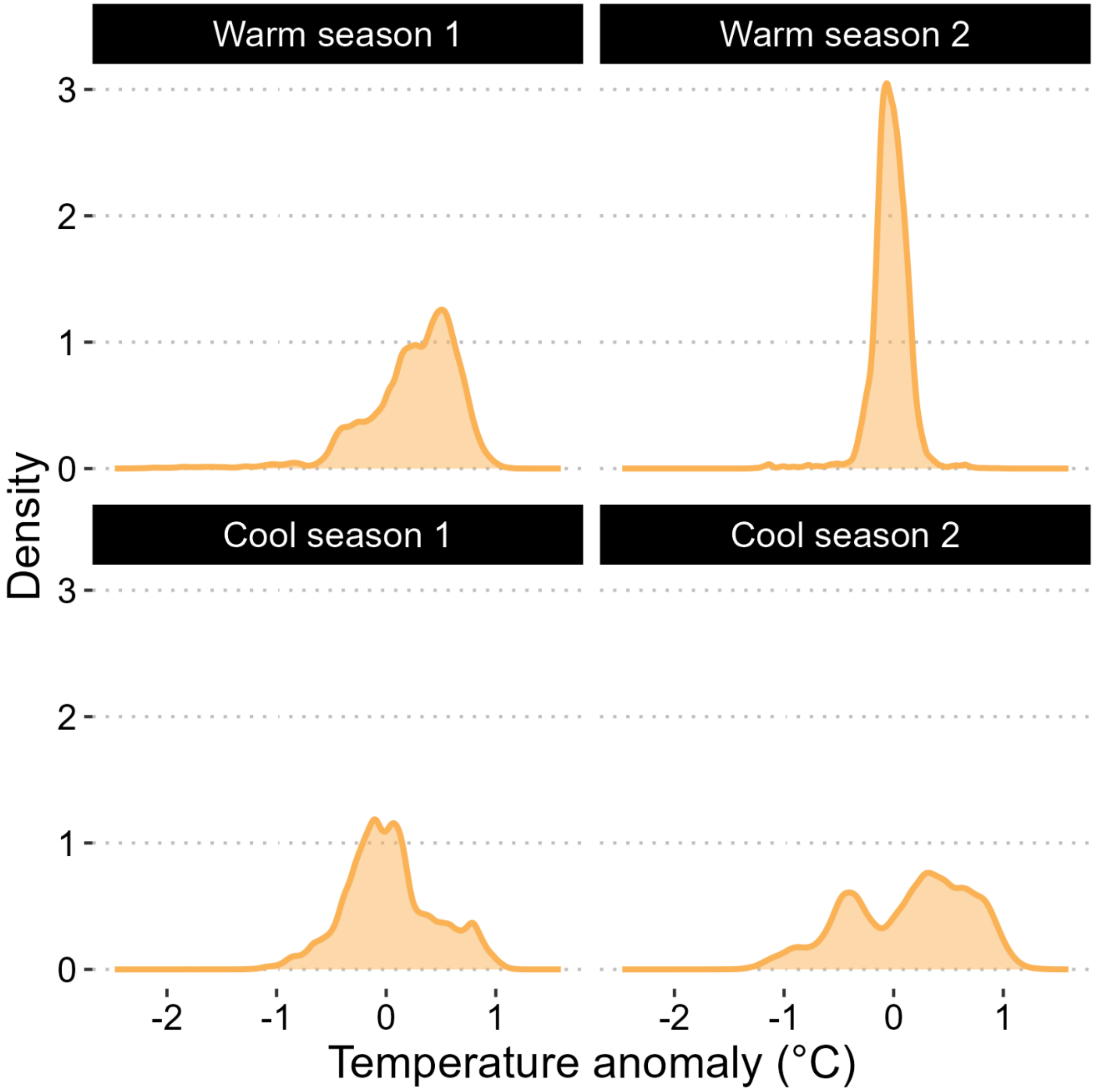


Figure S23. Density distributions of spatially explicit, 60-cm resolution, Random Forests predictions of temperature microclimate anomaly for high (95th percentile) temperature and solar irradiance conditions at four grassland study sites.

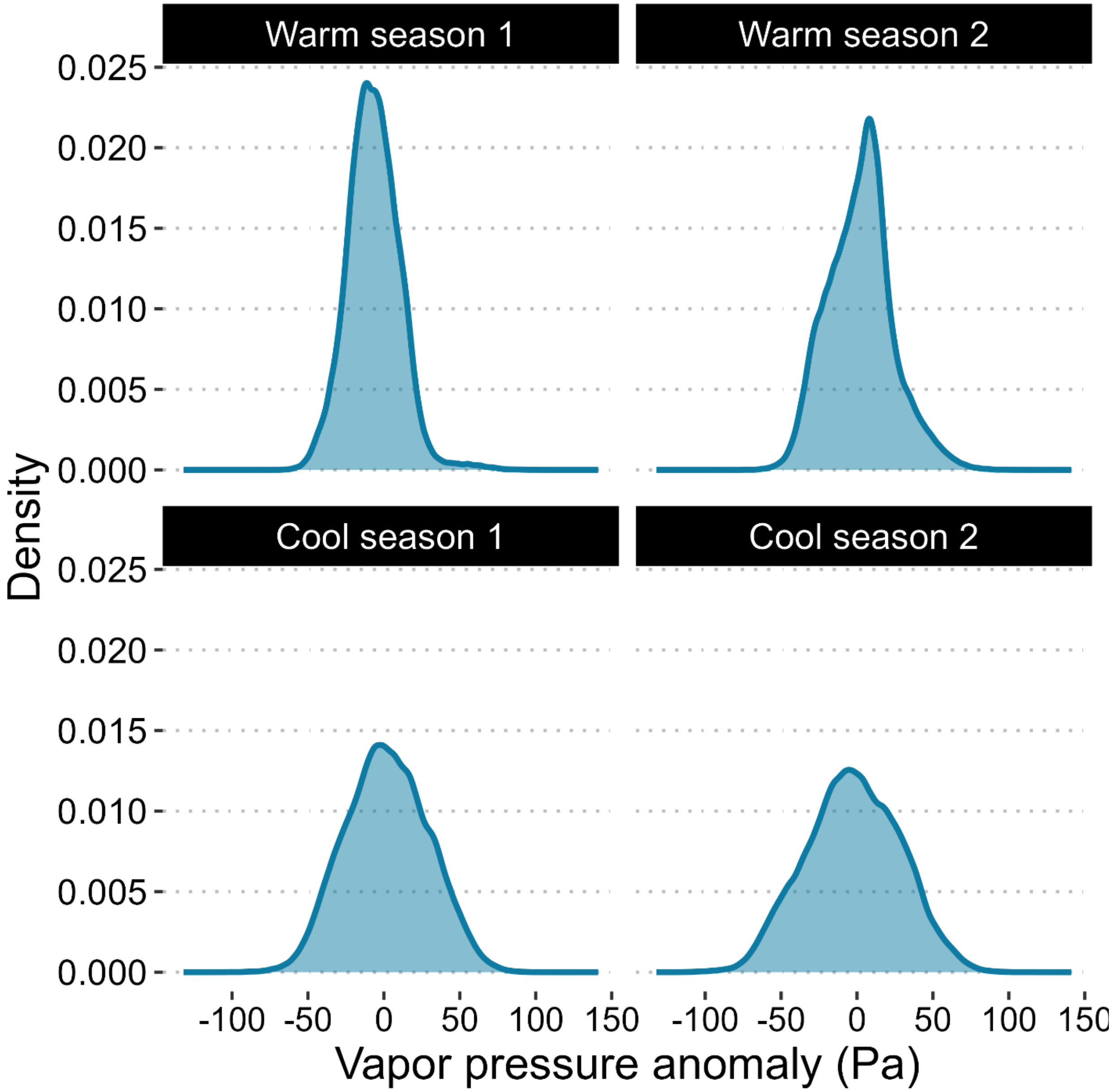


Figure S24. Density distributions of spatially explicit, 60-cm resolution, Random Forests predictions of vapor pressure microclimate anomaly for high (95th percentile) temperature and solar irradiance conditions at four grassland study sites.

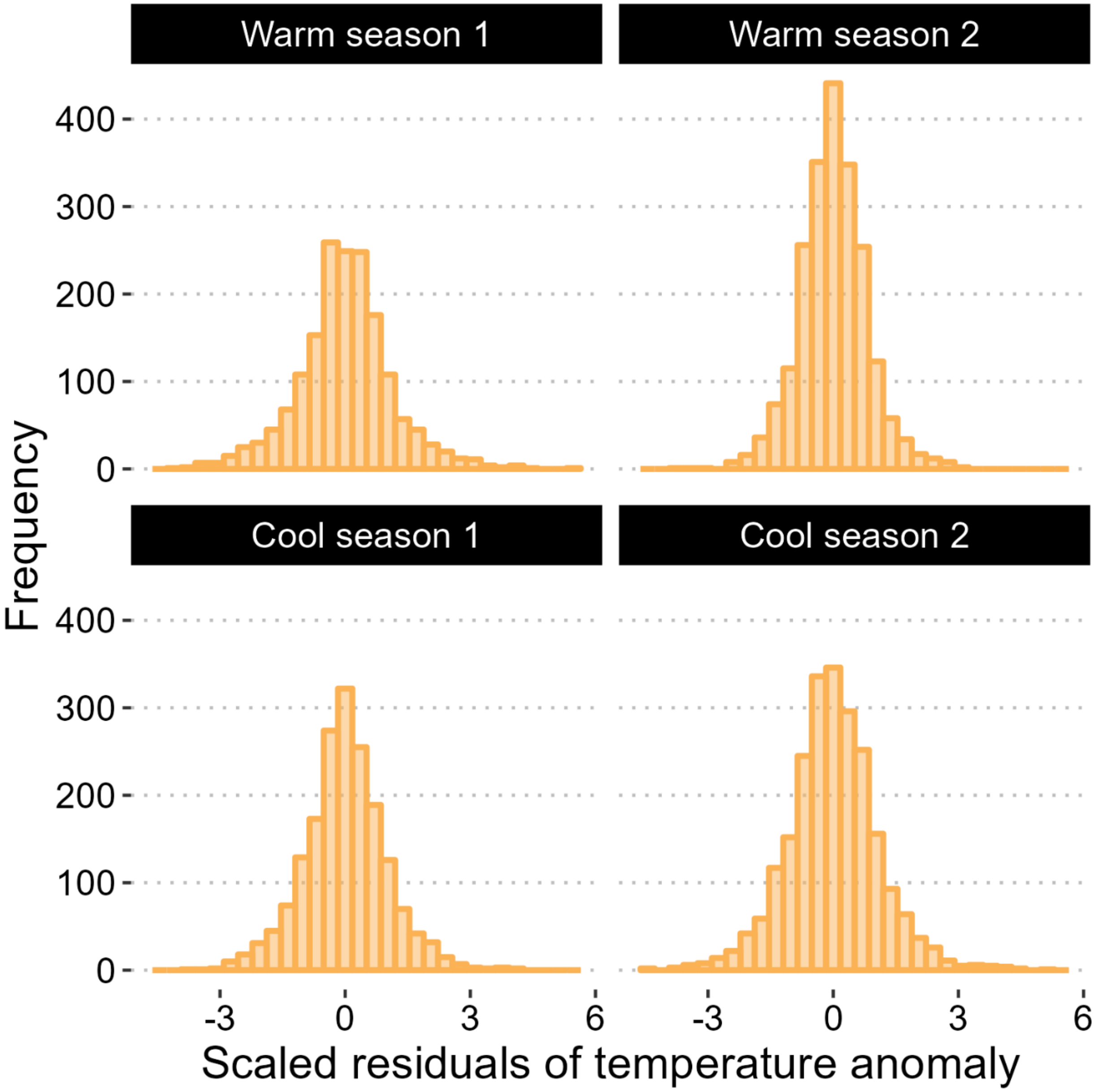


Figure S25. Histograms of residual error structure for Random Forests models of microclimate temperature anomaly at four grassland study sites in southern Wisconsin. Residuals have been scaled for easy comparison with vapor pressure models (Figure S26).

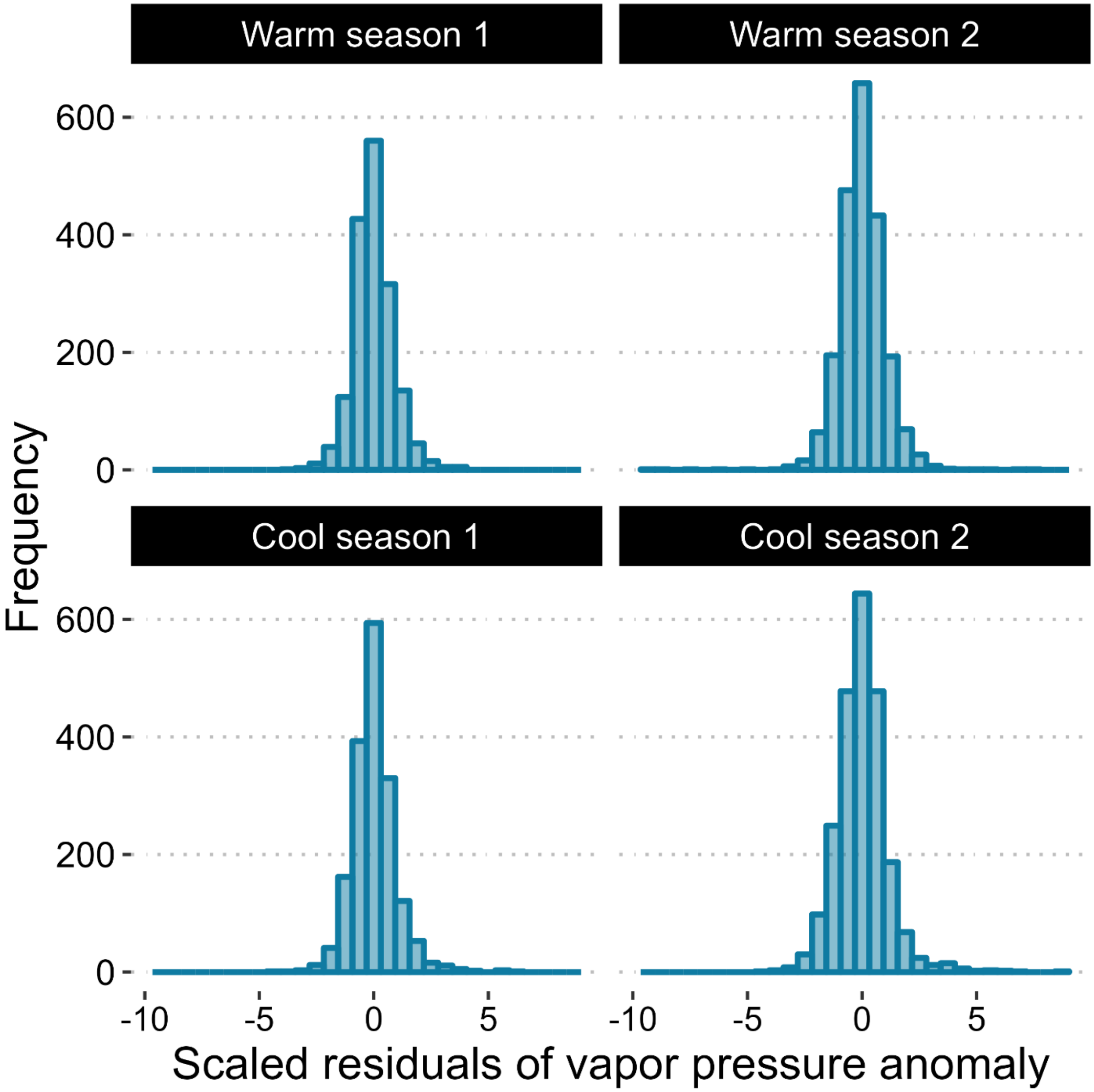


Figure S26. Histograms of residual error structure for Random Forests models of microclimate vapor pressure anomaly at four grassland study sites in southern Wisconsin. Residuals have been scaled for easy comparison with temperature models (Figure S25).

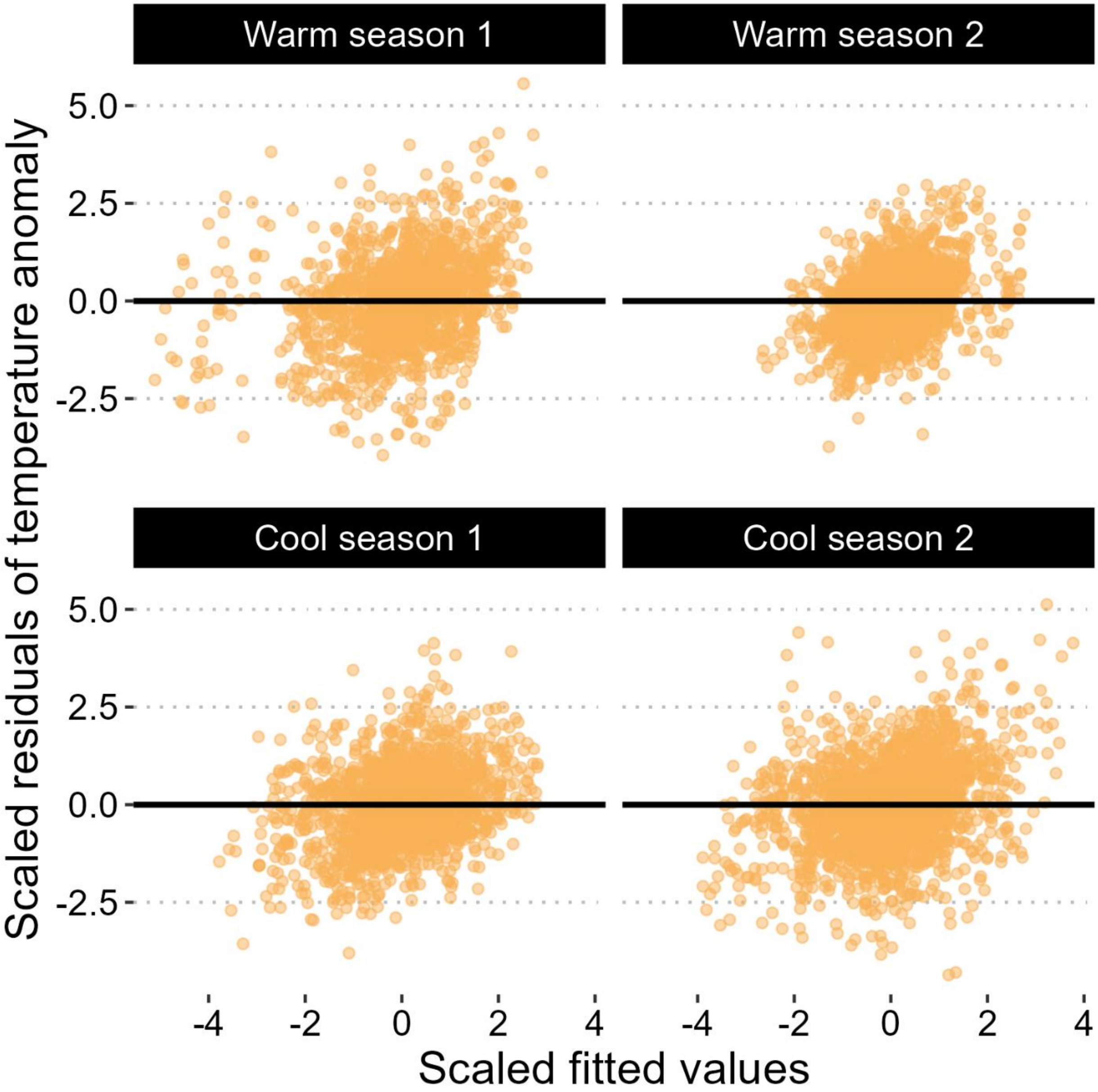


Figure S27. Scatter plots of residual error structure for Random Forests models of microclimate temperature anomaly at four grassland study sites in southern Wisconsin. Residuals and fitted values have been scaled for easy comparison with vapor pressure models (Figure S28).

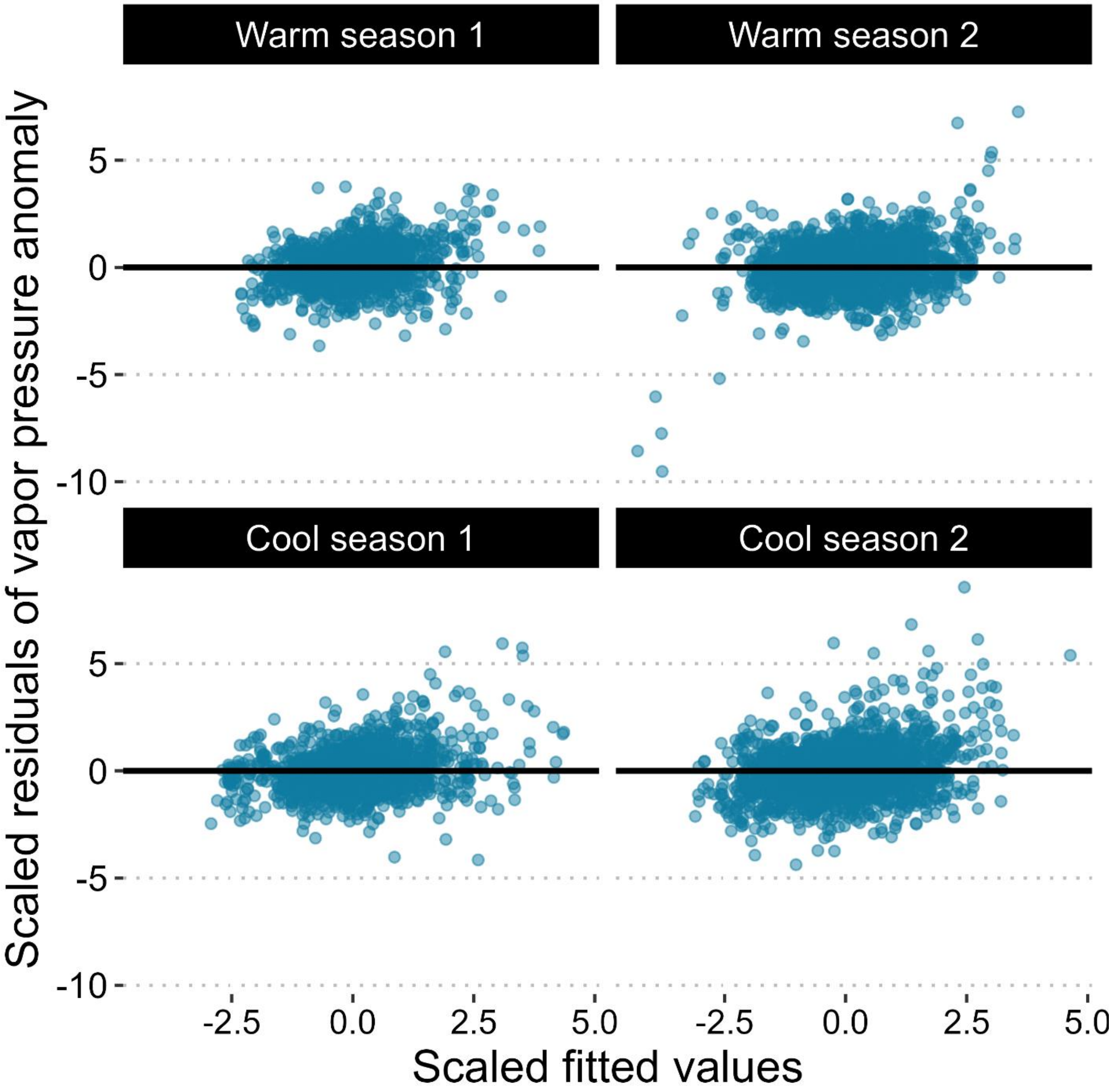


Figure S28. Scatter plots of residual error structure for Random Forests models of microclimate vapor pressure anomaly at four grassland study sites in southern Wisconsin. Residuals and fitted values have been scaled for easy comparison with temperature models (Figure S27).

Literature cited

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Chapter 2: Microclimatic exposure and species life history differences inform climate vulnerability in a grassland songbird community

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Author contributions: J. S. Bernath-Plaisted conceived experimental design, conducted fieldwork, performed analyses, created figures, and wrote manuscript text. C.A. Ribic conceptualized and advised project, and B. Zuckerberg conceptualized and advised project. All authors provided comments on manuscript drafts.

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Abstract

Assessment of species' vulnerability to climate change has been limited by a mismatch between coarse macroclimate data and the fine scales at which species select habitat. Habitat is an important mediator of climate, and fine-scale habitat features may permit species to exploit favorable microclimates, but habitat preferences and life histories of species can also constrain their ability to do so. Few studies have examined how habitat selection and life history can interact to affect microclimatic exposure. We leveraged fine-resolution models of near-surface temperature and humidity in temperate grasslands to understand how microclimates affect climatic exposure and demographics in a declining grassland bird community. We asked: 1) Do species select favorable nest-site microclimates? 2) Do habitat preferences limit the ability of species to access potentially favorable microclimates? 3) What are the demographic consequences of microclimatic exposure? We found limited evidence that grassland birds select beneficial cooler microclimates. Instead, many species appeared constrained by habitat preferences. While facultative generalists displayed flexibility to nest in denser vegetation that

provided thermal buffering, most obligate species were associated with more exposed microclimates. Nesting success in facultative species was not well explained by microclimate variables, but success in specialized grassland obligates declined with elevated microclimate temperatures. These findings suggest that habitat specialists may be more vulnerable to future temperature extremes because of a limited ability to take advantage of favorable microclimates. More broadly, this work illustrates how microclimate and species life history can interact to influence the potential vulnerability of species to climate change.

Significance Statement

Microclimates arise from fine-scale variations in vegetation and topography that create heterogeneity in climate conditions near the Earth's surface. Microclimate data are critical to understanding the vulnerability of species to climate change because they more realistically model conditions species experience in their habitats. We demonstrate that habitat can mediate microclimatic exposure and affect the reproductive success of declining grassland birds with implications for identifying differences in vulnerability among species. Grassland obligate species that nested in sparse vegetation were exposed to hotter and dryer conditions than species with the behavioral flexibility to use denser vegetation such as shrubs. Subsequently, obligate species suffered reduced nesting success in response to elevated microclimate temperatures while more generalist facultative species did not.

Introduction

In an era of climate change, species are increasingly subjected to unprecedented extremes of temperature and precipitation (Cook *et al* 2022, Murali *et al* 2023). Quantifying both current and future exposure of species to climate has therefore become critical to assessing the vulnerability of species (Foden *et al* 2019). Until recently, ecologists have relied on coarse resolution (typically ≥ 1 km^2) macroclimate data to model species-climate relationships (Potter *et al* 2013, Nadeau *et al* 2017). However, these data often do not reflect the climate conditions species experience in the environment or the scales at which they may select habitat (Nadeau *et al* 2017, Hannah *et al* 2014, Maclean and Early 2023). This is because variations in vegetation, topography, and biophysical processes near the Earth's surface create heterogeneity in climate at much finer scales (Bramer *et al* 2018)

Habitat is an important mediator of climate, and species habitat associations may have significant microclimatic consequences (Elmore *et al* 2017, Scheffers *et al* 2014). For example, the dense canopies of old-growth forests have a high capacity to moderate heat and ameliorate species declines in response to high temperatures (Kim *et al* 2022, McGinn *et al* 2023). By contrast, species in open systems may be more vulnerable to temperature extremes due to the absence of such forest canopy (Lauck *et al* 2023, Jarzyna *et al* 2016). Yet, even within open systems, microclimate heterogeneity may allow species to adaptively select habitats that confer thermal benefits and enable them to persist in stressful climate conditions (Hall *et al* 2016, Hovick *et al* 2014). Over longer time scales, such microrefugia can even prevent species extirpations under shifting climate regimes (Suggitt *et al* 2018). However, despite the availability of potentially favorable microclimates, species may also be constrained by life history traits (Riddell *et al* 2021) or competing selective pressures (Tieleman *et al* 2008) that prevent them from accessing microclimatic benefits. Therefore, our understanding of species' vulnerability to climate change could be improved not only by using microclimate data to realistically model exposure, but also a broader understanding of how species select microclimates and the consequences of such selection. Unfortunately, detailed microclimate data remain relatively rare (Brigham and N. Suding 2023), and few studies have examined the linkages between microclimates, selection, life history, and demographic consequences.

