

An integrated approach to restoring grassland function to working landscapes

by

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The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

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DEDICATION

This thesis is dedicated to my family and friends. Thank you all for your love and support. It has meant the world and I would not be here without you.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS.....	iv
ABSTRACT	v
CHAPTER 1. GENERAL INTRODUCTION	1
Prairies are Degraded	1
Opportunity in Working Lands.....	1
Thesis Foci and Organization	2
CHAPTER 2. BUTTERFLY LONG-TERM RESPONSE TO MANAGEMENT DIFFERS FROM SHORT-TERM RESPONSES.....	3
Abstract	3
Introduction.....	4
Methods	7
Results	11
Discussion	14
Acknowledgements	21
Figures and Tables	22
References	25
Supplementary Appendix	29
CHAPTER 3. EVALUATING THE UTILITY OF SPECIES DISTRIBUTION MODELS IN INFORMING CLIMATE CHANGE-RESILIENT GRASSLAND RESTORATION STRATEGY.....	36
Abstract	36
Introduction.....	37
Materials and Methods	39
Results	44
Discussion	46
Acknowledgements	51
Figures and Tables	52
References	56
Supplementary Appendix	59
CHAPTER 4. GENERAL CONCLUSION	60
Conclusions from Chapter 2	60
Conclusions from Chapter 3	60

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ABSTRACT

Nearly all of what was historically tallgrass prairie has been lost due to conversion to agriculture and increasing urbanization. This thesis focuses on strategies to restore native species diversity to working (i.e., agricultural) landscapes in the American Midwest. The practicality and efficacy of restoration of prairie function to working lands has been demonstrated for some taxa in the short-term (i.e., years 1-5), but the effects of continuing consistent management in the medium- and long-term are less studied. I focus here on butterflies and floral resources due to (1) the well-known sensitivity of butterflies to habitat changes (2) the likely concordant response between insect pollinators and floral resources due to their tight ecological relationship and (3) the ecosystem services provided by pollinators and the need to manage lands for such a service. Taken together, this body of work seeks to integrate empirical and modeling approaches to create a more holistic understanding of how grassland restoration strategies affect insect pollinators.

Management strategies are frequently recommended on the basis of only a few years of field sampling, after which, research often ceases and is replaced by opportunistic sampling by managers without a formal experimental framework. The first chapter of this thesis examines the effect of a continuous decade of consistent management with pyric-herbivory (i.e., various combinations of fire and grazing) on butterfly and floral resource plant communities. The management methods being considered here are burn-only (i.e., no grazing with the whole site burned once every three years) graze and burn (i.e., cattle grazing the entire site with a full-site burn once

every three years), and patch-burn grazing (i.e., cattle grazing the entire site with a burn on one third of the site every year). We find that not only do butterfly and floral resource communities vary in terms of abundance, species richness, and diversity among management strategies; they do so in a way that is not consistent with what is typically observed in studies conducted over a shorter time period (as will be more fully discussed in that chapter). Additionally, while the community composition of butterflies varies significantly among management types in three of the five study years, floral resource community composition does not vary significantly in any study year. This may be indicative of an effect of management on larval (i.e., caterpillar) resources that is not as impactful on the nectar resources upon which adult butterflies depend. The community composition variation in butterflies appears to be primarily driven by the hyper-abundance of particular families of butterflies in each of the three management types. These results demonstrate that short-term responses may not match long-term responses and thus indicate that field studies should take place—where feasible—over more sampling seasons such that management recommendations are more fully informed.

When restoring prairie function to working landscapes, one must plan for the effects of anthropogenic climate change. In the second chapter of this thesis, I focus on the potential changes in bioclimatic suitability to plant species included in a restoration seed-mix used to jump-start the reintroduction of a particular community of native plants. Using Species Distribution Modeling (SDM), I correlate occurrence records of a particular species with a suite of climatic variables to predict where suitable bioclimatic

conditions might be in the future. Given that SDMs can function well on publicly available data and are relatively intuitive in terms of how they infer changes to predicted distribution, they can be a powerful tool. However, the sheer number of distribution maps generated (one per species per climatic scenario) can be unwieldy in the context of restoration of entire plant communities. We sought therefore to assess whether modeled species exhibited conserved responses to climate change within functional groups. Our results indicate that for forbs, warm-season grasses, and legumes, species within a functional group tend to respond similarly to one another. Cool-season grasses, on the other hand, did not vary in a synchronous fashion, which may be indicative of more variable suitable conditions among species within this group. In addition, some functional groups tended to be much more sensitive (i.e., they demonstrated substantial changes between currently suitable areas and those predicted to be suitable in the future) to climate change conditions than others. Given that forbs tended to exhibit the most dramatic response to climate change, and other groups tended to exhibit more similar current and future distributions, managers interested in restoring flowering plant communities should consider either more southerly ecotypes or congeners to species of interest that are more tolerant of warmer and relatively drier conditions. One important caveat to the use of SDMs in restoration, however, is that such models are best applied at the continental scale (due to problematic assumptions of the role of microhabitat at small spatial scales), whereas land managers are likely interested in the regional or local spatial scale. More spatially precise estimates of the

impact of climate change should consider microhabitat, with the SDM outputs presented here and elsewhere informing the areas of interest.

Restoration of grassland function must occur in the immediate future if threatened prairie taxa are to be conserved. Such conservation may most profitably focus on increasing the ecological value of agricultural land because such lands occupy a majority of much of the American Midwest. The first chapter of this thesis indicates that the traditional length of field studies may be insufficient in capturing the full consequences of management for butterflies and floral resource. Additionally, single metrics for community response, though informative, are unlikely to be enough in quantifying the full scope of ecologically-meaningful community response and multivariate community composition methods must be included. The second chapter of this thesis suggests that plant species within a functional group generally demonstrate conserved responses to climate change and that functional groups respond differently to potential future conditions. This also serves as evidence that modeling approaches are a useful complement to field methods and can provide an added dimension in creating restoration plans effective in the short-and long-terms.

Collectively, the insights presented in this work demonstrate the need for restoration strategy to include many different approaches and emphasize ways in which management can be more likely to be successful in the long term.

CHAPTER 1. GENERAL INTRODUCTION

Prairies are Degraded

Since European colonization of the American Midwest, 99.9% of historic prairie habitat has been lost (Samson and Knopf 1994), primarily due to conversion to agriculture (Wright and Wimberly 2013). The remaining grassland habitat is often further degraded by the loss of twin ecosystem pressures vital to maintaining the diversity of grassland habitats: grazing by large mammals and periodic fire (Anderson 2006). Many of the plant species that typify grassland habitats share an evolutionary history with the—in many cases—functionally extirpated American bison (*Bison bison*) (Towne et al. 2005), and grazing by large mammals has been shown to serve as an important regulator of diversity (Rambo and Faeth 1999, Foster et al. 2003). Fire is critical in excluding woody plant species (Fuhlendorf and Engle 2004, Delaney et al. 2016), and can be important in controlling herbaceous invasives as well (Hall et al. 2012). Due to the co-evolutionary history of tallgrass prairie species with these two processes (Anderson 2006), restoration can most meaningfully be performed on lands where baseline management includes grazing by cattle (*Bos taurus*) or bison and periodic burning on at least part of the site (Pillsbury et al. 2011).

Opportunity in Working Lands

Working landscapes—here defined as lands that provide some economic value to humans that have not been entirely transformed to a different landcover type—present a valuable restoration opportunity in the context of extensive loss of historic prairie, given the overlap between ecological and economic goals on these lands (Polasky et al. 2005). Grazing by cattle provides a financial benefit for landowners, and cattle grazing has also shown to serve many of the same ecological functions as historic grazing by bison (Jackson 1999, Rambo and Faeth 1999, Fuhlendorf and Engle 2001, Towne et al. 2005, Delaney et al. 2016). The elimination of woody plants from grazed areas via fire likewise serves to increase the quality of forage for cattle on a recently burned area by increasing herbaceous cover and satisfies the fire-dependent nature of prairie habitats (Anderson 2006, Pillsbury et al. 2011).

Grazing and fire have also been shown to positively interact to benefit tallgrass prairie habitats (Fuhlendorf and Engle 2001, Delaney et al. 2016); grazing and fire benefit humans (directly by producing cattle, and indirectly via increased forage quality for the cattle respectively), but also can benefit native prairie species, so a combination of the two strategies is likely to be both a successful and practical tool in restoration efforts for prairie species. In short, by focusing Midwestern tallgrass prairie restoration effort on working landscapes, substantive ecological management can be performed in concert with financially motivated practices (Polasky et al. 2005).

Thesis Foci and Organization

Fortunately for those interested in restoring grassland function, the ability of working landscapes to serve as surrogate tallgrass prairie habitat has already been well documented (Debinski et al. 2011, Delaney et al. 2016, Bendel et al. 2018). The work presented herein focuses on two relatively less well explored components of grassland restoration in working lands that must be elucidated to better inform restoration strategy. The two chapters focus on the following research questions:

1. How do the long-term effects of management in working landscapes for butterflies and floral resource plants differ from the short-term impacts?
2. How might climate change affect the efficacy of seed-mixtures used to 'jump start' restoration of native plant communities?

CHAPTER 2. BUTTERFLY LONG-TERM RESPONSE TO MANAGEMENT DIFFERS FROM SHORT-TERM RESPONSES

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Abstract

The majority of pre-European colonization tallgrass prairie in the American Midwest has been lost, largely due to extensive conversion to agriculture. This loss of habitat has a corresponding negative effect on taxa that depend upon it. Pastureland managed with both periodic fire and grazing (“pyric-herbivory”) shows promise as a context for meaningful restoration of grassland function. The benefits of pyric-herbivory management to grassland insect pollinator abundance and diversity within—in some cases—one or two years have been effectively demonstrated in the short-term, but the effect of consistent long-term management has not. Here, we evaluate butterfly and nectar resource plant community response to several variants of pyric-herbivory management consistently implemented on sites for a decade. The particular management strategies considered here are: burn only (no grazing with a burn once every three years), graze and burn (same fire schedule as burn only but with cattle) and patch-burn graze (grazing by cattle on the site with a burn on one third of the site every year). While butterfly and nectar resource plant abundance were greater on sites with grazing and fire together than those with fire alone, diversity demonstrated the opposite pattern for both taxa. Species richness did not vary though community composition varied significantly among management types in different ways in

each year. Community composition differed largely due to which butterfly families were most abundant in each of the three types of management. In both our study and short-term responses observed in several previous studies, butterfly abundance increased in patch-burn grazed sites relative to those that were ungrazed and diversity displayed the opposite pattern. However, given the lack of concordance of response to management among species of the same family observed in short-term studies, the family-level signal quantified in our study seems an emergent property of long-term management. These results imply that managers interested in the long-term conservation of Nymphalids will need to focus on ungrazed management while those interested in either Lycaenid or Pierid restoration should focus on either patch-burn graze or graze and burn management respectively.

Introduction

More than 97% of historic grassland in North America has been lost (Samson and Knopf 1994), and in the Midwestern U.S., this is largely due to conversion to agriculture (Wright and Wimberly 2013). The remaining remnant tallgrass prairie is often less suitable for many prairie insect species due to the absence of large mammalian grazers, and the suppression of naturally occurring periodic fires. Prairie communities have evolved with grazers and fire as diversity stabilizing mechanisms (Anderson 2006), so restoration of historic grassland function is most effective on lands that incorporate both (Pillsbury et al. 2011).

Active pastureland has great potential for supporting many native grassland species because it includes mammalian grazing and frequently involves fire application (Polasky et

al. 2005). Low-to-moderate stocking rates of cattle grazing can be beneficial to prairie pollinator and floral taxa (Delaney et al. 2016) and prescribed fire improves cattle forage quality (Anderson 2006; Pillsbury et al. 2011). The interaction of fire and grazing is also important to successfully restoring prairie function, as fire mediates the use of the landscape by grazers by creating variation in forage quality and attractiveness to grazers (Fuhlendorf and Engle 2001; Delaney et al. 2016). Taken together, restoration efforts on pasturelands can provide substantive benefits to threatened prairie taxa.

While many studies have examined the effects of grassland management such as fire and grazing on insect and plant community responses within the first few years (Moranz et al. 2012; McGranahan et al. 2012, 2013; Delaney et al. 2015, 2016; Bendel et al. 2018), comparatively few have assessed whether the long-term effects are consistent with responses to the first few years of management (hereafter such responses will be referred to as “short-term”). A lack of consistency in response could mean either that a lack of response observed in the short-term may have a dramatic effect in later years post-management or that an initial dramatic response proves asymptotic or unstable in the long-term; either of these disconnects could prove disastrous for restoration planning and quantification of management outcomes for threatened taxa. Such potential temporal variation in response may be particularly problematic for pyric-herbivory management involving iterative applications of fire and grazing. Pyric-herbivory management methods often include one of burn only (burning the entire site once every three years), graze and burn (same burn schedule as burn only but with the cattle grazing the site each year), or

patch-burn graze (where one third of the site is burned every year on a rotating basis and cattle graze every year).

