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Degradation and restoration in remnant tallgrass prairie:
Grazing history, soil carbon, and invasive species affect community
composition and response to the fire-grazing interaction

by

Devan Allen McGranahan

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Co-majors: Sustainable Agriculture; Animal Ecology

Program of Study Committee:
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Iowa State University

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ACKNOWLEDGEMENTS

CHAPTER ONE

General Introduction

> Conservation is getting nowhere because it is incompatible with our Abrahamic concept of land. We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect. There is no other way for land to survive the impact of mechanized man, nor for us to reap from it the esthetic harvest it is capable, under science, of contributing to culture.
>
> —Aldo Leopold

A common convention for the introduction of research from the tallgrass prairie consists of describing the scarcity and fragility of what remains of the North American Pleistocene grasslands. I suspect that these statistics are meant to underscore the urgency of determining how these communities are composed and how they function, naturally, in order to successfully restore them to a natural state. It is hard, however, to escape the sense that such research constitutes the final examination of the last extant individual of some mysterious, soon-to-be-extinct species, kept this long behind the fingerprinted glass wall of an ecosystem zoo.

The chapters that follow are part of an attempt to pursue ecological inquiry positively, to understand our relationship with the world we inhabit as a constant interaction rather than a series of impacts. Sustainable Agriculture is the application of ecological knowledge to food systems. The ecological food system – nay, the greater ecological lifestyle – asks questions of the land, rather than making demands of it. Instead of approaching landscapes with the intent to manipulate it to achieve an *a priori* goal, ecologically-motivated agriculture seeks to determine what the ecology of the system is capable of producing at a sustainable rate.

Unfortunately, the ecological potential of most systems has been reduced by "the impact of mechanized man." The first chapter of this thesis represents research that seeks to understand not only the extent of our degradation, but also its nature, so that we might act in an ecological manner to reverse it. Chapter 2 explores this idea directly: how can we restore the native ecology of a system – in this case, the fire-grazing interaction – in order to restore the integrity of that system, and produce our food in the process? As an element of the ecological lifestyle, patch-burn grazing might not be as graceful as windfarms or as heart-warming as sun-ripened organic tomatoes. But recall that, ecologically, the majority of this continent, this Earth, was grassland before our species' tenure began. If we must reap, let it be the esthetic and nutritive harvest of restored, pre-historic range.

While the relevance of prairie vegetation to the study of Animal Ecology might not be immediately apparent, consider this axiom of the American bus system: The only reliable part of the experience is the certainty that there will be at least one crazy person on your bus. If you, as a passenger on a bus, look around and see no crazy people, then it necessarily follows that *you* are in fact the crazy person. Likewise, if we look around these fragmented, invaded, eroded, paved formerly glorious grasslands and can't find the animals, perhaps the animals are indeed us. Sociology and ecology split many decades ago and set about describing, in analogous terms, the structure and behavior of human and biotic communities, respectively. As we begin to "re-wild" the landscape, I hope we take pride in being the prairie's naturalized megafauna, and positively identify ourselves, in Leopold's words, as plain members and citizens of this biotic community.

CHAPTER TWO

Grazing history, soil carbon, and invasion by an exotic cool-season grass interact to shape composition of remnant tallgrass prairie in a working landscape

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Introduction

A central theme in applied ecology is the relationship between disturbance and the species composition of biological communities. Non-equilibrium theories (Connell 1978, Huston 1979) suggest that diversity is highest at moderate intensity or frequency of disturbance. Milchunas et al. (1988) proposed a grazing-specific model that described the expected response of rangeland communities to herbivory in terms of climate and the community's evolutionary history of grazing: diversity in communities with short evolutionary histories of grazing will decline more quickly than those with a longer history of grazing, and this effect is enhanced as aridity increases. The contribution of Milchunas et al. (1988) emphasizes the importance of understanding "disturbance" within the context of a specific system and its evolutionary history: responses to a disturbance are not consistent across systems with different evolutionary histories.

However, differences in community composition are not solely determined by differences in evolutionary history. Milchunas et al. (1988) overlook exotic species in their discussions of diversity in "climatically determined" or nonanthropogenic grasslands (as opposed to successional and agricultural grasslands, which are artificially created and maintained (Lauenroth 1979)). The modern problem with the focus on "natural" systems is

that the line between nonanthropogenic grasslands (rangelands) and anthropogenic grasslands (pastures) is blurred by the effects of anthropogenic activities bleeding into wildlands (Ellis and Ramankutty 2007).

To understand the role of disturbance in shaping community composition, one must recognize that invasive species are ecological actors even in "wildlands." Exotic species invasions have been documented in most of Earth's ecosystems, with significant effects on ecosystem processes (Vitousek et al. 1997, Levine et al. 2003, Ehrenfeld 2003, Brooks et al. 2004) and substantial environmental and economic impacts (Pimentel et al. 2005).

While ecologists have sought to explain the effects of disturbance on the relationship between diversity and invasion, this research has not produced much clarity. It is at least accepted that disturbance and resources (e.g., light, water and nutrients) interact to affect a community's invasibility and thus the community's composition, but the magnitude and direction of these effects often vary with community type and scale (Brown and Allen 1989, Dorrough et al. 2007). The interaction of herbivory, resources, and community composition has been studied in several communities (see meta-analysis by Proulx and Mazumder 1998). We present a conceptual model that describes these interactions in grassland ecosystems (Fig. 1).

There is general consensus that a range of disturbance exists wherein grazing has a positive effect on diversity, but the specific nature of the effect is dependent on the evolutionary history of grazing in the ecosystem, the system's limiting resources, and the frequency and intensity of grazing (reviewed in Olff and Ritchie 1998; see also Smith and Knapp 1999, Stohlgren et al. 1999, Hickman et al. 2004, Bock et al. 2007). All of the major disturbances in grasslands – grazing, fire, and mechanical disturbance of the soil – have been

shown to influence soil resources. Both fire and grazing influence plant-available nitrogen (Blair 1997, McNaughton et al. 1997). Fire regime and plant productivity interact to affect soil properties and processes (Prober et al. 2008). Excessive grazing and cultivation have deleterious effects on soil organic carbon (Mann 1986, Fuhlendorf et al. 2002, Guo and Gifford 2002), and the recovery to pre-disturbance carbon levels is very slow (Voroney et al. 1981, Kindscher and Tieszen 1998). Natural alterations to the soil-vegetation matrix include prairie dog burrows (Winters et al. 2002) and bison wallows (Coppedge and Shaw 2000, Trager et al. 2004). Invasive species benefit from such altered nutrient balances by thriving on levels below the optima of native species or taking advantage of surpluses not sequestered by the native community (Shea and Chesson 2002, Suding et al. 2004).

Our conceptual model also accounts for positive feedback by invasive species on soil nutrients (Fig. 1), such as increased nitrogen turnover in tallgrass prairie due to the more rapid decomposition of exotic cool-season grass tissue (Mayer et al. 2005, Vinton and Goergen 2006). More generally, invasive species have been implicated in ecosystem-level changes from nutrient and water cycling to fire regime (Vitousek et al. 1997, Levine et al. 2003, Ehrenfeld 2003, Brooks et al. 2004).

In this paper, we describe the composition of 9 remnant tallgrass prairie communities. We use grazing intensity, soil organic carbon, and invasion by exotic plant species to explain patterns of composition and suggest potential mechanisms behind these patterns. We are specifically interested in soil organic C as both an index of soil quality including nutrient availability because it is an indicator of soil degradation by cultivation based on the dramatic and almost immediate declines in soil organic C upon tillage (Voroney et al. 1981, Guo and Gifford 2002).

All of our sites are situated in a *working landscape*, in which conservation and restoration strategies and challenges differ from those in traditional parks and reserves (Fischer et al. 2006). All sites are in close proximity to a variety of land uses, including row crop agriculture, intensive grazing, and conservation/recreation public and private ownerships. Most have a history of grazing and some were grazed intensively up until the year before this study. As such, these sites have been exposed to a wide suite of potentially invasive species.

Of specific interest is the Eurasian, cool-season grass, tall fescue (*Festuca arundinacea* syn. *Lolium arundinaceum*), which was immediately observed to be a nearly ubiquitous and often abundant invader in this landscape (Engle et al., personal observation). Introduced to the United States in the 1940s as a forage grass (Bacon 1995), tall fescue is today the most abundant grass species in the eastern United States (Fribourg et al. 1991) and a frequent, difficult-to-control invader in tallgrass prairie (Washburn and Barnes 2000, Barnes 2004).