In this study, we sought to advance the ecological understanding of microclimates and habitat selection by leveraging a novel dataset consisting of fine-resolution spatiotemporal models of near-surface temperature and humidity in North American temperate grasslands (Bernath-Plaisted *et al* 2023b), and nesting data for a community of grassland songbirds. Grassland birds are among the most steeply declining avian assemblages in North America (Rosenberg *et al* 2019), and their demographics are sensitive to climate and weather—particularly high temperatures and drought conditions (Conrey *et al* 2016, Maresh Nelson *et al* 2023). Grassland birds also display strong interspecific variation in evolved vegetation preferences (Bernath-Plaisted *et al* 2023a, Knopf 1996). In particular, obligate species (e.g., specialist) and facultative species (e.g., more generalist) (Vickery *et al* 1999) may be exposed to different microclimates as a consequence of contrasting vegetation preferences. Facultative species often display greater flexibility to select nest sites in dense vegetation such as shrubs and forb clumps. Consequently, despite co-occurring within the same grassland ecosystems, grassland bird species may differ in microclimate exposure because of variations in habitat selection (Fig. 1).

Selection of the nest site represents a habitat choice with strong consequences for reproductive success in bird species (Chalfoun and Schmidt 2012), and in open grasslands, nest-site microclimate plays an important role in buffering eggs and nestlings from lethal climate conditions (Grisham *et al* 2016). Elevated temperatures can negatively affect nesting success directly through mechanisms such as evaporative water loss (EWL) and hyperthermia, which may cause nestling mortality (McKechnie and Wolf 2019) and egg unviability (Lundblad and Conway 2021). Temperature and humidity may also interact to affect the risk of such mortalities. For example, high temperatures and low humidities may increase rates of EWL, but high temperatures and saturating humidities can impair the dissipation of heat (van Dyk *et al* 2019). Microclimates may also affect success indirectly through behavioral trade-offs. For example, nest sites that are exposed to temperatures above critical thresholds may require adults to spend excessive time thermoregulating the nest at the expense of nestling provisioning—resulting in poor nestling body condition (van de Ven *et al* 2019).

Here, we employed a grassland dataset to address three primary questions exploring the importance of microclimates to breeding birds. 1) Does habitat heterogeneity allow grassland birds to select nest-sites with beneficial microclimates? We hypothesized that, given the sensitivity of grassland birds to elevated temperature and drought, species should select nest sites that reduce exposure to hot and dry conditions relative to random locations. 2) How do species' life histories and habitat preferences affect their ability to select optimal microclimates? If facultative species display greater flexibility to use dense vegetation, we hypothesized that they would receive more buffering from hot and dry conditions than obligate species nesting in sparser cover. 3) What are the consequences of microclimate exposure for species? We hypothesized that if exposure to hot and dry conditions negatively affects the thermoregulation and behavior of nesting birds, success should be lower for nests with greater microclimatic exposure to these conditions. Therefore, we also predicted that obligate species would show greater demographic sensitivity to temperature than facultative species due to differential exposure.

Results

Selection of nest-site microclimates

Comparison of microclimate conditions at nest sites with those at nearby random locations revealed that two shrub-associated species, grassland obligate Dickcissel (*n* = 33) and facultative species Red-winged Blackbird (*n* = 47), selected nest sites that were characterized by cooler temperatures (lower T_{max}) relative to nearby habitat (Fig. 2a; Table S1); Dickcissel also selected more humid sites (higher VP_{min}) relative to random locations (Fig. 2b); other species showed no statistical evidence of nest-site selection in relation to the microclimate variables we modeled (Table S1).

Habitat associations and microclimatic exposure

Though most species did not display evidence of microclimate selection *per se*, variation in habitat associations among species resulted in differing microclimatic exposures (Fig. 3). Species placed their nests, on average, in areas with differing vegetation densities ($F = 35.71$, df = 7, $P < 0.001$; additional nest-site vegetation data can be found in Fig. S1). Ground-nesting obligates like Eastern Meadowlark (*n* = 37) and Grasshopper Sparrow (*n* = 11) placed their nests in sparse vegetation compared to facultative species like Common Yellowthroat (*n* = 21) and Red-winged Blackbird (*n* = 47), as well as the shrub-nesting grassland obligate, Dickcissel (*n* = 33), all of which placed their nests in areas with significantly higher vegetation density (Fig. 4a). These differences in nest-site vegetation had microclimatic consequences. Nest sites within higher vegetation density experienced fewer days of exposure to potentially lethal air temperatures ($\beta = -0.44$, $SE = 0.10$, $P < 0.001$, $R^2 = 0.47$; Fig. 4b, Table S2) and dry conditions ($\beta = -0.38$, $SE = 0.11$, $P = 0.001$, $R^2 = 0.44$; Fig 4c, Table S3). For example, over a 22-day nesting cycle, the average Dickcissel nest with a VOR (Visual Obstruction Reading; e.g. density) of 60 cm would experience ~ 4 fewer days exceeding 39°C than the average Grasshopper Sparrow nest with a VOR of 20 cm. We also found that, on average, nests of grassland obligate species experienced a significantly higher proportion of heat exposure days than facultative species ($W = 5738$, $P = 0.002$). However, there was no difference in proportion of dry exposure days between these groups ($W = 4939$, $P = 0.377$).

Effects of microclimate on nesting success

We found that microclimate exposure at nest sites had reproductive consequences for breeding grassland birds. For grassland obligate species, T_{max} was the top model explaining daily nest survival ($\Delta AIC_c = 2.32$, $W_i = 0.51$; Table S4), and elevated temperatures negatively affected success ($\beta = -0.29$, $LCI = -0.51$, $UCI = -0.06$; Figure 4d). However, for facultative species, VP_{min}, T_{max}, and the null model were all competitive (Table S4), but the only predictor in these models with confidence intervals not overlapping zero was date (Table S5). Thus, we observed no similar effect of T_{max} on nesting success in facultative species.

Discussion

Climate change is an increasingly prevalent threat to animal populations globally (Spooner *et al* 2018). Predicting vulnerability of individual species to climate impacts requires an understanding of both exposure and demographic sensitivity (Foden *et al* 2019). However, the realized exposure of species to climate can be strongly mediated by the habitats they occupy (Kim *et al* 2022, Lauck *et al* 2023, Scheffers *et al* 2014). The habitat associations of species, and their behavioral flexibility to select beneficial microclimates, are likely key determinants in identifying vulnerable (or resilient) species. Here, we demonstrate not only the capacity of microhabitat to moderate exposure to climate in open grasslands, but also that evolved traits of habitat preference constrain which species can benefit from microclimatic heterogeneity.

Grassland birds are considered highly vulnerable to climate change (Wilsey *et al* 2019), both due to demographic sensitivity to climate (Conrey *et al* 2016, Maresh Nelson *et al* 2023, McCauley *et al* 2017), and association with grassland habitats that are often exposed to extremes of heat and drought (Murali *et al* 2023, Smith *et al* 2024). Although grasslands lack the temperature buffering capacity of forests (Lauck *et al* 2023, Jarzyna *et al* 2016, Suggitt *et al* 2011), fine-scale variation in vegetation density and microtopography in grasslands can still create significant thermal diversity (Bernath-Plaisted *et al* 2023b). Theoretically, breeding grassland birds could moderate exposure to hostile climate conditions through the selection of thermally buffered nest sites (Grisham *et al* 2016, Scherr and Chalfoun 2022). However, we found that grassland birds in our study appeared largely unable to access the coolest microclimates available. Out of 8 focal species, only Dickcissel and the facultative species, Red-winged Blackbird, selected nest sites that were significantly cooler than random locations. Both species are often shrub-associated with known preferences for dense vegetation, and it appears likely that—even for these species—cooler nest sites were a consequence of habitat association rather than selection for microclimates *per se.*

Consistent with previous work, nesting success for grassland obligates in our study declined with high ambient temperatures (Conrey *et al* 2016). Given this demographic sensitivity to temperature, adaptive selection theory predicts that grassland birds should have selected thermally buffered nest sites that were ostensibly available to them (Morris 2003). However, there are many ecological and methodological reasons that researchers often fail to detect such adaptive selection in nesting birds (Chalfoun and Schmidt 2012). These range from explanations as simple as small sample sizes to the complexities of life-time reproductive success and carry-over effects to other life-history phases, such as post-fledging survival (Chalfoun and Schmidt 2012). A limitation of our study is that we were not able to explicitly test such alternative hypotheses, but evolved life-histories and competing selective pressures provide a likely explanation for constraints on microclimate selection in nesting grassland birds.

Predation is typically the largest source of nest mortality in breeding birds, particularly in grassland and shrubland habitats, and thus predation risk is a strong selective force shaping avian life histories (Martin 1993). Grassland bird communities are characterized by distinct preferences for microhabitat structure, and individual species are often restricted to a narrow range of vegetation densities (Bernath-Plaisted *et al* 2023a, Knopf 1996, Wiens 1969). These preferences likely evolved under selective pressure both to reduce interspecific competition for nest sites and to escape predation risk by reducing nest density and diversifying the search image of nest locations (Martin 1988, Wiens 1969). Therefore, grassland birds may be constrained in microclimate selection either by perceived predation risk (e.g., nesting in sparse habitat may increase predator detection, but also exposure to heat and dry) (Tieleman *et al* 2008, Martin 2001), or habitat preferences shaped by selective pressures throughout their evolutionary histories (e.g., niche segregation, density effects, etc.) (Martin 1988). Regardless of mechanism, grassland obligate birds with strong preferences for relatively sparse vegetation cover appear to lack the behavioral flexibility to access cooler microclimates found in denser vegetation within the same grassland areas. There were clear microclimatic consequences associated with these habitat preferences, and high vegetation density at nest sites consistently reduced exposure to hot and dry conditions. As a result, nests of facultative species were exposed to significantly fewer days exceeding potentially lethal air temperatures than those of obligate species. This finding has implications for understanding interspecific differences in vulnerability to climate change and suggests that ground-nesting grassland obligates may be more threatened by future climate extremes than shrub-associated and facultative species.

Microclimates and microrefugia play an important ecological role in mediating the effects of climate change on animal species (Kim *et al* 2022, Suggitt *et al* 2018, Brigham and N. Suding 2023, McGinn *et al* 2023), and understanding how they influence species' habitat use and demographics can better inform our understanding of vulnerability (Neel *et al* 2021). Our results are significant not only because they demonstrate how microclimates can influence exposure and demographics even in open systems, but also because they highlight how species responses to microclimate may be individualistic and contingent on evolved life history. As the ecological relevance of microclimates has increasingly been recognized, maintaining thermal heterogeneity across landscapes has also emerged as a new climate adaptation strategy (Elmore *et al* 2017, Hovick *et al* 2014, Carroll *et al* 2016). While this is an important goal and one that may help to support biodiversity under climate change, it is also important to realize that not all species will benefit equally. Specialist species with inflexible habitat preferences may be constrained in their ability to benefit from thermal diversity, and such species will require alternative management strategies for conservation in a changing climate.

Materials and Methods

Study sites

We collected data 10 May – 10 August, 2020-2022 at 4 planted grasslands in southern Wisconsin, USA (~ 42° 55′ 11.45″, −89° 50′ 5.91″). Two of the 4 sites were dominated by a cool-season grass species, Smooth Brome (*Bromus inermis*), while the remaining sites were tallgrass prairie restorations planted with a diversity of native grasses and forbs. Both grassland types are commonly occupied by grassland birds in the midwestern United States (Jaster *et al* 2014, Byers *et al* 2017). Our sites were in Wisconsin's Driftless area—a region characterized by unglaciated rolling topography and diverse land cover including agriculture, forest, planted grassland, and prairie remnant. During the months of April-August of the study years, daily mean temperatures varied from -1.6 – 30 °C, and daily cumulative precipitation ranged from 0.0 – 5.5. cm (Fig. S2). Grassland sites ranged in size from 8.7-11.0 ha and were subject to management activities such as burning and spot mowing for invasive species at regular intervals. However, no burns were conducted at our sites during the study years, and all sites were ungrazed.

Study species

The most abundant grassland songbirds nesting at our sites included 5 obligate species: Bobolink (*Dolichonyx oryzivorus*), Dickcissel (*Spiza americana*), Eastern Meadowlark (*Sturnella magna*), Grasshopper Sparrow (*Ammodramus savannarum*), and Henslow's Sparrow (*Centronyx henslowii*), as well as 3 facultative species: Common Yellowthroat (*Geothlypis trichas*), Field Sparrow (*Spizella pusilla*), and Red-winged Blackbird (*Agelaius phoeniceus*). These species are all migratory and returned to our study region in April and May. Distributions of nest initiation dates by species for all nests monitored in our study are available in Fig. S3.

The habitat associations and nesting habits of our obligate and facultative focal species have been well described in Wisconsin (SI Appendix). Broadly, the grassland obligates in our study are ground-nesting species that select nest sites located in shallow ground depressions beneath small grass overhangs. Dickcissel is an important exception to this profile and typically builds nests above the ground in small shrubs, forbs, or dense grass clumps, and its nesting habits are like facultative species in this respect. The facultative species in our study were all observed to use a diversity of nest sites including shrubs, large and small forbs, grass clumps, and in the case of Red-winged Blackbird, even small trees. However, to ensure that our microclimate measurements were relevant, we only monitored nests located < 1 m from the ground.

Microclimate data

The microclimate product we used in the analyses described below is an application of recently developed spatiotemporal Random Forests models of near-surface grassland microclimate (Bernath-Plaisted *et al* 2023b). In short, these models were produced using hourly temperature and humidity observations from iButtons deployed systematically across study sites. These data were paired with UAS-collected (unpiloted aircraft systems, e.g., drones) LiDAR (light detection and ranging), and multi-spectral imagery of sites that were used to create spatial predictors of microclimate. These included canopy height, NDVI (normalized difference vegetation index), distance to wooded edge, elevation, topographic positioning, slope, aspect, and hill shade. Mesoclimate and weather data were also included as predictors in the models so that, for any day of the season and at any location within our study sites, an estimate of near-surface microclimate could be generated at a 60-cm resolution. For the present study, we used the model to produce estimates of daily maximum air temperatures (T_{max}) and daily minimum vapor pressures (VP_{min}) to capture extremes that might affect grassland birds. The two models had cross-validated accuracies of < 2 °C and < 0.10 kPa, respectively. We explored the possibility of using indices that included both temperature and humidity, such as wet-bulb temperature (WBT) and vapor pressure deficit (VPD), but in our data set, we found them to be highly correlated with air temperature, as well as each other. Thus, we chose to use air temperature and humidity individually for more parsimonious and orthogonal predictors that would still allow us to model interactions. Additional methodological details pertaining to microclimate models are available in SI Appendix.

Nesting data

Each year, we searched for nests daily from 15 May to 15 July. To locate nests, we searched sites once a week either by dragging a sisal rope through the grass to flush nesting birds, or later in the season when vegetation became too dense, walking sites systematically (Jaster *et al* 2014, Byers *et al* 2017). In addition to systematic searching, we located nests behaviorally by observing adults carrying nesting material and food (Jaster *et al* 2014). Finally, we found nests opportunistically while conducting other research activities. Once located, we marked nests non-invasively with survey flagging placed 5 m to the north and south of the nest. We monitored nests at 2–5-day intervals (typically 3) and recorded nest contents and activity at each visit. Nests were defined as successful if they fledged at least 1 young and failed if they did not and we followed common practices (Byers *et al* 2017) to determine nest fates (details are found in SI Appendix). We also calculated initiation date for each nest; in cases where initiation date was not known, dates were imputed using clutch size, incubation lengths, and known activity periods (details are found in SI Appendix).

We made typical grassland vegetation measurements at each nest within 1 week of termination. These included visual obstruction reading (VOR) in four cardinal directions using a Robel pole, percent cover of grass, forbs, shrubs, and bare ground using a Daubenmire frame, and vegetation height and litter depth measured at each corner of the frame using a Robel pole marked with centimeter gradations on one end. Following vegetation surveys, we used a sub-meter accuracy GPS unit (Trimble Geospatial, CA, USA) to measure each nest location within < 5 cm to ensure that we could accurately sample UAS imagery for nest locations.

Data analysis

All analyses were performed in Program R (R Core Team 2023). We scaled continuous predictors in our multivariate regression analyses and all correlations were < 0.7. For all tests of significance throughout our analyses, we used an alpha threshold of < 0.05. To assess the effect of microclimate on nest-site selection in grassland birds, we used conditional logistic regression implemented in the *survival* package (Therneau 2023). This allowed us to group nests and random points into strata such that each nest was matched with 5 unique random points. We sampled Random points within 50 m of matched nests to represent locations that were realistically accessible to each nesting pair. For each nest strata, we estimated T_{max} and VP_{min} using the spatial models described above for 7 days prior to the estimated initiation date (Scherr and Chalfoun 2022) and averaged these estimates to represent microclimate conditions during the week in which selection likely occurred. Nest-construction time in grassland birds can vary among species, by individual, and by time of season but we typically observed birds completing nests within 3-4 days during our study. Therefore, in averaging conditions for a full week prior to initiation, we accounted for the period in which pairs may have been prospecting for nest sites. For each species, we constructed univariate conditional logistic regression models comparing both T_{max} and VP_{min} at nest sites with the random points in each nest's respective strata. We chose to construct univariate models to avoid over-parameterizing models given small sample sizes for several species (Table S6).

To explore how differences in species habitat associations might influence their subsequent exposure to microclimate, we first compared mean nest-site VOR among species using a single-factor ANOVA for unequal variances with a Games-Howell test corrected for multiple comparisons. Second, to determine if vegetation conditions at the nest site can moderate exposure to high temperatures and dry conditions, we used the *gamlss* package (Rigby and Stasinopoulos 2005) to perform a zero-inflated beta regression (for details see SI Appendix) relating nest-site VOR to the proportion of active days for which each nest experienced $T_{max} > 39$ °C and $VP_{min} < 0.915$ kPa. We used these calculations as metrics of heat and dry exposure for each nest. We chose our temperature threshold because air temperatures beyond 39 °C can be increasingly lethal for eggs, nestlings, and even adult birds (McKechnie and Wolf 2019, Scherr and Chalfoun 2022). For vapor pressure, we could find no similar justification for a threshold in the literature, so we used the 20th percentile of all nest-site vapor pressure estimates as the upper cutoff to characterize the driest conditions that nests were exposed to during our study. In addition to the predictor of interest, VOR, we included study year and nest initiation date in models to account for temporal effects that would also influence broad exposure to temperature and humidity. For VOR and initiation date, we tested models with both quadratic and linear terms to account for the possibility of non-linear relationships. If quadratic terms were significant, we included them in models. Finally, to compare exposure to microclimate conditions between nests of obligate and facultative species, we also performed a Wilcoxon sum-rank test comparing heat exposure and dry exposure (as we define them above) between the two groups.

We used logistic exposure (Shaffer 2004) to examine the effects of microclimate on nesting success. Logistic exposure is a modified form of logistic regression that uses a custom link function to account for the length of exposure interval in modeling daily survival rate (DSR) (Shaffer 2004). We first conducted a preliminary analysis to determine if species' body mass interacted with air temperature to affect nesting success. Body size plays an important role in thermal regulation (McKechnie and Wolf 2019) and is often tested for in microclimate studies (Scherr and Chalfoun 2022). Our focal species ranged in average body masses from 10 g (Common Yellowthroat) to 92 g (Eastern Meadowlark). However, we found there was no significant interaction between T_{max} and body mass ($P = 0.314$), so we did not include body mass in subsequent analyses. We analyzed obligate and facultative species in separate models to determine if they responded differently to microclimate conditions, and we tested both time-specific and cumulative effects of microclimate, as well as the interaction between temperature and humidity, which can influence hyperthermia and EWL rates (van Dyk *et al* 2019). For each species group, we parameterized 7 models:

1) T_{max} + Date + Year (Daily temperature model)
2) VP_{min} + Date + Year (Daily vapor pressure model)
3) T_{max} X VP_{min} + Date + Year (Daily interactive model)
4) EXP_T + Date + Year (Cumulative temperature exposure model)
5) EXP_VP + Year (Cumulative dry exposure model)
6) EXP_T X EXP_VP + Year (Cumulative interactive exposure model)
7) Visit date + Year (null model)

We were not able to include dry exposure (EXP_VP) and visit date in the same models because they were correlated. We compared models using AIC_c model selection and selected the model with the lowest AIC_c score and considered models to be competitive for $\Delta AIC_c < 2.00$ (Burnham and Anderson 2002). We considered parameters to be informative *only* if 90%

confidence intervals did not overlap zero (Arnold 2010) *and* the model containing the parameter of interest occurred in the top model set (Burnham and Anderson 2002).

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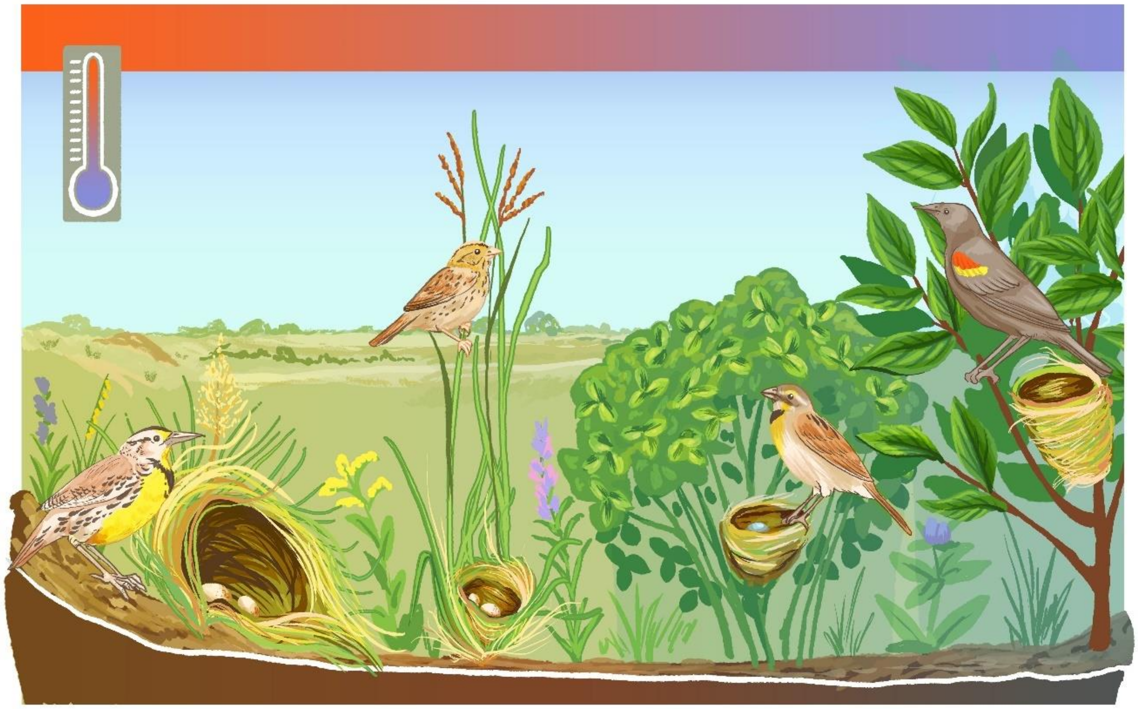

Figure 1. Conceptual figure showing hypothesized influence of species nesting habitat-associations on microclimate temperature exposure. For example, ground-nesting grassland obligates, such as Eastern Meadowlark (far left), and Henslow's Sparrow (center left) may be exposed to warmer nest-site temperatures while shrub-nesting species, such as Dickcissel (center right) and Red-winged Blackbird (far right), may benefit from cooler temperatures associated with dense vegetation. Artwork by L Kozik.

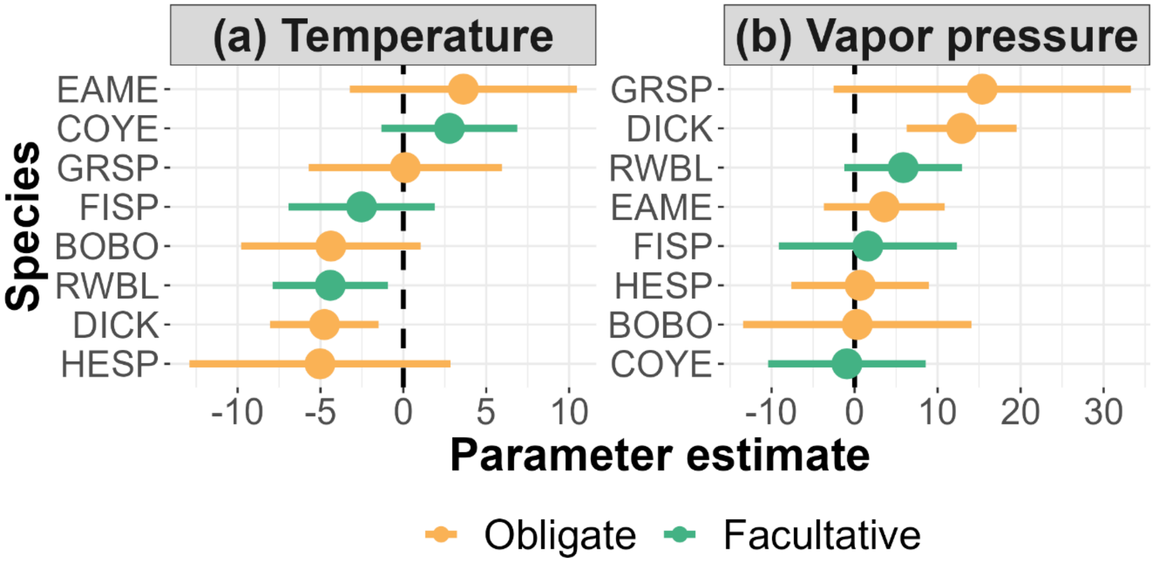

Figure 2. The effects of microclimate conditions on nest-site selection for a community of obligate and facultative grassland birds breeding in southern Wisconsin. Only Dickcissel (DICK) and Red-winged Blackbird (RWBL) showed evidence of selection for cooler microclimates relative to random locations **(a)**, and only Dickcissel responded to nest-site humidity and appeared to avoid dryer conditions **(b)**. Error bars denote 95% confidence intervals for $P < 0.05$. Species codes and sample sizes: Red-winged Blackbird (RWBL) = 47, Eastern Meadowlark (EAME) = 37, Dickcissel (DICK) = 33, Common Yellowthroat (COYE) = 21, Bobolink (BOBO) = 17, Henslow's Sparrow (HESP) = 17, Field Sparrow (FISP) = 12, Grasshopper Sparrow (GRSP) = 11.