Butterflies (Order: Lepidoptera) are a particularly vulnerable prairie taxon (Vogel et al. 2007). Within agricultural contexts butterfly abundance and diversity can be improved via management (McGranahan et al. 2012; Meehan et al. 2013; Berg et al. 2013), though butterflies do not always respond consistently in each consecutive year post-management (Woodcock et al. 2012). Despite this context dependency, managing for heterogeneity at both the site and landscape level has been shown to broadly benefit the species composition and diversity of butterfly communities (Berg et al. 2013; Slancarova et al. 2014; Welti and Joern 2018). Butterflies can also serve as indicators of how closely managed pastures match the composition of historic grasslands due to the tight association between butterflies and their host and nectar plants (Westgate et al. 2017). The utility of butterflies as indicators of particular plant presence can be particularly valuable in cases where the plant is small, difficult to find, or ephemeral and therefore infrequently found without its butterfly mutualist. Butterfly response to management therefore represents a conservative estimate of how other, less-specialized insect taxa might respond to differences in plant communities resulting from each management strategy.

By assessing the effect on butterfly communities of long-term consistent management (years 6-10 of management), we can identify long-term outcomes of management and highlight contrasts with the findings of short-term community responses. Such contrasts could be used to meaningfully inform—and perhaps modify—future changes to management based on preferred outcomes. We evaluated butterfly and nectar resource

plant communities annually for five additional years after the years presented by Moranz et al. (2012) on the same experimental sites managed with either burn only (BO), grazing and burning (GB), or patch-burn grazing (PBG). In brief, Moranz et al. (2012) found no variation in butterfly species richness, but found that a habitat generalist butterfly (*Cupido comyntas*)—representing the majority of their observed butterflies—was most abundant in patch-burn graze sites, while two habitat specialists (*Speyeria idalia* and *Ceryconis pegala*) and one generalist (*Danaus plexippus*) were most abundant in burn only sites. They also found no differences in butterfly community composition among management methods.

We hypothesized that (1) abundance, species richness, and diversity of both butterflies and nectar resource plants would be higher in sites managed with combinations of fire and grazing than in sites managed with fire alone, due to the most prevalent species assessed by Moranz et al. (2012) being most abundant in PBG sites, that (2) community composition of butterflies and nectar resources would differ among all three management methods given the longer history of management on the sites and attendant chances for community diversification, and finally that (3) the abundance of particular butterfly families would vary among management types, driving differences in butterfly community composition, as supported by the consistency of species' response to management within family demonstrated by Moranz et al. (2012).

Methods

Study Design

We evaluated the effect of three long-term grassland management approaches applied to entire pastures (a.k.a. sites) in the Grand River Grasslands ($N_{\text{sites}} = 10$; Figure

S2.1) of south-central Iowa (Ringgold Co.) and north-central Missouri (Harrison Co.). Sites were an average of 65.5 acres (± 16.9 SD) and have been either active pastureland, native prairies, or un-grazed restorations for the last ten years. All pasturelands were tallgrass prairie that has—to varying extents—been invaded by Eurasian exotic and invasive grasses (Moranz et al. 2012). All sites were divided into three equally sized “patches” where both sampling and management occurred.

Sites were managed with either burn-only (BO; N = 3), graze and burn (GB; N = 3), or patch-burn graze (PBG; N = 4) management. For both BO and GB sites, burns were applied to all three patches in the spring of 2015 and 2018. BO sites were either remnant native prairie (N = 2) or restorations with comparably high floral diversity (N = 1). GB sites were also given a patch-level treatment against an invasive grass common in the region (*Schedonorus phoenix*). Two of the three patches were sprayed with herbicide (glyphosate) and one of those two was additionally seeded with a native prairie plant seed-mix between the 2014 and 2015 sampling seasons, while the third patch was left as a control. Because these two treatments were applied to all GB sites used in our study, we are still able to proceed with those sites, though the patch-level management is likely to increase heterogeneity beyond what might be expected of typical GB management. For PBG sites, one patch was burned every spring, rotating among the three patches so that each patch was burned once every three years. Stocking rate of cattle on GB and PBG sites varied between 0.73 and 1.33 AUM/acre. These management methods were used consistently on these sites since 2007 (Moranz et al. 2012). This study includes only data collected from 2014 through 2018 to better focus on the latter half of the decade of management. It also

includes a smaller number of sites than the 13 sites examined in Moranz et al. (2012); some sites were dropped here due to inconsistencies in management over time.

Butterfly and Nectar Resource Transects

Sites were visited four times between the last week of May to the first week of August for 5 consecutive years (Moranz et al. 2012). These four visits were spread evenly through the field season, resulting in each site being visited (roughly) once every two weeks. During each visit, one of the two permanent transects located in the center of each of the three patches was sampled for both butterfly and floral resource communities (for a total of six transects per site and twelve total transect sampling events per site per season).

Butterflies were counted using a line-transect approach for 10 minutes per 100 meter transect (Moranz et al. 2012). Butterfly sampling was conducted between 0900 and 1730 where wind speed was less than 15 km/hour and it was at least 17°C (Bendel et al. 2018). All inflorescences within one meter of a random side of each transect were counted and identified to species in the field. Inflorescence structure and flower number within inflorescence varies among species so plants were counted by inflorescence rather than flower, consistent with Delaney et al. (2015). Due to our interest in variation in plant resources relevant to adult butterflies, only inflorescences of nectar-producing species were counted.

To assess full-season effects of management on butterfly and nectar resource communities, data for each species of both taxa were summed across all transects and all visits within a given year. These full-season butterfly and floral resource communities were

then used to calculate abundance, species richness, and Shannon diversity, and the abundance of each butterfly family.

Statistical Analysis

To test the effect of year (as a factor), management type, and their interaction on univariate butterfly and flower community metrics (i.e., abundance, species richness, and diversity), we used Residual Randomization in Permutation Procedure (RRPP) ANOVAs (Collyer and Adams 2018). Year was considered as a factor because the discrete, iterative application of the management strategies considered here was considered likely to respond in a non-linear fashion that analyses of year as a continuous variable would fail to assess. When the interaction term was non-significant, it was dropped, and the analysis was re-run without it. Permutation number was set at 10,000 to reduce the variability in exact statistical summary values inherent in a permutation-based method. Where management or year was significant, pairwise comparisons were performed within the perANOVA framework with a sequential Bonferroni adjustment (Holland and Copenhaver 1987).

To account for repeated sampling of sites through time, we utilized an approach specific to RRPP that is tantamount to performing a mixed model with site treated as a random effect. RRPP allows for specification of the reduced model against which each main effect is evaluated (Collyer and Adams 2018) such that one can assess whether a given model explains more of the variation in the data than another, user-specified, model; typical hypothesis testing does this, but the comparison is against a null model ($Y \sim 1$). Two models were run, one including management, year, and site as main effects without

specifying reduced models (i.e., comparing each main effect against the residuals of a null model), and a second model specifying that the “year” model was compared against a model including the term for site and that the “site” model compared against a model including the term for management. Though this variable-by-variable specification of the reduced model may seem complex, the resulting summary statistics require no special interpretation.

Abundance data for both taxa were log-transformed and floral species richness was square root transformed to meet model assumptions. All other univariate data met model assumptions without being transformed. All univariate figures were generated using the `ggplot2` (Wickham 2016) and `cowplot` (Wilke 2018) functions in R.

RRPP Multivariate ANOVAs (MANOVAs) were used on community composition data among management types within each year. Nonmetric Multidimensional Scaling (NMS) ordinations (Kruskal 1964) were performed on Jaccard presence/absence coefficients of community (Jaccard 1912) to visualize among management differences that were supported by MANOVA results. Both NMS ordinations and calculation of Jaccard coefficients were performed using the `vegan` package (Oksanen et al. 2018).

All data tidying, analysis, and plotting were performed in the R Statistical environment, version 3.3.1 (R Core Team, 2016).

Results

Over the five sampling years, we observed 8,526 butterflies of 49 different species and counted 513,795 inflorescences of 113 nectar-producing plant species (Table S2.1–5).

Our most abundant butterfly species was the Eastern-Tailed Blue (*Cupido comyntas*) with 2,316 sightings (27.2% of the total observed butterflies). Our most abundant floral species was birdsfoot trefoil (*Lotus corniculatus*) with 275,843 umbels counted (53.7% of all flowers counted for the project).

Neither butterflies nor floral resources responded to management strategy in a time-dependent fashion ($P_{\text{interaction}} \geq 0.1$), therefore all results below report results from models with main effects only.

Abundance, Species Richness, and Diversity

Abundance and diversity varied across management methods for both flowers and butterflies, though species richness did not differ for either group (Figure 2.1; Table 2.1). There were significantly more butterflies in patch-burn graze (PBG) and graze and burn (GB) sites than in burn only (BO) sites. Inflorescences followed a similar pattern, though only PBG sites had significantly more nectar-producing flowers than did BO sites (with the difference between GB and BO being non-significant). Diversity of butterflies and flowers was significantly higher in BO sites than PBG sites, with GB sites operating at an intermediate level of diversity that was not significantly different from either of the other management types.

Community Composition

In three of the five study years butterfly community composition varied significantly among management methods (Figure 2.2; Table 2.1), and this variation was always between

BO sites and one of the grazing treatments (once between BO and GB, once between BO and PBG, and finally between BO and both pyric-herbivory treatments).

In 2014—the year before the burn on BO and GB sites—butterfly communities on burn-only sites were significantly different from those on PBG sites, while the butterfly communities on GB sites were not different from either of the other management types (Figure 2.2; Table 2.1). In 2015—immediately following a full-site burn on BO and GB sites—there was no significant variation in butterfly community composition among management types. In 2016, BO sites had different butterfly communities than GB sites, but PBG was not different from GB or BO (Figure 2.2; Table 2.1). Butterfly community variation in 2017 followed the same pattern as 2014: BO and PBG differed, while GB was similar to both of the other management methods (Figure 2.2; Table 2.1). In 2018, as in 2015, (again, immediately following the full-site burn on GB and BO sites) there was no difference among management types. Within each of the five sampling years, floral resource communities did not significantly differ in any case ($p > \alpha$ in all cases).

Butterfly Family-Level Variation

To explore the observed differences in butterfly community composition among treatments, abundances of the three most common families of butterflies were analyzed in the same manner as the abundance of the whole butterfly community. Over five sampling seasons, we observed 2,385 butterflies in Lycaenidae (blues, coppers, hairstreaks, etc.), 2,201 in Nymphalidae (brush-footed butterflies), and 3,579 in Pieridae. Only 184 butterflies

in HesperIIDae (skippers) and 177 in Papilionidae (swallowtails) were observed across the 5 years, so these two families were left out of subsequent analyses.

There were significantly more Lycaenid butterflies on PBG sites than on burn-only sites and an intermediate number on GB sites that did not differ from either PBG or BO (Figure 2.3A). Nymphalids, on the other hand, showed the opposite pattern: significantly more were observed in BO than in PBG with GB having an intermediate number of Nymphalids. There were significantly more Pierids in GB and in PBG than in BO, but there was no difference between GB and PBG Pierid abundance. As with the other analyses, there were no significant across or among year effects (Table S2.6; Figure S2.2)

Discussion

Managing pastures with a combination of fire and grazing (as is the case in both GB and PBG sites) resulted in a significant increase in floral and butterfly abundance relative to sites managed with fire alone, though diversity was lower in these sites relative to ungrazed (e.g., BO) sites. The short-term (2007-09; (Moranz et al. 2012)) and long-term (2014-2018) effects of these management methods on nectar resource abundance were consistent: flowering ramets were most abundant in PBG sites, with somewhat fewer in GB sites, and even fewer in burn-only (BO) sites (Figure 2.1). These findings support previous work in this system showing that the interactive effects of fire and grazing (Fuhlendorf and Engle 2004) effectively increase the abundance of floral resources and butterflies.

The type of management did not affect the number of flower or butterfly species (Figure 2.1), as reported previously in the short-term response (Moranz et al. 2012) or in the

long-term response reported in this study. From this concurrence in results, and significant variation in the other response variables among management types, it appears that the species richness of butterflies and nectar resource plants is relatively static in both the short and the long term. While this does not account for species identity, it may be indicative of some resource limitation or lack of dispersal ability that management is unable to overcome. Burn-only sites demonstrated more heterogeneous communities (i.e., higher Shannon diversity) of both taxa than either of the other management methods (Figure 2.1). Burn-only sites (i.e., un-grazed restorations and native prairies), are often havens for disturbance intolerant prairie specialist butterfly species that do not tend to dominate communities. This could contribute to both the relatively low total abundance and relatively high diversity of butterfly and flower communities on these sites.

Considering the variation in abundance and diversity of both butterflies and nectar resource plants among management types, it is interesting that only butterfly communities showed significantly different community composition (Figure 2.2). Another study of the short-term response of butterfly communities to management (Bendel et al. 2018) found no difference in butterfly community composition between PBG and a variety of grazing only treatments, albeit in a different part of the tallgrass prairie ecoregion. Likewise, Delaney et al. (2016) found no difference between the butterfly community composition of PBG sites and those of GB sites. However, the findings of Moranz et al. (2012) on butterfly community variation in both 2008 and 2009 followed the same pattern as observed in our study: namely that BO sites were qualitatively more different from either GB or PBG sites than they were from one another. This similarity is in spite of Moranz et al. (2012) using Bray-

Curtis dissimilarity (a non-metric, relative abundance-based measure) which differs substantially from our use of Jaccard's distance (a metric, presence/absence measure).