Tall fescue merits such specific concern because it often hosts a fungal endophyte (Clay 1993, Bacon 1995, Malinowski and Belesky 2006). The symbiosis has been shown to confer several ecological advantages onto the grass that might increase its potential as an invasive species via all three of the invasion mechanisms – diversity (Clay and Holah 1999, Rudgers et al. 2004, Rudgers et al. 2005), resources (Elmi and West 1995, Malinowski et al. 2000), and enemy avoidance (Bacon 1995, Durham and Tannenbaum 1998, Tannenbaum et al. 1998, Malinowski and Belesky 2006).

We predict that tall fescue will be an important factor in community composition in these prairies. While the idea that a single invasive species can drive ecological change in a

community has recently been called into question (Gurevitch and Padilla 2004, Didham et al. 2005, MacDougall and Turkington 2005), it is unmistakable that in some instances a single species shows a disproportionate presence in invaded communities (Heidinga and Wilson 2002, Kissling et al. 2005, Gabbard and Fowler 2007, Somodi et al. 2008). We predict that grazing history, invasion by exotic species (specifically tall fescue) and altered soil organic C will each be effective in describing patterns of composition in the vegetation communities of these prairies. We use these results to suggest pathway(s) from our conceptual model (Fig. 1) that most influence community composition. Identifying the components of the disturbance-resource-invasion interaction that most affect community dynamics will potentially help managers and restoration ecologists focus effort on the elements of the system that are most likely to produce positive restoration outcomes.

Methods

Study Area

Our research was conducted within the Grand River Grasslands (GRG), an area of about 30,000 ha identified by The Nature Conservancy (TNC) for its potential for grassland conservation. The GRG spans the Iowa-Missouri state border and includes Ringgold County, Iowa, and Harrison County, Missouri.

We selected 9 prairie remnants identified by TNC as moderate to high in conservation value, based on identification of conservative prairie species (The Nature Conservancy, unpublished data). While each of our sites were selected for their known prairie elements, it is apparent that in many sites, at least sections have been subject to cultivation, terrace forming, and pond building, and that whatever prairie remnants remain might be constrained

to specific locations within the sites. Prairie size ranges from 15 to 31 ha. The prairies were generally dominated by two soil types, 172 Gara and 792 Armstrong, with slopes ranging from C to F. Some sites had been extensively grazed and unburned for several years prior to inclusion in the study, others had been left ungrazed and burned only a few years previous, while yet others had been without fire for several years. Grazing histories were determined from informal interviews with current and previous landowners and managers. Upon inclusion in the study, cattle stocked at moderate rates were added to six of the sites as part of long-term experimental treatments. Three prairies were left ungrazed.

Sampling

We used a permanent modified Whittaker plot design (Stohlgren et al. 1998) to sample the presence and abundance of native and exotic vascular plant species. The modified Whittaker plot methodology is effective in detecting rare species, including exotics (Stohlgren et al. 1998), and has the advantage of collecting abundance data in addition to accruing more accurate species lists. Each site had six plots. While the exact position of each site was determined randomly, possible locations were constrained to the two most dominant soil types (three plots on each) and controlled for catena.

Within our modified Whittaker plots, sampling occurred at four different scales: $0.5m^2$, $2.5m^2$, $250m^2$, and $500m^2$. Abundance data (relative cover) were sampled only within the 10 $0.5m^2$ quadrats based on the Daubenmire (1959) scale of cover classes: 0, <1%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95% 96-100%, indexed as 0, 1, 3, 16, 38, 63, 86 and 98, respectively. Overlapping layers of vegetation were taken into account by allowing sums of quadrat cover to exceed 100%. Above the $0.5m^2$ scale, only species presence was recorded.

For the purposes of the analyses in this paper, species found outside of the 10 quadrats but within the 500m^2 plot were assigned percent cover values of 0.001. Sampling occurred twice during the growing season – once in late May-early June and again in August – to account for community changes through different growing seasons. Maximum values for each species across both sampling periods were used in the analyses.

Soils were sampled in winter of 2006-2007 at a depth of 6cm located in the center grid cells (63 x 63m) in each site. Samples were analyzed for total organic carbon and expressed on a percent dry-weight basis. None of the soil sampling points fell within a Whittaker plot, so we used Geographical Information System (GIS) software to map soil organic carbon for each site by interpolating from sampled values using natural neighbor analysis (Sibson 1981). The interpolation produces isoclines giving probable ranges of soil carbon across each site. To estimate soil carbon of the Whittaker plots, we located each plot on the map and assigned an indexed value based on the soil carbon isocline.

Data Analysis

We used the ordination technique Non-metric Multidimensional Scaling (NMDS) to depict and relate the plant communities of the sampled remnant prairies. We used the Canberra distance measure to emphasize rare species. The NMDS was performed with the VEGAN package in Program R (Oksanen 2007). Community dissimilarity, a measure of beta diversity and turnover, was determined from the NMDS distance matrix. Community composition (as described by the ordination) was compared to tall fescue, total exotic cover, and various measures of diversity by regressing these variables on site scores of the first two ordination axes. We used Multivariate Analysis of Variance (MANOVA) on site scores to test for

differences between groups in ordination space, and Analysis of Variance (ANOVA) to test for differences in species richness and abundance between grazed and ungrazed groups.

In NMDS, the axes in the two-dimensional ordination simply represent the two dimensions explaining the greatest amount of variation in plant community composition. Because NMDS does not identify which elements of the community data account for this variation, we correlated the average relative cover of each species with axes 1 and 2 scores for each Whittaker plot. We considered species with a correlation $\geq |0.35|$ and fitted those species against the original NMDS axes.

Results

Community-level variation

Grazing history, followed by tall fescue abundance, and soil organic carbon explained variation in plant composition among 9 remnant tallgrass prairie communities. The relationship between tall fescue and soil C depended on grazing history: soil C explained more variation in historically severely grazed sites and tall fescue explained more variation in sites without a history of severe grazing. Dissimilarity among sites – a measure of beta diversity – was high. On a scale of 0 to 1, with 0 indicating identical community composition and 1 indicating completely dissimilar communities, mean Canberra distance between sites was 0.83 (+/- 0.01 s.e.). Within sites, Whittaker plot communities clustered together in the two-dimensional ordination space (fig. 2a).

Vegetation.—We observed 196 unique species across 51 dicot families and 3 grass subfamilies, in addition to sedges (Cyperaceae), which were not identified beyond family.

Across functional groups, we observed 129 flowering herbaceous (forb) species, 14 legumes, 18 warm-season grasses, 18 woody species and 14 cool-season grasses. Seventy-one percent of the total species were native.

Eleven species had a strong correlation with Axis 1, while 4 species had strong correlations with Axis 2 (fig. 3). With the exception of the native horse nettle (*Solanum carolinense*), exotic species were negatively correlated and native species positively correlated with axis 1. Tall fescue explained the most variation in axis 1 score in a linear regression (F = 99.58, p < 0.001, R^2 = 0.66). Of species correlated with axis 1 scores, tall fescue was by far the most abundant (fig. 4a). In this sense, axis 1 can be considered a gradient of tall fescue abundance, with sites scoring low on axis 1 having relatively low tall fescue cover. Tall fescue had no correlation with axis 2.

Pastures scoring farther to the right of axis 1 (Fig. 2a) contained more native plants species relative to exotic plant species, especially tall fescue, than those pastures along the left of axis 1. Axis 1 was positively correlated with native species richness (F = 64.76, p < 0.001, R^2 = 0.52) (Fig. 5b) and total native cover (F = 102.74, p << 0.001, R^2 = 0.68). Conversely, axis 1 was negatively correlated with exotic cover (F = 82.52, p < 0.001, R^2 = 0.69) (Fig. 5c). Interestingly, the relationship between total species richness and axis 1 was quadratic (F = 12.50, p < 0.001, R^2 = 0.30) (Fig. 5a).

Soil carbon.—Soil organic carbon at individual sampling points was highly variable, ranging from a low of 1.3% in the Pyland pastures to a high of 5.4% in Pawnee Prairie. Pasture averages were less variable, ranging from 2.1% in Ringgold North to 3.4% in Pawnee Prairie (fig. 6).

Soil organic carbon was not correlated with the first axis of the NMDS ordination. There was, however, a positive correlation with axis 2, although the correlation was relatively weak ($F = 7.47$, $p < 0.01$, $R^2 = 0.15$). Pastures at the top of axis 2 (fig. 2a) had more soil carbon, while pastures along the bottom of axis 2 were relatively carbon-poor. It is notable that although Pawnee and Ringgold North overlap greatly and group far to the right along axis 1, they each represent the extremes among pastures of high and low soil organic carbon, respectively.