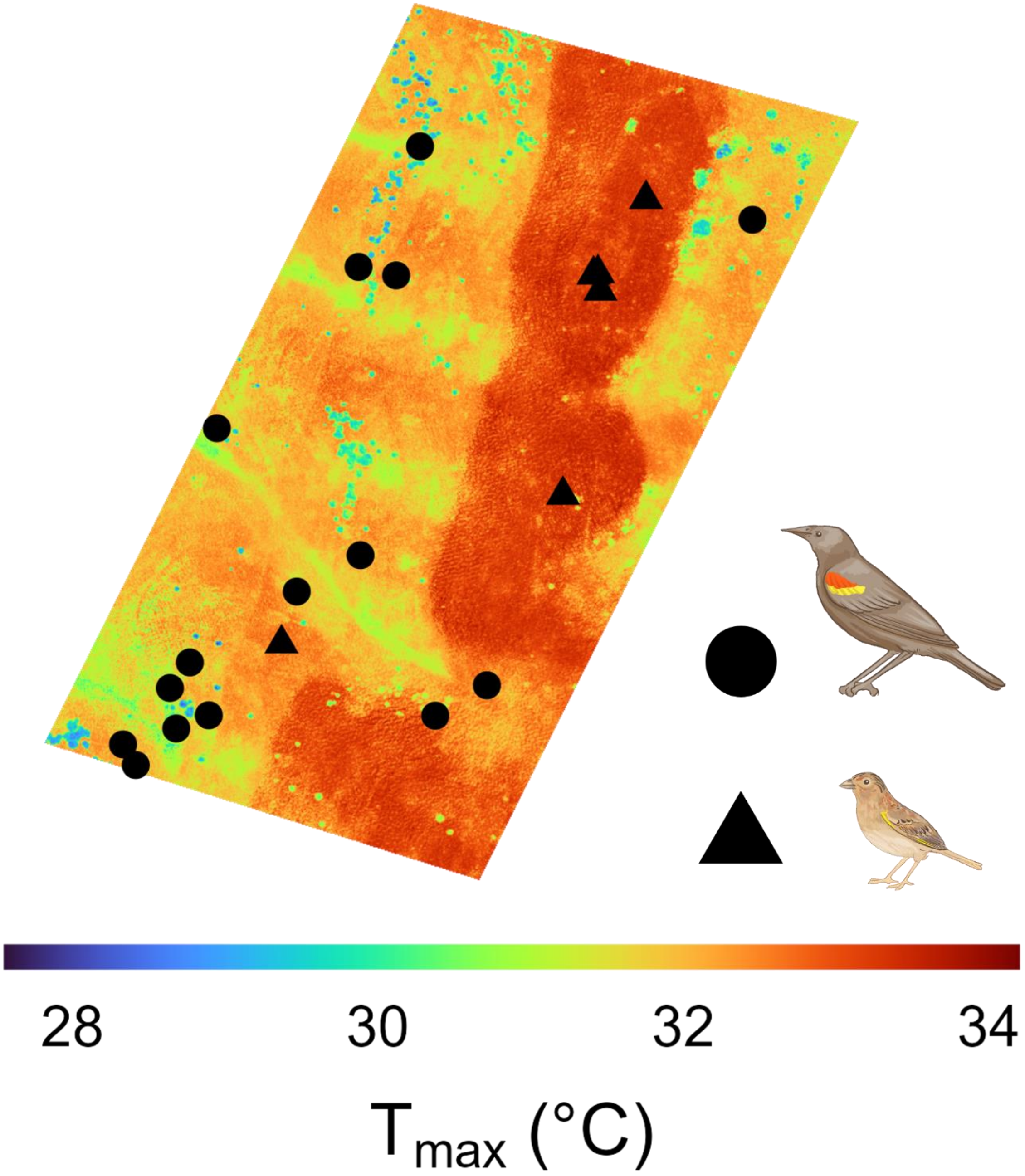

Figure 3. Grassland bird exposure to high temperatures can be influenced by habitat preferences. This map depicts the locations of Red-winged Blackbird nests (circles) and Grasshopper Sparrow nests (triangles) overlaid with 60-cm resolution microclimate predictions of daily maximum temperatures averaged across all days and years of the study for one of four study sites. Red-winged Blackbirds tended to nest in locations that provide thermal buffering, such as dense drainages and small shrubs, while Grasshopper Sparrows nested in exposed locations such as hilltops and short grass patches.

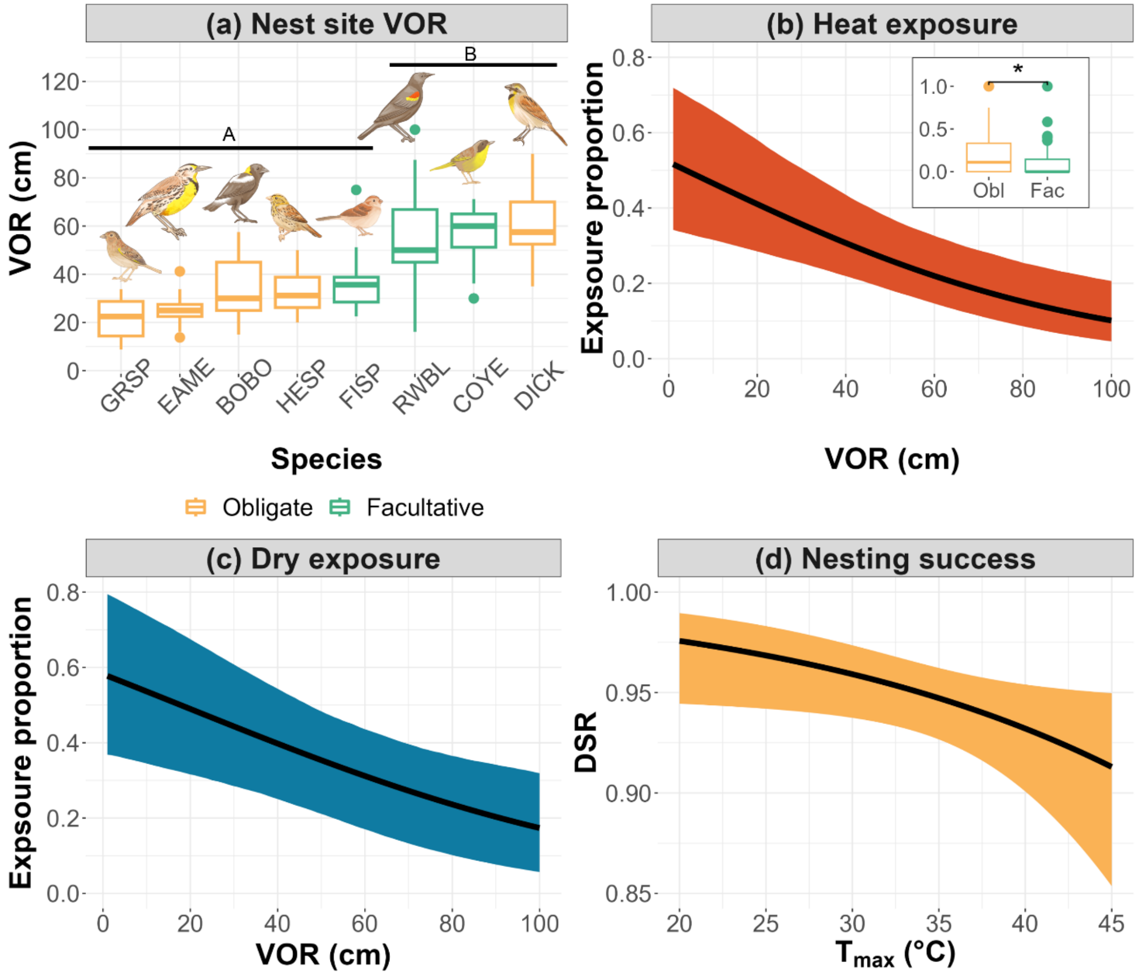

Figure 4. Grassland birds nest along a gradient of vegetation density that influences exposure to extremes of heat and dry. This microclimatic exposure to high temperatures can reduce nesting success, particularly for ground-nesting grassland obligates that use more exposed locations. Facultative and shrub/forb nesting species nested in locations with significantly ($P < 0.05$) higher vegetation density (VOR) than ground-nesting obligate species **(a)**. High vegetation densities subsequently reduced the proportion of days nests were exposed to high temperatures and facultative nest sites were significantly ($P = 0.002$) less exposed to heat than those of obligates **(b)**. Similarly, vegetation density also reduced exposure to drier conditions **(c)**. Daily nest survival (DSR) of grassland obligates declined with elevated daily maximum temperatures **(d)**. Shading denotes 95% confidence intervals around predictions.

Chapter 2: Supplemental Materials

Supporting information text

Study species

Obligate species. Bobolink is associated with mesic grassland and hayfields preferring vegetation heights of 15-35 cm, medium litter depths, and low to no cover of woody vegetation (Sample and Mossman 1997). Bobolink is an open-cup ground nester and selects nest sites with high concealment in grass and greater vegetation height relative to surroundings (Renfrew *et al* 2020). Dickcissel is also associated with vegetation heights of 15-35 cm and medium litter depths, but the species prefers a high ratio of forbs and the presence of some woody vegetation (Sample and Mossman 1997). Dickcissel is also an open-cup nester, but nests are typically placed above the ground and positioned in a dense vegetation clump, forb, or low woody plant (Sousa *et al* 2022). Eastern Meadowlark is found in a wide variety of grassland habitats with vegetation heights ranging from 10-35 cm in Wisconsin, high litter depths, and scattered trees and shrubs (Sample and Mossman 1997). The species constructs domed nests positioned in shallow ground depressions and typically selects nest sites with deeper litter than nearby locations (Jaster *et al* 2022). Grasshopper Sparrow is also widespread in Wisconsin grasslands and prefers shorter vegetation structure (5-20 cm) in Wisconsin with some bare ground cover, medium litter depth, and little to no woody vegetation (Sample and Mossman 1997). Grasshopper Sparrow nests are characterized by high concealment in small depressions or grass overhangs on the ground, and tunneled entrances (Vickery 2020). Henslow’s Sparrow is associated with relatively dense grassland vegetation (15-35 cm or sometimes greater), high litter depth, and low woody plant cover—though some shrub occurrence is tolerated (Sample and Mossman 1997). Henslow’s Sparrow nests may be placed directly on the ground in areas of high litter depth, at the base of small grass clumps, or several centimeters above the surface between grass stems (Herkert *et al* 2020).

Facultative species. Common Yellowthroat is found in a wide range of wetland, grassland, and secondary-growth habitats (Guzy and Ritchison 2020). In Wisconsin, Common Yellowthroat prefers mesic grasslands with tall and dense vegetation, and a shrub component (Sample and Mossman 1997). The species constructs open-cup nests which are generally < 10 cm above the ground and placed in grasses, reeds, forbs, and small shrubs (Guzy and Ritchison 2020). Field Sparrow is found in many open habitats and in Wisconsin it is associated with upland grasslands, mixed-shrub habitat, and woody edges (Sample and Mossman 1997). Field Sparrow constructs open-cup nests that may be placed in grass clumps, at the base of shrubs and forbs, or higher up in woody vegetation (Carey *et al* 2020). Finally, Red-winged Blackbird is an open habitat generalist found in many grassland and wetland areas (Yasukawa and Searcy 2020). It prefers taller and denser vegetation relative to most grassland bird species in Wisconsin (Sample and Mossman 1997). Red-winged Blackbird nests are open cup, and nest sites are extremely variable and may include grass clumps and reeds, forbs and shrubs, and small trees with the height of nests ranging widely (Yasukawa and Searcy 2020).

Modeling grassland microclimates

To model grassland microclimate for use in our grassland bird analyses, we applied previously developed and published grassland microclimate models (Bernath-Plaisted *et al* 2023). Here, we provide a summary of those methods intended to help readers understand and evaluate the application of models in the present study. For detailed methods on these microclimate models, readers should consult the original publication (Bernath-Plaisted *et al* 2023). Our models used 3 inputs to generate microclimate predictions:

1) Summaries of near-surface climate data collected by iButtons deployed systematically across grassland study sites at a 5-cm height in solar-shielded capsules from 15 May to 30 July 2020-22. These iButtons logged hourly measurements of temperature and relative humidity at locations spanning the range of environmental conditions at our study sites. For each iButton location, we extracted data and used temperature and relative humidity to calculate daily maximum temperature (T_{max}) and minimum vapor pressure deficit (VP_{min} using Teton's formula) to input as microclimate response variables.
2) UAS-collected LiDAR (flown once per season) and multispectral imagery (flown 3 times per season). These data were used to derive spatial environmental predictors of microclimate at a 60-cm resolution. Predictors included CHM (canopy height model), NDVI (normalized difference vegetation index), distance to wooded edge, DTM (digital terrain model), TPI (topographic positioning index), slope, aspect, and hill shade. For each iButton location and date, we extracted UAS predictors from the most recent flight at that site to ensure that vegetation predictors were as accurate as possible.
3) To account for the influence of broader climate conditions on microclimate estimates, we also incorporated gridded mesoclimate weather data at each site for each day of the study period. Mesoclimate variables at 2-km resolution included daily temperature, solar irradiance, precipitable water, and windspeed. These data were sourced from Solcast (www.solcast.com) and accessed via the company's free data program for researchers and students. We chose to use Solcast data in the place of Daymet, as used in the original publication because Daymet data were not yet available for all years of the study.

We used these 3 datasets to train Random Forest models of near-surface daily T_{max} and VP_{min} at each of our grassland study sites. Random Forests is a machine learning technique that excels at prediction and is capable of handling high dimensional data, interactions, and correlation (Breiman 2001, James *et al* 2013). To assess model accuracy, we performed *k*-fold cross-validation and calculated root mean squared error (*RMSE*) using iButton observations that were withheld during training. For the T_{max} model, RMSE = 1.79 °C and $R^2 = 0.94$; for the VP_{min} model, RMSE = 0.07 kPa and $R^2 = 0.97$. For each study site, on any day of the season, we were able to generate a raster of T_{max} and VP_{min} conditions at 60-cm resolution from which we could extract pixels for any nest or random location. For nests that were initiated prior to our data collection, we were able to generate microclimate predictions by assuming that environmental conditions from the first UAS flights in early May, which were conducted before most greening occurred, were representative of April conditions.

Assigning nest fates

Video surveillance studies have demonstrated that assigning nest fates based only on physical evidence found at the nest site can be challenging (Pietz and Granfors 2000, Burhans *et al* 2002). For example, some nest predators may leave the nest undisturbed (Pietz *et al* 2012). Therefore, we followed best practices to establish clear criteria for assigning nest fates and used all evidence available to us (Manolis *et al* 2000). We considered nests successful based on a combination of last known nestling age, observation of parents and feeding behavior, and visual detection of fledglings. We considered nests to have failed if there was physical evidence of predation or mortality (eggshell fragments, dead nestlings, damaged nests) or a lack of any parental activity at the nest near fledging age. In cases where evidence was ambiguous, we truncated observations to last known date of activity to avoid introducing uncertainty into data (Manolis *et al* 2000).

Imputing missing initiation dates

To accurately estimate spatiotemporal microclimate conditions for use in our nest-site selection analysis, it was necessary to estimate nest initiation date for each nest (to estimate microclimate conditions the week prior to nest initiation). For many nests, this was either known from finding the nest during the building or laying stage, or back dating based on hatch date and nestling ages. However, nest initiation date was unknown for ~25% of nests. This occurred primarily when a nest was found after the laying stage (i.e., during incubation) but failed before hatching.

Following Cox et al. 2012 (Cox *et al* 2012), to avoid removing these nests from our analysis, we estimated initiation dates using 3 pieces of information: 1) the length of time we observed a nest, 2) known incubation period of the species (12 days for most of our focal species), 3) apparent clutch size of the nest. For example, if a nest was observed to be active for 6 days, the incubation period of the species was known to be 12 days, and there were 3 eggs in the nest during the time we observed it, we used the following procedure to estimate initiation. First, we subtracted the length of the known activity period from the total incubation period: $12 - 6 = 6$. That is, given that we had observed the nest in incubation for at least 6 days, there could have been no more than 6 days remaining until the nest would have hatched. Second, because there was no way to know exactly how far into incubation the nest was when found, we performed a random draw across the range of remaining possibilities after accounting for known activity length (e.g., 1 to 6 days here). For this example. suppose we drew 3. Finally, we added the apparent clutch-size – 1 day (assuming 1 egg laid per day with incubation beginning with the last egg) to our random draw: $3 + 3 - 1 = 5$. Thus, we would impute initiation date as occurring 5 days prior to the day the nest was found in this example.

Zero-inflated beta regression models

Zero-inflated beta regression was a suitable choice for our analysis because our response variable was proportional (Douma and Weedon 2019), but it also contained a high frequency of zeros (> 20%) (Zurr and Leno 2018). The *gamlss* package allows fitting of a zero-inflated beta regression modeled using a three-parameter distribution (Rigby and Stasinopoulos 2005). The first two parameters determine the location, e.g., the primary relationship with predictors (Mu link, a logit function), and shape of the distribution (Sigma link function, a log function) while the third can model zeros as a separate process (Nu link, a logit function). Although the latter two parameters were not of direct interest to us from an inference perspective, accounting for them in the model improved our ability to model the relationships of interest and overall model performance. In the *gamlss* package, predictors for each of these parameters can be specified as formulae in separate arguments. In our case, we used the same predictors to model each parameter. Ecologically, we wanted to model zeros as a separate process because they were more likely to be determined by broader temporal effects than VOR. For example, a nest that was never exposed to hot macroclimate conditions would always have zero exposure days to high maximum temperatures at the microclimate scale regardless of nest-site vegetation. The *gamlss* package does not produce standard error estimates for predicted values when new data are provided (Rigby and Stasinopoulos 2005), therefore we boot-strapped 95% confidence intervals with 3000 iterations to estimate uncertainty in predictions.

Table S1. Model results for univariate conditional logistic regression assessing the effect of maximum temperatures and minimum vapor pressures on nest-site selection at the microclimate scale for 8 grassland bird species breeding in southern Wisconsin, USA, 2020-2022. The concordance statistic describes the area under the curve (AUC) characterizing a model's sensitivity and specificity. A concordance value of 1 indicates perfect model classification. Significant models ($P < 0.05$) are denoted with an asterisk*. Species codes and sample sizes: Red-winged Blackbird (RWBL) = 47, Eastern Meadowlark (EAME) = 37, Dickcissel (DICK) = 33, Common Yellowthroat (COYE) = 21, Bobolink (BOBO) = 17, Henslow's Sparrow (HESP) = 17, Field Sparrow (FISP) = 12, Grasshopper Sparrow (GRSP) = 11.

Species	**Model**	***β***	***SE***	***P*-value**	**Concordance**
BOBO	T_{max}	*-5.03*	*4.02*	0.211	0.58
	VP_{min}	*0.67*	*4.23*	0.875	0.53
COYE	T_{max}	*2.78*	*2.09*	0.184	0.57
	VP_{min}	*-0.92*	*4.84*	0.849	0.49
DICK	T_{max}*	*-4.76*	*1.67*	0.004	0.64
	VP_{min}*	*12.89*	*3.78*	<0.001	0.73
EAME	T_{max}	*3.62*	*3.49*	0.300	0.59
	VP_{min}	*3.57*	*3.71*	0.336	0.59
FISP	T_{max}	*-2.52*	*2.25*	0.262	0.60
	VP_{min}	*1.59*	*5.47*	0.770	0.57
GRSP	T_{max}	*0.12*	*2.97*	0.968	0.53
	VP_{min}	*15.37*	*9.13*	0.092	0.76
HESP	T_{max}	*-4.37*	2.76	0.114	0.60
	VP_{min}	*0.32*	1.38	0.964	0.51
RWBL	T_{max}*	*-4.41*	*1.78*	0.013	0.64
	VP_{min}	*5.86*	*3.62*	0.105	0.61

Table S2. Model results for a zero-inflated beta regression fitting the relationship between the proportion of active days a nest was exposed to microclimate temperatures > 39° C and nest-site VOR, nest initiation date, and study year for a community of grassland birds breeding in southern Wisconsin, USA, 2020-2022. Separate parameter estimates are provided for each of three model functions: 1) a *Mu* link on the logit scale modeling the distribution location/center (e.g., predictor relationship), 2) a *Sigma* link on the log scale modeling the distribution shape (e.g., spread), and 3) a *Nu* link on the logit scale modeling occurrence of zeros (e.g., the zero-inflated process).

Predictor	***β***	***SE***	***t*-value**	***P*-value**
Mu link				
VOR	-0.44	0.10	-4.28	< 0.001
Initiation date	2.85	0.87	3.27	0.001
Initiation date^2	2.34	0.89	-2.62	0.009
Year (2021)	0.95	0.18	5.21	0.000
Year (2022)	0.49	0.27	1.81	0.072
Sigma link				
VOR	0.01	0.01	1.39	0.164
Initiation date	-0.21	0.07	-2.89	0.004
Initiation date^2	0.00	0.00	2.35	0.020
Year (2021)	-0.91	0.39	-2.36	0.019
Year (2022)	-0.98	0.50	-1.97	0.051
Nu link				
VOR	0.02	0.01	1.56	0.121
Initiation date	-0.34	0.09	-3.95	< 0.001
Initiation date^2	0.00	0.00	3.56	< 0.001
Year (2021)	-0.25	0.47	-0.54	0.588
Year (2022)	1.62	0.49	3.31	0.001

Table S3. Model results for a zero-inflated beta regression fitting the relationship between the proportion of active days a nest was exposed to microclimate vapor pressure below the 20th percentile and nest-site VOR, nest initiation date, and study year for a community of grassland birds breeding in southern Wisconsin, USA, 2020-2022. Separate parameter estimates are provided for each of three model functions: 1) a *Mu* link on the logit scale modeling the distribution location/center (e.g., predictor relationship), 2) a *Sigma* link on the log scale modeling the distribution shape (e.g., spread), and 3) a *Nu* link on the logit scale modeling occurrence of zeros (e.g., the zero-inflated process).

Predictor	***β***	***SE***	***t*-value**	***P*-value**
Mu link				
VOR	-0.38	0.11	-3.59	< 0.001
Initiation date	3.96	0.81	4.87	< 0.001
Initiation date^2	-3.63	0.81	-4.47	< 0.001
Year (2021)	0.96	0.19	4.93	< 0.001
Year (2022)	1.41	0.31	4.49	< 0.001
Sigma link				
VOR	0.05	0.16	0.32	0.751
Initiation date	-4.47	1.28	-3.49	0.001
Initiation date^2	3.79	1.14	3.32	0.001
Year (2021)	-0.91	0.39	-2.28	0.023
Year (2022)	-2.62	0.42	-6.27	< 0.001
Nu link				
VOR	0.31	0.21	1.52	0.130
Initiation date	-5.88	1.46	-4.02	< 0.001
Initiation date^2	5.15	1.40	3.66	< 0.001
Year (2021)	-0.27	0.46	-0.58	0.566
Year (2022)	1.44	0.48	2.99	0.003

Table S4. AIC Model selection results for logistic exposure models assessing the effects of microclimate on daily nest survival for a community of obligate and facultative grassland songbirds breeding in southern Wisconsin, USA, 2020-2022. Sample sizes: obligate = 115; facultative = 80.

Model	**K**	**LogLik**	**AIC$_c$**	**ΔAIC$_c$**	**W$_i$**
Obligate					
T_{max} + Date + Year	5	-191.24	392.6	0.00	0.51
T_{max} X VP_{min} + Date + Year	7	-190.34	394.9	2.32	0.16
Date + Year (Null model)	4	-193.49	395.1	2.46	0.15
Exp_T + Date + Year	5	-192.88	395.9	3.28	0.09
VP_{min} + Date + Year	5	-193.21	396.6	3.95	0.07
Exp_T X Exp_VP + Year	6	-194.16	400.5	7.91	0.01
Exp_VP + Year	4	-196.43	400.9	8.33	0.01
Facultative					
VP_{min} + Date + Year	5	-143.73	297.7	0.00	0.32
Date + Year (Null model)	4	-145.07	298.3	0.62	0.23
T_{max} + Date + Year	5	-144.49	299.2	1.52	0.15
T_{max} X VP_{min} + Date + Year	7	-142.59	299.6	1.92	0.12
Exp_T + Date + Year	5	-145.04	300.3	2.63	0.09
Exp_T * Exp_VP + Year	6	-144.16	300.6	2.95	0.08
Exp_VP + Year	4	-147.38	302.9	5.24	0.03

Table S5. Parameter estimates for variables appearing in the top model set (ΔAICc < 2) for logistic exposure models assessing the influence of microclimate on daily nest survival for a community of obligate and facultative grassland songbirds breeding in southern Wisconsin, USA, 2020-2022. Sample sizes: obligates = 115; facultative = 80.

Predictor	β	**LCI**	**UCI**	**z-value**	***P*-value**
Obligate					
T_{max}	-0.29	-0.51	-0.06	-2.09	0.036
Date	-0.22	-0.42	-0.03	-1.87	0.063
Year (2021)	-0.18	-0.79	0.38	-0.50	0.615
Year (2022)	-0.87	-1.51	-0.26	-2.29	0.022
Facultative					
T_{max}	-0.16	-0.42	0.08	-1.08	0.281
VP_{min}	0.26	-0.01	0.52	1.59	0.110
Date	-0.45	-0.68	-0.23	-3.17	0.001
Year (2021)	0.20	-0.55	0.89	0.46	0.645
Year (2022)	0.19	-0.55	0.88	0.46	0.649

Table S6. Species sample sizes for nests of obligate and facultative grassland songbirds located and monitored in southern Wisconsin, USA, 2020-2022.

Species	**Notation**	**Group**	**Nests**
Red-winged Blackbird	RWBL	Facultative	47
Eastern Meadowlark	EAME	Obligate	37
Dickcissel	DICK	Obligate	33
Common Yellowthroat	COYE	Facultative	21
Bobolink	BOBO	Obligate	17
Henslow’s Sparrow	HESP	Obligate	17
Field Sparrow	FISP	Facultative	12
Grasshopper Sparrow	GRSP	Obligate	11
All obligate	-	-	115
All facultative	-	-	80

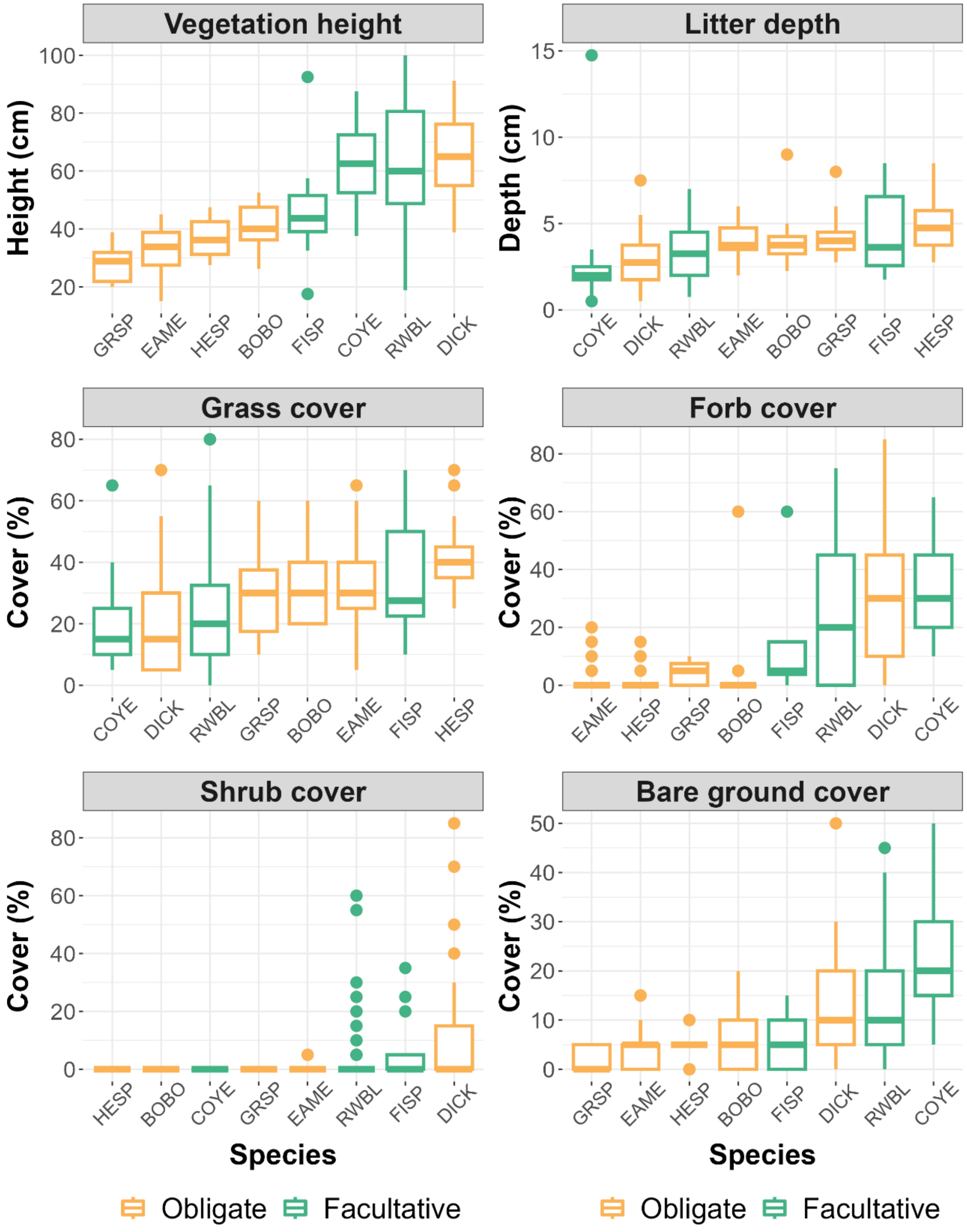

Figure S1. Comparison of nest-site vegetation measurements among 8 species of grassland songbird species breeding in southern Wisconsin, USA, 2020-2022. Species codes and sample sizes: Red-winged Blackbird (RWBL) = 47, Eastern Meadowlark (EAME) = 37, Dickcissel (DICK) = 33, Common Yellowthroat (COYE) = 21, Bobolink (BOBO) = 17, Henslow's Sparrow (HESP) = 17, Field Sparrow (FISP) = 12, Grasshopper Sparrow (GRSP) = 11.