Notably, the two years where butterfly community composition did not vary significantly among management types in our study (2015 and 2018) are the two years following the full-site burns applied to GB and BO sites (Figure 2.2). These two years are the only years where all study sites were at least partially burned. Thus, the short-term effects of prescribed fire on the physical structure of vegetation appear to promote a conserved butterfly community composition, regardless of grazer presence or long-term management history.

Given that we found among-management composition variation for butterfly communities but not for floral resource communities, and that we used a presence/absence metric for quantifying community differences (Jaccard 1912), we can infer that different butterfly species tended to occupy sites under different management styles, but that this is not true for nectar resource plant species. This variation in butterfly community composition occurred despite the fact that all three management methods contained the same species richness of flowers and of butterflies. This is particularly surprising because floral resource community composition does not vary, indicating that different butterfly communities are surviving on similar adult floral resources. This apparent disconnect in the tight relationship between butterflies and nectar resource plants (Westgate et al. 2017) may be due to the presence of different larval resource plants under each management method. We counted ramets of flowering plants, but only for those plants that produce nectar. As such, the response to management of non-flowering plants that provide larval

resources for particular butterfly species was not included in our analysis. Some larval resource plants were incidentally recorded, but only in cases where the larval resource plant also serves as a nectar resource for adult butterflies. The overlap between adult and larval plant requirements only occurs for a minority of the observed butterfly species in this study (e.g., Monarchs, *Danaus plexippus*), so the data presented here are not well-suited to testing whether larval resource plants respond in the same ways that adult resource plants do. Future research would ideally focus on quantifying both adult and larval resource plant response to treatment so that the impact of management on all parts of the butterfly lifecycle can be better clarified.

As hypothesized, the abundance of butterflies in different families varied among management types (Figure 2.3) and explains some of the variation in community composition. For instance, Nymphalid butterflies (Family: Nymphalidae) had more individuals on BO sites than on PBG sites, likely due to the relative prevalence of habitat specialists (e.g., *Cerycyonis pegala*, *Speyeria aphrodite*, *S. idalia*, etc.) in that family (Vogel et al. 2007). Of the five Nymphalid species assessed by Moranz et al. (2012), three did not respond to management (*Danaus plexippus*, *Speyeria cybele*, *Phyciodes tharos*) while two (*Speyeria idalia*, *Cerycyonis pegala*) followed the same pattern reported here at the Nymphalid family level. Bendel et al. (2018) found that one of their Nymphalid species (*Phyciodes tharos*) did not respond to grazing-only treatments or to PBG while their other (*Speyeria idalia*) was much more abundant in grazing-only sites than in PBG. Given the relatively high frequency of specialist life histories within Nymphalidae, it may be the case that single species are able to respond differently than others in the family. That being said,

it is likely that in aggregate, specialist butterflies will be most abundant where their floral and larval resources are most abundant, which is frequently within an un-grazed context (especially when the site in question is a remnant native prairie) due to extreme grazing intolerance of some prairie specialist plants. The consistency between the short-term response of a few species (Moranz et al. 2012) and the long-term response of the family as a whole is promising for managers concerned with long-term support of Nymphalids.

The variation among management types in Lycaenidae is likely driven by the fact that 97% of our observations of Lycaenids (2,316 butterflies of 2,385 total) were the same species (*Cupido comyntas*). Generally, Lycaenidae contains a mix of generalist and specialist butterflies (Vogel et al. 2007) and is the most abundant family on PBG sites, which offer the greatest habitat variation within a single site (Fuhlendorf and Engle 2004; McGranahan et al. 2012; Ricketts and Sandercock 2016). Moranz et al. found that the population density of *C. comyntas* did not vary significantly in the short term among the same management types presented here (2012), indicating that long-term management has different implications for at least this super abundant species than does the short-term. A previous study examining butterfly diversity in flowering strips between agricultural lands and streams also found that *C. comyntas* was their most abundant butterfly despite the much more heavily modified context (Reeder et al. 2005), indicating that this species, and possibly other members of the family, can be expected to maintain abundance in even intense agricultural settings. This species shares some patterns with other published Lycaenid responses: Bendel et al. (2018) found that a different Lycaenid butterfly (*Lycaena helloides*) was dramatically more abundant in PBG sites than grazing-only sites. Lycaenidae frequently use plants of the

legume family (Fabaceae) as larval resources, which tend to be more abundant in sites managed with cattle, so the increased abundance of Lycaenidae may be a product of the plethora of larval resources available.

Pieridae is largely a family of generalists in this region (Vogel et al. 2007) and their abundance was highest in the two management methods that involve cattle grazing in addition to fire. Sites managed with cattle have a more continuous level of disturbance than burn-only sites, and generalist species can be expected to benefit most under such conditions. Similarly to the response of the Lycaenid included in Moranz et al. (Moranz et al. 2012), the two species of Pieridae (*Colias eurytheme* and *C. philodice*) did not significantly vary with management in either 2008 or 2009. However, our results suggest that, given more years of management, Pierids become significantly more abundant on grazed sites than on un-grazed sites. It is likely that the disturbance-tolerant generalists in this family are able to persist on these sites even after several consecutive years of grazing by cattle removes and excludes many of the more sensitive floral resources that specialist butterflies depend upon.

The significant response of all three analyzed family-level abundances—though not a perfect proxy the response of particular species—provides valuable insight for managers interested in promoting species for which few data are available. Insofar as different butterfly families are primarily associated with a variety of habitats (Vogel et al. 2007), or have variable degrees of responsiveness to restoration action (Waltz and Covington 2004), the most abundant butterfly family under each type of management also gives implicit evidence of which floral families and habitat structures correlate with management. This is

useful in identifying what resources are available for other pollinators and non-pollinating insect taxa under particular management types and, by extension, which management should be used to achieve desired outcomes.

One caveat to the interpretation of the results presented here is the aforementioned patch-level treatment of GB sites with herbicide and seed-mix addition. While all graze and burn sites were treated this way—and thus we are still able to present results from graze and burn sites as a single, coherent management type—it is likely that this additional management increased heterogeneity within the site relative to what is “typical” of graze and burn management. In the context of our results, it is not possible to untangle the effects of graze and burn management from the results of herbicide application, so future studies may wish to focus on identifying response to particular management strategies at the site level with and without such within-site management.

Taking these findings together, if managers define ‘success’ as simple abundance of butterflies or nectar resource flowers, pastures managed with combinations of fire and grazing may constitute a dramatic improvement on outcomes typical of un-grazed restorations or even native prairies. If, however, the emphasis is on heterogeneous communities or more specific compositions that support rare species and species of conservation concern (e.g., *S. idalia*), then restoration without the use of cattle may still be preferable. This supposition is somewhat complicated by the lack of native prairie sites including cattle grazing in this study; inclusion of this scenario in future research would be valuable in clarifying the degree of resilience to grazing specialist butterfly host plants demonstrate.

Regardless, the long-term outcomes of managing pastureland for butterflies and nectar resource plants are promising in terms of promoting ecological and economic ends in working pastureland. Future work should focus on identifying more of the time-dependent outcomes of ongoing management, such that a better understanding of the mechanisms driving the short and long-term can be achieved.

Acknowledgements

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Figures and Tables

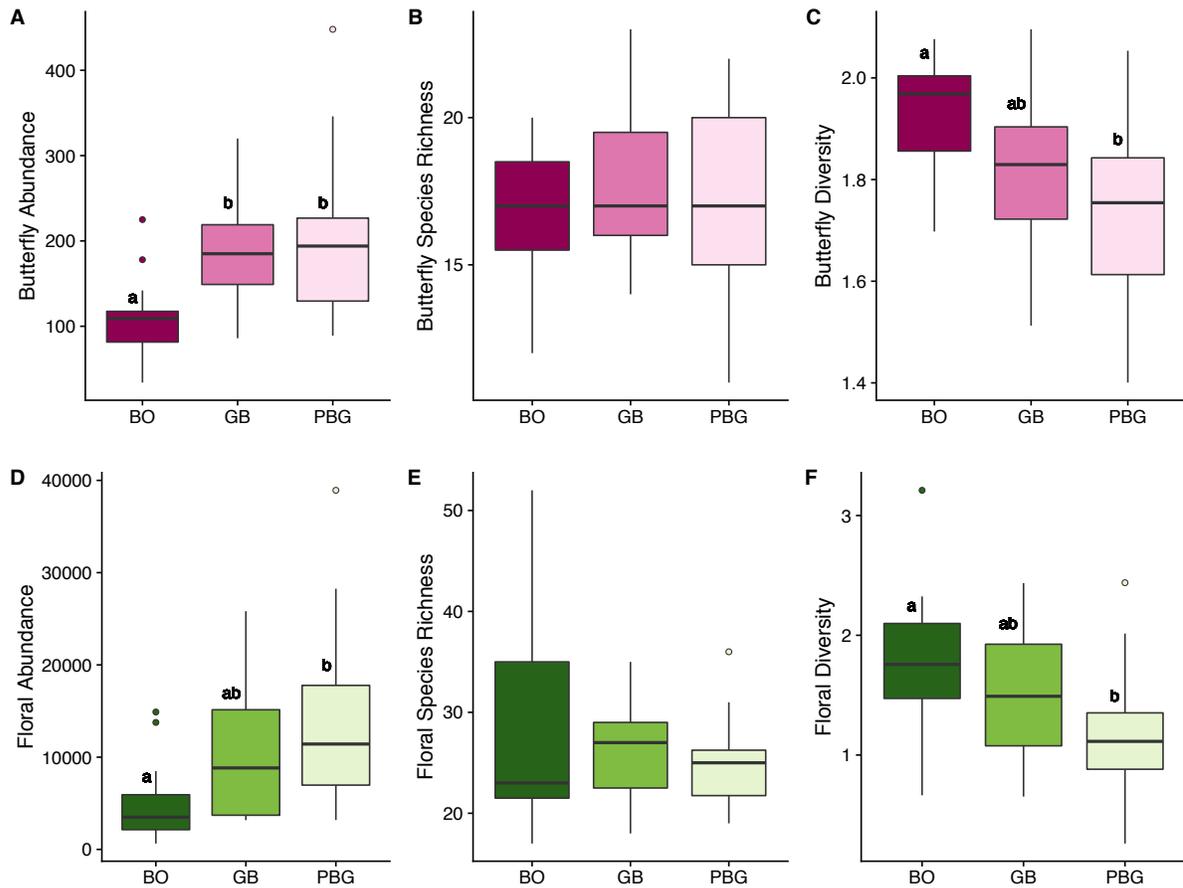


Figure 2.1. Butterfly and floral resource abundance and diversity vary among management types, but species richness did not. Data are presented without respect to the five sampling years (2014-2018) due to the lack of a time-dependent effect of treatment. The top row of plots (A-C) summarizes butterfly community metrics, while the bottom row (D-F) summarizes floral resource community metrics. In all panels x-axis acronyms are as follows: BO = burn-only, GB = graze and burn, PBG = patch-burn graze. Lowercase letters indicate patterns of significance within plots, such that boxplots that do not share a letter are significantly different from one another. Boxplots without letters indicate no among-group differences. Standard boxplot format was used where boxes indicate median (dark middle line), and first and third quartiles (top and bottom of box) while whiskers show 1.5 times the inter-quartile range.