Grazing history

Pastures with a history of grazing separated from ungrazed sites in ordination space (Exact $F = 47.38$, $p < 0.001$; Fig. 2b). Several measures of species richness and abundance differed between these groups (Fig. 7). On average, historically grazed sites had larger species lists than ungrazed sites ($F = 7.80$, $p < 0.01$) because grazed pastures contained more exotic species ($F = 140.64$, $p < 0.001$). Native species richness did not vary significantly across the two groups ($F = 1.97$, $p = 0.17$). Native species abundance was greater in historically ungrazed prairies ($F = 8.19$, $p < 0.01$), while historically grazed prairies had more exotic species ($F = 59.14$, $p < 0.001$) including tall fescue ($F = 28.43$, $p < 0.001$).

Grazed group.—In the historically grazed group, total species richness (S_T) correlated with scores along both axes. There was a positive relationship between S_T and axis 1 scores ($F = 36.96$, $p < 0.001$, $R^2 = 0.51$), and a negative relationship with axis 2 ($F = 6.50$, $p = 0.02$, $R^2 = 0.14$). Tall fescue accounted for 14% of the variation along the second axis ($F = 6.75$, $p = 0.01$), but very little variation along axis 1 ($F = 3.48$, $p = 0.07$, $R^2 = 0.06$). Soil C had a negative correlation ($F = 6.00$, $p = 0.02$, $R^2 = 0.12$) with axis 1 in the grazed group, and no relationship with axis 2.

Ungrazed group.—Soil C explained 41% of the variation along axis 2 in the historically ungrazed group (F = 20.90, p < 0.001) and had no relationship with axis 1. Whereas tall fescue explained 66% of the entire variation along axis 1 in Figure 2a, this effect was primarily due to the strong negative relationship ($R^2 = 0.65$) with axis 1 in the historically ungrazed group.

Plotting this relationship revealed an interesting pattern of tall fescue as a function of axis 1 (Fig. 8). For Whittaker plots in ungrazed pastures with axis 1 scores below 0.3, tall fescue explained 20% of the variation along axis 1, and none of the variation along axis 2 (F = 10.7, p < 0.01 and F = 0.93, p = 0.34, respectively). For this sub-group of historically ungrazed sites, native species richness was positively correlated with axis 1 scores (F = 26.64, p < 0.0001, $R^2 = 0.40$) and total species richness was negatively correlated with axis 2 scores (F = 28.30, p < 0.001, $R^2 = 0.42$).

The ungrazed sub-group scoring greater than approximately 0.3 along axis 1 had very little or no tall fescue. The remaining variation along axis 1 (beyond 0.3) was negatively correlated with total exotic cover (F = 12.92, p < 0.01, $R^2 = 0.46$). Soil C (F = 14.13, p < 0.01, $R^2 = 0.48$) and total species richness (F = 8.37, p = 0.01, $R^2 = 0.34$) were positively correlated with axis 2.

Discussion

We sampled the composition of the vegetation communities and soil carbon concentration in 9 remnant prairie pastures in Ringgold County, Iowa and Harrison County, Missouri. We found considerable variation in community composition among pastures, and

found relationships between this variation and our predicted elements of ecological

degradation: history of intense grazing, tall fescue invasion and soil organic carbon paucity.

Pastures formed distinct groups in ordination space based on historic grazing

intensity. These results are consistent with previous research comparing the communities of

grazed and ungrazed sites (Altesor et al. 2006). Our grazed pastures were characterized by

higher species richness on account of exotic species, particularly introduced forage species

such as tall fescue, smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*),

and red and white (*Trifolium* spp.) clover. Soil C and tall fescue correlated with variation

within each of the groups, but the strength of these correlations switched between groups. In

the historically intensively-grazed pastures, soil C explained the most variation along axis 1,

indicating that it has the strongest relationship with the composition of grazed communities.

This might represent a gradient of disturbance, perhaps intensity of grazing and/or

mechanical soil degradation – i.e. tillage – at the extreme end. Unfortunately, we were unable

to classify grazing history beyond whether it was known to have occurred within the recent

memory of landowners and managers, and cannot explore this gradient further with regard to

stocking rate or other features of herbivory (e.g., season and frequency of grazing).

A more evocative effect of disturbance is suggested by the quadratic relationship

between total species richness and axis 1 (Fig. 5a). The curve suggests the theoretical

relationship between diversity and disturbance as predicted by many non-equilibrium

theories (Connell 1978, Huston 1979, Milchunas et al. 1988). Considering the end points of

axis 1lie at opposite extremes in terms of grazing history, it is tempting to conclude that the

midpoint of axis 1 – which corresponds to the peak of the species richness curve – represents

a moderate intensity of (or intermediate time since) disturbance where high diversity is

maintained. Rather than a direct effect of disturbance intensity, however, it is clear that the high species richness near the midpoint (0) of axis 1 is produced by the intersection of two opposite trends: declining exotic species richness (Fig. 5c) and increasing native species richness (Fig. 5b) along axis 1. These trends are best explained independently in the context of groups with similar grazing history, rather than as a single, quadratic relationship at the landscape scale. Angermeir (1994) argues that conflating exotics with native species can compromise the usefulness of diversity in ecological research and management. At the very least, these data underscore the importance of distinguishing between exotic and native species when studying the relationship between disturbance and composition in real-world communities, lest ecologically-meaningful patterns go overlooked.

Tall fescue abundance was most explanatory of variation at the landscape level, and remained an important factor in explaining variation within both historically grazed and ungrazed pastures. We believe it is telling that tall fescue consistently had correlations with site scores along NMDS axes at several scales, unlike any other exotic species, total exotic cover or total exotic richness. Tall fescue was certainly a common species throughout the landscape, but it was most abundant in grazed pastures.

The greatest amount of within-group variation occurred along axis 1 in the grazed group (Fig. 2b). This variation might indicate two sub-groups within sites without a history of intense grazing, delineated by the transition that appears at approximately 0.35 along axis 1 (Fig. 8). Variation within the sub-groups appears to be derived from different sources: S_T, S_N, and tall fescue cover correlated with variation within the < 0.35 sub-group, while S_N, soil C, and exotic cover correlated with variation in the > 0.35 sub-group. We believe that these sub-groups reflect differences in land ownership and management. The Richardson tract is

privately owned, borders cultivated agricultural land, and has the highest average abundance

of tall fescue of all the pastures (Fig. 4b). Pawnee and Ringgold North are both state-owned

properties, are buffered by other conservation lands, and have little to no tall fescue. While

data on fire histories was not explicitly collected in this study, conversations with past and

current managers indicate that only the state-owned properties have a recent history of fire

management. As prescribed fire is an effective means of controlling invasive species

(DiTomaso et al. 2006), it is possible that a history of fire suppression and a close proximity

to source populations has created an invaded sub-group within the historically ungrazed

communities.

Implications for restoration

On the whole, these results support our general model relating disturbance, soil

resources, and exotic species invasion to community composition (Fig. 1). When we consider

the different and occasionally opposite relationships between these factors and the variation

in communities that share a common disturbance history, it becomes clear that the relative

contributions of each factor are variable.

Based on the data presented here, we propose a dichotomous schema designed to

describe the relative influence of these factors in this working landscape (Fig. 9). The model

begins by differentiating sites by grazing history and considers the effects of tall fescue

invasion and soil C condition separately within the grazed-ungrazed groups. Such a

framework allows managers to understand the hierarchies of effect within ecosystems and

identify priorities and goals for restoration and/or control.

In our model (Fig. 9), current and potential tall fescue invasions determine the

urgency and intensity of recommended management practices in these grasslands. Sites that

currently have no tall fescue are not free from management concern in a working landscape: even without the facilitation of past or current agricultural activity within the boundaries of the site, high propagule availability in the landscape can eventually overwhelm even the most ecologically resistant sites (e.g., Von Holle and Simberloff 2005).

Once tall fescue has established, it is critical to determine what level of invasion constitutes a management priority. The first step consists of identifying thresholds where tall fescue abundance effects significant change in key ecosystem processes. Percolation theory (Gardner et al. 1987, Turner et al. 1989) suggests that the spread of a disturbance (e.g., fire, Hargrove et al. (2000)) across a matrix (e.g., a grassland landscape) is drastically reduced when approximately 59% of that matrix is not conducive to propagation. Thus, we might expect that 59% canopy cover of tall fescue represents a critical threshold beyond which fire will not spread. This would have system-wide consequences, as fire suppression promotes the encroachment and eventual dominance of woody species such as eastern redcedar (*Juniperus virginiana*) at the expense of herbaceous species (Engle et al. 1987, Briggs et al. 2002).