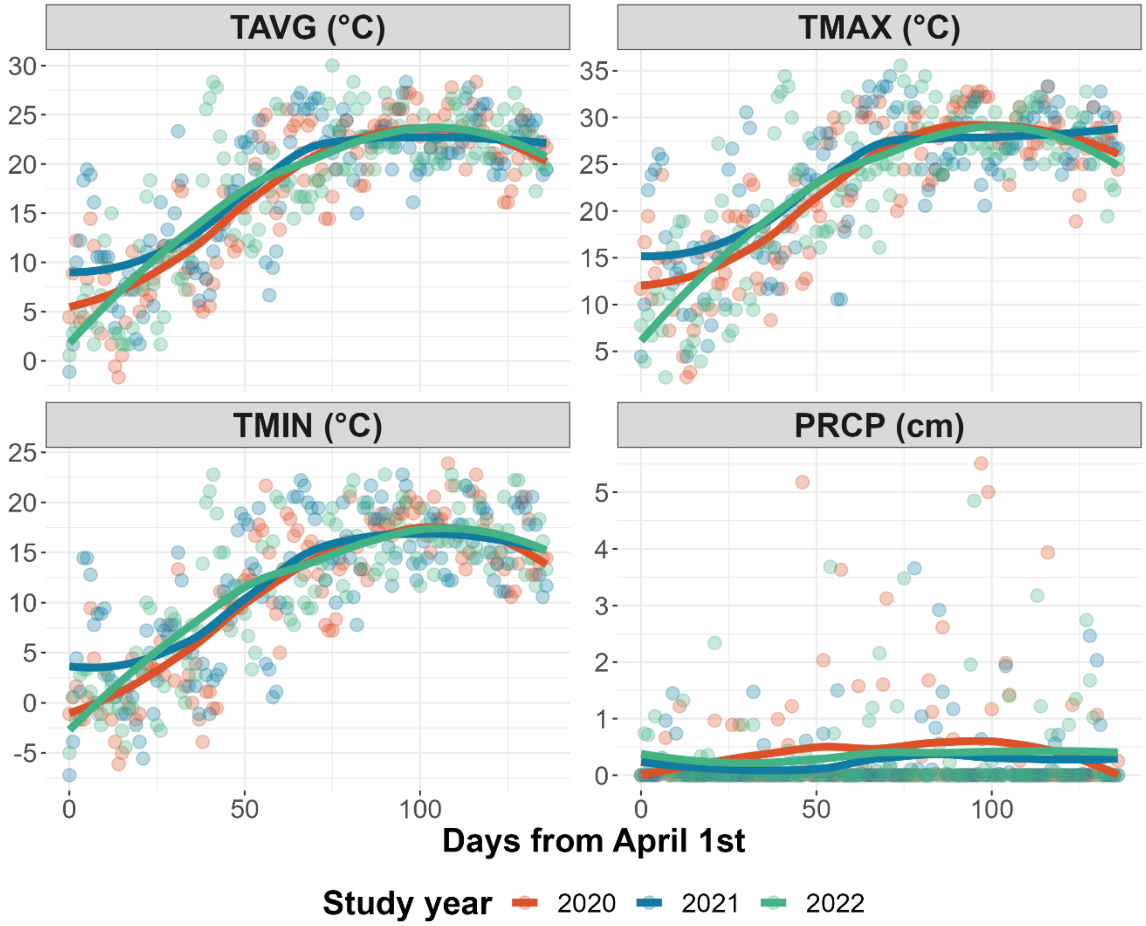

Figure S2. Regional climate summary data for grassland sites during the study years and months. Panels display daily average (TAVG), maximum (TMAX), and minimum (TMIN) air temperatures, and cumulative precipitation (PRCP) for the Dane County area from 1 April – 15 August 2020-2022. Points are the raw observations and solid lines are smoothed (Loess) trends. Weather data are sourced from https://www.ncei.noaa.gov/cdo-web/, Dane County Regional Airport station.

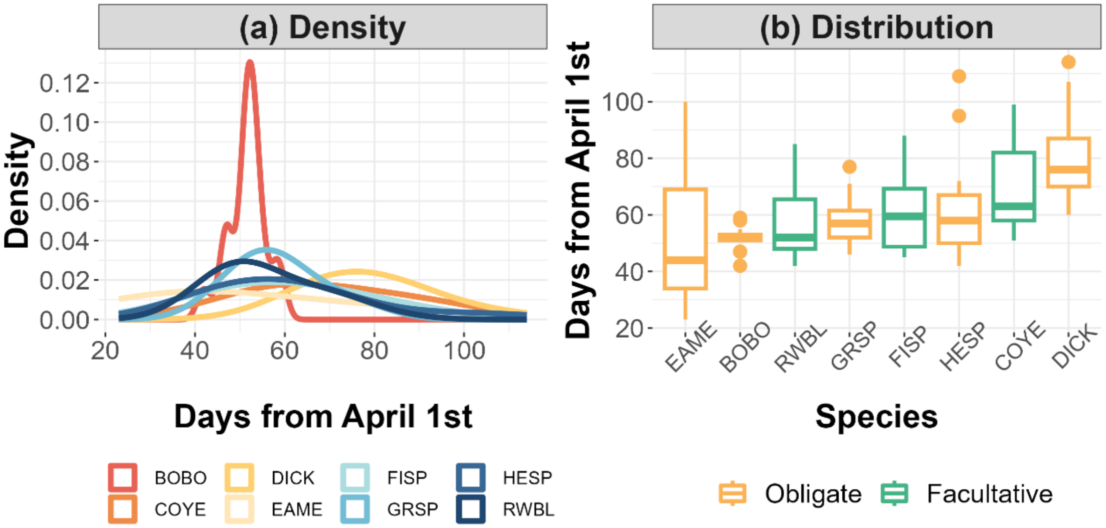

Figure S3. Summary of nest initiation dates by species for nests included in the study. Density plots **(a)** and boxplot distributions **(b)** of nest initiations for 8 grassland bird species breeding in southern Wisconsin, USA. Data from 3 study years, 2020-2022 are combined in this figure. For nests with unknown initiation dates, dates were imputed based on the established species incubation periods, estimated clutch sizes, and length of observation (see SI Appendix). Species sample sizes are: Red-winged Blackbird (RWBL) = 47, Eastern Meadowlark (EAME) = 37, Dickcissel (DICK) = 33, Common Yellowthroat (COYE) = 21, Bobolink (BOBO) = 17, Henslow’s Sparrow (HESP) = 17, Field Sparrow (FISP) = 12, Grasshopper Sparrow (GRSP) = 11.

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Chapter 3: A Climate Adaptation Menu for North American Grasslands

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Abstract

North American grasslands are climate-vulnerable biomes that provide critical ecosystem services and support biodiversity. However, grasslands are often neglected in climate policy and treaties, and they are underrepresented in ecological climate-adaptation literature. We sought to synthesize existing knowledge on climate adaptation in North American grasslands to provide resources and guidance for grassland managers facing increasing climate change impacts. We leveraged data from a systematic review and solicited input from management professionals at workshops to create a Grassland Climate Adaptation Menu—a referenced, hierarchical list of specific grassland management tactics nested under broader adaptation strategies. Our review revealed that although the number of published studies examining grassland-climate topics is increasing, relatively few make actionable recommendations for adaptation. Among studies that did make recommendations, landscape-planning principles such as conserving grasslands in future climate refugia and enhancing connectivity were the most commonly recommended practice types, but there were also suggestions for site-level management such as adjustments to fire and grazing, improved seed-sourcing and restoration practices, increased heterogeneity and biodiversity, use of assisted migration, and management of microclimate conditions. The Grassland Climate Adaption Menu incorporates eight general strategies and 32 approaches in a structured format designed to help managers translate concepts into actions.

Introduction

Grasslands currently occupy approximately 40% of the world's land surface (Gibson 2009, White *et al* 2000). In North America, grasslands are continentally distributed and encompass a diversity of natural and planted habitats. Globally, grassland biomes provide trillions of dollars in ecosystem services that are both critical to the maintenance of biodiversity and to sustaining human well-being (Bengtsson *et al* 2019, Liu *et al* 2022, Zhao *et al* 2020). Key ecosystem services provided by grasslands include food, fiber, and animal production (O'Mara 2012, White *et al* 2000), erosion control and soil production (Saviozzi *et al* 2001, Wu *et al* 2020), water quality and runoff reduction (Bengtsson *et al* 2019, Zhao *et al* 2020), pollination services (Holland *et al* 2017, Sexton and Emery 2020), and wildlife habitat (Bernath-Plaisted *et al* 2023a, Davidson *et al* 2012, Hanberry *et al* 2021). Currently, grasslands store ~30-35% of the world's terrestrial carbon stock (Ahlström *et al* 2015, White *et al* 2000), and importantly, ~90% of carbon in grasslands is stored belowground in soil (Bai and Cotrufo 2022), where it is protected from release during disturbance events such as fire (Viglizzo *et al* 2019).

Despite their importance to such ecosystem services, grasslands are threatened by many anthropogenic stressors and are often undervalued for their conservation and ecosystem service benefits. Globally, grasslands have been reduced to 26-45% relative to historic extents (Hoekstra *et al* 2005), and most remaining grasslands are highly fragmented (Augustine *et al* 2021, Scholtz and Twidwell 2022). Grasslands also tend to receive less protection (Hoekstra *et al* 2005) and policy attention (Bardgett *et al* 2021, Bengtsson *et al* 2019) than forested systems, and they are frequently left out of international treaties and climate agreements (Gibson and Newman 2019). In North America, ~50% of original grasslands have been lost to threats including agricultural expansion, energy development, woody encroachment, urbanization, and deliberate afforestation (Briske *et al* 2024, Lark *et al* 2015, Ott *et al* 2021, Van Auken 2009). This habitat loss has been exacerbated by the degradation of many grasslands by invasive species, fire suppression, and homogenized grazing practices (Bardgett *et al* 2021, Fuhlendorf *et al* 2012, Grant *et al* 2020, Ratajczak *et al* 2016). Anthropogenic climate change now presents a further threat to grassland systems, and the biodiversity and services that they support (Gibson and Newman 2019, Lavorel 2019).

Global surface temperatures have increased by 1.1°C since the pre-industrial era, and greenhouse gas emissions have continued to rise over the last decade increasing the likelihood that mean warming will exceed 2°C by mid-century (Calvin *et al* 2023). Broadly, grassland regions in North America are projected to experience increased intensity and frequency of summer droughts, elevated maximum temperatures, and an increase in heavy precipitation events in some areas (Calvin *et al* 2023, Gibson and Newman 2019). The Central Grasslands form a tri-national region that constitutes the largest contiguous grassland remaining in North America, and one of the largest on earth (Scholtz and Twidwell 2022). By 2040-2070, northern parts of this region will experience increases in average maximum temperature of at least 4°C (Fig. 1a). Central and southern grassland regions will likely see reduced precipitation, while many northern areas will receive increased rainfall (Fig. 1b). However, these precipitation gains may be offset by greater evaporative water loss and moisture deficits (e.g., drier soils due to high evaporation) throughout the Central Grasslands region (Fig. 1c). Grasslands may be especially vulnerable to increasing temperatures associated with climate change because they lack the buffering capacity of forest canopy to moderate microclimate extremes (Suggitt *et al* 2011), and because they often occur at low elevations where the velocity of climate change is greater (Dobrowski *et al* 2013, Loarie *et al* 2009).

Climate change may affect the ecology and functioning of grassland systems in numerous ways and will likely create new management challenges, as well as exacerbate existing ones (Gibson and Newman 2019, Lavorel 2019). Changes in temperature extremes as well as the timing and intensity of precipitation will fundamentally alter the productivity and phenology of grassland plants (Fraser 2019), nutrient cycling, and ecosystem processes (Henry 2019). For example, elevated temperatures and drought may reduce forage quality and grazing capacity

(Holechek *et al* 2020), shift fire seasons (Yurkonis *et al* 2019), and reduce carbon sequestration (Felton and Goldsmith 2023). Greater climate variability and occurrence of extreme events (particularly concerning precipitation), elevated CO_2 levels, and earlier growing seasons may favor the dominance of invasive species and facilitate woody encroachment—invasive species may be better able to capitalize on longer growing seasons, and woody plants can put on biomass more rapidly with higher CO_2 concentrations, and both groups may also benefit from intense precipitation events. (Catford and Jones 2019, Goodale and Wilsey 2018, Kulmatiski and Beard 2013, Morgan *et al* 2007). Increased drought and evaporative water loss may also result in the drying of grassland-embedded wetlands and subsequent loss of wetland habitat and ecosystem services in places like the Prairie Pothole Region (Londe *et al* 2024, Zhang *et al* 2021). Finally, the management of grassland wildlife will also be affected by climate change with many species experiencing range shifts and losses (Wilsey *et al* 2019), elevated demographic stress and disease risk (Conrey *et al* 2016, Poje *et al* 2020), altered movement patterns (Bateman *et al* 2015), and phenological mismatches (Freimuth *et al* 2022).

Given these diverse challenges and the threats they pose to the functioning of grassland ecosystems, there is a need for actionable management recommendations to help grassland managers adapt to a changing climate (Miller Hesed *et al* 2023). Climate adaptation can be defined as any adjustment to the management of systems intended to reduce the risk and impacts of climate change (Handler *et al* 2022, Swanston *et al* 2016). While there is an increasingly wide array of broad principles available to managers to help guide climate adaptation, information on specific adaptation practices is often sparse and many recommendations made in literature are not locally actionable (Cady *et al* 2023, Handler *et al* 2022). In particular, grassland biomes are underrepresented in ecological climate-adaptation literature (Cady *et al* 2023, LeDee *et al* 2021), and guidance tailored to grassland management under climate change is generally lacking.

To address these gaps, our goal was to synthesize current recommendations about climate adaptation in grassland ecosystems and create an adaptation menu to address the unique and pressing adaptation needs of North American grasslands. There were three objectives involved in the development of this menu: 1) Conduct a systematic literature review to provide an overview of recommended climate adaptation practices in grasslands, and assess the current state of research on this topic; 2) Combine recommendations extracted from our review with expert opinion and input from managers to produce a structured Grassland Climate Adaptation Menu; and 3) Demonstrate a real-world application of the menu through a case study with grassland managers.

Methods

Systematic Review

We used the ISI Web of Science (WOS) database to conduct a systematic literature review. To target articles that researched the effects of climate change in North American grasslands or discussed topics broadly relevant to grassland climate adaptation, we constructed a search string using Boolean operators. We used these operators to link key terms describing climate change, habitat, and topics related to ecological response and management of grasslands (including restoration). Thus, our search used the following structure on WOS: TS = (first climate term OR second climate term) AND TS = (first habitat term OR second habitat term…) AND TS = (first ecological term OR second ecological term…). Using this structure, any article that contained at least one term from each argument in any of the title, abstract, or keywords would be returned.

Our climate terms included only “climate change” and “global warming” as we wanted to identify not simply articles that related climate variables to grassland ecology (e.g., temperature, precipitation), but rather those that examined, discussed, or acknowledged the impacts of change in these climate conditions on grasslands. Our habitat terms included grassland, “old field”, parkland, pasture, prairie, rangeland, and savanna as we felt these were the most used terms to describe grassland habitats in North America. Finally, our ecological topic keywords included numerous terms describing possible response taxa (e.g., plants, birds, invertebrates, etc.), grassland ecosystem services (e.g., “ecosystem functioning”, hydrology, soil, etc.), and grassland management/adaptation topics (e.g., fire, grazing, invasive species, translocation, etc.). The full search string exactly as entered in WOS is available in Appendix S1. WOS initially returned 8423 records when we searched these terms. Before abstract screening, we used WOS filters for country (selecting only Canada, Mexico, and United States) and record type (removing books) leaving 4201 records (Fig. S1).

The lead author screened abstracts of all remaining records for relevance based on three criteria. First, if the study was field-based, we ensured that data collection occurred in North America (WOS country filters are often not precise). Global datasets that included North America were also included, as well as reviews on topics that could be broadly applied to any grassland system. Second, we confirmed that data collection occurred in grassland habitat, or that the topic was focused on a grassland system. We excluded studies that were focused on other similar ecosystems, such as sagebrush. However, we included studies of grassland-embedded wetlands, as we felt these were highly relevant to the management of grasslands in regions such as the Prairie Potholes and Playa Lakes. Finally, we assessed whether the analysis or topic of the study explicitly addressed the effect of climate change on some aspect of ecology or management in grasslands. Thus, we excluded studies that, for example, were concerned with climate change projections in grassland regions, but did not address any kind of ecological response or context, studies that examined the relationship between climate and a grassland response but said nothing about climate change or its implications, and studies that were entirely agriculturally focused (e.g., drought tolerance of crops, cattle weight gain practices, etc.), but did not address any of the ecological consequences associated with agricultural management decisions.

Following abstract screening, the lead author and two trained assistants extracted vote count (i.e., summarizing the number of studies on given topics or making certain recommendations) data from all relevant records. We extracted the following variables: publication year, country where data were collected (Canada, Mexico, or United States; reviews and global studies were classified as “multiple”), state or province, grassland topic in relation to climate change (fire, grazing, human dimensions, invasive species, organismal response, restoration, soil and nutrients, wetlands and hydrology, woody encroachment, other, or multiple), focal taxa (if the study was organismally focused; bird, herpetofauna, invertebrate, mammal, plant, soil fauna, or multiple), and grassland type (arid, grassland-embedded wetland, Mediterranean, mixed-grass, old field, planted/pasture, savanna, shortgrass, tallgrass, other, or multiple). Finally, we assessed whether each article had made what we considered to be one or more coherent management recommendations (see Textual Analysis section below) concerning climate adaptation in grassland ecosystems and assigned each record a binary “Yes” or “No.” We summarized vote count data from all relevant studies to provide an overview of interest in the topic over time and breakdowns of studies by grassland type, ecological/adaptation topic, and taxonomic focus.

Qualitative Textual Analysis and Extraction

A primary objective of our review was to extract management recommendations for climate adaptation actions in grassland ecosystems to include in the Grassland Climate Adaptation Menu. Thus, for each relevant article, we manually scanned the discussion, conclusion, management implications, and relevant review sections for clear statements about management in relation to climate change adaptation. We extracted and stored relevant text passages for each article, and articles could contain multiple recommendations. We considered passages to be coherent recommendations if they clearly stated specific actions that could be taken to achieve adaptation goals. However, we excluded passages that were vague or provided insufficient detail and context to be actionable. For example, many studies stated that their results had important implications for climate change but did not provide specific details describing how their findings could be applied. Similarly, studies often called for additional research, made vague statements about future implications, or discussed their findings in the context of advancing theory or improving certain types of models, but failed to connect these advances to management. After all recommendation passages were compiled, we assigned each passage a practice category so that we could summarize what types of recommendations are commonly made. These practice categories were not created *a priori* but rather were informed by the types of recommendations that we frequently observed during the review. Practice categories included adjustments to grazing systems, adjustments to prescribed fire, assisted migration, climate matching seeds, conservation stocking rates, future habitat refugia and connectivity, habitat heterogeneity, incentivizing conservation actions, increasing biodiversity (including richness, functional diversity, and genetics), managing invasive species, managing microclimate conditions, managing woody encroachment, providing resources to managers, restoring hydrology, soil amendments, and other recommendations. Recommendations that fell into the “other” category were often too system-specific to fit general categories or were recommended too rarely to be given a designated category.

Menu Development

We followed a similar approach to previously published Climate Adaptation Menus (e.g., Handler et al., 2022; Janowiak et al., 2021; Schmitt et al., 2022; Staffen et al., 2019; Swanston et al., 2016) in developing the Grassland Climate Adaptation Menu. After completing our literature review, we collated and synthesized both specific management recommendations extracted in textual analysis and broader adaptation concepts gleaned from the literature we reviewed into a tiered list of adaptation strategies, approaches, and tactics (Fig. 2). As in previous menus, we used the terms *strategy*, *approach*, and *tactic* as defined by Swanston et al. (2016). *Strategies* are defined as broad adaptation responses that describe major management goals under climate change, *approaches* are more detailed responses that consider how a strategy could be applied in different instances, and *tactics* are specific, prescriptive management actions taken to implement strategies and approaches.

Following the development of an initial draft menu, we solicited input on the menu from management professionals by hosting three virtual manager workshops. The first workshop was held in February 2021 and two subsequent events were held in August 2021 and February 2022. The first workshop was attended only by U.S. Forest Service staff while subsequent workshops were attended by management professionals from a diversity of non-governmental organizations as well as state and federal natural resource agencies. We followed Handler et al. (2022) in structuring our workshops, and participants were split into groups and asked to apply the Grassland Climate Adaptation Menu in combination with the Adaptation Workbook (https://adaptationworkbook.org/) —a planning process developed by the Northern Institute of Applied Climate Science (NIACS), a collaborative, multi-institutional organization led by the USDA Forest Service—to real life grassland management projects. The Adaptation Workbook consists of a structured five-step process (Swanston *et al* 2016): 1) *Define* management objectives; 2) *Assess* vulnerability to climate change; 3) *Evaluate* objective given vulnerability; 4) *Identify* adaptation practices; 5) *Monitor* the effectiveness of management actions. It was during this fourth step, that participants were asked to use the Grassland Climate Adaptation Menu to identify strategies, approaches and tactics that were appropriate for the management goals they had defined. Following these breakout sessions, we brought participants back together for a group discussion to receive general feedback and comments on the draft menu. We revised the menu in accordance with these comments using feedback from all workshops. An example meeting agenda and workshop feedback form are available in Appendix S2 and Appendix S3, respectively.

Results and Discussion

Literature Review Findings

Our systematic review of literature examining the effects of climate change on North American grasslands and their management identified 863 studies spanning the years 1990-2023 (Fig. 3a). Consistent with a recent review on climate change in grasslands globally (Hager and Newman 2019), we found that interest in the topic appears to have increased substantially over the last two decades. However, only 23% of studies (Fig. 3a) on grasslands and climate change included in our review made coherent recommendations for climate adaptation and management. While we acknowledge that our review was not exhaustive given the breadth of the topic and possible key terms, these results are likely representative and speak to a broader need for specificity in management surrounding climate change (Cady *et al* 2023, Heller and Zavaleta 2009, LeDee *et al* 2021). Many of the studies identified in our review made vague or general statements about climate change but failed to provide sufficient detail or specificity to inform management, while others emphasized the general importance or novelty of their work but made little attempt to link results to management. We encourage authors of future work on climate change in North American grasslands to elevate actionable recommendations associated with their findings when possible.

Our review also identified geographic and taxonomic biases in existing grassland climate-change literature that highlight potential information gaps. First, although we gathered studies from across North America including Canada, Mexico, and the United States, as well as global datasets that included North America, most existing studies (78%) were conducted in the United States (Fig. 3a). Similarly, not all grassland ecosystems were evenly represented in literature, and the effects of climate change were most studied in tallgrass prairie, accounting for 19% of studies (although studies examining multiple grassland types were the most common), while systems like shortgrass prairie (which is geographically more extensive) were more poorly represented at 4% (Fig 3b). Finally, among all studies for which a focal taxon could be identified (*n* = 668), 67% were focused on plants while, for example, only 9%, 3%, and 2% examined climate change effects on grassland birds, invertebrates, and mammals, respectively (Fig. 3c). Studies that focused on the management of grassland herpetofauna under climate change were almost completely absent from the literature. Filling these taxonomic knowledge gaps and increasing our understanding of how climate change affects a diversity of grassland species will be important for informed adaptation planning, as species groups may have unique needs and respond differently to both climate and management practices.

The studies included in our review focused on a diversity of climate adaptation topics in grasslands, but the relationship between grassland organisms and climate variables was the most common subject, while the effect of climate on management issues was less frequently addressed (Fig. 3c). The studies that we considered to provide clear adaptation guidance (n = 203) collectively made 335 recommendations which we classified into practice categories (Fig. 3d). The most recommended practice types comprised landscape-level planning activities such as conserving grasslands in regions where climate is likely to remain suitable for grassland species (e.g., Bateman et al., 2020), and improving habitat connectivity to facilitate range shifts and gene flow (e.g., Perkins, Ahlering, & Larson, 2019). However, recommendations were also made for site-level management. For example, alternative grazing schemes to increase ecosystem services (e.g., Döbert et al., 2021), enhancing resilience through increased biodiversity (e.g., Catford, Dwyer, Palma, Cowles, & Tilman, 2020), restoring grasslands with seed-mixes that are better matched to future climate (e.g., Galatowitsch, Frelich, & Phillips-Mao, 2009), conservation stocking as drought mitigation (e.g., Fritts et al., 2018), and managing for heterogeneity (e.g., Bachelet et al., 2011) and thermal diversity (e.g., Patterson, Grundel, Dzurisin, Knutson, & Hellmann, 2020) were all consistently suggested. We incorporated these types of practices, and many others, into the Grassland Climate Adaption Menu discussed below.

Grassland Climate Adaptation Menu and Practices

We developed a menu of strategies (overarching management goals), approaches (more detailed responses for a given project or site), and example tactics (specific management practices) intended to support managers in implementing climate adaptation in North America's grassland ecosystems. Like previously published adaptation menus for other ecosystems (e.g., Handler et al., 2022; Janowiak et al., 2021; Schmitt et al., 2022; Staffen et al., 2019; Swanston et al., 2016), the Grassland Climate Adaptation Menu is hierarchical and designed to help managers translate broad management goals to specific actions (Fig. 2). We created the menu using a synthetic approach and combined data from a systematic review and input from management professionals to create a detailed list of adaptation practices tailored for grasslands. The resulting Grassland Climate Adaption Menu includes 8 general strategies (Table 1; Fig. 4), and 32 targeted approaches (Table 1). We also provide 145 example tactics to illustrate how adaptation strategies could be implemented in specific contexts (Appendix S4). The version of the menu found in Appendix S4 includes referenced narrative text for each strategy, approach, and example tactic. Here, we present a tabular summary of the menu (Table 1) and provide a brief discussion of practices associated with each strategy.