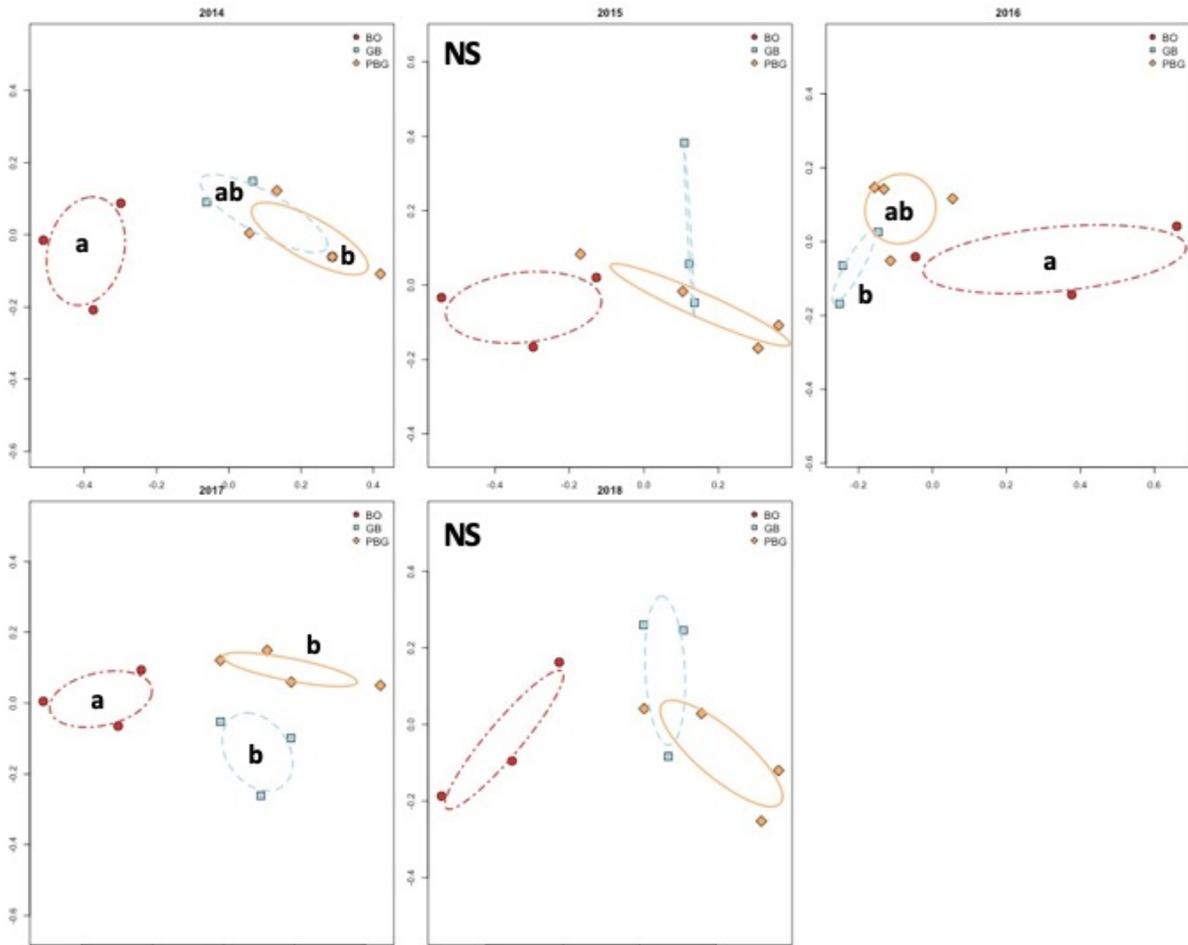


Figure 2.2. Butterfly communities were significantly different among adaptive management methods in most study years, as visualized by nonmetric multidimensional scaling ordination. Each management method has a unique point shape, ellipse line type, and color that matches those found in the site map (Figure S1). Red circles with a dot-dash ellipse line show burn-only (BO) community composition. Blue squares with a dashed line show graze and burn (GB) butterfly communities while patch-burn graze (PBG) communities are shown in orange diamonds with a continuous line. Lowercase letters indicate patterns of significance within each year's plot such that ellipses that do not share a letter are significantly different from one another. Stress measures for each nonmetric multidimensional scaling ordination are as follows: 2014 = 0.002, 2015 = 0.048, 2016 = 0.022, and 2017 = 0.029, 2018 = 0.069. The "NS" in the top-left corner of 2015 and 2018 stands for non-significant variation in community composition among management methods. Visual differences that may appear "significant" within those two ordinations can be attributed to NMS procedure maximizing between-point differences in a non-metric fashion.

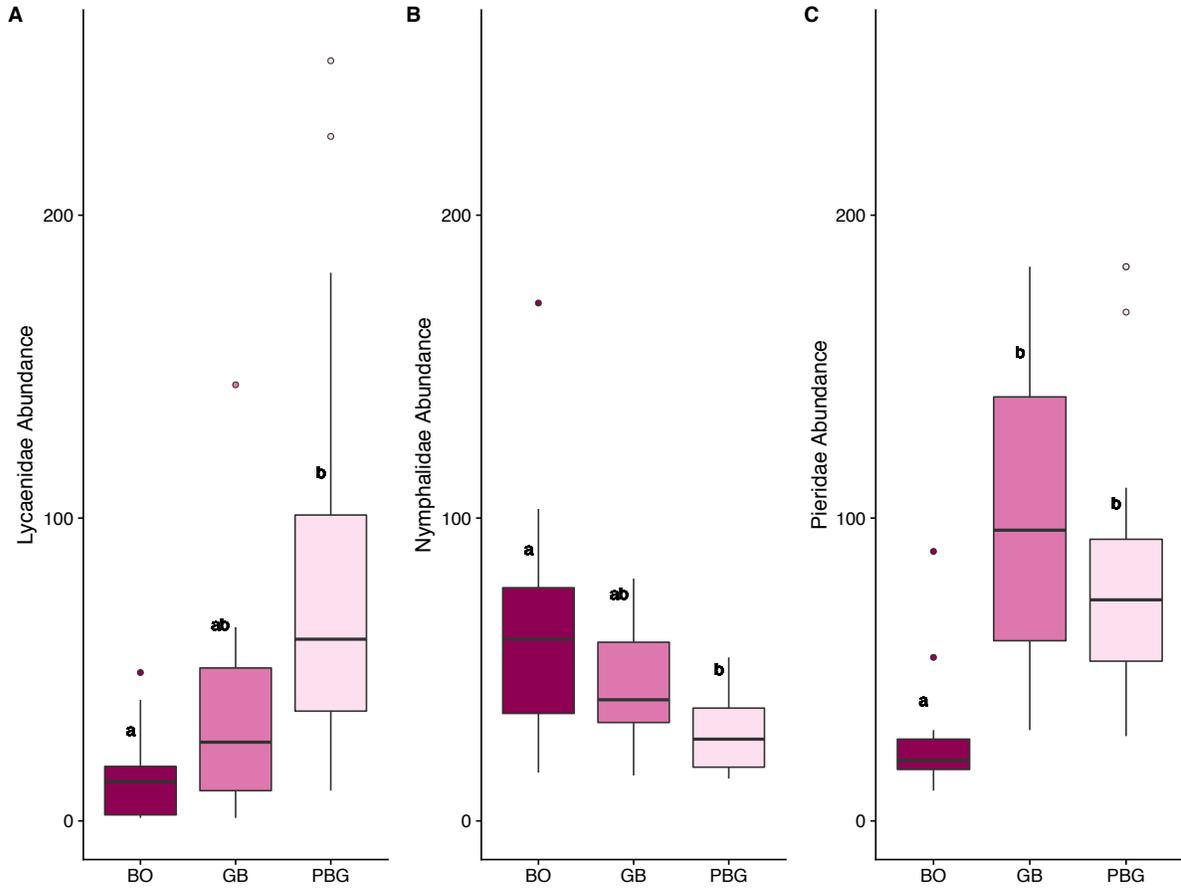


Figure 2.3. Butterfly families respond differently to each management method. Data are presented without respect to the five sampling years (2014-2018) due to the lack of a time-dependent effect of treatment. Lowercase letters indicate patterns of significance within plot such that boxplots that do not share a letter are significantly different from one another. Boxplots without letters indicate no among-group differences. Standard boxplot format was used.

Table 2.1. Summary statistics from permutational ANOVA for among-management approach analyses and, where relevant, results of pairwise comparisons.

Fig	Response	F	Df	Z	P	BO - GB	GB - PBG	BO - PBG
1	Butterfly #	10.69	2, 49	2.25	< 0.001	$\alpha = 0.025$ P = 0.001	$\alpha = 0.05$ P = 0.890	$\alpha = 0.017$ P < 0.001
1	Butterfly S	2.99	2, 49		0.741	–	–	–
1	Butterfly H'	10.18	2, 49	2.20	< 0.001	$\alpha = 0.025$ P = 0.077	$\alpha = 0.05$ P = 0.191	$\alpha = 0.017$ P < 0.001
1	Floral #	11.03	2, 49	2.29	< 0.001	$\alpha = 0.025$ P = 0.029	$\alpha = 0.05$ P = 0.159	$\alpha = 0.017$ P < 0.001
1	Floral S	0.49	2, 49		0.619	–	–	–
1	Floral H'	6.35	2, 49	1.84	0.004	$\alpha = 0.05$ P = 0.192	$\alpha = 0.025$ P = 0.087	$\alpha = 0.017$ P < 0.001
2	2014 Butterfly Com.	3.04	2, 9	2.39	0.013	$\alpha = 0.025$ P = 0.027	$\alpha = 0.05$ P = 0.930	$\alpha = 0.017$ P = 0.003
	2015 Butterfly Com.	2.07	2, 9	2.23	0.022	NS	NS	NS
2	2016 Butterfly Com.	2.54	2, 9	2.73	0.005	$\alpha = 0.017$ P = 0.003	$\alpha = 0.05$ P = 0.224	$\alpha = 0.025$ P = 0.034
2	2017 Butterfly Com.	2.94	2, 9	3.44	0.001	$\alpha = 0.025$ P = 0.006	$\alpha = 0.05$ P = 0.211	$\alpha = 0.017$ P = 0.001
	2018 Butterfly Com.	1.32	1, 6		0.292	–	–	–
	2014 Floral Com.	1.11	2, 9		0.300	–	–	–
	2015 Floral Com.	1.97	2, 9	1.91	0.032	NS	NS	NS
	2016 Floral Com.	1.84	2, 9	1.81	0.040	NS	NS	NS
	2017 Floral Com.	1.66	2, 9		0.056	–	–	–
	2018 Floral Com.	0.94	1, 6		0.421	–	–	–
3	Lycaenidae #	13.66	2, 49	2.41	< 0.001	$\alpha = 0.017$ P < 0.001	$\alpha = 0.025$ P = 0.030	$\alpha = 0.05$ P = 0.074
3	Nymphalidae #	11.58	2, 49	2.33	< 0.001	$\alpha = 0.05$ P = 0.144	$\alpha = 0.025$ P = 0.017	$\alpha = 0.017$ P < 0.001
3	Pieridae #	31.24	2, 49	3.07	< 0.001	$\alpha = 0.017$ P < 0.001	$\alpha = 0.05$ P = 0.460	$\alpha = 0.025$ P < 0.001

Management acronyms are as follows: burn only = BO; graze and burn = GB; patch-burn graze = PBG.

Response symbols are as follows: # = abundance, S = species richness, H' = Shannon diversity, Com. =

Community composition, Z scores are only provided for significant analyses ($P < 0.05$). A “–” is used for tests where pairwise comparisons were not run, and “NS” for tests where pairwise comparisons were run but were not significant after adjusting for multiple comparisons.

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Supplementary Appendix

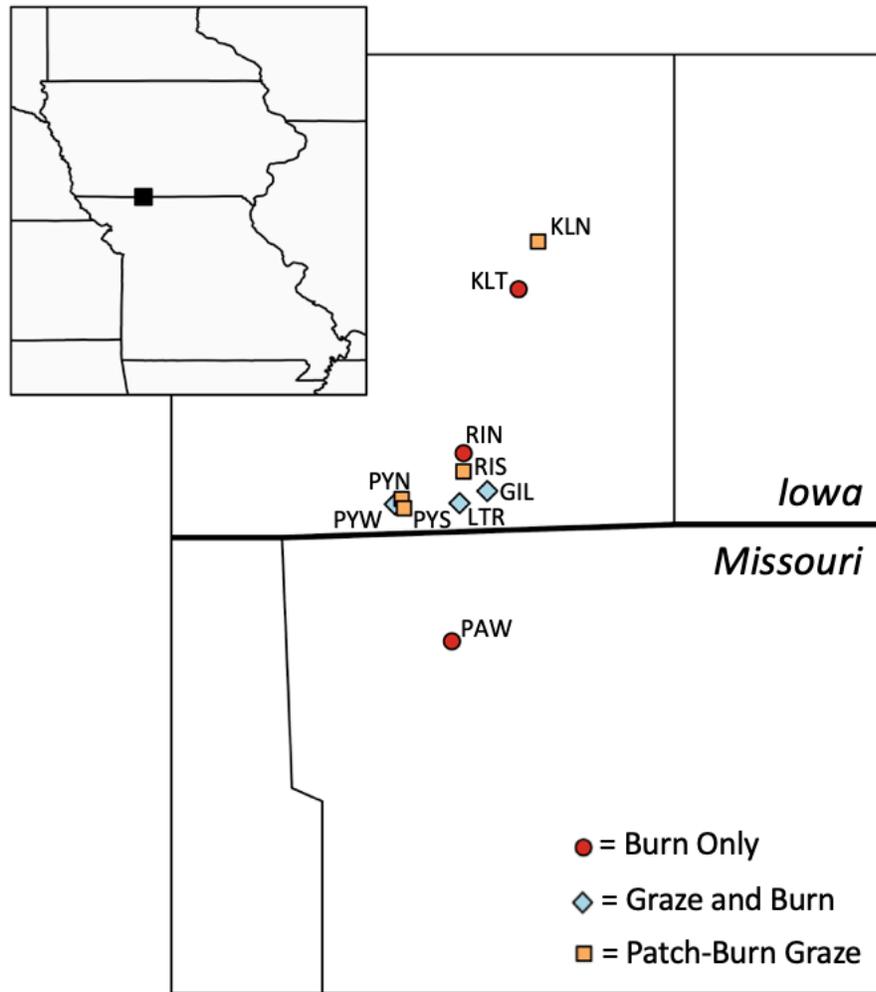


Figure S2.1. Map of study sites with state map inset. Thin lines show county borders. Site abbreviations are as follows: KLN = Kellerton North; KLT = Kellerton Tauke; RIN = Ringgold North; RIS = Ringgold South; GIL = Gilliland; LTR = Lee Trail; PYN = Pyland North; PYS = Pyland South; PYW = Pyland West; PAW = Pawnee Prairie.

Table S2.1. Butterfly species abundances in 2014.