Because restoration costs increase in proportion to increased degradation (Milton et al. 1994), there is an incentive to identify and address symptoms of degradation at an early stage (Whisenant 1999). *State-and-transition* models (Westoby et al. 1989) help managers predict stages of ecosystem degradation and identify pathways communities follow as they transition between states. In the state-and-transition framework, the point at which management and/or natural events precipitate the transition from one state to another is referred to as a *threshold* (Briske et al. 2006). A *state* is generally defined as "a recognizable,

resistant and resilient complex of 2 components, the soil base and the vegetation (Stringham et al. 2003)."

We can hypothesize on what the potential states of our grasslands might be. Fifty-nine percent tall fescue cover might represent a threshold where an otherwise stable, fully-functioning grassland transitions to a tall fescue-dominated system characterized by rapid nutrient cycling and infrequent fire. The next stable state would likely consist of eastern redcedar-dominated woodland. From our results, historically severely grazed sites are at a greater risk of crossing this threshold. Under the hypothetical percolation model that assumes a threshold at 59% tall fescue cover, none of our pastures would appear to be at immediate risk of transitioning to eastern redcedar woodland (Fig. 4b), although all 3 Pyland sites, Gilleland and especially Richardson are high in tall fescue abundance. Predictably, these 5 sites cluster together in ordination space (Fig. 2a), and (except for Richardson) comprise the historically grazed group (Fig. 2b).

Whisenant (1999) and Briske et al. (2006) identify stages of degradation that are characterized by modified or reduced function in primary processes and the beginnings of native species loss. Briske et al. (2006) defines this stage as the "exotic species state." Whisenant (1999) lists herbivory manipulation and fire among potential management options for repairing systems with damaged but functioning primary processes. From an ecological restoration perspective, it appears that restoring historic disturbance regimes, including fire and grazing (Fuhlendorf and Engle 2001, Fuhlendorf et al. in press), while the system is still within the stable grassland state is the most effective way to reduce tall fescue abundance and increase the dominance of native species in these remnant grasslands.