Strategy 1. Restore and Maintain the Extent of Grasslands Across the Landscape. Despite the importance of climate change, habitat loss remains the greatest threat to ecosystems and species globally (Caro *et al* 2022). In the North American Great Plains, roughly 6,500 km^2 of grassland is converted to cropland annually (WWF 2024). Climate change and land-use change can have synergistic effects on species and ecosystems (Northrup *et al* 2019), and continued investment in the conservation and restoration of grasslands is a prerequisite to any successful climate adaptation. Targeting investments in large and intact grasslands may provide the best returns, as not only do these areas support high biodiversity and stable metapopulation structures (Augustine *et al* 2021, Scholtz and Twidwell 2022), but intact landscapes also display greater resilience to climate perturbations (Martin and Watson 2016). Similarly, identifying regions where future climate is likely to be suitable for target species (Fig. 4a) (Grand, Wilsey, Wu, & Michel, 2019), or prioritizing grasslands that support greater heterogeneity and resilience, such as topographically complex areas (Anderson *et al* 2023, Duquette *et al* 2022a), are also tactics that can delineate climate-informed priorities. Mitigating future habitat conversion is also important. For instance, as increased precipitation in some grassland areas may incentivize future crop expansion (King *et al* 2018), removing crop-insurance subsidies for converted native grasslands can help discourage conversion (Lark 2020). Proactive land-use planning around energy leases is also critical, particularly as future solar expansions throughout North America may drive massive land-use shifts (Ott *et al* 2021). Regulating where these leases can go and incentivizing new installations in previously disturbed landscapes (agricultural and urban areas, landfills, old lease sites) rather than intact native grassland could help reduce habitat losses.

Strategy 2. Increase Landscape-scale Resilience Under Future Climate Conditions. Landscape-level processes such as connectivity play an important role in climate resilience (Anderson *et al* 2023). However, North America's grasslands are highly fragmented (Augustine *et al* 2021, Wimberly *et al* 2018). This fragmentation may exacerbate climate change by inhibiting species movements and range shifts (Bateman *et al* 2015, Nixon *et al* 2016) and preventing gene flow of adaptive climate phenotypes (Cullingham *et al* 2023). In grasslands, connectivity (Fig. 4b) can be improved through tactics such as maintaining native vegetation buffers throughout riparian corridors (Cole *et al* 2020), implementing prairie strips in agricultural areas (Schulte *et al* 2017), managing powerline rights-of-ways for native vegetation (Garfinkel *et al* 2023), and using wildlife-friendly fencing to reduce ungulate movement barriers (Jones *et al*

2018). Alternatively, rather than directly connecting habitat areas, strategic investment in patches that can serve as steppingstones between larger grasslands can also be effective (Herrera *et al* 2017, Wimberly *et al* 2018). Such steppingstones may even act as climate refugia depending on their locations (Grand *et al* 2019), and these patches might buy time for species to adapt or continue shifting their ranges (Hannah *et al* 2014). In agricultural regions, the use of government programs such as the Conservation Reserve Program (CRP) may provide one mechanism to introduce additional grassland habitat patches on the landscape (Spencer *et al* 2017).

Strategy 3. Maintain Fundamental Ecosystem Functioning in Grasslands. North American grassland**s** in the Anthropocene are highly degraded ecosystems (Augustine *et al* 2021, Bardgett *et al* 2021, Samson *et al* 2004), and although they still provide many critical ecosystem services, these services are sensitive to management decisions (Sollenberger *et al* 2019). Thus, a focus on maintaining the fundamental functions of grasslands will likely be compatible with current goals while helping to increase resilience to future climate threats. For example, transitioning from continuous to rotational and adaptive multi-paddock (AMP) grazing systems can enhance soil quality and carbon sequestration, particularly at lighter stocking rates (Bai and Cotrufo 2022, Teague and Kreuter 2020, Zhou *et al* 2017). In other cases, soil amendments such as biochar or low levels of nitrogen fertilization may be appropriate to mitigate reduced productivity and forage quality from increases in temperature and CO_2 concentrations (Augustine *et al* 2018, Mayer and Silver 2022). Maintaining grassland structure and function by emulating natural disturbances is another major focus of grassland management. For example, Increasing the frequency of prescribed fire to match natural regimes (Ratajczak *et al* 2016), and conducting burns with higher intensities (Scholtz *et al* 2022), can help prevent ecosystem state-shifts from increasing woody encroachment. Intentional management of grassland hydrology is also important, and tactics like removing legacy drain tiles (Fig. 4c) (Becker, Becker, & Doro, 2021; Biebighauser, 2007), controlling woody plant species with high water uptakes (Acharya *et al* 2017), and retaining agricultural wetlands on private lands (Swartz *et al* 2019) can help to sustain ecosystem services in grassland-embedded wetlands under increasing drought.

Strategy 4. Increase Biodiversity and Heterogeneity in Grassland Communities. Biodiversity is known to promote resilience and stability in grassland ecosystems (Tilman *et al* 2006, Wang *et al* 2019), and in a climate context, biodiversity can be viewed as a portfolio effect by which genetically and functionally diverse communities have increased adaptive capacity under climate variability (Catford *et al* 2020, Cowles *et al* 2016, Whitney *et al* 2019). The use of diverse seed mixes from multiple climates-zones, as well as the introduction of locally adapted phenotypes from areas that better resemble future climates across species' ranges are widely recommended tactics to increase biodiversity and drought tolerance in grassland plant communities (Havens *et al* 2015, Nolan *et al* 2023, Phillips-Mao *et al* 2016). Similarly, the selection of plants with specific functional traits (Fig. 4d), such as different carbon pathways (e.g. C4 plants), nutrient cycling roles (e.g., legumes), and leaf morphologies (e.g., narrow-leafed species for drought), are also often recommended (Craine et al., 2013; Havrilla, Bradford, Yackulic, & Munson, 2023; Volaire, Barkaoui, & Norton, 2014). Managers may also seek to enhance grassland biodiversity by managing for structural heterogeneity through alternative fire and grazing schemes, variable stocking rates, and variable burn intensities (Duquette *et al* 2022b, 2022a, Hill *et al* 2017, Hovick *et al* 2015).

Strategy 5. Reduce the Impacts of Ecological and Climate Stressors. Many grassland organisms are already threatened by the loss of grasslands and various sources of habitat degradation (Bernath-Plaisted *et al* 2023a, Hanberry *et al* 2021). Increasing frequency and intensity of extreme climate events will likely compound these stressors and further threaten grassland communities (Maresh Nelson *et al* 2023, Murali *et al* 2023, Ratajczak *et al* 2019). However, managers can take steps to lessen these impacts both by actively seeking to mitigate climate effects and reducing background stressors. For example, increasing grassland-embedded wetlands on the landscape to moderate precipitation extremes (Ferreira *et al* 2023), irrigating smaller grasslands (Greenwood *et al* 2016), and deploying artificial water sources for wildlife (Rich *et al* 2019) can help reduce the impacts of severe drought. Likewise, the effects of extreme heat can be mitigated for some organisms by retaining taller vegetation as microclimate refugia (Bernath-Plaisted *et al* 2023b). In some cases, management can also address grassland phenology changes driven by climate change. For example, seeding grassland sites with plants that have diverse flowering phenologies may help to prevent timing mismatches for pollinators (Fig. 4e) (Guzman *et al* 2021). Finally, addressing other ecological stressors with management actions, such as fire and herbicide for woody encroachment (Scholtz *et al* 2018), targeted grazing to reduce invasives (Firn *et al* 2013), and reduced pesticide use on agricultural lands to protect pollinators and birds (Main *et al* 2021, Stanton *et al* 2018) can also help species persist under increasingly challenging conditions.

Strategy 6. Adjust Site-level Management to Align with New Climate Conditions. Grasslands are disturbance-maintained ecosystems, and they often require intensive management (Samson *et al* 2004). However, changing climate conditions could make it increasingly challenging to implement traditional management regimes. Therefore, adaptive shifts in the timing, intensity, and types of management activities may be required. For example, in many regions, prescribed burns are typically conducted during relatively cool and wet spring periods. As springs become hotter and earlier, these activities may need to shift to fall and even winter

(Yurkonis *et al* 2019). Similarly, rangeland productivity and forage quality may decline with increasing drought and CO_2 levels creating challenges for grazing (Holechek *et al* 2020). Thus, producers and managers may wish to consider conservation stocking rates to avoid rangeland degradation during droughts (Fig. 4f) (Briske *et al* 2015, Joyce *et al* 2013). The management of grassland-embedded wetlands may also be affected by climate change, and increased variability in precipitation could alter hydroperiods in wetlands that are important for waterfowl and amphibians. One tactic managers can use to address this issue is to maintain wetlands of different sizes at grassland sites, as smaller wetlands can sustain longer hydroperiods in some cases (Tsai *et al* 2007). Grassland restoration practices may also need to change as seed establishment becomes more difficult with greater climate variability (Lyons *et al* 2023). Practices such as restoring microtopography and stone cover to create "safe-sites" for establishment (Biederman and Whisenant 2011), climate-informed seed sourcing (Bower *et al* 2014), and inoculating propagules with beneficial microbes (Docherty and Gutknecht 2019) could help to foster better establishment. Finally, phenological shifts associated with climate change could worsen existing management conflicts. For instance, mowing in agricultural grasslands is a major source of nest mortality for grassland birds (Tews *et al* 2013), and earlier greening of vegetation will increase the overlap of nesting and haying activities—a conflict that may require management adjustments to resolve (McGowan *et al* 2021).

Strategy 7. Facilitate Transitions Under Climate Change. It is generally accepted that many grassland species will shift their ranges northwards to track suitable climate space (Hovick *et al* 2016)—though not all species will (McCauley *et al* 2017). Managers can help facilitate such transitions when appropriate, especially for species that may be limited by disjunct ranges or poor dispersal capability, through approaches such as assisted migration programs

(Cullingham *et al* 2023, McKone and Hernández 2021). Using procedures to identify species with high exposure and poor dispersal can help mangers to select priority species for intervention (Barber *et al* 2016). In grassland plant communities, managers can also facilitate transitions by observing native grassland species that perform well under extreme droughts and supporting the expansion of these species locally and regionally (Fig 4g) (Griffin-Nolan *et al* 2019). In other cases, transitions will occur at the ecosystem rather than species-level and although some grasslands will be lost to woody encroachment and sea-level rise (Crosby *et al* 2016, Jones 2019), opportunities for grassland conservation may also emerge. For instance, there may be an incentive to return marginal croplands to permanent cover as changing climate conditions require increasing inputs for low yields in some regions (Lark *et al* 2020). Finally, situations may arise where the best decision is simply to avoid wasting resources on poor conservation investments. Managers can use so-called conservation triage frameworks to decide when it is better to allocate resources elsewhere (Bottrill *et al* 2008).

Strategy 8. Engage Human Communities in Grassland Conservation Adaptation. There has always been a strong connection between grasslands and human communities, and many of the services that grasslands provide are cultural and economic (Nowak-Olejnik *et al* 2020, Zhao *et al* 2020). North American grasslands are working landscapes, and they have played important roles in food production in both pre-colonial and modern times (O’Mara 2012, Roos *et al* 2018). In Canada and the United States, 80% of remaining grasslands are privately managed (Bernath-Plaisted *et al* 2023a). Therefore, continued efforts to support private landowners in grassland management are critical (Morgan *et al* 2019), and there is an opportunity to include climate priorities in government programs and incentivize adaptation practices like improved grazing to increase carbon sequestration, etc. (Ayambire *et al* 2021).

Ensuring that agency staff are trained and able to assist landowners on climate-specific issues is also key (Wiener *et al* 2020). Non-profit and government entities can also leverage grassland properties by using grassbank strategies (e.g., forage reserve) by which they allow emergency grazing by local producers during forage shortfalls in exchange for conservation practices (Gripne 2005). Indigenous tribes are also important stakeholders in grassland management, and engaging with tribes about grassland climate adaptation, respecting indigenous knowledge (IK), and expanding the reach of Farm Bill benefits to include tribal landowners are all important tactics. Outside of economic incentives and programs, human communities of all kinds can also be engaged to participate in active management activities that support climate adaptation. For example, both woody encroachment and invasive species challenges will be exacerbated by climate change, but communities can be engaged in local burn cooperatives (Fig. 4h) and regional invasive species monitoring and prevention campaigns to combat these threats (Goodwin *et al* 2012, Twidwell *et al* 2013)

Menu Use

We developed the Grassland Climate Adaptation menu to be flexible and it can be used both for the management of local sites, and broader landscape planning, as it contains a mix of approaches and example tactics that operate at different spatial scales. The menu is intended to be used in conjunction with a structured planning process, such as the Adaptation Workbook (https://adaptationworkbook.org/), but it can also stand on its own for some uses. The menu has a well-defined hierarchical structure intended to help managers bridge the gap between broad adaptation goals and specific actions (Fig. 2). Strategies are the broadest tier of the menu and can be thought of as statements of intent describing overarching management goals (e.g., increase biodiversity and heterogeneity of grassland communities). Approaches are more detailed and describe methods for the implementation of a broader strategy. For example, an approach to implementing our example strategy of increasing grassland biodiversity could be to enhance functional diversity in grassland restorations and plantings. Tactics, the final tier of the menu, describe prescriptive management practices that can be taken to achieve the management goals identified in previous steps. For this example, overseeding restorations with high-diversity mixes could be an appropriate tactic. Importantly, while strategies and approaches are somewhat broad and apply to many situations, tactics can be very specific and need not be limited to the examples we list. In many cases (such as in the case study discussed below), managers will use the menu structure to aid in articulating their own tactics.

Case Study

To demonstrate the use of the Grassland Climate Adaptation Menu, The Nature Conservancy (TNC) in MN, ND, SD, agreed to use the menu and the Adaptation Workbook in the development of a climate adaptation plan for Samuel H. Ordway Prairie (Fig. 5), a TNC property located within the Leola Hills Conservation Area. This area spans the borders of North and South Dakota, USA, and is an example of high-quality Prairie Potholes habitat with 64% native prairie cover comprising ~141,640 ha of grassland (Miller *et al* 2022). Leola Hills is also located within TNC's Resilient and Connected Network, a designation identifying landscapes expected to have high ecological value and resilience under a changing climate (Anderson *et al* 2023). Ordway Prairie is representative of the Leola Hills Conservation Area, and TNC included both regional and local priorities in the adaptation plan they developed. The Leola Hills region is projected to experience increasing annual temperatures over the coming decades with more rapid increases in nighttime and winter temperatures. Like much of the ecoregion, increased drought frequency and severity as well as extreme precipitation events are also predicted (Miller *et al* 2022). Interactive maps of projected temperature and precipitation changes under various warming scenarios for the Leola Hills Conservation Area can be viewed on TNC's ArcGIS Dashboard. The TNC team was interested in incorporating climate adaptation strategies into their existing conservation planning for Ordway Prairie and the Leola Hills Conservation Area.

TNC had previously established three main conservation priorities for Ordway Prairie and the Leola Hills Conservation Area: 1) Managing ecosystems for biodiversity, 2) Improving and maintaining habitat connectivity, and 3) Supporting producers in improving rangeland conditions and the economic viability of their operations (Miller *et al* 2022). The team used the Adaptation Workbook to formally consider how these goals might be affected by climate change and develop a regional climate adaptation plan. They identified numerous potential challenges including, increased risk of conversion to cropland with longer growing seasons, loss of forage capacity with increased drought, loss of water resources from drying wetlands, water quality issues associated with increased sediments during extreme precipitation events, increased dominance of invasive species with earlier growing seasons, challenges to establishment in restorations under climate change, increased rates of woody encroachment, and narrowing windows for prescribed fire. The TNC team selected approaches from the menu that could help address such challenges and identified tactics that would best achieve their goals (Table 2). This case study provides a good example of menu use because it demonstrates the diversity of approaches and tactics, the use of the tool for both local and regional activities, and the flexibility for users to tailor it to their needs.

Conclusion

North American grasslands are threatened both by past and current agricultural conversion (WWF 2024) and increasingly by future climate change (Gibson and Newman 2019). To maintain and enhance the biodiversity and ecosystem services that these biomes support, adaptation through active management and conservation planning will be important (Ansley *et al* 2023, Miller Hesed *et al* 2023, Sollenberger *et al* 2019). However, actionable management recommendations for climate adaptation are often difficult to identify, particularly for grassland ecosystems (Cady *et al* 2023). To assess the state of knowledge regarding climate adaptation in North America's grasslands, and to provide better guidance for grassland managers, we conducted a systematic literature review of adaptation practices in grasslands and developed a Grassland Climate Adaptation Menu. The menu is a structured, hierarchical list of broad strategies and more specific approaches designed to help managers translate their adaptation goals into prescriptive actions. The menu contains dozens of example adaptation tactics targeted for grassland management and discusses the most widely recommended actions in literature such as protecting future habitat and enhancing connectivity, adjusting grazing systems to increase heterogeneity and carbon sequestration, shifting the timing and intensity of prescribed fire, restoring grassland-embedded wetlands, improving seed-sourcing practices to increase diversity and climate-zone representation, assisted migration, managing microclimates to buffer organisms from extremes, and many others. Our review also revealed that, consistent with the previous findings (Cady *et al* 2023, LeDee *et al* 2021), many studies on ecological-climate topics fail to provide actionable management practices. As climate change becomes an increasingly important focus of ecological management, we draw attention to this issue in grasslands, and we urge researchers and ecologists who publish on climate topics in grasslands to better emphasis how their findings can be applied to climate adaptation.

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Tables

Table 1. A tabular summary of strategies, approaches, and example tactics from the Grassland Climate Adaptation Menu. Strategies characterize broad goals for the management of grasslands in a climate change context while approaches describe more specific ways a strategy might be implemented for a given project or management site. Tactics are prescriptive practices nested under each approach, and need not be limited to the examples we provide. A full narrative version of the menu including all example tactics and references is available in Appendix S4.

Adaptation strategies	Adaptation approaches and example tactics
1. Restore and maintain the extent of grasslands across the landscape	1.1 Conserve existing intact grasslands *Example: prioritize intact core grassland areas*[1]
	1.2 Mitigate major mechanisms of grassland conversion *Example: regulate new energy leases on undeveloped grasslands*[2]
	1.3 Create or maintain grassland habitats that include heterogeneity and redundancy in site types and environmental conditions *Example: implement site-level management that promotes heterogeneity, such as patch-burn grazing*[3]
	1.4 Restore or establish grasslands in locations expected to remain suitable under future climate conditions *Example: incorporate climate priorities into government permanent cover programs*[4]
2. Increase landscape-scale resilience under future climate conditions	2.1 Maintain or create movement corridors *Example: use prairie strips to enhance grassland connectivity through agricultural areas*[5]
	2.2 Reduce fragmentation and create habitat steppingstones *Example: consider landscape context when prioritizing conservation investment*[6]
	2.3 Protect habitat along species range edges *Example: focus conservation efforts on the northern edge of species distributions in anticipation of range shifts*[7]
3. Maintain fundamental ecosystem functioning	3.1 Maintain or restore nutrient cycling *Example: apply soil amendments like biochar to increase soil organic matter and productivity*[8]
	3.2 Emulate natural disturbance processes from grazing *Example: protect remaining native grazers such as prairie dogs*[9]
	3.3 Emulate natural disturbance processes from natural and indigenous fire

Adaptation strategies	Adaptation approaches and example tactics
	Example: allow prescribed fire to burn with varying intensity to mimic wildfire and create heterogeneity[10]
	3.4 Maintain or restore hydrology *Example: exclude cattle from riparian areas to prevent bank erosion and maintain water quality*[11]
	3.5 Maintain pollination services *Example: strengthen pollination networks by increasing floral diversity*[12]
4. Increase biodiversity and heterogeneity in grassland communities	4.1 Maintain or enhance genetic diversity of ecological communities *Example: overseed grassland restorations with seed mixes from multiple collection zones*[13]
	4.2 Maintain and restore a diversity of native plants and functional groups *Example: diversify tame pasture and planted forage with greater functional diversity (e.g., legume/grass mixes) and consider plant tolerances for future climate conditions when selecting forage*[14]
	4.3 Maintain and restore heterogenous vegetation structure *Example: create refugia by leaving taller patches of vegetation unburned*[15]
	4.4 Maintain or restore grassland-embedded wetland vegetation *Example: remove legacy sediments to control weedy and invasive species*[16]
5. Reduce the impacts of ecological and climate stressors	5.1 Reduce the impact of climate on ecosystem functioning *Example: restore grassland-embedded wetlands to regulate flooding and provide moisture refuiga*[17]
	5.2 Reduce the impact of climate on grassland wildlife *Example: maintain and deploy natural and artificial water sources for grassland wildlife to mitigate drought*[18]
	5.3 Control woody encroachment *Example: implement prescribed fire with higher intensities than natural fire regimes to control invasions*[19]
	5.4 Control invasive species *Example: manipulate timing and intensity of grazing to target invasive species*[20]
	5.5 Promote beneficial management practices on agricultural lands *Example: reduce or delay mowing and haying activities in agricultural grasslands to avoid destroying grassland bird nests*[21]

Adaptation strategies	Adaptation approaches and example tactics
6. Adjust site-level management to align with new climate conditions	6.1 Adjust the timing, frequency, and intensity of management actions (such as fire, grazing, and mechanical treatments, etc.) *Example: adopt flexible burn schedules that can accommodate shifting fire windows such as winter burns*[22]
	6.2 Adjust planting and restoration practices to promote establishment of grassland vegetation under climate change *Example: create "safe sites" for seed establishment and enhance diversity by restoring microtopography and stone cover*[23]
	6.3 Adjust the management of grassland-embedded wetlands to account for changing precipitation and hydroperiods *Example: install infrastructure and vegetation features that control the flow of water and sediments (e.g., one-rock damns, swales)*[24]
7. Facilitate transitions under climate change	7.1 Promote climate-tolerant plant genotypes and facilitate community shifts to better align with future climate conditions *Example: facilitate transition of plant communities by seeding restorations with all climate-viable species theoretically within dispersal distance*[25]
	7.2 Engage in assisted migration to facilitate species range shifts *Example: prioritize species for assisted migration based on expected range loss and dispersal capability*[26]
	7.3 Convert non-grassland systems to grassland where climate can no longer support current land use *Example: identify locations where forest-ecotones are shifting to savanna and facilitate this shift through prescribed burns*[27]
	7.4 Identify where investment in grassland conservation is a poor use of resources *Example: elect not to pursue high-cost measures in favor of spending resources elsewhere*[28]
8. Engage human communities in grassland conservation and adaptation	8.1 Respect and incorporate indigenous knowledge and values in grassland management *Example: Partner with indigenous-led natural resources agencies to develop joint adaptation practices and co-stewardship projects on issues of cultural importance to indigenous peoples*[29]
	8.2 Invest in outreach and support for landowners and producers *Example: explicitly include climate adaptation practices (e.g., payments for carbon sequestration and pasture rest etc.) in programs and ensure that agency staff are*

Adaptation strategies	Adaptation approaches and example tactics
	trained to advise landowners on climate topics[30]
	8.3 Develop and promote economic incentives for grassland climate adaptation on private lands *Example: create branding and markets for sustainably produced grassland products, such as the Audubon Society's Bird Friendly Land label*
	8.4 Involve communities in management activities *Example: engage communities in regional invasive species monitoring and prevention campaigns*[31]

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[1](Scholtz and Twidwell 2022), [2](Ott *et al* 2021), [3](Fuhlendorf *et al* 2012), [4](Cunningham 2022), [5](Schulte *et al* 2017), [6](Herse *et al* 2020), [7](Nixon *et al* 2016), [8](Mayer and Silver 2022), [9](Haun *et al* 2024),[10](Hill *et al* 2017), [11](Krall *et al* 2021), [12](Guzman *et al* 2021), [13](Havens *et al* 2015), [14](Rojas-Downing *et al* 2018), [15](Steenvoorden *et al* 2019), [16](Beas *et al* 2013), [17](Ferreira *et al* 2023), [18](Rich *et al* 2019), [19](Scholtz *et al* 2022), [20](Firn *et al* 2013), [21](Tews *et al* 2013), [22](Yurkonis *et al* 2019), [23](Biederman and Whisenant 2011), [24](Pierce *et al* 2012), [25](McKone and Hernández 2021), [26](Barber *et al* 2016), [27](Kodero *et al* 2024), [28](Bottrill *et al* 2008), [29](Mucioki 2024), [30](Wiener *et al* 2020), [31](Goodwin *et al* 2012).

Table 2. Example approaches and tactics selected by The Nature Conservancy staff in a case study application of the Grassland Climate Adaptation Menu for Samuel H. Ordway preserve and the Leola Hills Conservation Area located in the Dakota's, USA. The Climate Challenges column describes challenges to management goals driven by climate change that The Nature Conservancy team sought to address with the menu. The parenetical numbers refer to indexing of approaches and tactics in the full menu (Appendix S4).

Climate Challenges	**Selected Approaches**	**Selected Tactics**
Increased risk of conversion of rangeland to cropland with longer growing seasons	Mitigate major mechanisms of grassland conversion (*1.2*)	Invest in private lands outreach to establish more grassland and wetland easements (*1.2.2*)
Drier summers may inhibit establishment of native plants in restorations	Maintain or enhance genetic diversity of ecological communities (*4.1*)	Improve seed-sourcing practices to include greater diversity of climate zones and increase adaptive capacity (*4.1.1*)
Farm Bill policies (e.g. crop insurance) have greater impact on producer decisions than climate change	Invest in outreach and support for landowners and producers (*8.2*)	Support mentoring programs for ranchers to facilitate learning and adoption of adaptation strategies (*articulated by TNC*)
Climate change and land-use changes may threaten water quality through increased agricultural runoff and sediments	Maintain or restore hydrology (*3.4*)	Use freshwater resilience maps and models to prioritize easements and riparian buffers (*articulated by TNC*)
Fewer burn days during the traditional spring burn season and more extreme weather will make prescribed fire difficult to implement	Adjust the timing, frequency, and intensity of management actions (*6.1*)	Adopt more flexible burn schedules that extend into other seasons, such as fall in this case (*6.1.1*)
Precipitation increases may facilitate woody encroachment	Emulate natural disturbances with fire (*3.3*)	Increase frequency and coverage of burns to better control woody species (*3.3.1*)

Figures

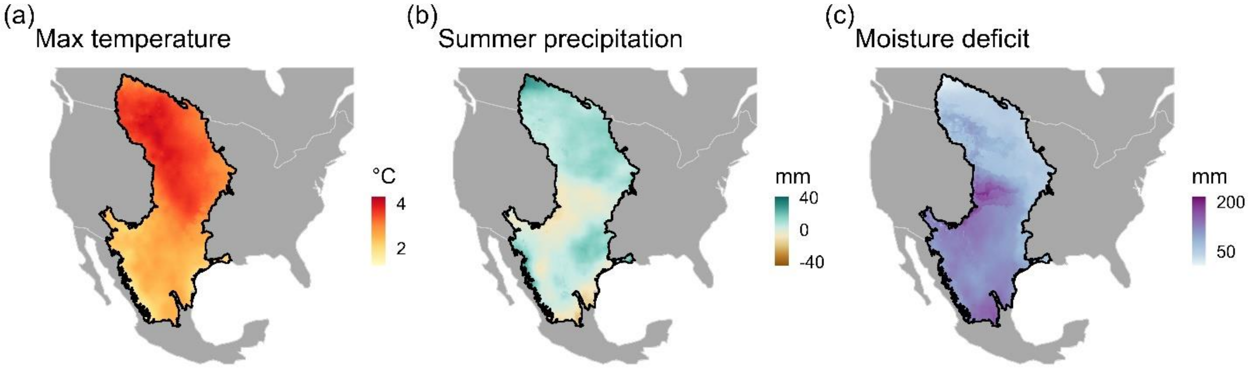


Fig. 1. Projected changes between current climate normals and normals by 2040-2070 for the North American Central Grasslands region—North America's largest remaining continuous grasslands. The largest maximum temperature increases are projected to occur in the Northern Great Plains **(a)**, Mean summer precipitation may increase through much of the Northern Great Plains, while parts of the south and central plains will become increasingly dry **(b)**, and nearly the entire Central Grassland regions will experience greater climatic moisture deficits (a measure of evaporation potential and soil drying) likely resulting in more arid conditions **(c)**. Climate data are generated from CMIP6 (ensemble models for SSP245 emissions scenario) models and sourced from the AdaptWest Project (adaptwest.databasin.org). The Central Grasslands boundary file is available from the U.S. Fish and Wildlife Service at https://gis-fws.opendata.arcgis.com/datasets/fws::north-american-central-grasslands/explore.