Scientific Name	Burn Only			Graze and Burn			Patch-Burn Graze			
	KLT	PAW	RIN	GIL	LTR	PYW	KLN	PYN	PYS	RIS
<i>Asterocampa celtis</i>		2								
<i>Boloria bellona</i>		2		3		5	1	3	2	
<i>Celastrina neglecta</i>					1					1
<i>Cercyonis pegala</i>	14	29	19	20		2	2	3	3	4
<i>Chlosyne nycteis</i>				1						
<i>Colias eurytheme</i>	9	7	4	19	29	41	35	62	33	42
<i>Colias philodice</i>	7	6	11	34	25	98	22	104	61	35
<i>Cupido comyntas</i>	40	31	5	44	63	144	81	250	180	66
<i>Danaus plexippus</i>	1	4	2	2	4	10	5	9	7	1
<i>Epargyreus clarus</i>				1					1	
<i>Euptoeita claudia</i>									1	
<i>Junonia coenia</i>										1
<i>Limenitis arthemis</i>								1	1	1
<i>Lycaena dione</i>		1	1	2			3	1		
<i>Megisto cymela</i>				3						
<i>Nymphalis antiopa</i>									1	
<i>Papilio cresphontes</i>	1	1	1					2		1
<i>Papilio glaucus</i>		1	2	2	2	4		2	3	3
<i>Papilio polyxenes</i>					1					
<i>Phyciodes tharos</i>	7	13	5	8	5	3			3	14
<i>Pieris rapae</i>	2		2	11		1	5	1	1	1
<i>Polites peckius</i>								2		1
<i>Polites themistocles</i>	1			2	1	2	9	5	1	
<i>Polygonia interrogationis</i>		2								1
<i>Pyrisitia lisa</i>		1	5		1	4	1	1	1	3
<i>Satyrium edwardsii</i>									1	
<i>Satyrium titus</i>		6	1							
<i>Speyeria cybele</i>	2	19	9	5	1	3	4	2	4	10
<i>Speyeria idalia</i>	33	98	48	3	2	2	2			5
<i>Vanessa atalanta</i>		1	1			1				1
<i>Vanessa cardui</i>									1	
<i>Vanessa virginiensis</i>		1	2	6	3		3		1	1

Site abbreviations are as follows: KLN = Kellerton North; KLT = Kellerton Tauke; RIN = Ringgold North; RIS = Ringgold South; GIL = Gilliland; LTR = Lee Trail; PYN = Pyland North; PYS = Pyland South; PYW = Pyland West; PAW = Pawnee Prairie.

Table S2.2. Butterfly species abundances in 2015.

Scientific	Burn Only			Graze and Burn			Patch-Burn Graze			
	KLT	PAW	RIN	GIL	LTR	PYW	KLN	PYN	PYS	RIS
<i>Boloria bellona</i>		2				3		1	10	1
<i>Celastrina ladon</i>	1								2	
<i>Celastrina neglecta</i>		1						1		
<i>Cercyonis pegala</i>	9	6	24	3	5		2		1	3
<i>Colias eurytheme</i>	8	9	4	13	33	27	46	38	25	7
<i>Colias philodice</i>	25	12	10	39	49	84	114	129	55	27
<i>Cupido comyntas</i>	20	12	2	4	4	5	46	33	18	10
<i>Danaus plexippus</i>	7	10	5	2	4	8	1	8	7	4
<i>Epargyreus clarus</i>						1				
<i>Erynnis baptisiae</i>		2								
<i>Junonia coenia</i>			1	2	1					
<i>Limenitis archippus</i>	1			2						
<i>Lycaena hyllus</i>				1						
<i>Megisto cymela</i>		1						1	1	
<i>Nymphalis antiopa</i>			1							
<i>Papilio cresphontes</i>			1			1				2
<i>Papilio polyxenes</i>	2	3	3		2	3	5	1	5	3
<i>Phyciodes tharos</i>		1	13	6	13	1	13		3	5
<i>Pieris rapae</i>	21	9	5	111	31	25	23	16	12	10
<i>Polites themistocles</i>		1						2	2	
<i>Polygonia comma</i>	2	1		1				1		2
<i>Polygonia interrogationis</i>			1		1				2	2
<i>Satyrrium titus</i>				1						
<i>Speyeria cybele</i>	3	10		2	7	14	1	2	7	8
<i>Speyeria idalia</i>	8	28	17		1	9			1	2
<i>Thymelicus lineola</i>						1				
<i>Vanessa atalanta</i>	2	1		1	4	1	1	1	3	2
<i>Vanessa cardui</i>	2			2	1	1		1		1
<i>Vanessa virginiensis</i>					1					

Site abbreviations are as follows: KLN = Kellerton North; KLT = Kellerton Tauke; RIN = Ringgold North; RIS = Ringgold South; GIL = Gilliland; LTR = Lee Trail; PYN = Pyland North; PYS = Pyland South; PYW = Pyland West; PAW = Pawnee Prairie.

Table S2.3. Butterfly species abundances in 2016.

Scientific	Burn Only			Graze and Burn			Patch-Burn Graze			
	KLT	PAW	RIN	GIL	LTR	PYW	KLN	PYN	PYS	RIS
<i>Anatrytone logan</i>	1			1				1		
<i>Ancyloxypha numitor</i>					1					
<i>Boloria bellona</i>	1	1	1	8	19	14	1	6	12	11
<i>Celastrina neglecta</i>		1		1					1	
<i>Cercyonis pegala</i>	18	13	2	6	5	2	27		7	2
<i>Chlosyne gorgone</i>				1						
<i>Chlosyne nycteis</i>					1	1				2
<i>Colias eurytheme</i>	34	3	3	88	110	40	36	40	32	17
<i>Colias philodice</i>	17	7	4	42	31	32	27	22	16	10
<i>Cupido comyntas</i>	46	14	1	51	20	44	51	101	102	49
<i>Danaus plexippus</i>	1	1	2			1	1		1	
<i>Epargyreus clarus</i>		3		5	2		1			1
<i>Erynnis baptisiae</i>					1	1				
<i>Euphyes bimacula</i>		1						1		
<i>Euphyes vestris</i>		3		1						
<i>Junonia coenia</i>	1			15	7	1	1		3	5
<i>Limenitis archippus</i>				1	1					
<i>Limenitis arthemis</i>						1			1	2
<i>Lycaena dione</i>	2									
<i>Lycaena hyllus</i>	1			3						
<i>Nathalis iole</i>	1		1				1			1
<i>Papilio cressphontes</i>			1	3		2			1	1
<i>Papilio glaucus</i>	1			1				1	1	1
<i>Papilio polyxenes</i>	3	1	2	7	2	1	5	2	4	2
<i>Phyciodes tharos</i>	1	2	2	12	12	15	11	3	4	1
<i>Pieris rapae</i>	36	7	4	50	42	24	46	22	23	9
<i>Polites peckius</i>				1	2	1		15		
<i>Polites themistocles</i>				1	5		1			
<i>Polygonia interrogationis</i>				1						
<i>Pyrisitia lisa</i>	1		1					1		
<i>Speyeria cybele</i>		6	4			4	2	4	5	10
<i>Speyeria idalia</i>	12	12	5		1	1	2	1	3	1
<i>Thymelicus lineola</i>			1							
<i>Vanessa atalanta</i>	1	1		1						
<i>Vanessa virginiensis</i>					1				1	

Site abbreviations are as follows: KLN = Kellerton North; KLT = Kellerton Tauke; RIN = Ringgold North; RIS = Ringgold South; GIL = Gilliland; LTR = Lee Trail; PYN = Pyland North; PYS = Pyland South; PYW = Pyland West; PAW = Pawnee Prairie.

Table S2.4. Butterfly species abundances in 2017.

Scientific	Burn Only			Graze and Burn			Patch-Burn Graze			
	KLT	PAW	RIN	GIL	LTR	PYW	KLN	PYN	PYS	RIS
<i>Anatrytone logan</i>					1					
<i>Ancyloxypha numitor</i>	1			1			1	9	2	
<i>Boloria bellona</i>				7	2	20		2	11	2
<i>Cercyonis pegala</i>	11	16	30		3	10		1	6	1
<i>Chlosyne nycteis</i>				2						
<i>Colias eurytheme</i>	11	1	10	40	73	16	7	33	21	10
<i>Colias philodice</i>	3	4	6	16	18	15	20	35	20	5
<i>Cupido comyntas</i>	7	1	1	61	14	30	52	225	95	37
<i>Danaus plexippus</i>	3	1	8	5	7	1	4	4	4	
<i>Epargyreus clarus</i>		3		1						
<i>Erynnis baptisiae</i>								1	1	
<i>Euphyes vestris</i>		2						1		
<i>Junonia coenia</i>	1	2	9	23	7	8	1	1	3	2
<i>Limenitis archippus</i>	1				1					
<i>Lycaena dione</i>	2								1	
<i>Lycaena hyllus</i>							1	1		
<i>Nathalis iole</i>								1		
<i>Papilio cresphontes</i>					1				2	
<i>Papilio glaucus</i>			1		2			2	2	1
<i>Papilio polyxenes</i>	1		1	1	1		1	2	3	1
<i>Phyciodes tharos</i>	10	8	12	34	43	21	6	4	7	10
<i>Pieris rapae</i>	11	4	8	28	21	13	10	19	11	13
<i>Polites peckius</i>	1			1	5			1		2
<i>Polites themistocles</i>				3	7			2		
<i>Polygonia comma</i>		1				1			2	
<i>Polygonia interrogationis</i>			1							
<i>Pyrisitia lisa</i>		1	3							
<i>Speyeria cybele</i>	1	19	4	3	3	4	1	1	2	4
<i>Speyeria idalia</i>	5	7	7		1				2	1
<i>Vanessa atalanta</i>	1	3		1			1			
<i>Vanessa cardui</i>	1	1			1	1	1		1	
<i>Vanessa virginiensis</i>						1	2	1		

Site abbreviations are as follows: KLN = Kellerton North; KLT = Kellerton Tauke; RIN = Ringgold North; RIS = Ringgold South; GIL = Gilliland; LTR = Lee Trail; PYN = Pyland North; PYS = Pyland South; PYW = Pyland West; PAW = Pawnee Prairie.

Table S2.5. Butterfly species abundances in 2018.

Scientific	Burn Only			Graze and Burn			Patch-Burn Graze			
	KLT	PAW	RIN	GIL	LTR	PYW	KLN	PYN	PYS	RIS
<i>Anatrytone logan</i>					1		1			
<i>Ancyloxypha numitor</i>	1						1	1		
<i>Asterocampa celtis</i>			1							
<i>Boloria bellona</i>	4	7		5	6	26	7	8	10	15
<i>Cercyonis pegala</i>	9	11	25			5	2	1		
<i>Chlosyne nycteis</i>	6	1		4	4	2		1		1
<i>Colias eurytheme</i>	8	6	5	21	24	29	30	28	29	21
<i>Colias philodice</i>	10	8	5	4	10	26	24	15	15	13
<i>Cupido comyntas</i>	13	15	1	14	1	26	77	77	18	14
<i>Danaus plexippus</i>	7	11	13	3	6	13	3		7	5
<i>Epargyreus clarus</i>		3		4	7	3	1	1	1	1
<i>Erynnis baptisiae</i>	1		1		1				1	1
<i>Euptoeita claudia</i>						2				
<i>Hylephila phyleus</i>									1	
<i>Junonia coenia</i>		1		2						
<i>Limenitis archippus</i>	2							1		
<i>Limenitis arthemis</i>			1					1		
<i>Lycaedies melissa</i>	1						24			
<i>Lycaena dione</i>			1	2						1
<i>Lycaena hyllus</i>									1	
<i>Megisto cymela</i>										1
<i>Nathalis iole</i>			1							
<i>Papilio crespontes</i>			1		2	1			2	1
<i>Papilio glaucus</i>	2		3		2	1		1	4	1
<i>Papilio polyxenes</i>	2	1	3	1	3	3	5	10	4	3
<i>Pholisora catullus</i>										1
<i>Phyciodes tharos</i>	27	10	7	12	9	13	21	3	3	11
<i>Pieris rapae</i>	8	6	5	4	10	11	19	11	10	18
<i>Polites peckius</i>				1	1		2	4		1
<i>Polites themistocles</i>					5	1			2	
<i>Pyrisitia lisa</i>	1		1	1		7	2		2	1
<i>Speyeria cybele</i>	2	26	12	8	1	13	3	6	7	16
<i>Speyeria idalia</i>	4	33	24		4	6			2	4
<i>Thorybes bathyllus</i>					1	1				
<i>Vanessa atalanta</i>	1	2								
<i>Vanessa virginiensis</i>		1			1		2		2	1

Site abbreviations are as follows: KLN = Kellerton North; KLT = Kellerton Tauke; RIN = Ringgold North; RIS = Ringgold South; GIL = Gilliland; LTR = Lee Trail; PYN = Pyland North; PYS = Pyland South; PYW = Pyland West; PAW = Pawnee Prairie.

Table S2.6. Summary statistics for among-year analyses.

Figure	Response	F	Df	Z	P
S2A	Butterfly #	0.93	4, 49	-0.095	0.559
S2B	Butterfly S	2.01	4, 49	0.585	0.279
S2C	Butterfly H'	2.94	4, 49	0.681	0.251
S2D	Floral #	1.07	4, 49	-0.072	0.550
S2E	Floral S	0.74	4, 49	-0.469	0.700
S2F	Floral H'	0.56	4, 49	-0.640	0.757

Response symbols are as follows: # = abundance, S = species richness, H' = Shannon diversity. F statistics are the result of comparing mean squares of a model with year (as a factor) against a null model including site (i.e., $H_1: Y \sim \text{Year}$, $H_0: Y \sim \text{Site}$).