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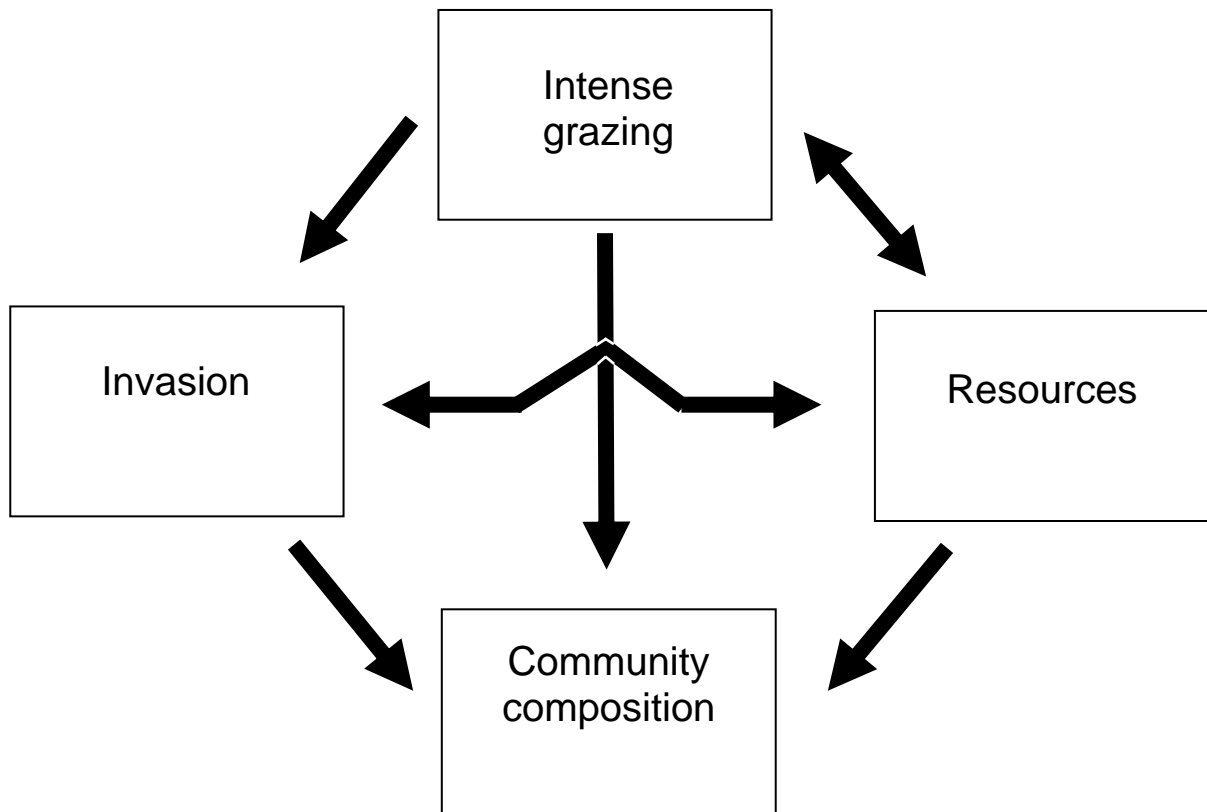
Fig. 1: Conceptual model describing the general relationships between disturbance, invasion, and resources as they affect community composition.
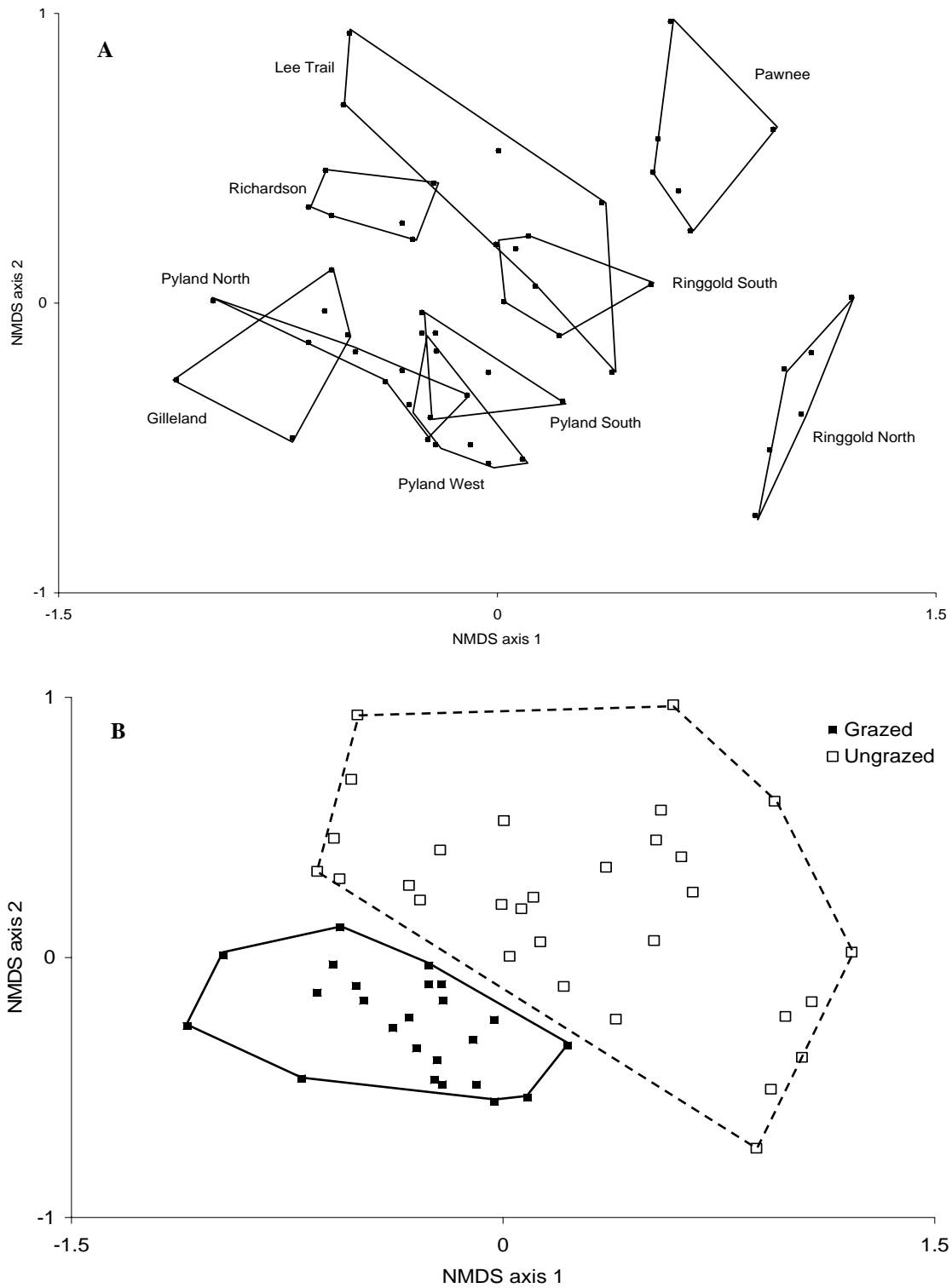
Fig. 2: (A) Plot of NMDS of plant species composition showing community clusters at the pasture level. Points represent individual modified Whittaker plots, while convex hulls enclose the six plots within the named pastures. (B) Same NMDS plot as above, except grouped by history of intense grazing.
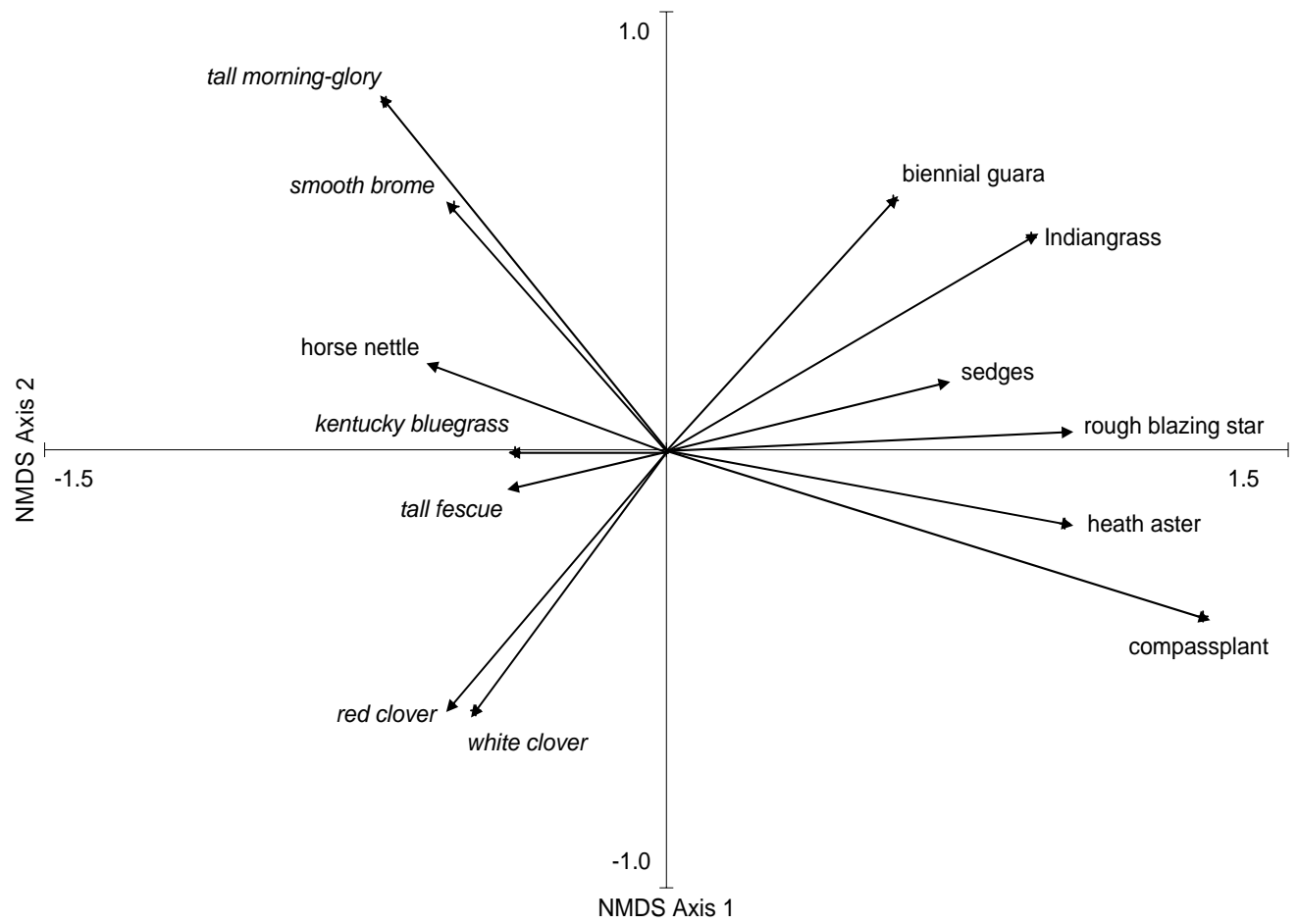
Fig. 3: Vectors of species correlated ($R^2 \geq |0.35|$) with NMDS axes 1 and 2.
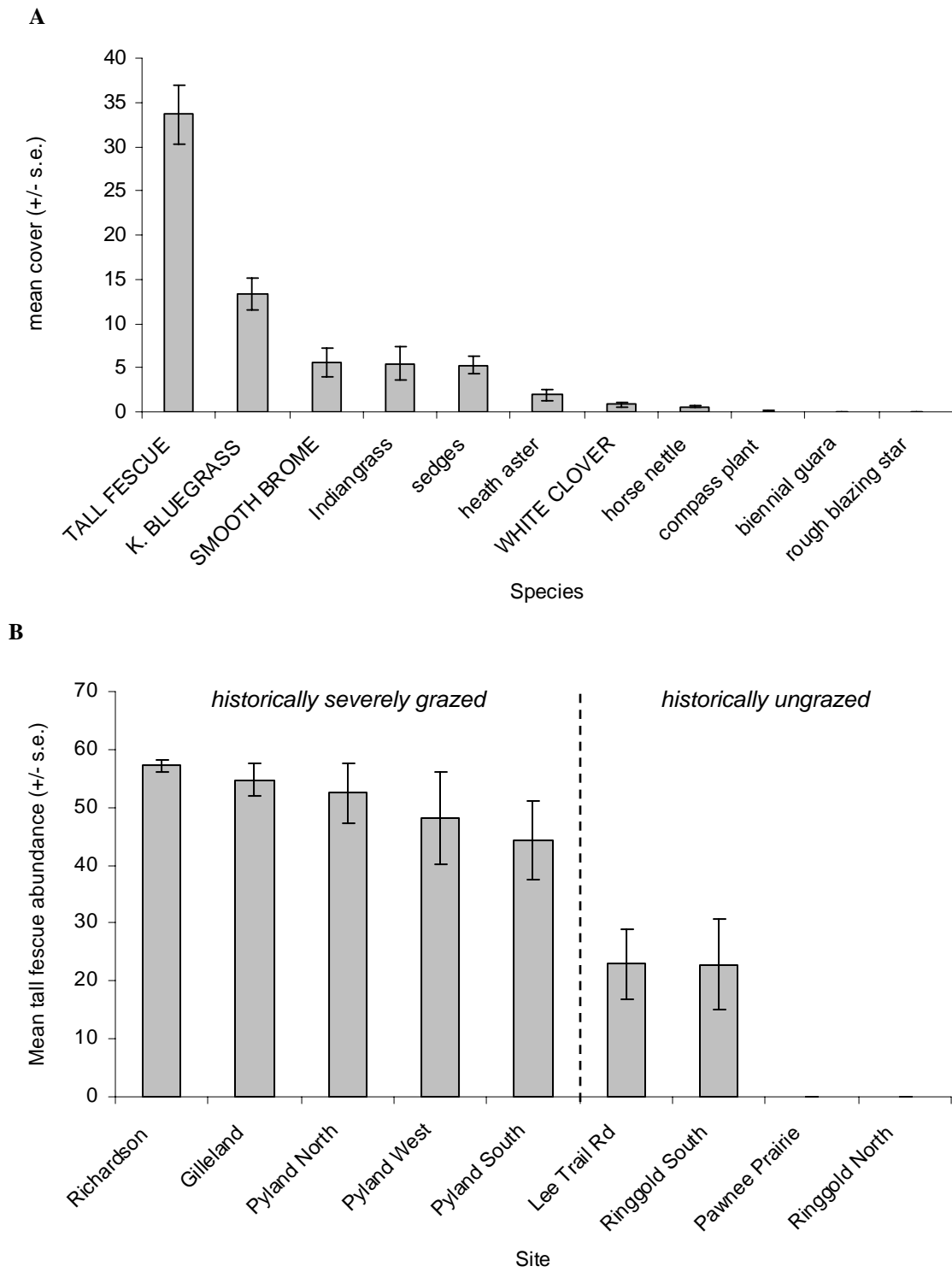
A