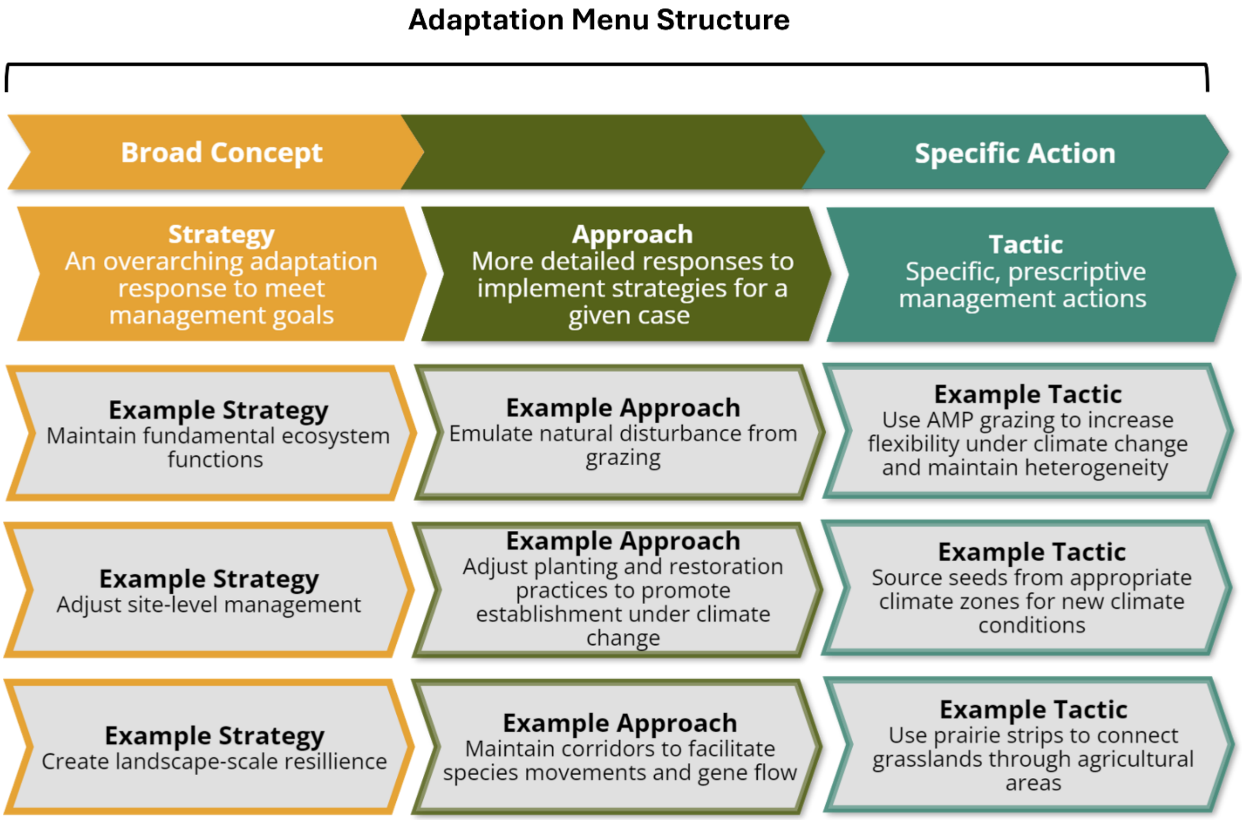


Fig. 2. The tiered structure of the Grassland Climate Adaptation Menu is intended to help managers move from broad concepts to specific management actions. Strategies (yellow) represent broader adaptation responses to meet general management goals, approaches (green) are more detailed ways to implement a strategy for a given site, species, or problem, and finally, tactics (teal) are specific, prescriptive actions taken to achieve adaptation goals in a particular instance.

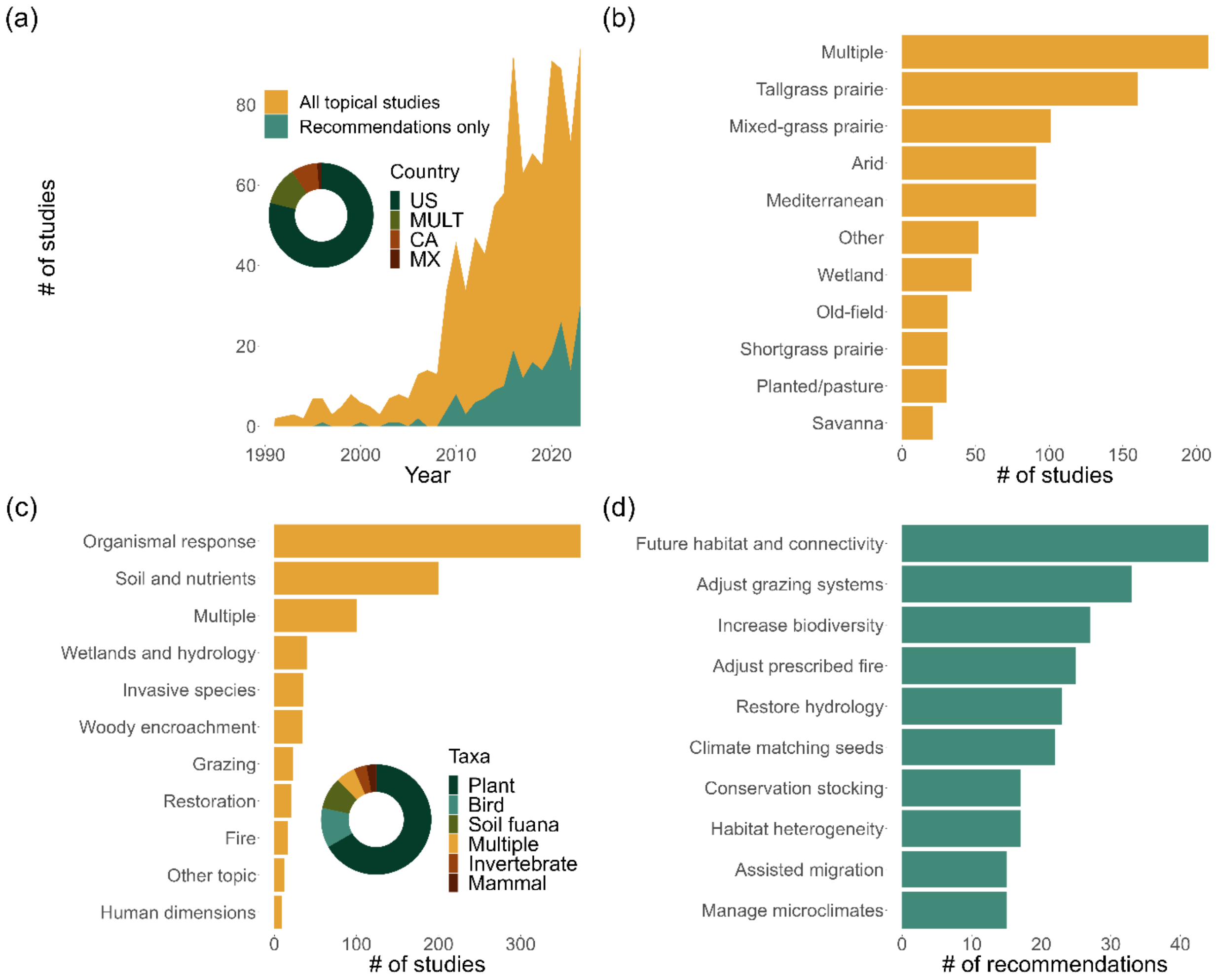
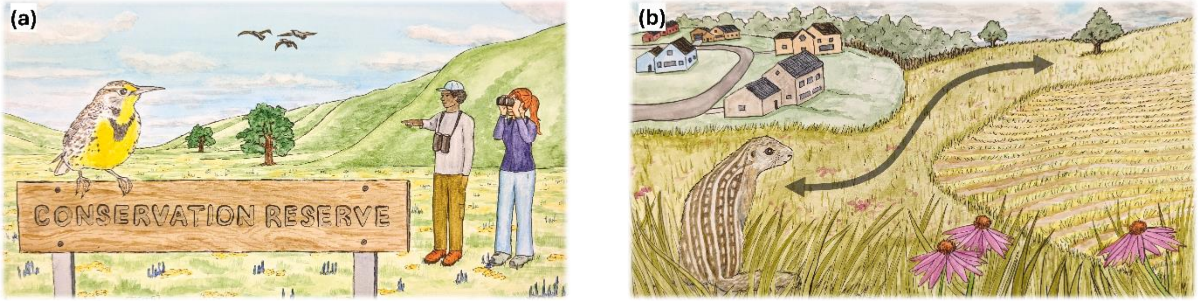
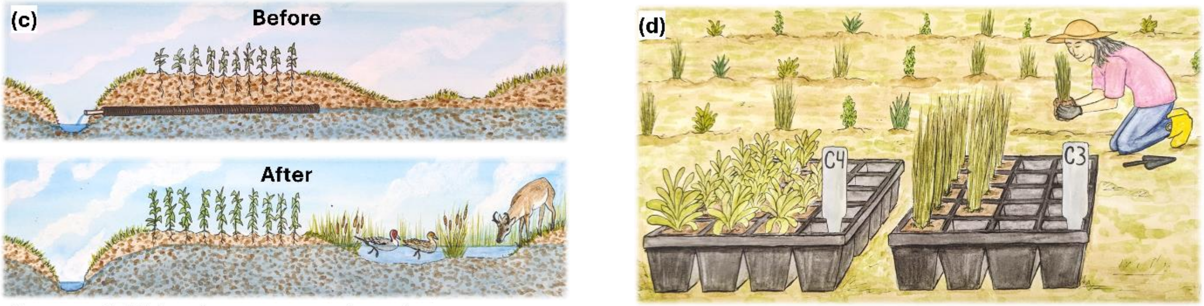


Fig. 3. Summaries of vote-count data from a systematic review examining the effects of climate change on grassland management in North America (*n* = 863). Interest in the topic has been increasing, but only a small proportion of studies made clear management recommendations for grassland climate adaptation **(a)**; studies have been conducted in a variety of grassland types in North America with tallgrass prairie receiving the most research attention **(b)**; the studies in our review focused on a range of topics, and the most frequently examined topic was the relationships between grassland organisms and climate variables (*n* = 373); among all studies, the taxonomic focus was biased towards plants, while other taxa were understudied **(c)**; the ten most commonly identified grassland climate adaptation practices **(d)**.



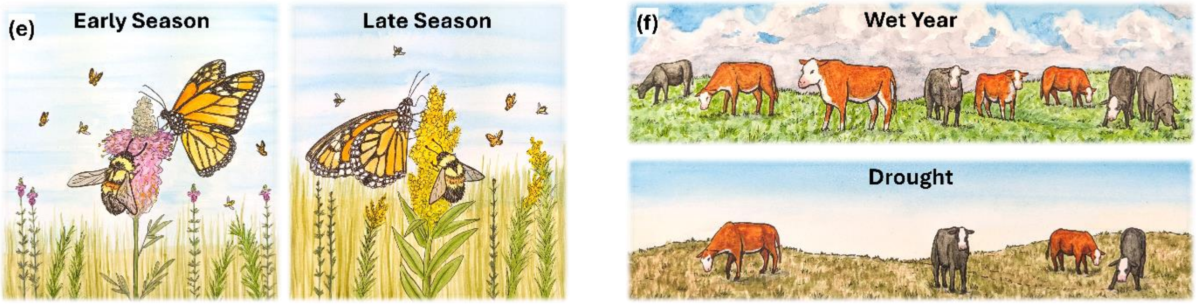
Strategy 1. Maintain and restore grassland extent
Example: Establish reserves in future climate refugia

Strategy 2. Increase landscape-scale resilience
Example: Increase habitat connectivity



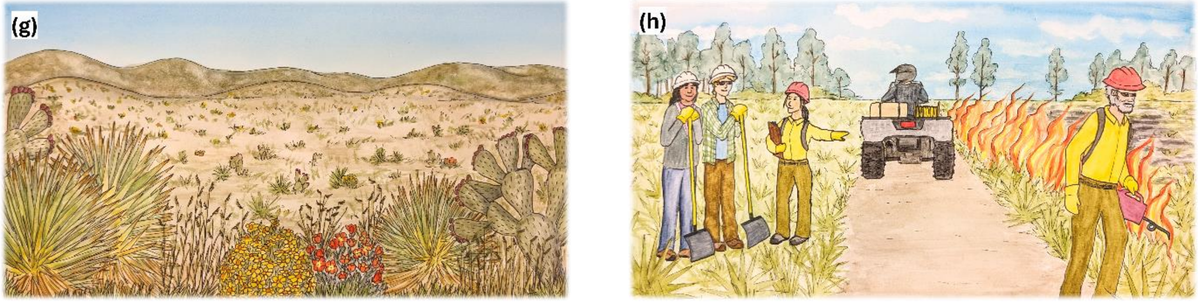
Strategy 3. Maintain ecosystem function
Example: Restore hydrology

Strategy 4. Increase biodiversity and heterogeneity
Example: Include functional diversity in plantings



Strategy 5. Reduce the impact of stressors
Example: Ensure pollinator resources season long

Strategy 6. Adjust site-level management
Example: Conservation stocking during drought



Strategy 7. Facilitate transitions
Example: Plant drought tolerant species

Strategy 8. Engage human communities
Example: Promote burn cooperatives

Fig. 4. Depictions of example adaptation tactics for each of the eight broad strategies **(a-h)** identified in the Grassland Climate Adaptation Menu. Artwork by V. Doebley at Wild Earth Lab.

Fig. 5. The Nature Conservancy's Samuel H. Ordway preserve is located in the Leola Hills Conservation Area, South Dakota, USA. The preserve is a largely intact mixed-grass prairie characteristic of the Prairie Potholes Regions and provides habitat for grassland birds and pollinators, as well as grazing capacity. Samuel H. Ordway served as a case study for the Grassland Climate Adaptation Menu, which was used to aid in creating a regional climate adaptation plan for the Leola Hills Conservation Area. Photo by Nate Powazki.

Chapter 3: Supplemental Materials

Appendix S1: Web of Science Search Terms

(((TS=(“climate change” OR “global warming”)) AND TS=(grassland OR "old field" OR parkland OR pasture OR prairie OR rangeland OR savanna)) AND TS=(adapt* OR amphibian OR animal OR avian OR biodiversity OR bird OR community OR "conservation planning" OR demog* OR "ecosystem service*" OR "ecosystem function*" OR encroach* OR exotic OR fire OR genetic* OR graz* OR hay* OR hydro* OR herp* OR insect OR invasive OR invert* OR mammal OR microb* OR mowing OR plant OR population OR productivity OR reptile OR reserve OR resili* OR restor* OR soil OR translocat* OR vegetation OR wildlife)) NOT TS=(Africa OR Asia OR Australia OR Argentina OR Britain OR Brazil OR China OR Eur* OR England OR France OR Germany OR Mongolia OR U.K. OR Russia OR "South America" OR Tibet*)

Appendix S2: Sample Workshop Agenda

Grassland Climate Adaptation Menu Workshop Agenda

Objectives

1. Become familiar with observed and projected climate change trends and impacts for the region.
2. Use the Adaptation Workbook process to consider climate change impacts and develop climate change adaptation plans for multiple large conservation landscapes
3. Gather feedback on the NIACS Grassland Adaptation Menu.

Agenda

Pre-work

- Before the first session, each landscape team should complete the worksheet for Step 1: Goals and Objectives.
- Goals are broad statements that describe a desired future condition and can have a longer time horizon (20 years or more). Objectives are specific, measurable statements that describe how you will attain the overall goal. You can have multiple objectives within a single goal, and objectives can have shorter or longer timeframes.
- Goals and objectives do not need to specifically address climate change adaptation. They should be written to reflect your conservation and management priorities. Part of the Adaptation Workbook is to scrutinize whether the individual objectives are still feasible, and then to develop adaptation actions that can help accomplish those objectives.
- *Optional*: arrange an introductory call to give an overview of the Adaptation Workbook process and answer any questions about articulating management goals and objectives.

Session 1 – Adaptation Workbook Steps 1 & 2

- Introductions (10 min.)
- Overview of Adaptation Workbook (15 min.)
- Review goals and objectives for each landscape and discuss any lingering questions (20 min.)
- Presentation from Northern Plains Climate Hub on climate change trends and climate vulnerability of northern plains grasslands and forests (60 min. including discussion)
- Small-group discussion: (60 min)
    - What are the priority climate impacts in your landscape?
    - How might climate change play out differently in your landscape than elsewhere in the region?
- Large-group discussion and next steps (15 min.)
- Before the next session, review NIACS Grassland Climate Adaptation Menu.

Session 2 – Adaptation Workbook Steps 3 & 4

- Review Step 2 discussion and lingering climate change questions (15 min.)
- Small-group discussion: (45 min.)
    - Discuss the feasibility of the Goals and Objectives for your landscape.
    - Does climate change significantly reduce the feasibility of any objectives? Do some objectives need to change?
- Large-group discussion to recap feasibility ratings (30 min.)
    - What were some of the climate change challenges your groups discussed? What were some of the climate change opportunities?
        - **Challenges to Meeting Management Objective with Climate Change:** Things that will make it harder to achieve the management objective due to climate change. ***Focus on challenges within control of your management (not global markets, policies, etc.)*
        - **Opportunities to Meeting Management Objectives with Climate Change:** Things that will make it easier to achieve the management objective due to climate change. ***Focus on challenges within control of your management (not global markets, policies, etc.)*
    - What is the feasibility of meeting your objectives under "business as usual" management?
    - Are there specific objectives that have a lower feasibility than others? Why?
- TNC Resilient and Connected Lands Tool (15 mins)
- Introduce NIACS Adaptation Menus (15 min.)
- Small-group work: (45 min.)
    - Brainstorm adaptation actions and tailor them to your landscape.
- Recap and next steps (15 min.)

Session 3 – Adaptation Workbook Steps 4 & 5

- Lingering questions about developing adaptation actions (15 min.)
- Small-group work: (45 min.)
    - Continue to brainstorm adaptation actions and tailor them to your landscape.
- Large-group discussion to review adaptation ideas (30 min.)
- Small-group discussion: (45 min.)
    - How will you know if your adaptation actions are effective? What monitoring will be necessary to guide future decisions?
- Feedback on Grassland Climate Adaptation Menu (30 min.)
- Recap and next steps (15 min.)

Appendix S3: Sample Grassland Adaptation Menu Feedback Form

Feedback Questionnaire – Grassland Adaptation Menu

What did you like about the menu?

What about the menu could use improvement?

Are there missing topics in the menu?

Other comments:

Appendix S4: Grassland Climate Adaptation Menu

Introduction to the Grassland Climate Adaptation Menu

Grasslands are highly threatened ecosystems globally (Hoekstra *et al* 2005, Scholtz and Twidwell 2022), yet they are also of great ecological, economic, and cultural importance providing dozens of ecosystem services (Bengtsson *et al* 2019, Zhao *et al* 2020). Unfortunately, climate change presents a significant threat to grasslands, and the wildlife, ecosystem services, and human communities that they support (Gibson and Newman 2019, Bardgett *et al* 2021). In North America, major grassland regions are projected to experience elevated temperatures, and more frequent and extreme droughts, but also increases in rainfall and extreme precipitation events in some regions (Calvin *et al* 2023, Gibson and Newman 2019). These changes will be coupled with elevated CO_2 concentrations, shifting and lengthening growing seasons, and increased climate variability. Thus, managers will face many challenges in maintaining the integrity and functionality of grassland ecosystems in the coming decades.

The purpose of this document is to provide managers with a tool to facilitate the planning and implementation of climate adaptation actions developed specifically for grassland ecosystems. Like other climate adaptation menus published by the U.S Forest Service and the Northern Institute of Applied Climate Science (NIACS) (https://forestadaptation.org/), the Grassland Climate Adaptation Menu is a structured hierarchy of management practices that move from broad concepts to specific actions. The menu is divided into three tiers including *strategies*, *approaches*, and *tactics* after Swanston et al. (2016). Strategies identify broad adaptation objectives, approaches are more specific methods used to implement strategies, and tactics are concrete, prescriptive actions taken for a given site or management application. Importantly, the menu is designed to be flexible, and multiple strategies and approaches may be used in combination. Further, though we provide many example tactics likely to be widely applicable, managers may also use the menu to aid in articulating other tactics that are more specific to a given location or objective. We also note that there is occasional redundancy in tactics, as some are relevant to multiple approaches. Finally, as in previous adaptation menus, the Grassland Climate Adaptation Menu is also designed so that it can be used in tandem with the Adaptation Workbook (Swanston *et al* 2016) and its online companion tool (https://adaptationworkbook.org/), or other climate adaption planning processes. The Adaption Workbook describes a five-step decision-making process to help managers *define* management objectives, *assess* climate threats, *evaluate* management objectives given climate vulnerabilities, *identify* adaptation approaches and tactics (using the menu), and create effectiveness *monitoring* plans. Below, we present a tabular summary of the Grassland Climate Adaptation Menu strategies and approaches, as well as a more detailed narrative version including example tactics and references.

Adaptation Strategies	Adaptation Approaches
1. Restore and maintain the extent of grasslands across the landscape	1.1. Conserve existing intact grasslands and high-value sites
	1.2. Mitigate major mechanisms of grassland conversion
	1.3. Create or maintain grassland habitats that include heterogeneity and redundancy in site types and environmental conditions
	1.4. Restore or establish grasslands in locations expected to remain suitable under future climate conditions
2. Increase landscape-scale resilience under future climate conditions	2.1. Maintain or create movement corridors
	2.2. Reduce fragmentation and create steppingstones
	2.3. Protect habitat along species range edges
3. Maintain fundamental ecosystem functioning in grasslands	3.1. Maintain or restore soil quality and nutrient cycling
	3.2. Emulate natural disturbance processes from grazing
	3.3. Emulate natural disturbance processes from natural and indigenous fire
	3.4. Maintain or restore hydrology
	3.5. Maintain pollination services
4. Increase biodiversity and heterogeneity in grassland communities	4.1. Maintain or restore genetic diversity of ecological communities
	4.2. Maintain and restore a diversity of native plants and functional groups (e.g., C3 and C4)
	4.3. Maintain and restore heterogenous vegetation structure
	4.4. Maintain or restore grassland-embedded wetland vegetation
5. Reduce the impacts of ecological and climate stressors	5.1. Reduce the impacts of climate on ecosystem functioning
	5.2. Reduce the impacts of climate on grassland wildlife
	5.3. Control woody encroachment
	5.4. Control invasive species
	5.5. Promote beneficial practices on agricultural lands

Adaptation Strategies	Adaptation Approaches
6. Adjust site-level management to align with new climate conditions	6.1. Adjust timing, frequency, and intensity of management actions (such as fire, grazing, and mechanical treatments etc.)
	6.2. Adjust planting and restoration practices to promote establishment of grassland vegetation under climate change
	6.3. Adjust the management of grassland-embedded wetlands to account for changes in hydroperiod, precipitation events, and drought
7. Facilitate transitions under climate change	7.1. Promote climate-tolerant plant genotypes and facilitate community shifts to better align with future climate conditions
	7.2. Engage in assisted migration to facilitate species range shifts
	7.3. Convert non-grassland systems to grassland where climate can no longer support current landcover
	7.4. Identify areas where continued investment in grassland conservation is a poor use of resources and allow transition
8. Engage human communities in grassland conservation and adaptation	8.1. Respect and incorporate indigenous knowledge and values in grassland management
	8.2. Invest in outreach and support for landowners and producers
	8.3. Develop and promote economic incentives for grassland climate adaptation and conservation on private lands
	8.4. Involve communities in management activities

GRASSLAND CLIMATE ADAPTATION MENU—COMPLETE NARRATIVE WITH EXAMPLE TACTICS

Strategy 1. Restore and maintain the extent of grasslands across the landscape

Grasslands are highly threatened ecosystems that have suffered conversion on a massive scale with only ~5% of grasslands protected globally (Hoekstra *et al* 2005). In North America, ~50% of original grassland extents have already been lost, and for some biomes such as tallgrass prairie, conversion rates have exceeded 90% (Augustine *et al* 2021, Comer *et al* 2018). Consequently, grassland species are fundamentally habitat-limited, and many of the ecosystem services that grasslands provide may be disrupted or disappear entirely (with or without climate change) if grassland losses continue. Therefore, restoring grassland habitat and preventing further conversion could be viewed as a prerequisite to any successful climate adaptation at large scales. Investment in maintaining grassland extent is a no-regrets strategy that will provide both present and future benefits. The approaches and tactics below provide some suggestions for conservation mechanisms, priorities, and planning in a climate context. Though most of the approaches in this menu are intended to be locally actionable, we appreciate that those related to landscape-scale planning may be beyond the control of managers operating locally. However, we felt it was important to articulate these broader goals to support regional planning efforts. Further, we believe some managers may find it useful to consider how their local activities fit into a larger climate adaptation context.

Approach 1.1. Conserve existing intact grasslands and high-value sites

Before European settlement, connected and intact native grasslands and savanna covered vast swaths of central North America (Samson *et al* 2004), and these large grassland landscapes facilitated ecosystem processes like natural fire regimes and movement of large grazers, supported high biodiversity, and stable meta-population dynamics (Augustine *et al* 2021, Scholtz and Twidwell 2022). Importantly, large and intact natural areas may also be more resilient to climate extremes (Martin and Watson 2016, Zuckerberg *et al* 2018). Today, large tracts of native grassland have become rare in many regions, and conserving these core grassland areas is an important priority both under climate change and for grassland conservation generally.

Example tactics

1.1.1 Focus landscape-scale habitat protection and restoration efforts in areas where habitat quality is highest (e.g., core intact grassland areas) (Comer *et al* 2018, Scholtz and Twidwell 2022).

1.1.2 Target previously undervalued landscapes or those that may have disproportionate impacts on species. For example, the Chihuahuan Desert grasslands of Mexico have been identified as a critical, and rapidly disappearing overwintering habitat for a large number of grassland birds that breed in the Great Plains, so investment in conserving these grasslands might have a high return for these species (Pool *et al* 2014).

1.1.3 Expand existing protected areas (Wulder *et al* 2018).

Approach 1.2. Mitigate major mechanisms of grassland conversion

Conversion to row-crop agriculture has historically been the single greatest source of grassland habitat loss in North America, and it remains a primary driver of conversion (Lark *et al* 2015, WWF 2024). As climate change advances, some regions of the Great Plains are likely to see greater precipitation and longer growing seasons, which could trigger additional conversion—particularly in northern grasslands (King *et al* 2018, Olimb and Robinson 2019). Energy development also occupies a substantial and rapidly increasing footprint in North American grasslands (Ott *et al* 2021), and it is critical that the increasing need for large wind and solar installations during the transition to clean energy is balanced with the need to protect intact grasslands. Conservation planning to ensure that future land use changes are focused in previously disturbed areas rather than intact grassland will be essential to long term preservation of large grasslands.

Example tactics

1.2.1 Remove perverse incentives in crop insurance by implementing and expanding provisions such as "sodsaver," which prevent crop insurance subsidies on converted native grasslands (Lark 2020).

1.2.2 Protect intact grassland patches in heavily impacted landscapes through conservation easements, Farm Bill programs, and land exchanges (Keyser *et al* 2019, Lichtenberg 2019). For example, CRP has benefited many grassland bird species by creating habitat in agricultural regions and slowing population declines (Pavlacky *et al* 2022).