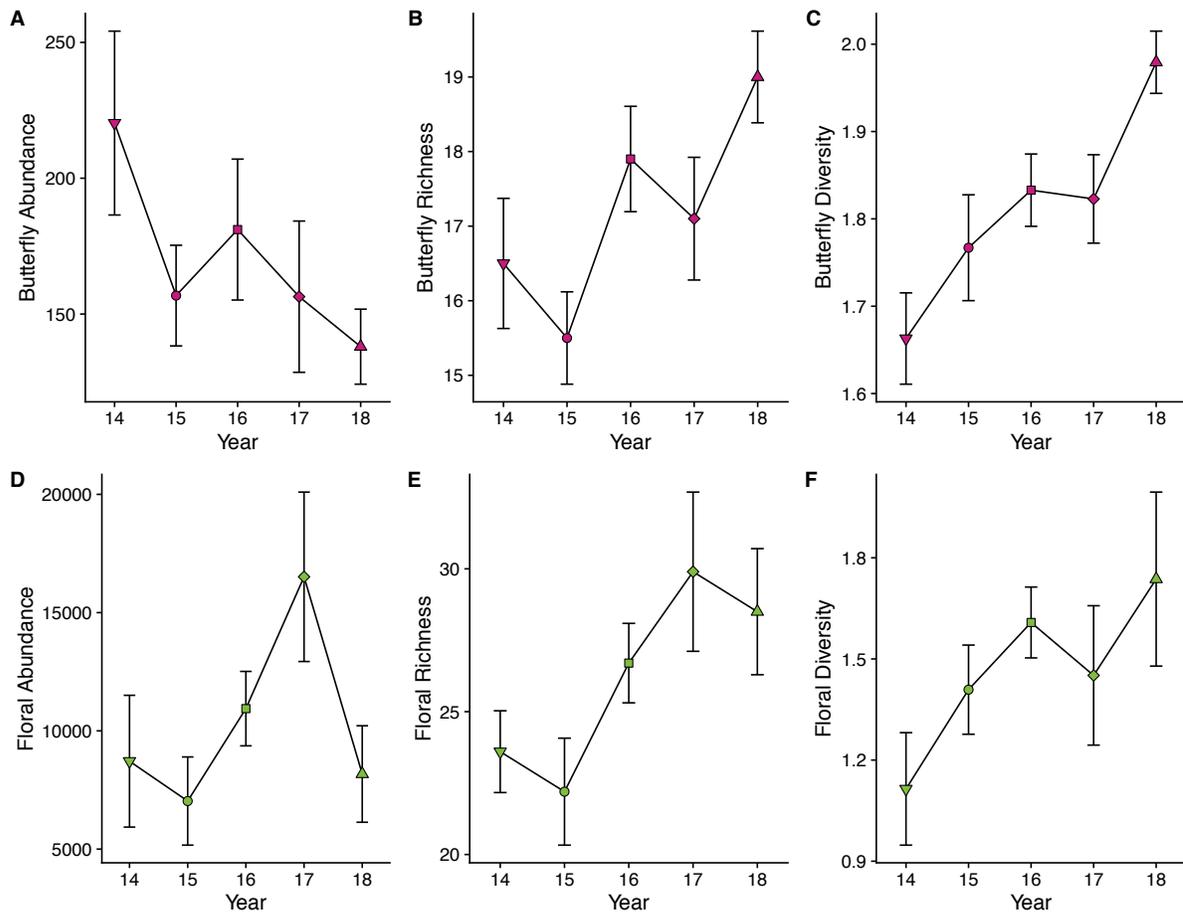


Figure S2.2. Butterfly and floral resource variation among years. Points are across treatment, within-year averages, and error bars show standard error. No among year-analyses proved significant ($p \gg 0.1$), though year was treated as a factor to better capture response to management at discrete time points.

CHAPTER 3. EVALUATING THE UTILITY OF SPECIES DISTRIBUTION MODELS IN INFORMING CLIMATE CHANGE-RESILIENT GRASSLAND RESTORATION STRATEGY

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Abstract

Tallgrass prairie ecosystems in North America are heavily degraded and require effective restoration strategies if prairie specialist taxa are to be preserved. One common management tool used to restore grassland is the application of a seed-mix of native prairie plant species. While this technique is effective in the short-term, it is critical that species' resilience to changing climate be evaluated when designing these mixes. By utilizing species distribution models (SDMs), species' bioclimatic envelopes—and thus the geographic area suitable for them—can be quantified and predicted under various future climate regimes, and current seed-mixes may be modified to include more climate resilient species or exclude more affected species. We evaluated climate response on plant functional groups to examine the generalizability of climate response among species of particular functional groups. We selected fourteen prairie species representing the functional groups of cool-season and warm-season grasses, forbs, and legumes and we modeled their responses under both a moderate and more extreme predicted future. Our functional group 'composite maps' show that warm-season grasses, forbs, and legumes responded similarly

to other species within their functional group, while cool-season grasses showed less inter-species concordance. The value of functional group as a rough method for evaluating climate-resilience is therefore supported, but candidate cool-season grass species will require more individualized attention. This result suggests that seed-mix designers may be able to use species with more occurrence records to generate functional group-level predictions to assess the climate response of species for which there are prohibitively few occurrence records for modeling.

Introduction

Prairies in the United States are among the most degraded habitats in the world (Larson et al. 2011), and as such, have necessitated active restoration, particularly for the plant communities historically found in these systems (Vogel et al. 2007; Debinski et al. 2011; Pillsbury et al. 2011; Delaney et al. 2015). The addition of native plant seeds via seed-mixes is one restoration tool used to speed the re-colonization of degraded prairies by native prairie plant species (Dickson & Busby 2009; Larson et al. 2011). However, the composition of seed-mixes can be limited by seed availability, cost of seeds from rare plants, or even a focus on particular seed ecotypes, thus restricting the possible combinations of species in a seed-mix used for a given area. The number of different species and relative abundance of seeds included in a given seed-mix must then be considered from ecological, economic, and logistical perspectives, and the success of the end-product is often judged years after the seed-mix is first implemented (Dickson & Busby 2009). Given the need for viable restoration strategies in prairies, it is imperative that

restoration efforts be successful in longer timeframes than is usually feasible for empirical monitoring. Modeling approaches can serve as a valuable tool in this regard, especially when the input data are easily collected or publicly available.

In particular, species distribution models (SDMs) can be used relatively easily (Kane et al. 2017) to assess how the effectiveness of species in a restoration seed-mix will change under different future climate predictions, and seed-mix composition can then be modified in the present without the need to wait years for experimental results. SDMs are used to predict the environmental suitability of a continent or landscape for individual species both in present conditions and under a variety of future climate change scenarios (Soberón & Nakamura 2009; Elith et al. 2011). These models correlate current occurrence records of a species with the temperature and precipitation in that area to generate a prediction of the bioclimatic envelope for individual species, which can then be projected across a current or future landscape (Pearson & Dawson 2003; Araújo & Guisan 2006; Soberón & Nakamura 2009; Elith et al. 2011). Climate data alone are sufficient predictors at macro-ecological scales (Pearson & Dawson 2003), which increases the potential utility of these models to managers and researchers working with limited resources. These models are generally considered to generate robust predictions even in the absence of data on biotic factors, land-use, and soil type (Thuiller et al. 2004; Pearson et al. 2007), making them especially useful for species for which publicly available data are sparse or for projects where it is not feasible to collect occurrence records prior to model construction. By employing SDMs on prairie plant species used in a seed-mix currently in use in southern Iowa, the impact of possible climatic futures can be quantified and the utility of SDMs in recommending

changes to seed-mix composition may be assessed. In addition, including multiple species from each of several functional groups (e.g. cool-season grasses, warm-season grasses, forbs, and legumes) can allow the conservation of response within functional group to be examined. This functional group-level response is especially relevant given the potential for functional group predictions to be used as a proxy for species without prerequisite data for their own models.

We hypothesized that (1) plant functional groups will show relatively conserved responses to changing climate and (2) most modeled species will show increasing suitability in the northern extent of their range and decreasing suitability in the southern edges of their range regardless of how conserved the response is within functional group.

Materials and Methods

Species Selection

To best assess the relevance of this modeling approach to managers, we retrieved publicly available occurrence records for all 26 tallgrass prairie plant species in a seed-mix currently used in the American Midwest. Of this initial pool, only fourteen species were selected for modeling based on sufficient occurrence records. These species represent four functional groups: cool-season (C_3) grasses, warm-season (C_4) grasses, forbs (here defined as non-leguminous flowering plants), and legumes (Table 3.1). While this functional group approach leaves three of the functional groups presented here with relatively few included species, the limited number of species with enough occurrence records to model is likely to be a constraint encountered by managers using this approach, so modeling proceeded

despite the reduced representation in some groups. Species occurrence records across North America were obtained from the Global Biodiversity Information Facility, the University of California Berkeley's Eco Engine, and the BISON database from United States Geological Survey via their packages in the R statistical environment—version 3.3.1—, “rgbif”, “ecoengine”, and “rbison” respectively (Ram 2016; Chamberlain 2016; Chamberlain et al. 2016). Only data that met Darwin Core standards (Wieczorek et al. 2012) were used. Records from outside of the tallgrass prairie region were included to ensure that the full range of environmental conditions each species has been observed to exist in was represented in our models.

Predictor Selection

All data for the climate-predictor variables were obtained from the WorldClim Global Climate Dataset—version 1.4—at a 2.5-minute resolution (an area of $\sim 5 \text{ km}^2$ at the equator) using the same latitude and longitude bounds as those used for species occurrence data. This broad scale (both in terms of pixel size and spatial extent of model) was selected to prevent inappropriately fine interpretation of model outputs, as this has been indicated as an area of concern in projects utilizing presence-only modeling (Yackulic et al. 2013). WorldClim uses data from a large number of surface meteorological stations and applies an interpolation algorithm to generate spatially gridded data (Hijmans et al. 2005). Initially, all models are informed by eight bioclimatic (BIOCLIM) variables: mean temperature for the wettest (BIO8), driest (BIO9), warmest (BIO10), and coldest (BIO11) quarters averaged from 1960 to 1990 as well as the mean precipitation for the same quarters (BIO16 through 19

respectively). These variables were selected because they are the finest temporal BIOCLIM variables and are thus most likely to represent the intra-annual climatic variation species must tolerate. Only BIOCLIM variables with a Pearson correlation coefficient of less than 0.7 with the other BIOCLIM variables at occurrence locations were included in training each model; this value was reduced from the 0.75 threshold used by Kane *et al.* (2017) due to the use of a greater number of predictor variables. Correlation was assessed on a per-species basis (Pearson & Dawson 2003; Elith *et al.* 2010). The predictor variables used for each species are found in Table S3.1.

SDMs for the mid-21st century (2041-2060) were built with the projected climate from the National Center for Atmospheric Research (United States) CCSM4 global climate model (GCM) in two Representative Concentration Pathway (RCP) emissions scenarios (RCP 4.5 and 8.5). The CCSM4 GCM predicts an average increase of 2.5°C across North America for RCP 4.5 and a 4.4°C average increase for RCP 8.5, and neither predicted future shows an average change of more than 1 cm in rainfall. Hereafter RCP 4.5 is referred to as the “moderate” future and RCP 8.5 as “extreme” future. The CCSM4 GCM is thus an ideal candidate for suitability response comparisons between possible future conditions because of the effective standardization of most variables other than temperature. This GCM also shows relatively low error frequency when compared to the observed climate for parts of North America (Rupp *et al.* 2013). Additionally, by using only RCPs from the same GCM, we control for any differences in model convention in the construction of these climate datasets, and therefore eliminate suitability prediction differences that are mere artifacts of GCM construction.

Modeling Methods

Current and future SDMs for each of the selected species were created with the modeling software MaxEnt version 3.3.3k (Elith et al. 2011) through its interface with the R statistical environment. Occurrence records were thinned in multivariate environmental space to account for potential oversampling of environmental conditions following from geographic sampling bias (de Oliveira et al. 2014) via principal components analysis (PCA) of the predictor variables associated with each occurrence record. The points were plotted against PC1 and PC2 and one record was randomly selected wherever multiple records overlapped. All models constructed had 40 or more occurrence records after environmental thinning (Table S3.1), to stay well above the recommended 25 minimum number of occurrence records (Pearson et al. 2007).

For each species, corrected Akaike Information Criterion (AICc) values were compared between models with MaxEnt's regularization parameter (β) set at 0.5, 1, 2, 3, 4, or 5, and the model with the lowest AICc was selected (Warren & Seifert 2011). After each species' current distribution model was generated, projections into each predicted future were conducted for each species. In order to limit extrapolation, all models constructed used the default "clamping" option within MaxEnt such that climate values outside of those used to train the model are treated as if they were the end of the training range (Elith et al. 2011). All suitability predictions are made in the logistic output format such that predictions range from 1 (100% probability of presence) to 0 (0% probability of presence) on a continuous scale (Phillips & Dudík 2008).