B

Fig. 4: (A) Abundance of 11 species correlated (P<0.05) with NMDS axis 1. Invasive species in CAPITALS. (B) Abundance of tall fescue by pasture, with history of severe grazing denoted. Pastures lacking a bar had either no tall fescue cover or <1% tall fescue cover.
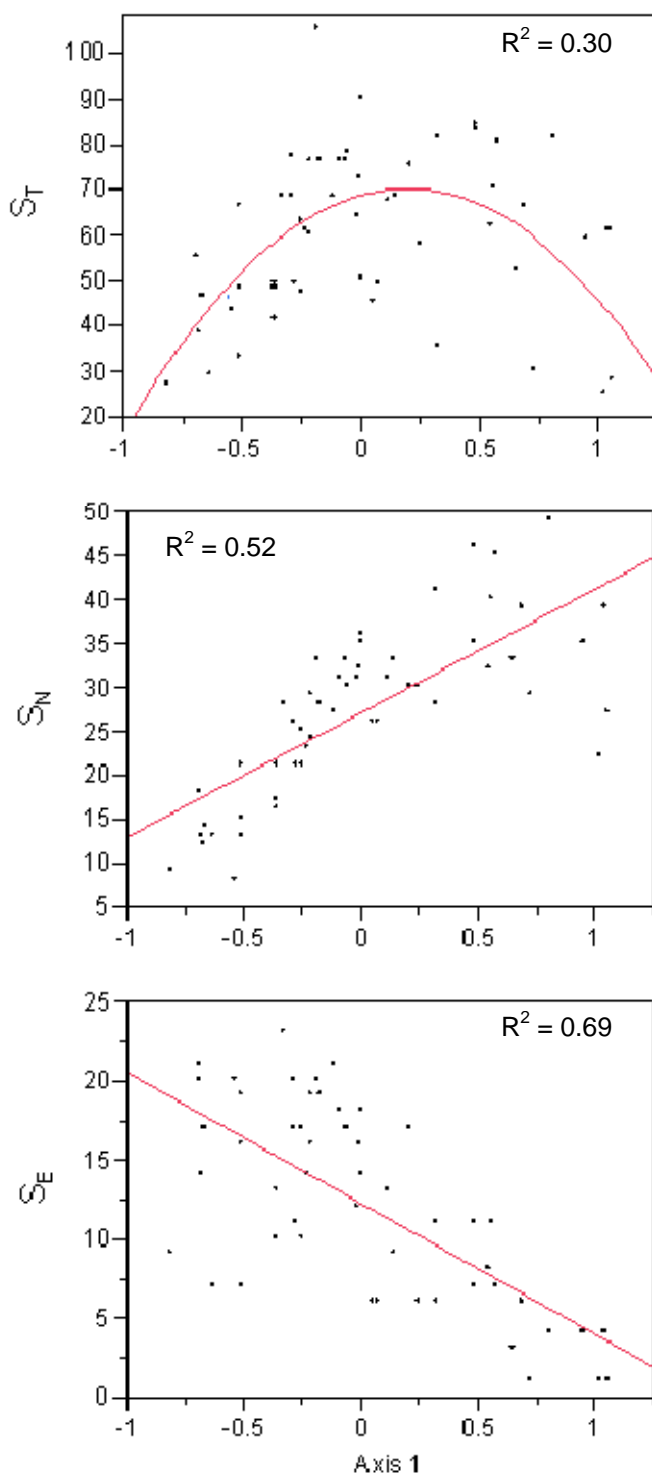
Fig. 5: (A) Quadratic relationship between total species richness (S_T) and NMDS axis 1 site scores, showing apparent maximum richness around 0.25. (B) Linear positive relationship between native species richness (S_N) and Axis 1 site scores. (C) Linear negative relationship between exotic species richness (S_E) and Axis 1 site scores.

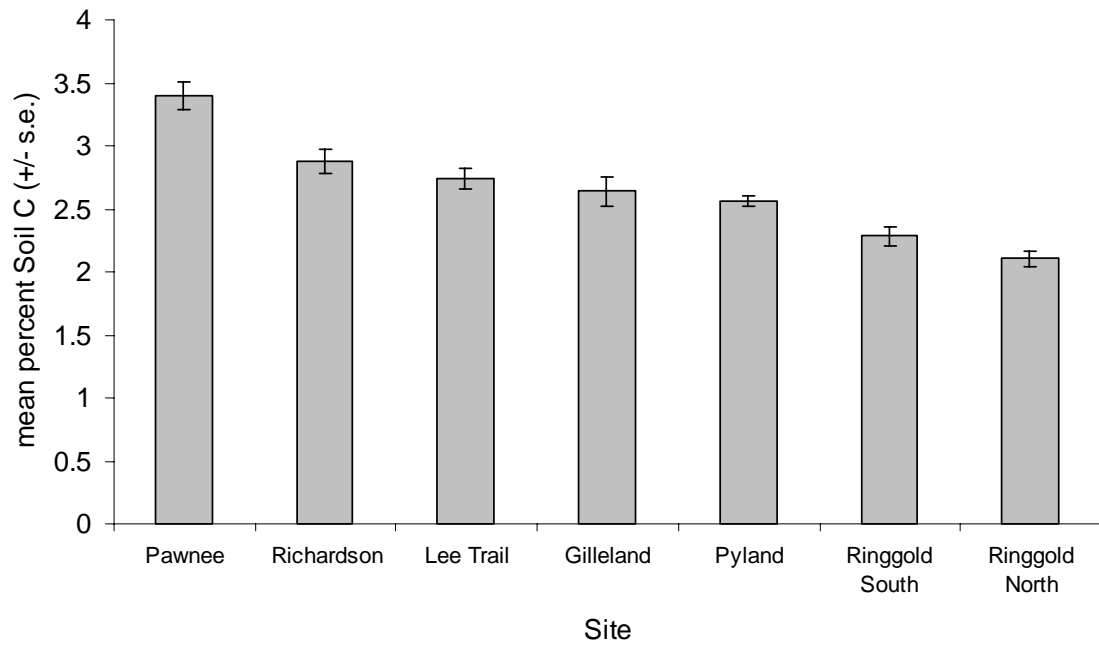Fig. 6: Histogram showing the mean (± s.e.) soil organic carbon (C) for 9 remnant prairie pastures (the 3 Pyland tracts are grouped together in this analysis).
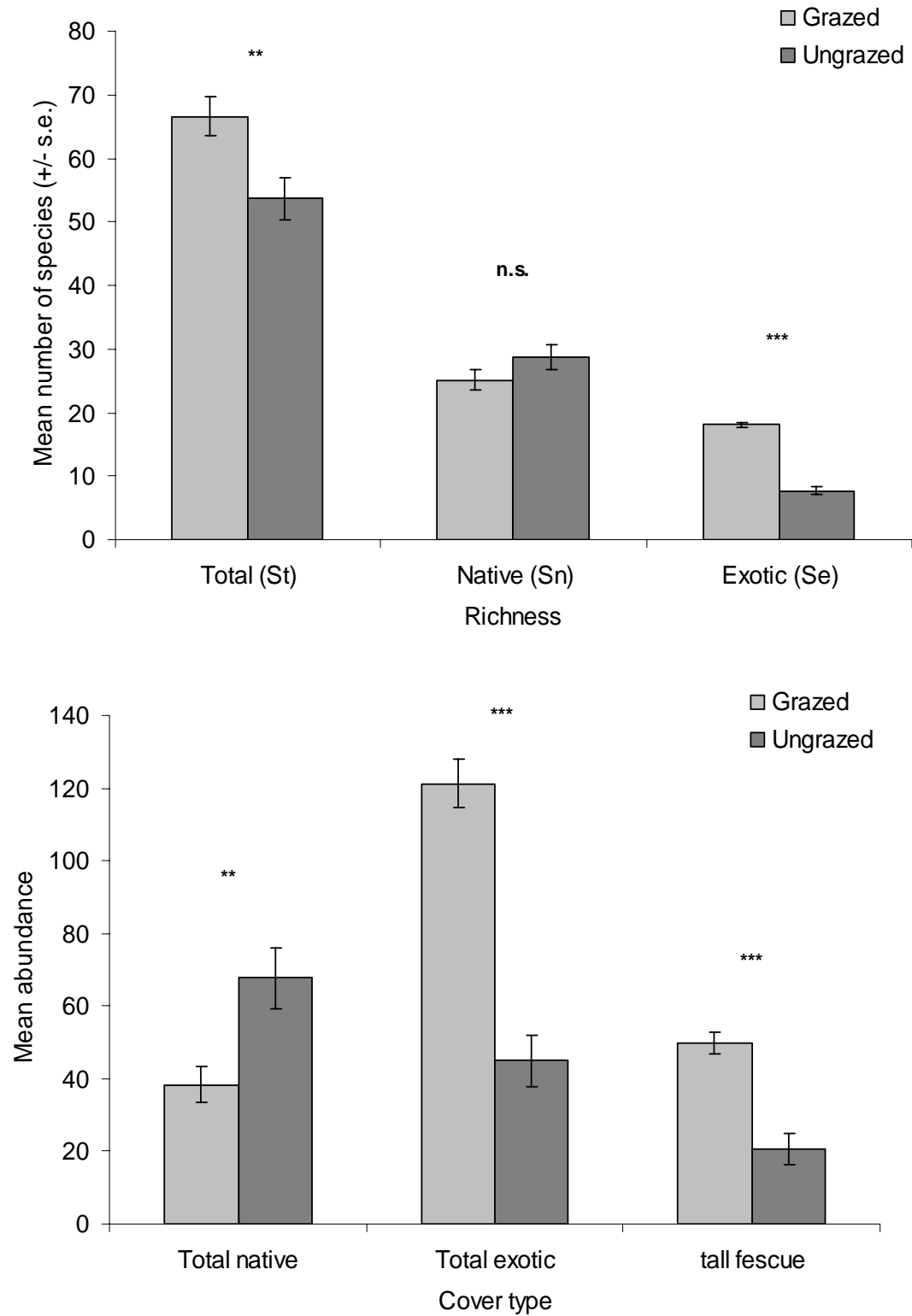
Fig. 7: Comparison of community measures across grazed and ungrazed sites.
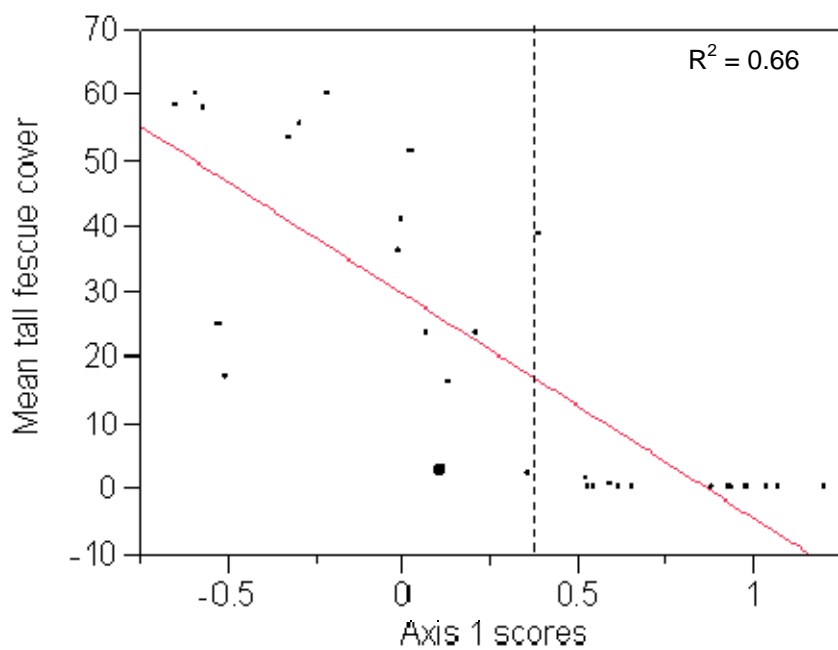
Fig. 8: Tall fescue abundance versus Axis 1 site scores for ungrazed sites, denoting the transition at approximately 0.3 on axis 1.