1.2.3 Encourage grasslands planted for biofuel to be managed for wildlife, and promote the use of agricultural waste in place of biofuel crops to reduce grassland losses to biofuel production (Robertson *et al* 2012).

1.2.4 Use conservation planning to determine optimal locations for new energy development installations (such as landfills, agricultural areas, or previously disturbed habitat) and discourage conversion of intact grasslands for future lease sites (Ott *et al* 2021).

Approach 1.3. Create or maintain grassland habitats that include heterogeneity and redundancy in site types and environmental conditions

North American grasslands evolved under the influence of multiple disturbance processes (e.g., fire and grazing) that resulted in heterogenous vegetation structures (Fuhlendorf *et al* 2006, Samson *et al* 2004). This disturbance-driven heterogeneity also interacted with inherent heterogeneity in soil, topography, and hydrology creating additional diversity (Duquette *et al* 2022a). Heterogeneity is often considered to be foundational for grassland biodiversity and rangeland health (Fuhlendorf *et al* 2017), and in a climate adaptation context, habitat heterogeneity can also play an important role in creating thermal diversity that may provide refugia for grassland organisms under climate change (Bernath-Plaisted *et al* 2023b, Hovick *et al* 2014). Therefore, maintaining and protecting heterogeneity in grasslands, and ensuring redundancy in site types, are likely helpful in creating resilience.

Example tactics

1.3.1 Prioritize the protection of grasslands that contain heterogeneity in soil types, topographic complexity, plant communities, and riparian zones (Bachelet *et al* 2011, Duquette *et al* 2022a). For example, the nature conservancy has created a tool that identifies habitats expected to have high natural resilience to climate change based on topographic complexity and connectivity that managers could leverage (Anderson *et al* 2023).

1.3.2 Protect grassland-embedded wetlands to preserve heterogeneity and wetland ecosystem services For example, in Iowa, USDA easements on wetlands in agricultural areas supported habitat for amphibians, grassland birds, and pollinators, and sequestered carbon (Mushet and Roth 2020).

1.3.3 Restore and protect grassland sites that span spatial gradients in climate conditions and elevation. For example, a study of arthropod diversity in grasslands showed that protecting a natural range of variation in conditions had a greater influence on species richness than site-level management for a protected lands network (Pryke and Samways 2015).

1.3.4 Implement site-level management regimes that promote structural diversity, such as patch-burn grazing (e.g., allowing cattle to freely graze in pastures with burn and unburned areas) or conducting less complete prescribed burns (Fuhlendorf *et al* 2012).

1.3.5 Ensure redundancy of site types and ecotones across protected area networks to avoid losing unique communities as climate change affects different areas disproportionately (Halpin 1997)

<u>Approach 1.4. Restore or establish grasslands in locations expected to remain suitable under future climate conditions</u>

While conserving existing habitat is critical, climate change is expected to result in dramatic range losses and shifts for many grassland species (Kane *et al* 2017, Wilsey *et al* 2019), as well as changes in the distribution of grassland habitat itself (Jones 2019). Thus, conservation planning to predict where species will be in the future, coupled with efforts to preserve or create habitat in these places is an important component of adaptation planning for many grassland species (Grand *et al* 2019)

Example tactics

1.4.1 Use climate projections and species distribution models (SDMs) to model where grassland species will have future suitable habitats and delineate conservation priorities based on these projections (Nixon *et al* 2016). For example, for grassland birds, grasslands located in the Northern Great Plains and southern Canada have been identified as future habitat strongholds under climate change (Grand *et al* 2019).

1.4.2 Advocate for incorporation of climate priorities in large-scale grassland conservation mechanisms such as the Conservation Reserve Program (CRP) in the United States, and the reinstatement of the Permanent Cover Program (PCP) or other similar program in Canada to preserve grasslands under shifting agricultural zones (Cunningham 2022).

1.4.3 Take advantage of climate-driven habitat shifts to create new grassland regions, such as by pre-emptively introducing prescribed fire in regions where forests are shifting to savanna or creating flooded grassland habitat in areas where sea-level rise is displacing other vegetation (Bachelet *et al* 2011).

Strategy 2. Increase landscape-scale resilience under future climate conditions

Resilience is broadly defined as the capacity of ecosystems to recover from disturbance (Dakos and Kéfi 2022). At the landscape-scale, resilience requires the maintenance of large spatial processes that affect the ecology of species, such as connectivity (Cumming 2011). North American grasslands are highly fragmented landscapes, which may make isolated populations of grassland species more likely to be extirpated under climate variability, prevent gene flow, and interfere with the movements of species (Augustine *et al* 2021, Tack *et al* 2015, Wimberly *et al* 2018). This is critical, as grassland species may respond to climate change by tracking climate conditions through range shifts in the long term (Pfeifer-Meister *et al* 2013), and within-range dispersal to avoid climate extremes in the near-term (Bateman *et al* 2015). Further, genetic variants and locally-adapted phenotypes of species in certain regions may be better adapted to future climate conditions (Anderson *et al* 2015, Cullingham *et al* 2023, Johnson *et al* 2015). Thus, allowing free movement of individuals (or seeds) from these populations across the landscape may enhance climate resilience and adaptive capacity of species.

Approach 2.1 Maintain or create movement corridors

Corridors that facilitate the movement of species across the landscape are important in fragmented biomes such as grasslands (Öckinger and Smith 2008). These allow for the movement of migratory species, such as birds and butterflies (Hill and Renfrew 2019), as well as local dispersal and range expansions of other species, including plants that rely on animal movements for pollination and dispersal (Tewksbury *et al* 2002). Even narrow strips of habitat can act as corridors, and tactics like prairie strips and protecting riparian corridors can help increase connectivity (Naiman *et al* 1993, Schulte *et al* 2017).

Example tactics

2.1.1 Use geospatial information and animal movement data to identify and protect new and existing migratory corridors and dispersal routes for target species. This approach has been used to identify conservation priorities for sensitive grassland species like Greater Prairie-chicken (Roy and Gregory 2019).

2.1.2 Protect riparian habitat in grassland areas through grazing exclosures and habitat buffers to create corridors with high biodiversity and connectivity (Cole *et al* 2020).

2.1.3 In agricultural areas, use prairie strips to create dispersal corridors through low-quality habitats (e.g., cropland matrix) (Schulte *et al* 2017).

2.1.4 Plant powerline rights-of-ways and roadsides with native grassland plants to create grassland habitat corridors (Garfinkel *et al* 2023, Russell *et al* 2005).

2.1.5 Install wildlife bridges and underpasses on busy roads in grassland areas and use wildlife-friendly fences (e.g., for Pronghorn etc.) to reduce movement barriers (Jones *et al* 2018).

Approach 2.2 Reduce fragmentation and create steppingstones

In addition to connecting habitat patches directly through corridors, increasing the size of habitat patches, and reducing the distance between them can also increase landscape connectivity and reduce fragmentation. Large habitat patches often provide better habitat for grassland species and may be more resilient to climate change (Augustine *et al* 2021, Ribic *et al* 2009, Zuckerberg *et al* 2018). At the same time, smaller habitat patches can also provide steppingstones to facilitate species range shifts and act as refugia (Hannah *et al* 2014). Thus, efforts to expand existing habitat patches and strategically create or preserve habitat patches that can functionally reduce fragmentation may create greater resilience.

Example tactics

2.2.1 Consider landscape context in prioritizing habitat conservation and restoration, and target patches near other large grasslands, or those that may help connect other patches. Landscape context has consistently been shown to be important for species like grassland birds (Herse *et al* 2020).

2.2.2 Invest in expanding protected areas to increase the size and number of habitat patches on the landscape (Fore *et al* 2015).

2.2.3 In agricultural grassland areas, merge habitat patches by restoring cropland to permanent cover at key locations. This could be accomplished through Farm Bill programs, easements, or other forms of land acquisition (Spencer *et al* 2017).

Approach 2.3 Protect habitat along species range edges

Populations living at the edges of a species' range often experience more extreme or novel environmental conditions relative to those in the core range. Consequently, these populations may harbor unique local adaptations and genetics that may better prepare them for climate change adaptation (Rehm *et al* 2015). Range edges can also provide refugia from climate extremes affecting the core range—particularly for mobile species like grassland bird species (Bateman *et al* 2015)—and serve as launching points for species range shifts with a changing climate. Therefore, special attention should be given to conserving range-edge habitats for species of high conservation interest when possible.

Example tactics

2.3.1 Focus conservation efforts at the northern edge of distributions for target species in anticipation of future range shifts (Nixon *et al* 2016).

2.3.2 Use conservation planning to create habitat corridors that span/connect species' ranges (Dixon *et al* 2006).

2.3.3 At northern range boundaries, protect grassland habitat along prairie-forest ecotones where forests are anticipated to decline under future climate change (Frelich and Reich 2010).

Strategy 3. Maintain fundamental ecosystem functioning in grasslands

Grassland vegetation, soil, and wetlands provide many ecosystem services including erosion control, carbon sequestration, water resources, food and fiber, and biodiversity (Zhao *et al* 2020). However, these services can only be sustained through the maintenance of grassland structure and function. Grasslands are disturbance-maintained ecosystems that occur in areas where precipitation is too low and irregular to support woody vegetation (Gibson 2009), and or where fire and grazing maintain herbaceous structure (Samson *et al* 2004). In modern times, the grazing of domestic cattle and prescribed fire have become the primary disturbance mechanisms in most North American grasslands (Samson *et al* 2004). These activities are critical to maintaining grasslands by preventing woody encroachment, creating heterogeneity that supports biodiversity, and redistributing nutrients (Fuhlendorf and Engle 2004, Fuhlendorf *et al* 2006, Ratajczak *et al* 2016). Similarly, protecting grassland-embedded wetlands, and considering how land use and management activities impact soil health are also fundamental to maintaining the integrity of grasslands (Conant *et al* 2017, Rhodes *et al* 2023). The impacts of climate change on grasslands at any given location will largely be beyond the control of local managers but ensuring that grasslands are properly maintained can help increase the integrity and resilience of grassland services now and under future climate regimes.

Approach 3.1 Maintain or restore soil quality and nutrient cycling

Grassland soils are some of the most productive in the world because grassland plants allocate a high proportion of resources below ground (e.g. extensive root systems) creating high soil organic carbon and diverse soil microbiomes. Consequently, grassland soils sequester large amounts of carbon and provide productive conditions for agriculture, grazing, and diverse native plant communities. However, grassland soils are also highly sensitive to management type and intensity, as well as climate forcings (Bai and Cotrufo

2022, Mayel *et al* 2021). There are many tools available to managers to maintain and improve grassland soil quality. Some examples include rotational grazing to enhance carbon sequestration (Holechek *et al* 2020), increased plant diversity to improve soil health and nutrient utilization (Tilman *et al* 1996), and the use of soil amendments to improve productivity under changing climate conditions (Mayer and Silver 2022).

Example tactics

3.1.1 Apply prescribed fire to increase nutrient turn-over (Augustine *et al* 2014).

3.1.2 Use carbon-rich soil amendments such as biochar to increase soil organic carbon and primary productivity (Mayer and Silver 2022).

3.1.3 Use lime soil amendments to combat anthropogenic acid deposition and increase productivity in acidic soils (Heyburn *et al* 2017).

3.1.4 Promptly restore diverse native cover following a surface disturbance in grasslands to reduce erosion and prevent the establishment of invasives (Walsh and Rose 2022).

3.1.5 Minimize soil compaction by reducing the use of heavy machinery where possible and taking other mitigation steps (e.g., debris mattes, dual tires, rubber tracks) (Batey 2009).

Approach 3.2 Emulate natural disturbance processes from grazing

Native mammalian grazers played a critical role in the evolution and maintenance of grassland ecosystems (Gibson 2009, Samson *et al* 2004). Although domestic cattle have largely replaced native grazers in this role following European settlement of the Great Plains, modern grazing practices have often created homogenous range conditions that tend to reduce biodiversity and may be less beneficial for rangeland health (Fuhlendorf *et al* 2012). Grassland managers can enhance heterogeneity, biodiversity, and soil health by implementing alternative grazing practices that more closely resemble historic grazing regimes, (Duquette *et al* 2022a, 2022b, Fuhlendorf *et al* 2006), and by protecting native grazers that remain on the landscape (Haun *et al* 2024). In some cases, mowing and mechanical clearing can also act as surrogates for grazing disturbance (Collins *et al* 1998).

Example tactics

3.2.1 Implement rotational grazing and adaptive multi-paddock (AMP) systems to improve flexibility under changing climate, increase structural heterogeneity, and increase carbon sequestration (Teague and Kreuter 2020).

3.2.2 Protect remaining native grazers such as Prairie Dogs (*Cynomys sp.*), which have been linked to greater grassland bird diversity, for example (Haun *et al* 2024).

3.2.3 Reintroduce larger native grazers such as bison (*Bison sp.*) in large and connected grassland areas to restore more heterogeneous grazing patterns and improve the tolerance of herds to heat and drought relative to cattle (Harms 2022). In tallgrass prairie, bison reintroduction has been shown to improve grassland plant diversity and resilience (Ratajczak *et al* 2022).

3.2.4 Where grazing is not practical, use spot-mowing or mechanical removal of woody species to maintain grassland vegetation structure and emulate disturbance (Halpern *et al* 2012, Miller *et al* 2017).

Approach 3.3. Emulate natural disturbance processes from natural and indigenous fires

Like grazing, fire is a fundamental process that has contributed to the maintenance of grassland ecosystems and structural heterogeneity over time (Gibson 2009, Samson *et al* 2004). Before European settlement, fires in North American grasslands occurred naturally and were applied with intention by indigenous peoples (Roos *et al* 2018). Fire can improve soil quality (Augustine *et al* 2014), control invasive species (Glassman *et al* 2023), and increase grassland bird diversity (Fuhlendorf *et al* 2006, Hovick *et al* 2015). Importantly, fire is also one of the primary tools available to combat woody encroachment (Scholtz *et al* 2022)—a management issue likely to get worse with climate change (Van Auken 2009).

Example tactics

3.3.1 Conduct prescribed fire at sufficient frequency to mimic natural fire regimes and control woody species, particularly in more mesic tallgrass ecosystems where fire plays a greater role in controlling woody species (Ratajczak *et al* 2016).

3.3.2 Allow prescribed fires to burn with varying intensities, including incomplete burns, to mimic the heterogeneity of wildfire. One way this can be done is by incorporating more information on weather, time of day, and fine-fuels into burn plans to achieve different results (Hill *et al* 2017).

Approach 3.4 Maintain or restore hydrology

Grassland-embedded wetlands are important components of many grassland ecosystems and they contribute to local water resources (Bengtsson *et al* 2019), inherent heterogeneity (Duquette *et al* 2022a), and wildlife habitat (Niemuth and Solberg 2003). Under climate change, they may also become increasingly valuable as hydrological refugia (McLaughlin *et al* 2017). However, grassland-embedded wetlands are often threatened both by surrounding land uses and changes in precipitation patterns associated with climate change (Londe *et al* 2024, McKenna *et al* 2021).

Example tactics

3.4.1 Remove drain tiles and allow wetlands to reform (Biebighauser 2007). Recent advances in remote sensing have made it easier to locate old drain tiles, using drones for example (Becker *et al* 2021).

3.4.2 Control woody species invasions that may deplete water tables (because woody plants have higher water uptake rates) (Acharya *et al* 2017).

3.4.3 Reduce groundwater withdrawals in recharge areas (e.g., playa lakes, prairie potholes). For example, use dryland-appropriate crops and invest in more efficient irrigation systems to reduce water use (Rhodes *et al* 2023).

3.4.4 Retain livestock ponds and agricultural wetlands to provide permanent mesic habitats within grasslands (Knutson *et al* 2004, Swartz *et al* 2019).

3.4.5 Consider the impacts of adjacent land use on water runoff and wetland recharge. For example, grazing and burning can increase wetland recharge by reducing vegetation retention of run off (Johnson and Poiani 2016).

3.4.6 Maintain plant litter in grasslands to help to retain soil moisture and boost productivity (Deutsch *et al* 2010).

3.4.7 Exclude cattle from riparian areas to protect water quality and prevent bank erosion with loss of riparian vegetation (Krall *et al* 2021).

Approach 3.5 Maintain pollination services

Pollination is an essential ecosystem service provided by grasslands that plays an important role in agriculture as well as in supporting biodiversity (Hanberry *et al* 2021, Zhao *et al* 2020). Pollinators in North American grasslands are already threatened by habitat loss, domesticated bees, and pesticides (Hanberry *et al* 2021), and climate change will likely further threaten pollinators through drought, reduced floral resources, and phenological mismatch (Brown *et al* 2016, Gallagher and Campbell 2017, Petanidou *et al* 2014). Therefore, management to support pollinator species may be needed to maintain pollinator services under climate change.

Example tactics

3.5.1 Maintain and improve pollinator networks by increasing floral diversity throughout the growing season (Guzman *et al* 2021, Orford *et al* 2016, Timberlake *et al* 2019).

3.5.2 Ensure that floral resources are replaced with native species following invasive species control actions, as some non-native plants do provide important forage for pollinators. For example, a study in oak savanna documented butterflies using 83% non-native forage (Rivest *et al* 2023).

3.5.3 Retain unburned areas as pollinator refugia, as different pollinator groups (e.g., bees vs butterflies) may respond differently to fire (Hanberry *et al* 2021, Leone *et al* 2022).

Strategy 4. Increase biodiversity and heterogeneity in grassland communities

Biodiversity contributes to stability and resilience in grassland ecosystems (Tilman *et al* 2006, Wang *et al* 2019a), as species may differ in sensitivity to variation in climate extremes, competition with invasive species, and different forms of disturbance (Catford *et al* 2020). In a climate adaptation context, enhancing the diversity of communities and leveraging existing genetic and phenotypic variation across the range of species may be a conceptually simple and effective way to create greater resilience in the face of climate change (Ahlering and Binggeli 2022, Craine 2013, Galatowitsch *et al* 2009). This can be accomplished through a diversity of approaches and tactics such as climate-appropriate seed-sourcing practices (Nolan *et al* 2023), more incorporation of functional diversity in plantings (Havrilla *et al* 2023), and management practices that create heterogeneity (Fuhlendorf and Engle 2004).

<u>Approach 4.1 Maintain or enhance genetic diversity of ecological communities</u>

Many species with relatively large geographic ranges display variation in genetics and locally adapted phenotypes across these ranges (Galliart *et al* 2019, Gray *et al* 2014). Particularly in grassland plants, some genetic variants may be better able to tolerate temperature and precipitation extremes, and including these genotypes in plantings and restorations may not only increase resilience to climate disturbances like drought, but also facilitate rapid evolutionary response to novel conditions under climate change (Avolio *et al* 2013, Whitney *et al* 2019). Similarly, sourcing seeds that are adapted to climate zones more like projected future conditions (such as hotter and dryer portions of species' ranges), or representing a greater diversity of climate zones in seed mixes, can make grassland restorations more resilient to climate extremes (Ahlering and Binggeli 2022, Nolan *et al* 2023).

Example tactics

4.1.1 Overseed grasslands and restorations with seed mixes from multiple collection zones to increase genetic diversity, or match seed-sourcing with projected future climate zones (Havens *et al* 2015).

4.1.2 Introduce propagules from range edges or hotter and dryer climate zones to increase genetic diversity and introduce genotypes that may be better adapted to future conditions (Phillips-Mao *et al* 2016).

<u>Approach 4.2 Maintain and restore a diversity of native plants and functional groups (e.g., C3 and C4)</u>

Generally speaking, biodiversity is positively associated with many aspects of ecosystem functioning (Hooper *et al* 2005, van der Plas 2019). In grasslands, greater plant diversity can improve primary productivity, soil health, and pollinator diversity under climatic variability (Cowles *et al* 2016, Hanberry *et al* 2021, Schaub *et al* 2020, Tilman *et al*

1996, Volaire *et al* 2014). One key functional distinction between grassland plants is the use of alternative carbon pathways where C3 species tend to perform better in cooler conditions (but also higher CO_2 concentrations) while C4 species are generally more tolerant of heat (Havrilla *et al* 2023). Other kinds of functional traits may also be important to incorporate, such as narrow-leafed plants that display greater drought tolerance (Craine *et al* 2013), or plant groups that perform specific nutrient cycling functions like legumes (Volaire *et al* 2014). Increasing different kinds of biodiversity and functional diversity in grasslands can be viewed as a kind of bet-hedging under increasing climate variability and will likely help to improve the overall resilience of many grassland communities.

Example tactics

4.2.1 Prioritize the conservation of grasslands with high species richness or rare species. This can be accomplished through the use of biodiversity hotspot analyses performed for major grassland regions such as the Great Plains (e.g., Gary, Mougey, McIntyre, & Griffis-Kyle, 2019).

4.2.2 Diversify pastures and planted forage to include greater functional diversity (e.g., including legumes) and consider future climate conditions in forage selection. A study in Michigan identified perennial ryegrass (*Lolium multiflorum*) and red clover (*Trifolium patense*) as a more resilient tame-species composition than many traditional forage species used in the Midwest, for example (Rojas-Downing *et al* 2018).

4.2.3 Overseed grassland restorations with high-diversity mixes including both C3 and C4 species (Piper 2014).

4.2.4 Although woody plants must generally be controlled in grasslands, in some cases, allowing a low-density of native shrub species may enhance functional diversity and act as thermal refugia for some species. For example, multiple studies have documented the use of shrubs as thermal refugia by grassland birds (Palmer *et al* 2021, Ruth *et al* 2020).

Approach 4.3 Maintain and restore heterogenous vegetation structure

Maintaining structural heterogeneity is considered a key management goal in grasslands (Fuhlendorf *et al* 2017), and heterogeneous grasslands support increased biodiversity for many taxa (Duquette *et al* 2022a, Fuhlendorf *et al* 2006, Johansen *et al* 2019, McGranahan *et al* 2018), as well as promote nutrient cycling (Bloor *et al* 2020). Further, greater structural diversity in grasslands may also create thermal heterogeneity, which could allow species to buffer themselves from climate extremes through selection of microhabitat (Bernath-Plaisted *et al* 2023b, Carroll *et al* 2016, Hovick *et al* 2014). These microclimates appear to be of special importance to insects and pollinators, which may require refugia from management practices that homogenize conditions and reduce cover (Gardiner and Hassall 2009, Hanberry *et al* 2021, Thomas *et al* 2009).

Example tactics

4.3.1 Implement disturbance regimes that foster structural heterogeneity, such as rotational grazing, patch-burn grazing, variable stocking rates, and incomplete burns (Duquette *et al* 2022b, Hovick *et al* 2015).

4.3.2 Restore distinct vegetation patches by planting species-mixes of contrasting heights (Lengyel *et al* 2020).

4.3.3 Create refugia by leaving taller patches of vegetation unburned or un-mowed (Bernath-Plaisted *et al* 2023b, Steenvoorden *et al* 2019).

4.3.4 Restore and maintain microtopography (including ant mounds) which may support heterogeneity in plant phenologies to support pollinators (Hansen *et al* 2023).

Approach 4.4. Maintain or restore grassland-embedded wetland vegetation

Grassland-embedded wetlands are an important component of grassland biodiversity, and in the Prairie Pothole region, they once occupied 20-60% of the landscape (Seabloom and van der Valk 2003). Like upland grasslands, species and functional diversity in wetland vegetation can enhance stability and resilience to climate extremes (Brotherton and Joyce 2015). Wetland vegetation can also play important roles in soil stabilization and flood control (Acreman and Holden 2013, Ford *et al* 2016).

Example tactics

4.4.1 Control the invasion of woody and non-native species in wetlands as these can reduce native plant diversity and alter surrounding grasslands (Dahl *et al* 2020).

4.4.2 Remove legacy sediments to control weedy and invasive species; augment seed banks as needed to enhance richness following treatment (Beas *et al* 2013).

4.4.3 Create prescribed burn plans for wetland units, particularly in ungrazed areas where woody species and invasives may be poorly controlled (Sonnier *et al* 2023).

4.4.4 In agricultural areas, buffer wetlands with native vegetation strips to reduce sediments and maintain water quality (Haukos *et al* 2016, Stephenson *et al* 2024).

Strategy 5. Reduce the impacts of ecological and climate stressors

Grassland ecosystems and the organisms that inhabit them face numerous stressors and sources of habitat degradation (Augustine *et al* 2021, Bardgett *et al* 2021). These include many of the traditional focuses of grassland management such as woody encroachment (Morford *et al* 2022, Scholtz *et al* 2018b), invasive species (Grant *et al* 2020, Printz and Hendrickson 2015), fire suppression (Ratajczak *et al* 2014a, Samson *et al* 2004), and grazing challenges (Fuhlendorf *et al* 2012, Samson *et al* 2004). Climate change is likely to exacerbate and interact with many of these management issues, as well as expose grassland organisms to increasingly extreme environmental conditions (Murali *et al* 2023, Ratajczak *et al* 2019). Consequently, mitigating the effects of both existing ecological stressors and emerging climate stressors is an important aspect of grassland climate adaptation.

Approach 5.1 Reduce the impacts of climate on ecosystem functioning

Climate change is projected to bring elevated temperatures, more frequent and severe drought, and more intense precipitation events to many grassland areas in North America (Calvin *et al* 2023, Cook *et al* 2022, Patricola and Cook 2013). Climate extremes can negatively impact the integrity of grassland ecosystems in many ways. For example, heat and drought can reduce the primary productivity of grassland plant communities (Carroll *et al* 2021, Smith *et al* 2024), and extreme precipitation events may trigger flooding and erosion. Clearly, managers cannot control what kinds of climate extremes occur at grassland sites, but there are management actions that can be taken to help reduce the ecological impacts of these events.

Example tactics

5.1.1 Maintain and restore grassland-embedded wetlands, as wetlands can capture excess runoff during precipitation events providing flood mitigation, and also store water to reduce drought stress (Ferreira *et al* 2023).

5.1.2 For smaller properties, consider active irrigation to mitigate extreme drought (Greenwood *et al* 2016).

5.1.3 On rangelands, implement conservation stocking rates during drought to prevent overgrazing when primary productivity is low (Briske *et al* 2015).

Approach 5.2 Reduce the impacts of climate on grassland wildlife

Many grassland organisms are sensitive to temperature and precipitation conditions, and grassland species will likely be increasingly exposed to novel and extreme climate events (Murali *et al* 2023). For example, grassland birds suffer reduced nesting success with elevated maximum temperatures, drought, and heavy precipitation (Conrey *et al* 2016, Maresh Nelson *et al* 2023). Phenological shifts associated with climate change may also be problematic for grassland wildlife such as pollinators, which may become increasingly mismatched with floral resources (Freimuth *et al* 2022, Pyke *et al* 2016). Therefore, managers may wish to take targeted, site-level actions to buffer vulnerable species from climate extremes.

Example tactics

5.2.1 Maintain and deploy natural and artificial water sources for mammals and other wildlife to mitigate the effects of drought (Rich *et al* 2019, Rosenstock *et al* 1999).

5.2.2 Minimize withdraw and drainages, and manage adjacent land uses (e.g. grazing instead of cropland) to maintain wetland hydroperiods for waterfowl during droughts (Londe *et al* 2024, McKenna *et al* 2021).

5.2.3 During heatwaves and droughts, refrain from intensive management activities (e.g., mowing) that may reduce vegetation cover, which might provide thermal and moisture refugia for some species (Bernath-Plaisted *et al* 2023b).

5.2.4 Enhance the diversity of flowering plants at sites, and include both early and later-flowering species in seed mixes to provide season-long floral resources for pollinators (Guzman *et al* 2021).

Approach 5.3 Control woody encroachment

Woody encroachment is a significant threat to grasslands globally and in North America (Morford *et al* 2022, Scholtz *et al* 2018b, Van Auken 2009). Woody species may degrade grasslands by reducing vegetation cover and promoting erosion (Li *et al* 2022), depleting water tables (Acharya *et al* 2017), and reducing habitat quality for some grassland bird species (Andersen and Steidl 2022). In some cases, woody encroachment can lead to ecosystem state-shifts that are difficult to reverse (Ratajczak *et al* 2014b). Woody encroachment is expected to increase with climate change as shrubs benefit from elevated CO_2 levels (Manea and Leishman 2019). Therefore, controlling woody encroachment may help to reduce ecological stressors in grassland ecosystems, especially as climate change advances.