All models were evaluated by the area under the receiver-operator characteristic curve (AUC) (Merow et al. 2013; Kane et al. 2017). Cross-validation by resampling k -folds ($k = 5$) was performed to obtain a more discriminant AUC value, and for all models mean AUC was greater than 0.82, indicating robust model performance for all species distribution models (Table S3.1). While AUC has been criticized as a method of model evaluation (Fourcade et al. 2018), our use of relatively few BIOCLIM variables (average of five predictor variables across all 14 species), coupled with our restriction of interpretation to climatic suitability rather than realized distribution both minimizes inflation of AUC and allows for relaxed predictor selection at the outset.

Due to our interest in the similarity of response of species within the same functional group rather than the response of particular species—and the high number of species-specific output models generated as a result of this process (42 total)—only composite maps are presented here to facilitate evaluation of functional group response. Composite maps demonstrate the number of modeled species that performed at or better than a given threshold of suitability. Composite maps presented here use 50% as that threshold such that each map demonstrates high suitability explicitly while allowing for equal interpretation of low suitability (e.g., if two species are doing well in a given area that means that the remainder of the species are not above the suitability threshold). A limitation of this approach is the loss of much of the gradient of suitability response but given the dramatic increase in interpretability to non-specialist audiences and likely relevance of such interpretability to managers, we continued in this vein.

Results

Cool-Season Grasses

Cool-season grasses did not exhibit a conserved response to either predicted future (Figure 3.1). All three cool-season grass species were predicted to have greater than 50% suitability in only small and isolated areas outside of the American Midwest. However, in the RCP 8.5 predicted future, bioclimatic suitability for two of the three species was above the threshold throughout much of Iowa, Nebraska, and Kansas. There were areas in the Southeast and Northern Midwest for which all three species had low predicted suitability, so this offers partial support for this functional group sharing certain conditions that are unsuitable while the specific tolerances to less negative conditions vary by species. Interestingly, agreement between species of this group increased from present conditions to moderate future and increased further from the moderate to extreme future.

Warm-Season Grasses

In contrast to the apparent lack of consensus in cool-season grass response, warm-season grasses tended to respond similarly in both future conditions (Figure 3.2). Not only did all three species show greater than 50% future suitability throughout the vast majority of the American Midwest, for much of the Eastern half of the nation, two species remained above that threshold. Additionally, all three species showed below 50% suitability in the American southeast, and this area of low suitability remained consistent between the two RCPs. The area of overlapping suitability nearly doubled in size from present conditions to the moderate future though remained largely static between the two future predictions.

Forbs

More forb species were modeled than any other functional group in this project, making the observed conservation of response among those species even more striking. Not only does the area of above 50% suitability overlap for nearly all modeled species; most species are also below the threshold when any one is (Figure 3.3). Areas of suitable conditions are largely in the American Northeast and most of that area is projected to be suitable for at least five of the six modeled forb species. While in RCP 4.5 very little of the American Midwest is suitable for even one species, in RCP 8.5 this area is projected to be suitable for at least one species (and in many areas as many as three).

Legumes

While only two legume species had sufficient occurrence records for modeling, and our inferential abilities are therefore limited, the areas of consensus are of note. The American Midwest is projected to be suitable for both legume species in both futures (Figure 3.4), though the specific area is somewhat north of the suitable area for warm-season grasses and west of forb areas. As with warm-season grasses, the area in present conditions predicted to be suitable for all modeled legumes virtually only expands from present to either future condition, indicating that some groups may be sufficiently climate-resilient that they can be maintained in current areas while also introduced into previously inhospitable areas.

Discussion

While we hypothesized that species within each functional group would have conserved responses to changing climate, this appears to only be partially true; while forb response was highly conserved, warm-season grass and legume response were less so and there were very few areas of consensus among cool-season grasses. This indicates that while functional group may be a good predictor for climate response for some functional groups, there are some limitations. The relatively few species per functional group is particularly limiting to our assessment of the value of functional group as a predictor of species' response, though is likely to be equally limiting to managers using SDMs to inform restoration strategy. Additionally, though we hypothesized that all species would likely shift northwards (i.e., suitability would decline in the southern-most areas and increase in the northern-most areas) only forbs exhibited this response. Given these findings, it is clear that functional group is not an equally good predictor of response to climate change across the four functional groups used here. Further exploration of functional group response to climate change—particularly with a greater number of modeled species per group—will lend valuable insight into the climate-resiliency of different groups. An alternative avenue to merely increasing the number of species per group would be to use the physiological tolerances of each species to define more ecologically relevant groups for modeling. Such an approach would be extremely valuable to improving the relevance of SDMs and would also dramatically increase the precision of management recommendations from such models.

For Midwestern restorations using seed-mixes, warm-season grasses and legumes can be expected to have some resilience to changing climate because these groups show high suitability in the Midwest in both future conditions (Figures 2 and 3). This response makes them better candidates for inclusion in seed-mixes than many cool-season grass or forb species. However, it should be noted that both of those less-resilient functional groups do have members for whom the Midwest remains suitable (Figures 1 and 4), so some species-specific modeling may be valuable. Also, for restorations being conducted in the southern or eastern Midwest, even under the most severe predicted future all functional groups (and virtually all modeled species) have predicted suitability above 50%, indicating that responses to climatic change may be less extensive in those areas, at least in the near-term.

The variability in suitability response between the two grass functional groups may be explained by the current prevalence of warm-season grasses in areas of hotter conditions. Moderately increasing surface temperatures appear to remain within the tolerance of warm-season grasses—at least initially—in a way that is less expected for cool-season grasses. This would also help explain the northward expansion of warm-season suitability insofar as unsuitable (i.e., cold) conditions in the northern United States would become more suitable (i.e., warmer) in the future. One caveat particularly relevant to the discussion of the two grass functional groups' responses is that the terms 'warm-season' and 'cool-season,' while useful, should not be taken to be absolute predictors of thermal tolerance. As brought up earlier, quantification of true physiological responses of these

species will invariably lead to increased quality of result and should be pursued in future studies.

A factor that is left unconsidered here but is likely to affect distributions and suitability for these functional groups in particular is the impact of changing atmospheric CO₂ levels on the different photosynthetic modes of cool and warm-season grasses (C₃ and C₄ photosynthesis respectively). C₄ photosynthesis allows for more carbon concentration, and hence more chemically efficient photosynthesis reactions in low CO₂ environments, than does C₃ photosynthesis (Taiz et al. 2014). This physiological difference is likely to affect the response of grasses to anthropogenic climate change (Griffith et al. 2017), and could exacerbate the projected responses of these functional groups. However, it is improbable that a functional group or species predicted to experience extremely low suitability in a given area because of some combination of temperature and rainfall will be able to surmount these constraints if the concentration of atmospheric CO₂ becomes more advantageous for its photosynthetic mode.

In contrast to the grass species, and despite the larger number of forb species included, suitability changes were highly consistent across species (Figure 3.3). This was also the case for both warm-season grass and legume response, but the consensus among forb species is particularly noteworthy because it is conserved in a novel area and included many more species than other functional groups. It is also valuable to consider that the number of species for which suitability is predicted to be above 50% increases in the Midwest from present conditions to moderate future and even further from moderate to extreme future, though never to the extent of agreement found in the Northeast.

Given that only two legume species included in the seed-mix drawn from here had numerous enough occurrence records for model construction, generalizations about this functional group are especially limited. That being said, areas suitable for one species tended to be suitable for both across the majority of the modeled landscape, and the same was true for unsuitable conditions (Figure 3.4). The legume functional group also exhibited very little change between the two future conditions, which may be indicative of at least some resilience of this functional group to changing climate. This seems particularly the case when considering that the suitable area only increases from present to either futures' predicted conditions.

The results presented here demonstrate that warm-season grasses, forbs, and legumes may be expected to show some consistency in responding to a warming world. Therefore, when species from within these functional groups are being evaluated for inclusion in seed-mixes, modeling of other members of the functional group—either individually or collectively as shown here—may provide valuable insights. Desired cool-season grasses may require more of a single-species approach because generalization across the functional group does not appear to be supported. Additionally, our results indicate that the general assumption of northern range shifts in response to climate change may not always be robust for these plant species. It is important however to reiterate that given the constraints of the limited number of species in each functional group, the strength of our inferences is correspondingly reduced. In assessing the potential utility of these models to informing restoration plans, choosing species for modeling from only those in use in a particular seed-mix is likely to dramatically reduce the scope of conclusions that can be

drawn. For restoration planners interested in using this type of modeling approach, it will likely be more effective to either model species of interest individually or choose functional groups of interest and then model many species within those groups (regardless of whether or not those species are typically in a seed-mix).

In interpreting these results, it is also important to note that our models make no attempt to include soil, current land-use, biotic interactions, or other known biologically relevant factors in informing the predictions of current and future habitat suitability. In some cases, scientists and managers may be interested in predicting climate-change induced distribution changes at a finer spatial scale or including these variables. A microhabitat model is more appropriate for delving into this type of question than is a MaxEnt-style SDM (Araújo & Guisan 2006; Araújo & Luoto 2007). Likewise, a more mechanistically specific model will be better able to clarify how photosynthetic mode (e.g. C_3 versus C_4) may buffer against or increase susceptibility to changing climate (Griffith et al. 2017). A more specific model is also likely to be able to evaluate the relative importance of each of these factors and potentially account for changes to the species-environment relationship that MaxEnt assumes to be constant. Nonetheless, the results presented here can serve to indicate areas where microhabitat models may be most profitably applied. Future models specific to the American southeast, Northern Great Plains, and upper Midwest could assist in understanding the potential microhabitat-scale impacts of climate change for these important prairie species.

The ability of SDMs to create continent-scale models from relatively few occurrence records, as demonstrated here, is remarkably useful as a complement to experimental

restoration approaches and finer-scale modeling methods. By including both modeling and on-the-ground techniques, restoration projects will be better informed and will be more likely to restore and conserve the habitats and communities that will exist into the future, rather than solely replicating those communities that existed without consideration for the effects of a changing climate.

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Figures and Tables

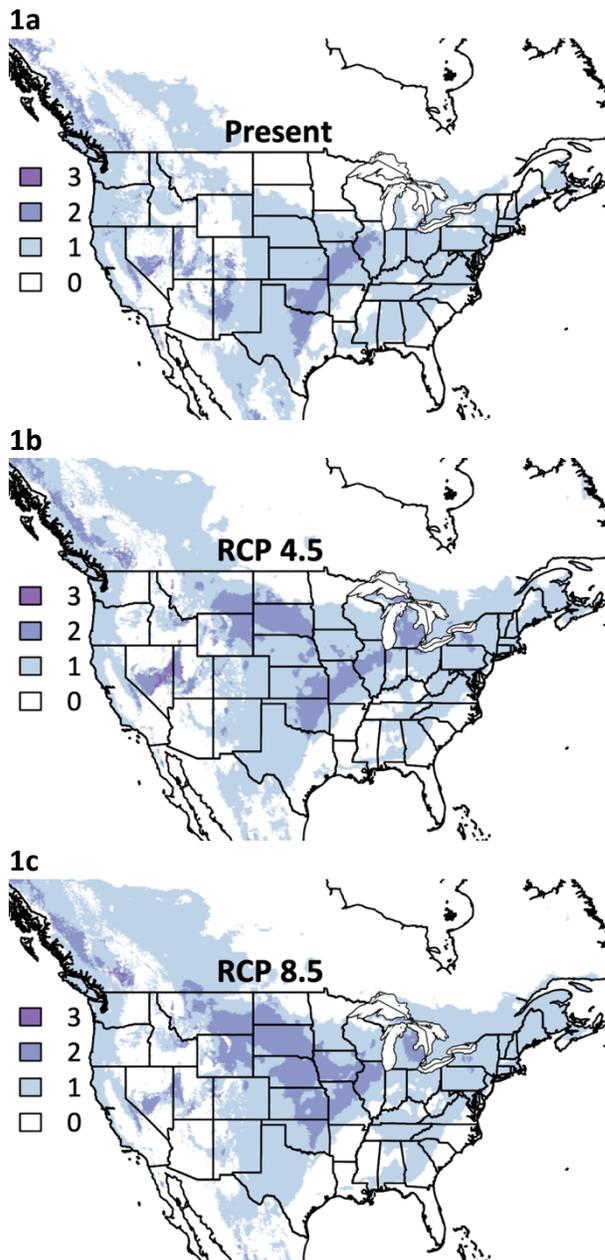


Figure 3.1. Composite Map of Cool-Season Grass (1a) Current Distribution and Response to (1b) RCP 4.5 and (1c) RCP 8.5. Colors indicate the number of species where suitability is predicted to greater than or equal to 50%. Darker colors indicate areas where bioclimatic suitability is above the threshold for more species. Included species are *Elymus virginicus*, *Koeleria macrantha*, and *Stipa spartea*. Time period is identified in the top of each panel.