Fig. 9: A dichotomous schema representing pathways of disturbance-driven effects on grassland composition in a working landscape. Endpoints suggest management strategies for restoration and invasive species control within communities determined by each unique hierarchy of effects.

CHAPTER THREE

Patch-burning increases grazer selection for an invasive cool-season grass in degraded tallgrass prairie remnants

Manuscript to be submitted to Ecological Applications [1]

Introduction

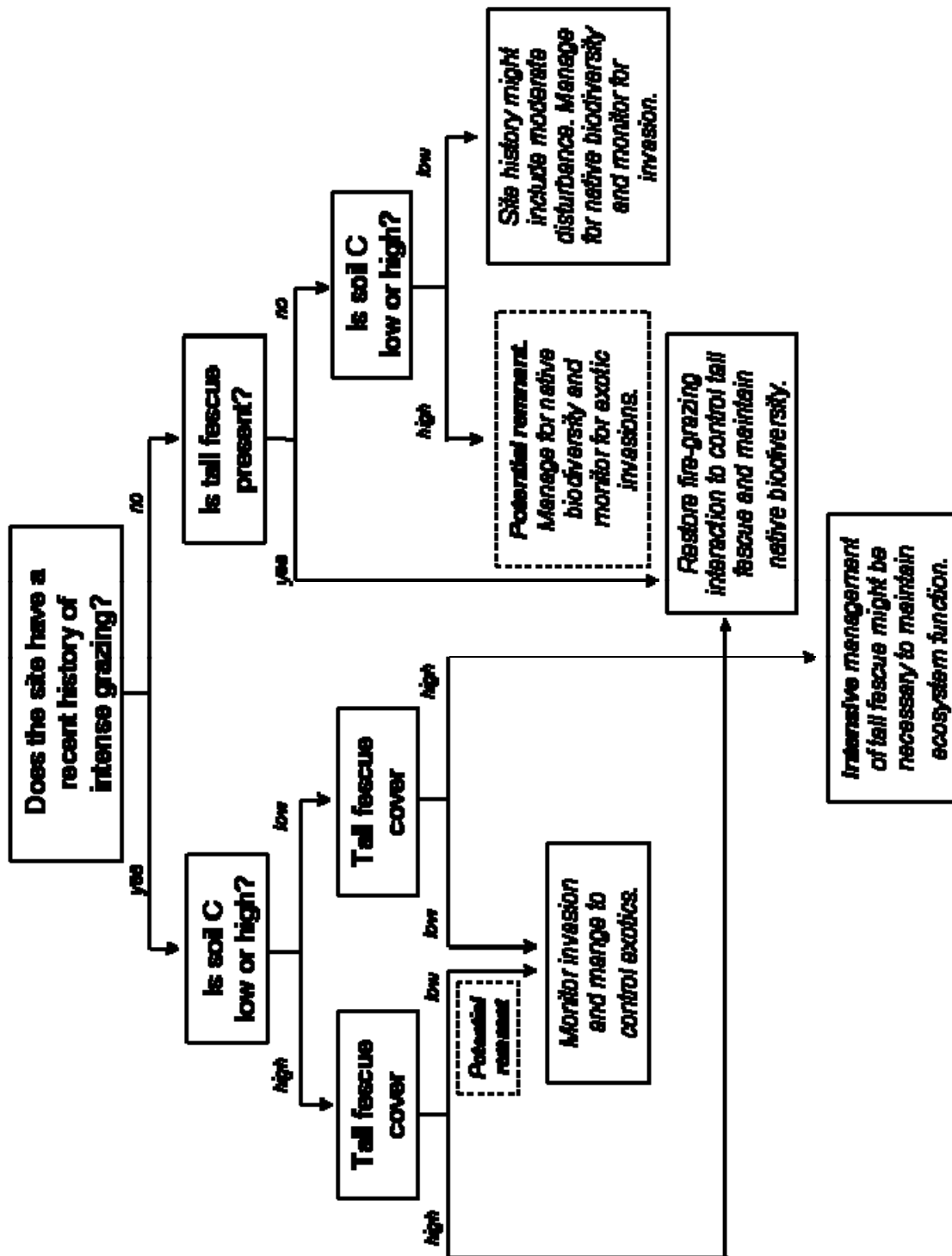Considerable research has focused on the relationship between native plant communities and exotic species, especially the mechanisms and processes that influence whether a given species will become invasive (Davis et al. 2000, Stohlgren 2002, Shea and Chesson 2002, Levine et al. 2003). Meanwhile, applied ecologists and managers have grappled with controlling existing invasions. Invasive species are the second-greatest threat to native biodiversity (behind habitat loss; Wilcove et al. 1998), and alter ecosystem processes such as fire regime (Mack and D'Antonio 1998, Brooks et al. 2004) and nutrient and water cycling (Vitousek et al. 1997, Levine et al. 2003, Ehrenfeld 2003).