Example tactics

5.3.1 Increase the frequency of prescribed fire intervals to prevent and slow woody encroachment (Ratajczak *et al* 2016, 2014b).

5.3.2 Implement prescribed fire with higher intensity than natural fire regimes in the area to increase the efficacy of shrub control where invasions are advanced (Scholtz *et al* 2022).

5.3.3 Combine fire with herbicide applications to address major woody plant invasions (Scholtz *et al* 2018a).

5.3.4 Engage in mechanical removal of shrubs, especially when the return of natural fire intervals is not adequate to reverse encroachment (Lett and Knapp 2005).

Approach 5.4 Control invasive species

Invasive species are a form of habitat degradation that widely affects North American grasslands (DeKeyser *et al* 2013, Grant *et al* 2020, Samson *et al* 2004). Non-native plants can stress grassland ecosystems in many ways such as reducing plant diversity (Kobiela *et al* 2017), altering soil properties (Koteen *et al* 2011), decreasing insect abundance (Litt *et al* 2014), and lowering reproductive success in grassland birds (Coon *et al* 2022). Climate change will likely make invasive species increasingly problematic in grasslands as many non-native plants could benefit from earlier growing seasons and increased precipitation in some regions (Catford and Jones 2019).

Example tactics

5.4.1 Target invasive species with herbicide applications (Ruffner and Barnes 2010).

5.4.2 Manipulate timing and intensity of grazing to target invasives (Firn *et al* 2013).

5.4.3 Use prescribed fire to combat invasive species, and take advantage of climate events such as drought to maximize negative effects on non-native species (Havill *et al* 2015).

5.4.4 Target invasive species with mowing to help give native species a competitive advantage (Wilson and Clark 2001).

5.4.5 Promptly establish native cover after disturbance to prevent invasive establishment, and integrate invasive control efforts with post-treatment native seeding to control re-establishment (Bucharova and Krahulec 2020, Pyke *et al* 2013).

5.4.6 Minimize cutting of new roads and maintain "roadless refugia" areas where non-native species will be less likely to invade (Gelbard and Harrison 2003).

5.4.7 Ensure that cattle are being fed native forage before introducing to a property, as cattle can vector invasive species through droppings (Chuong *et al* 2016).

Approach 5.5 Promote beneficial management practices on agricultural lands

Conversion of grasslands to agriculture is the primary cause of historic and current grassland habitat loss in North America (Augustine *et al* 2021, Samson *et al* 2004, WWF 2024). Consequently, most remaining grassland habitats are embedded in agricultural landscapes, and many grassland organisms also use agricultural habitats and thus are affected by the management of these lands (Holzschuh *et al* 2008, Suraci *et al* 2023). Similarly, the management of croplands can also affect the ecosystem functioning of adjacent grasslands through erosion, surface runoff, and nutrient enrichment (Schulte *et al* 2017). Promoting agricultural practices that benefit grassland wildlife and sustain ecosystem services may help to support grasslands as they come under increasing climate stress.

Example tactics

5.5.1 Retain semi-natural areas and prairie strips in croplands to increase biodiversity and reduce leaching and runoff (Kemmerling *et al* 2022, Schulte *et al* 2017).

5.5.2 Reduce the use of lethal neonicotinoid compounds which have contributed to the decline of pollinators and grassland birds (Main *et al* 2021, Stanton *et al* 2018)—use integrated pest management (IPM) alternatives (Furlan and Kreutzweiser 2015).

5.5.3 Promote regenerative farming practices such as diversified cropping and no-till agriculture (LaCanne and Lundgren 2018) No-till practices, can improve soil quality in grassland-adjacent cropland and provide better habitat for some grassland species (VanBeek, Brawn, & Ward, 2014).

5.5.4 Plant winter cover crops to reduce erosion and enhance soil quality (Blanco-Canqui *et al* 2015).

5.5.5 Manage post-harvest crop residuals to provide food resources for migrating waterfowl and cranes (Sherfy *et al* 2011).

5.5.6 Reduce or delay mowing and haying activities in agricultural grasslands and road-side ditches to avoid destroying grassland bird nests (Tews *et al* 2013).

Strategy 6. Adjust-site level management to align with new climate conditions

Grasslands are intensively managed ecosystems, and managers often engage in activities such as burning, grazing, and mowing to maintain structure and function in grasslands (Davison and Kindscher 1999, Samson *et al* 2004). However, as climate conditions shift and extremes become increasingly common, managers may need to consider adjusting the timing, intensity, and types of management activities they implement as part of a climate adaptation strategy. Likewise, new practices may be needed to improve the success of grassland restoration efforts under climate change (Lyons *et al* 2023), and maintain the integrity of grassland-embedded wetlands (Londe *et al* 2023).

Approach 6.1 Adjust timing, frequency, and intensity of management actions (such as fire, grazing, and mechanical treatments, etc.)

Climate is an important mediator of many grassland management activities and may affect how impactful these practices are, or whether they can be implemented at all. For example, increased drought may reduce the sustainability of grazing (Holechek *et al* 2020), and changing climate conditions could reduce or shift traditional windows for prescribed burns (Yurkonis *et al* 2019).

Example tactics

6.1.1 Adopt flexible burn schedules that can accommodate shifting windows rather than attempting to follow rigid prescriptions (Yurkonis *et al* 2019)

6.1.2 Reduce stocking rates to avoid rangeland degradation and minimize economic risk under increasing drought frequency (Joyce *et al* 2013)

6.1.3 Adjust haying dates to track green-up patterns in grasslands, but avoid haying during critical nesting periods for grassland birds, which may not advance their phenology at the same pace (McGowan *et al* 2021)

6.1.4 Perform management activities when climate conditions are optimal. For example, woody-species control activities can be performed in wet years to increase the chances of herbaceous re-establishment (D'Odorico *et al* 2012)

Approach 6.2 Adjust planting and restoration practices to promote establishment of grassland vegetation under climate change

Given the extent of grassland loss in North America to-date (Comer *et al* 2018), restoration of grassland habitat is critical to the conservation of grassland biodiversity. However, under a more variable and extreme climate, practitioners of grassland restoration must seek to create diverse and resilient grassland communities that can successfully be established under a broader range of conditions (Lyons *et al* 2023).

Example tactics

6.2.1 Create "safe sites" for seed bed establishment and enhance diversity by restoring microtopography and stone cover (Biederman and Whisenant 2011)

6.2.2 Remove top soil before restoration or temporarily plant with high-productivity crops to remove agricultural nutrient legacies that homogenize restorations (Lyons *et al* 2023)

6.2.3 Account for the condition of microbial and fungal communities at restoration sites. Inoculating some plants with appropriate microbes, and certain kinds of cellulose additions can enhance establishment and carbon sequestration (Docherty and Gutknecht 2019, Lyons *et al* 2023)

6.2.4 When sourcing seeds, reference climatically defined seed transfer zones (STZ) to select appropriate species for new climate conditions, and create diverse and resilient seed mixes (Bower *et al* 2014)

Approach 6.3 Adjust the management of grassland-embedded wetlands to account for changes in hydroperiod, precipitation events, and drought

Changes in temperature and precipitation associated with climate change may change the hydrology of grassland-embedded wetlands. However, these changes will vary widely depending on the aridity of the region, as well as variation in projected precipitation changes (Fay *et al* 2016). Thus, some wetlands may experience drying, reduced hydroperiods, and loss of productivity while others may experience increased water levels and sediments from heavy precipitation. These changes could also interact with shifts in agricultural land-use associated with climate change, which are likely to reduce wetland productivity through increased water withdraws (Rashford *et al* 2016). Consequently, management actions specific to local hydrological conditions may be needed to maintain grassland-embedded wetlands in a changing climate.

Example tactics

6.3.1 Minimize cropland near wetlands, as this land use can deplete water levels in natural wetlands (Rashford *et al* 2016, Tsai *et al* 2007)

6.3.2 Install infrastructure and vegetation features that control the flow of water and sediments (e.g., one-rock damns), and also allow for timed release of water (such as flood irrigation of fields for migrating shorebirds and waterfowl) (Pierce *et al* 2012)

6.3.3 Maintain both large and small wetlands in management units, as small wetlands may have longer hydroperiods in some cases (Tsai *et al* 2007). This can help to maintain the continuity of water resources for amphibians and waterfowl.

Strategy 7. Facilitate transitions under climate change

While many of the practices in this menu could be classified as resistance strategies—aimed at avoiding and reducing the negative effects of climate change—planning for and facilitating inevitable changes is also an important part of climate adaptation (Lynch *et al* 2021). For example, some grassland areas will almost certainly be lost to woody species with increasing CO_2 concentrations and changing precipitation patterns (Jones 2019), while coastal grasslands like salt marsh may experience dramatic losses from sea-level rise (Crosby *et al* 2016). Understanding and acknowledging these changes, and in some cases actively helping to facilitate them for more desirable outcomes may help managers to prepare for ecological transitions and avoid investing in management actions that will fail. In other cases, grasslands will persist but the types of species and communities that inhabit them may shift (Fridley *et al* 2016). In these cases, there may be a role for managers to play in facilitating range shifts for vulnerable species and supporting transitions to new ecological communities (Robillard *et al* 2015).

Approach 7.1 Promote climate-tolerant plant genotypes and facilitate community shifts to better align with future climate conditions

Grassland plant communities may shift in composition under a changing climate. In some cases, species that are already present may become more or less dominant based on their climate tolerance traits (Griffin-Nolan *et al* 2019). In other cases, introducing plant genotypes best suited to new climate conditions may also be helpful (Phillips-Mao *et al* 2016).

Example tactics

7.1.1 Facilitate the transition of entire grassland plant communities by seeding high diversity restorations with all viable species that would theoretically be able to disperse across an unfragmented landscape and could survive under projected changes to a given climate zone (McKone and Hernández 2021).

7.1.2 Observe which existing species perform well under climate extremes (e.g., drought-tolerant species) and facilitate the expansion of these species locally or through translocation (assuming they are not invasive) (Griffin-Nolan *et al* 2019).

7.1.3 Introduce the best-suited genotypes for each species based on projected climate conditions and local adaptation across areas of species ranges (Galliart *et al* 2019, Phillips-Mao *et al* 2016).

Approach 7.2 Engage in assisted migration to facilitate species range shifts
As climate change advances, species (especially mobile animals) may actively shift their ranges through dispersal to track suitable climate space (Hovick *et al* 2016). However, less mobile species such as plants, or species with highly disjunct ranges, may require assisted migration to reach future habitats (Cullingham *et al* 2023, Wang *et al* 2019b).

7.2.1 Determine which species are priorities for assisted migration based on projected range losses and dispersal capability (Barber *et al* 2016, Hällfors *et al* 2017).

7.2.2 Translocate individuals from southern populations that may be better adapted to warmer conditions (Brambila *et al* 2023), or focus on particular species needed to fill specific functional roles as other species are extirpated (Havrilla *et al* 2023)

Approach 7.3 Convert non-grassland systems to grassland where climate can no longer support current landcover
Although grassland losses may be inevitable in some regions, there could also be opportunities for grassland gains as climate change reshapes land-uses in North America. Locally, managers may be able to identify regions or properties where a proactive conversion to grassland from a competing land use might be justifiable.

Example tactics

7.3.1 Forests and savanna ecosystems in some regions of North America will shift towards grassland structures with increasing fire frequency and decreasing moisture (Bachelet *et al* 2011, Kodero *et al* 2024). Identifying such locations, and facilitating this transition, could be a means to offset other grassland losses and be more sustainable than maintaining forested landcover in drying climates.

7.3.2 Marginal croplands provide another opportunity to create new grasslands. Often, these properties were originally grasslands, and they require intensive input for low yields (Lark *et al* 2020). Converting such marginal agricultural lands to grassland could be increasingly practical under climate change, as the ecosystem services and carbon sequestration benefits from doing so become greater.

Approach 7.4 Identify areas where continued investment in grassland conservation is a poor use of resources and allow transition

Optimal allocation of limited resources has always been a component of so-called conservation triage (Bottrill *et al* 2008). As climate change advances, natural resources will likely become increasingly strained, and climate conditions may simply not support the grassland communities they once did. In such cases, it will be important to realistically assess whether investing in intensive management to maintain a grassland property is worthwhile, or whether greater conservation returns could be achieved elsewhere, and transition must simply be allowed.

Example tactics

7.4.1 Elect not to pursue high-cost or socially unpopular measures in favor of spending resources elsewhere. For example, irrigating natural grasslands during a drought might be expensive and unpopular with local producers. Instead, those resources could be spent restoring a higher-value property with drought-tolerant vegetation

7.4.2 Use grassland properties of lower ecological value, or high management costs, as natural experiments to learn about how grassland communities respond to changing climate conditions without intervention.

Strategy 8. Engage human communities in grassland conservation and adaptation

Human communities have always been closely linked to grassland landscapes, and grasslands provide many social, cultural, and economic services (Nowak-Olejnik *et al* 2020, Zhao *et al* 2020). In pre-colonial times, indigenous peoples used fire to maintain grasslands for hunting and nomadic agriculture (Kimmerer and Lake 2001, Roos *et al* 2018). In the modern era, the majority of the world’s food production occurs on grasslands (O’Mara 2012), and grassland regions often provide the homes and livelihoods of farmers, ranchers, indigenous peoples, and rural communities. Engaging the public, businesses, and the people who live in and depend on working grassland landscapes is critically important to grassland conservation now and in the future.

Approach 8.1. Respect and incorporate indigenous knowledge and values in grassland management

Indigenous Knowledge (IK) is a broad term describing the accumulated cultural knowledge of indigenous peoples regarding ecological systems. Although IK operates through a different paradigm than Western science, it is also empirically based and has already made contributions to conservation science (Huntington 2000). In grasslands globally, IK has found particular application in grazing systems (Molnár *et al* 2020). Respecting and including IK in conversations around grassland climate adaptation may not only improve science, but it can also foster greater inclusion.

Example tactics

8.1.1 Engage and build relationships with local indigenous communities regarding the management of grasslands in homelands or ceded territories

8.1.2 Consult with Tribal Historic Preservation Officers, elders, and other knowledge holders to learn about the historical and present community relationships with an area

8.1.3 Partner with indigenous-led natural resources agencies to develop joint adaptation practices and co-stewardship projects on issues of cultural importance to indigenous peoples (Mucioki 2024)

Approach 8.2 Invest in outreach and support for landowners and producers

Approximately 80% of grasslands in Canada and the United States are privately managed (Bernath-Plaisted *et al* 2023a). Therefore, engaging and supporting private landowners in grassland conservation and climate-informed management is a potentially huge component of successful adaptation in North American grasslands. Many government agencies and non-profit organizations already devote significant resources to providing cost-shares, incentives, and technical support to landowners (Morgan *et al* 2019), and continuing to expand the reach of these programs and incorporating climate adaptation practices should be a priority.

Example tactics

8.2.1 Continue to implement successful landowner programs that fund grassland conservation and sustainable practices (see Bernath-Plaisted, Correll, et al., 2023 for more information on programs in North America). In the United States, Farm Bill programs such as the Conservation Reserve Program (CRP) and Environmental Quality Incentives Program (EQIP) have been successful in creating permanent cover, providing wildlife-friendly fencing, and funding infrastructure needed to transition to rotational grazing. All these practices are beneficial from a climate adaptation standpoint. Increasing funding caps for such programs and making Farm Bill benefits available to all indigenous lands are important expansions to support climate adaptation.

8.2.2 Explicitly include climate adaptation practices in private lands programs, such as prioritizing properties that may be climate resilient, payments for reduced stocking and pasture rest, and payments for increased carbon sequestration from permanent cover and improved grazing practices. Additionally, ensure that agency staff and private lands biologists are trained to advise landowners on climate adaptation (Wiener *et al* 2020)

Approach 8.3 Develop and promote economic incentives for grassland climate adaptation and conservation on private lands

Balancing producer livelihoods with grassland conservation and adaptation goals will likely be key to the success of these endeavors (Keyser *et al* 2019). Therefore, there is a strong need to develop economic incentives that can make sustainable grassland management feasible and desirable from a landowner perspective. This could be accomplished through a variety of methods, such as direct payment for ecosystem services (PES), easements, and branding surrounding sustainable practices.

Example tactics

8.3.1 Pay landowners directly for ecosystem services provided by practices like maintaining permanent cover, sequestering carbon, rotational grazing, managing for heterogeneity, or providing habitat for threatened grassland species (Ayambire *et al* 2021, Mishra *et al* 2021).

8.3.2 Invest in grassland conservation easements (Braza 2017).

8.3.4 Provide "grassbanks" that local ranchers can use during times of drought in exchange for participation in conservation practices (Gripne 2005).

8.3.5 Create branding and markets for sustainably produced grassland products, such as the Audubon Society's Bird-Friendly Land label associated with their Conservation Ranching Initiative.

8.3.6 Engage corporate entities in grassland conservation. For example, energy companies may be incentivized to improve environmental management or fund conservation efforts to avoid federal listing of grassland species.

Approach 8.4 Involve communities in management activities

Involving communities in management actions and decisions can increase the effectiveness of management, foster stakeholder investment in natural resources, and serve as an opportunity to educate and engage the public on ecological topics (Danielsen *et al* 2007, Swart *et al* 2018). Grasslands offer natural opportunities for such engagement, as many of the management activities conducted on these lands may also affect producers living in local communities.

Example tactics

8.4.1 Organize burn-cooperatives that can provide resources and expertise to help landowners manage woody encroachment and increase heterogeneity on their properties (Twidwell *et al* 2013).

8.4.2 Engage communities in regional invasive species monitoring campaigns to look out for and recognize invasive species, and take preventive steps like cleaning boots and equipment to help control the spread of non-native plants (Goodwin et al., 2012).

8.4.3 Hold outreach events where community members can participate in conservation activities like restoration plantings and seed collection for rare plants.

8.4.4 Promote the use of citizen science on climate-related topics in grasslands, such as monitoring changes in phenology or the presence of sensitive grassland wildlife (Lewandowski and Oberhauser 2017).

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Supporting Figures

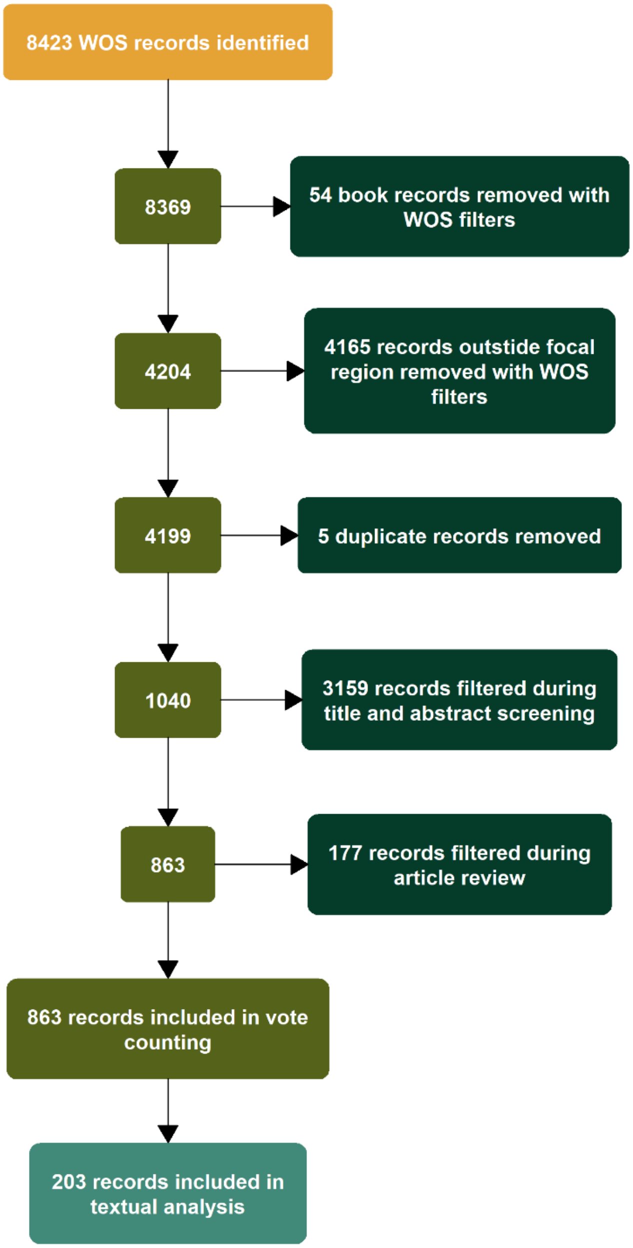

Figure S1. PRISMA diagram for systematic review on climate adaptation in North American grasslands. The diagram shows records returned by a Web of Science search on 2 January 2024, and how records were filtered at different stages of screening during the review.

Dissertation Epilogue

In the coming decades, climate adaptation will likely become a primary objective of natural resource management. North America's grasslands are highly endangered, climate-vulnerable ecosystems that already face numerous stressors such as fragmentation, woody encroachment, and invasive species. Thus, preparing these degraded biomes for climate change is of particular importance—especially given the critical ecosystem services that grasslands provide. The first two chapters of this dissertation explored the potential for microclimate models to inform grassland climate adaptation and elucidate the climate change ecology of a declining grassland songbird community. The final chapter of this work moved beyond microclimates to synthesize broader knowledge on grassland climate adaptation and create a structured menu of management practices to support the implementation of climate adaptation. Below, I briefly highlight a few themes that have emerged from this research and provide some further personal reflections.

On the benefits and limitations of microclimate data in ecology and climate adaptation

The world is getting smaller, or rather it is becoming more finely grained. There can be no question that the spatiotemporal resolution of remote-sensing products has increased dramatically in recent decades, and I expect that this progression will continue into the near future. The day may not be far away when high-quality, centimeter-resolution microclimate datasets will be available for every ecosystem on Earth (in fact, platforms such as *NicheMapR* are already beginning to do just that), and researchers will not have to go to the lengths I have to address microclimate questions. My dissertation work has contributed to a growing body of research demonstrating how microclimate data can improve various aspects of our ecological science. Some examples of this improvement include better-performing species distribution models, more informed climate vulnerability assessments, and revealing new aspects of species' ecology and behavior. In fact, it would be strange if microclimate data did not furnish such advancements. Like any other type of ecological data, improving the detail and quality of climate data should improve our prediction and inference. However, my dissertation work also demonstrates a limit to the ecological application of microclimate data to climate adaptation problems. While understanding microclimate-habitat relationships can surely inform the assessment of species vulnerability, it may not always offer fresh solutions for their conservation. Highly specialized species, by definition, may have little flexibility to access microclimates other than those found in their core habitats. For these species, adaptation approaches that focus on heterogeneity and thermal diversity may be likely to fail. That said, I believe there is already evidence that intentional management of the thermal environment is an adaptation practice worth consideration in many cases, and microclimate datasets are essential to determining which cases these may be.

On climate adaption, being specific, and writing about management

Ecology, like any specialized discipline or subculture, is awash in nebulous terminology—those widely used and rarely defined terms that come in and out of fashion like clothing. Climate adaptation, like resilience, is (I think) an important term that has occasionally suffered from this type of abuse. During the review I conducted for my third chapter, I found it satisfying, and inspiring at times, to catalog many specific practices and ideas for addressing the inevitable effects of climate change in North American grasslands. However, the diversity of these practices in scale of application, goal, and intention, and method of execution almost defies lumping under a single term. Climate adaptation does not imply that the effects of climate change can somehow be solved, mitigated, or managed away—that is a fantasy. Instead, what all climate adaptation practices offer, no matter how disparate, is a way of framing management problems around *adapting* to a new reality. Sometimes, this may involve a practice that can truly lessen a certain kind of climate impact, sometimes it may simply mean staying the course with fundamental management, and in other cases, it may be an acknowledgment that we must plan for unavoidable changes. In all these cases, I submit that recommendations for climate adaptation must be specific to be useful. What is the threat to which we are adapting? What is a realistic objective given that threat? What actions can be taken? Under what circumstances might those actions be effective?

Yet, such specificity appears difficult to come by in published literature. During my review, not only did I find that few studies articulated any clear recommendation for adaptation, but I noticed repeatedly the vague and arm-waving statements tossed into the final sentences of papers to hint at a broad relevance to climate change adaptation. There has always been an epistemological divide between science purely for the advancement of knowledge and applied science to solve real-world problems, but it seems to me a great waste that we should publish so extensively on the ecological effects of climate change but say so little about managing them. So why should this be the case? I believe there are two non-mutually exclusive explanations. First, as others have suggested, it seems probable to me that current trends in scientific publishing are pushing authors to promote broad concepts, exciting narratives, and big data. By contrast, system-specific work, local field-based studies, and gritty details are becoming unfashionable, or more to the point, un-fundable. Yet it is precisely these system-specific insights that are often most useful for informing management. As Lawton (1999, *Oikos,* 84.2, 177-192) observed, the natural world is governed more so by contingency than generality, and we may find that there is a limit to the application of broad concepts to local management. The second explanation is simpler, and perhaps less nefarious: it is difficult for researchers to write effectively about management. I venture to state that *most* ecological researchers, no matter how applied their interests, are not management practitioners. As scientists, not only must we tread carefully to avoid overstating our findings and qualify our statements with nuance and measures of uncertainty, but we also may lack direct experience with the management that we must recommend. I struggled with this very doubt as I compiled recommendations for my third chapter. Though I have conducted fieldwork in many grasslands under various management regimes, I simply do not have the lived experience of implementing each practice I encountered in the literature or seeing how the results differ for this ecotone or that property, or under these climate conditions, etc. Thus, it was sometimes difficult for me to know what information managers would find useful and what would simply be more words on the page. In truth, generalities are simply much easier to write about than specific details, which often require much greater knowledge and experience. I am not aware of any practical solution to these dilemmas beyond increased efforts to co-produce science with managers, and a great deal of humility, earnestness, and attention to detail.

The lost landscape: personal reflections on the conservation of North American grasslands

Having now devoted my early career to the study and conservation of grasslands and grassland birds, I have often reflected on the fates of these unique environments and the wonderful diversity of species that inhabit them. When I have found myself standing in a prairie, whether surrounded by Compass Plant and Purple Coneflower in Wisconsin’s tallgrass or watching a

Ferruginous Hawk glide across the horizon from a sparse hilltop in Alberta's mixed-grass prairie, I have lamented the fact that I never had the chance to see these landscapes in their unbroken splendor. Natural history accounts describe a lost landscape where buffalo and pronghorn roamed without fences, where wildfire maintained dazzling diversity, and where grassland birds were abundant rather than disappearing. This was a time when the state of Illinois was nearly covered in tallgrass prairie, though now only corn grows in its place. It is with some sadness that I must confront the fact that I too am standing in a lost landscape—one that may yet be lost to future generations. In 2021 alone, 1.6 million acres of grassland in the United States and Canada were converted to cropland, and each year, losses to agricultural, energy development, suburban sprawl, and woody encroachment continue. It is not difficult to imagine a future in which Eastern Meadowlark will be a rare sighting (in some places, this has already come to be), or where children can no longer run outside to search for great green and yellow striped Monarch Butterfly caterpillars on Common Milkweed each spring. Although I hope that my science will contribute in some small way to avoiding this fate, I am also keenly aware that the problem of grassland conservation is not one of scientific understanding, but rather one of societal values, economics, and externalities that go unnoticed, or are misunderstood, by the public. With that in mind, I have included at the conclusion of this document a Photographic Epilogue containing images of grassland landscapes and species taken throughout my doctoral fieldwork. Thus, in the unlikely event that an unknown reader cracks this volume at some future date, they may find something more inspirational to reflect on than facts and figures.

---Fin---

Photographic Epilogue