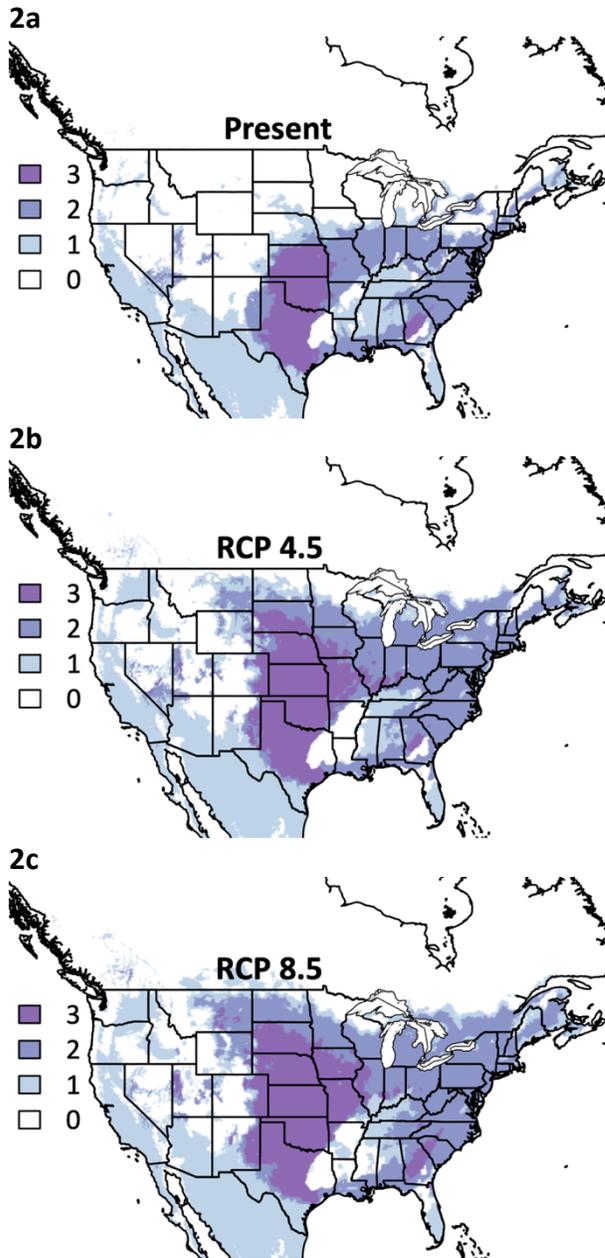


Figure 3.2. Composite Map of Warm-Season Grass (2a) Current Distribution and Response to (2b) RCP 4.5 and (2c) RCP 8.5. Colors indicate the number of species where suitability is predicted to be greater than or equal to 50%. Darker colors indicate areas where bioclimatic suitability is above the threshold for more species. Included species are *Bouteloua curtipendula*, *Schizachyrium scoparium*, and *Sorghastrum nutans*. Time period is identified in the top of each panel.

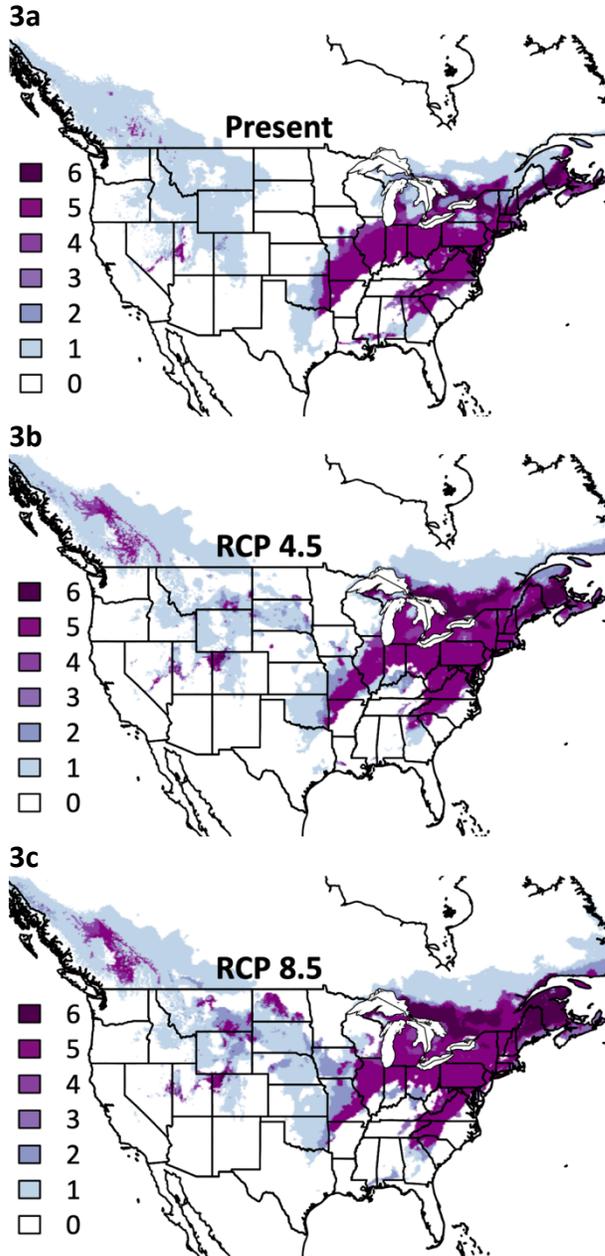


Figure 3.3. Composite Map of Forb (3a) Current Distribution and Response to (3b) RCP 4.5 and (3c) RCP 8.5. Colors indicate the number of species where suitability is predicted to be greater than or equal to 50%. Darker colors indicate areas where bioclimatic suitability is above the threshold for more species. Included species are *Asclepias incarnata*, *A. syriaca*, *A. tuberosa*, *Drymocallis arguta*, *Lobelia siphilitica*, and *Monarda fistulosa*. Time period is identified in the top of each panel.

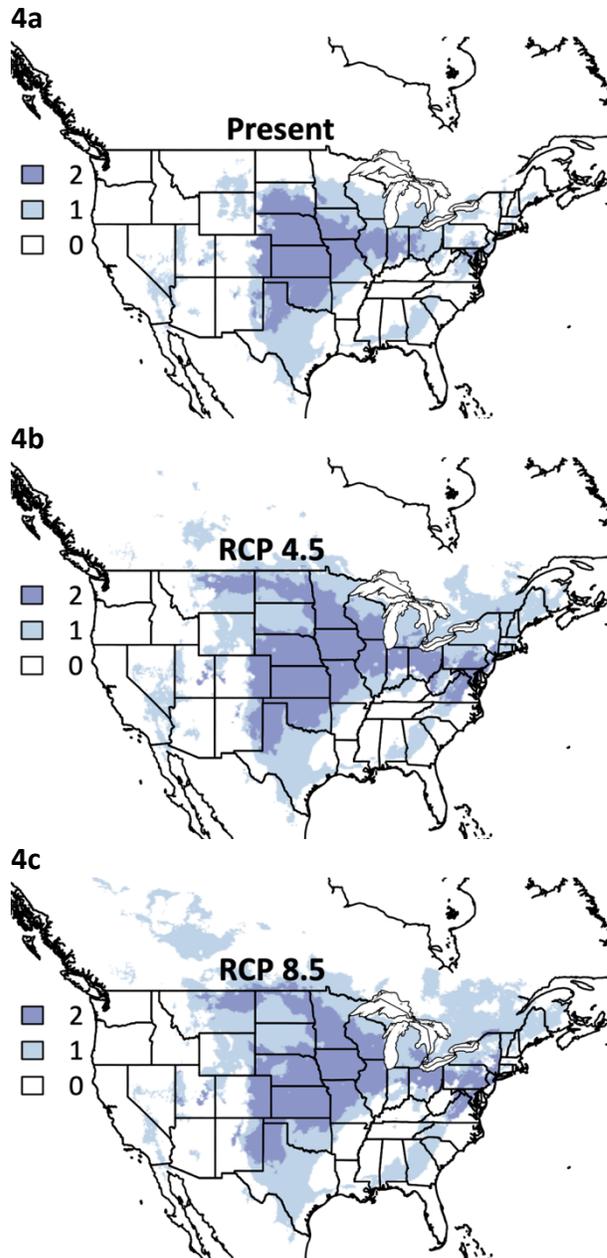


Figure 3.4. Composite Map of Legume (4a) Current Distribution and Response to (4b) RCP 4.5 and (4c) RCP 8.5. Colors indicate the number of species where suitability is predicted to greater than or equal to 50%. Darker colors indicate areas where bioclimatic suitability is above the threshold for more species. Included species are *Amorpha canescens* and *Dalea candida*. Time period is identified in the top of each panel.

Table 3.1. Functional Groups of Modeled Species.

Functional Group	Scientific Name	Common Name
Cool-Season (C ₃) Grass	<i>Elymus virginicus</i> (L.)	Virginia Wildrye
	<i>Koeleria macrantha</i> (Ledeb.) Schult.	Prairie Junegrass
	<i>Stipa spartea</i> (Trin.) Barkworth	Porcupine Grass
Warm-Season (C ₄) Grass	<i>Bouteloua curtipendula</i> (Michx.) Torr.	Sideoats Grama
	<i>Schizachyrium scoparium</i> (Michx.) Nash	Little Bluestem
	<i>Sorghastrum nutans</i> (L.) Nash	Indian Grass
Forb	<i>Asclepias incarnata</i> (L.)	Swamp Milkweed
	<i>Asclepias syriaca</i> (L.)	Common Milkweed
	<i>Asclepias tuberosa</i> (L.)	Butterfly Milkweed
	<i>Drymocallis arguta</i> Lehm.	Prairie Cinquefoil
	<i>Lobelia siphilitica</i> (L.)	Blue Lobelia
	<i>Monarda fistulosa</i> (L.)	Wild Bergamot
Legume	<i>Amorpha canescens</i> Pursh	Leadplant
	<i>Dalea candida</i> Michx. ex Willd.	White Prairie Clover

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Supplementary Appendix

Table S3.1. Modeled species with model training and evaluation metrics

Scientific Name	Common Name	Functional Group	Predictor Variables	N	β	Mean AUC
<i>Elymus virginicus</i>	Virginia Wildrye	C ₃ Grass	8, 9, 10, 16, 17	74	1	0.918
<i>Koeleria macrantha</i>	Prairie Junegrass	C ₃ Grass	9, 10, 16, 17, 18	59	1	0.865
<i>Stipa spartea</i>	Porcupine Grass	C ₃ Grass	8, 9, 16, 17	43	1	0.873
<i>Bouteloua curtipendula</i>	Sideoats Grama	C ₄ Grass	8, 9, 10, 16, 17, 19	65	1	0.910
<i>Schizachyrium scoparium</i>	Little Bluestem	C ₄ Grass	8, 9, 10, 16, 17	91	0.5	0.870
<i>Sorghastrum nutans</i>	Indian Grass	C ₄ Grass	8, 9, 10, 16, 17	69	0.5	0.899
<i>Asclepias incarnata</i>	Swamp Milkweed	Forb	8, 9, 10, 16, 17	88	1	0.876
<i>Asclepias syriaca</i>	Common Milkweed	Forb	8, 9, 10, 16, 17	74	0.5	0.897
<i>Asclepias tuberosa</i>	Butterfly Milkweed	Forb	8, 9, 10, 16, 17	65	0.5	0.919
<i>Drymocallis arguta</i>	Prairie Cinquefoil	Forb	8, 10, 11, 16, 17	43	1	0.880
<i>Lobelia siphilitica</i>	Blue Lobelia	Forb	8, 9, 10, 16, 17	41	0.5	0.917
<i>Monarda fistulosa</i>	Wild Bergamot	Forb	8, 9, 10, 17	79	2	0.824
<i>Amorpha canescens</i>	Leadplant	Legume	8, 9, 16, 17	78	1	0.839
<i>Petalostemon candida</i>	White Prairie Clover	Legume	8, 9, 10, 16, 19	41	1	0.936

Predictor Variable numbers indicate which BIOCLIM variables* were used in that model. N is the number of occurrence records used after environmental thinning, and β is the value of MaxEnt's regularization parameter used to construct the model. Mean AUC is the average across the 5 *k*-folds.

* worldclim.org/bioclim

CHAPTER 4. GENERAL CONCLUSION

Conclusions from Chapter 2

Abundant, speciose, and diverse communities of butterflies and flowers can be managed for on active pastureland in both the short- and long-term. Interestingly, community composition for butterflies varies among management types, but that is not the case for floral resource communities, which indicates some as yet unquantified indirect effects of management.

Managers can successfully restore butterfly communities to working landscapes with only minor changes in stocking rate, but the specific composition of such communities—and relative abundances of different families—varies by management type and with years of consistent application. This necessitates careful restoration strategizing, as well as recurring sampling for taxa of interest in order to ensure management does not have unintended, perhaps negative, consequences after consecutive years of continuous treatment. Further exploration of effects of management on caterpillars and on larval host plants may better elucidate some of the mechanisms behind the observed butterfly community responses reported here.

Conclusions from Chapter 3

Climate models can be a useful tool when used in concert with traditional, field-based approaches. By limiting our suite of species to only those that are currently included in a particular seed-mix (and subsequently removing species without sufficient occurrence records for model construction) we correspondingly limit the scope of our functional group level inference. However, the areas in single-species models (and low-replication functional group “composite maps”) that demonstrate highest—or lowest—suitability can serve to indicate areas that might be particularly valuable for smaller scale models or those that include microhabitat factors. Taken together, species distribution models (SDMs) are a useful tool when utilized in combination with other restoration approaches but are unlikely be sufficient alone.