The term "invasive species" is applied to a broad range of life forms across almost every ecosystem on Earth (Pimentel et al. 2005). In this paper, however, we focus on exotic plant invaders in native grasslands, particularly in North America, where farmers and ranchers spend more than $5 billion annually in the control and management of invasive species, and suffer an even greater loss in productivity (Babbit 1998). The cost of invasive species management is high because of the resource-intensive nature of common control methods, such as herbicide application, and mechanical and manual removal (Mack et al. 2000). For example, the cost of keeping a 160-acre grassland free of eastern redcedar

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[1] Submission is contingent on at least one more year of data collection and re-analysis.

(*Juniperus virginiania*) with prescribed fire is $10 per acre, but mechanically removing mature stands of trees can range from $40 to $90 per acre (Bidwell et al. 2002). Herbicide control costs of spotted knapweed (*Centaurea maculosa*, an invader of North American rangelands), are only justifiable when substantial forage increases are the result, regardless of the treatment's efficacy (Griffith and Lacey 1991). On top of the economic costs of chemical control are the environmental implications of widespread herbicide application in our ecosystems (e.g., Battaglin et al. 2005).

Given the high economic and environmental costs of intensive, technological methods for the management of invasive species, there is a motivation for less costly methods with fewer negative ecosystem impacts. Zavaleta et al. (2001) endorse an entire ecosystem perspective in invasive species control, to minimize secondary effects and maximize longevity of positive results. Implicit in this argument is the importance of identifying and understanding the processes of the focal ecosystem in a natural context, and making attempts to restore those functions.

Both fire (DiTomaso et al. 2006) and grazing (Olson and Lacey 1994, Frost and Launchbaugh 2003) are natural processes that have been used to control invasive species in native grasslands. However, some invasive species are able to persist despite fire or grazing when these methods are independently applied (Dwyer et al. 1964, Madison et al. 2001, Barnes 2004, Munger 2004).

The fire-grazing interaction

Rather than use intensive methods to control invasive species resistant to independently-applied fire or grazing, Fuhlendorf and Engle (2004) suggest patch-burn

grazing as an alternative approach. Patch-burn grazing capitalizes on the interaction of fire and grazing, rather than relying on their independent effects alone. Fuhlendorf et al. (in press) argue that fire and grazing interact so tightly in the landscape that they act as a single disturbance, referred to as *pyric-herbivory*. When applied to modern grasslands, patch-burn grazing replicates the disturbance patterns of pre-settlement North American rangelands, wherein large herbivores concentrate their grazing on recently burned patches to create a heterogeneous landscape mosaic (Fuhlendorf and Engle 2001). This concentration of grazing pressure on burned patches has an effect on grassland communities that is unique from fire or grazing alone (Collins and Smith 2006).

It is reasonable, then, to predict that the effects of the fire-grazing interaction on invasive species might differ from either fire or grazing applied alone. Indeed, Fuhlendorf and Engle (2004) showed that patch-burn grazing reduces invasion of sericea lespedeza (*Lespedeza cuneata*), an invasive species in North American grasslands known to be promoted by fire (Munger 2004) and avoided by grazers (Dwyer et al. 1964). Patch-burn grazing also was more effective in limiting the annual spread of sericea lespedeza than traditional, homogeneity-based pasture management (Cummings et al. 2007).

Mechanistically, patch-burn grazing works by drawing grazers to the succulent regrowth of the burned patch – the "magnet effect" (Archibald et al. 2005) – and overriding the tendency of grazers to select forage on a plant-by-plant level (Stuth 1991). Repeated grazing in the burned patch creates a "grazing lawn" (McNaughton 1984) in which grazers are presumably unable to distinguish preferred forages by individual species. The result is the inadvertent consumption of otherwise less-desired species along with preferred forage. Complementary to the "magnet effect" is that grazers avoid unburned patches for their lower

proportion of nutritious forage and the physical barriers presented by accumulated litter (Stuth 1987, Vallentine 1990).

In this paper, we report on tall fescue (*Festuca arundinacea* syn. *Lolium arundinaceaum*) defoliation under patch-burn grazing in remnant tallgrass prairie degraded by invasion from exotic forage species. We predict that contrast in vegetation structure between burned and unburned patches will increase tall fescue tiller defoliation in the recently-burned patch of patch burn-grazed pastures when compared to pastures grazed and burned in their entirety every third year. We also predict that increasing tiller defoliation in the burned patches will reduce the abundance of tall fescue in patch-burn grazed pastures.

Introduced in the 1940s as a forage species (Bacon 1995), tall fescue is now the most abundant grass in the eastern United States (Fribourg et al. 1991) and has become a troublesome invader in many humid and sub-humid native grasslands within the region (Barnes et al. 1995, Washburn and Barnes 2000, Barnes 2004). Control of invasive tall fescue has proven difficult: prescribed fire is not effective against tall fescue in native grass communities (Madison et al. 2001, Barnes 2004). Likewise, grazing alone is an ineffective means of control in mixed stands if grazers avoid tall fescue in favor of other species.

Like many cool-season grasses, tall fescue is often host to a symbiotic fungal endophyte (Clay 1993) that has been shown to have several adverse effects on livestock (reviewed in Malinowski and Belesky 2006). While it might seem counterintuitive and perhaps even negligent to encourage intensive grazing on a species with so many known toxic effects, we predict that cattle will suffer no negative effects from consuming tall fescue in the grazing lawn. Firstly, cattle are capable of "detoxifying" after consuming toxic forage by periodically abstaining from that forage when alternatives are available (Pfister 1997).

Secondly, endophyte-infected tall fescue has been shown to have lower concentrations of alkaloids after repeated defoliation (Belesky and Hill 1997), suggesting that tall fescue in patch-burned pastures might actually be better for cattle than tall fescue under homogeneously managed pastures.

Methods

Study area

This study was conducted in the Grand River Grasslands, a 30,000 ha landscape of mixed agriculture, recreation, and conservation land including Ringgold County, Iowa and Harrison County, Missouri (Fig. 1). We selected six grassland parcels with known elements of tallgrass prairie (The Nature Conservancy, unpublished data), although the pastures varied in the quality of native vegetation and the extent to which they were invaded by exotic species, primarily forage grasses and legumes (see previous chapter). Observations of forage residue in fall of 2005 and spring 2006 and conversations with managers indicated that the majority of our sites had been intensively grazed at heavy stocking rates prior to their inclusion in this study. Each site was dominated by soil types 179 Gara and 792 Armstrong, and slopes ranged from C to F. The sites varied in size from 15 to 31 ha.

Each pasture was moderately stocked (target rates = 0.53 Animal Unit Months [AUM]/ha (1.25 AUM/acre) in 2006, 0.42 AUM/ha (1.00 AUM/acre) in 2007 and 2008) with cows from local cattle owners, and included both spring-calving and fall-calving cows. The grazing season extended from early May to mid-October. Cows received no additional feed beyond forage available in the pastures and mineral supplements.

These six grazed sites were divided into two treatment groups: three pastures were patch-burned – i.e., a third of the pasture (one patch) is burned every year (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2004) – while the other three pastures are burned in their entirety every three years (hereafter referred to as "control pastures" as they were not patch-burned). In this manner, any given patch is managed for a three-year fire return interval. We used ground-truthed, remotely-sensed imagery to create patch boundaries that made use of natural fuel breaks (trails, gullies, etc.) while ensuring equal divisions of the pastures. Fires were conducted in the spring between snowmelt and the beginning of the growing season (2006: no fire, pre-treatment year; 2007: April fires; 2008: mid-March fires). Fire spread in 2007 was limited in part due to extensive live material in the fuelbed, so in 2008 we attempted to burn before the cool-season grass component of the plant community broke dormancy.

Tall fescue selectivity

We sampled tall fescue defoliation by cattle by recording the number of grazed and ungrazed leaves of 100 tillers per patch, and measuring the height of the longest leaf of each. We sampled tillers along the 25-m center line of two permanently-marked modified Whittaker plots in each patch (see Methods in McGranahan (2008) for a description of the modified Whittaker plot, including the criteria for their location in this study). In 2006, the first 150 tall fescue tillers encountered, beginning from the northernmost point of the 25m transect, were measured. In subsequent years, the nearest tillers from either side of the 25m transect were measured at 1m intervals, for a total of 50 tillers per plot (100 tillers per patch). For the purpose of analysis, we randomly selected 50 of the 150 tillers per plot from the 2006

dataset. Tall fescue tillers were sampled in late July in all three years. In this paper, we report both the proportion of ungrazed tillers and the relative height of grazed tillers (versus ungrazed tillers within the same patch) for each treatment. We used multiple linear regressions to test for treatment effects over time, and pair-wise Analysis of Variance (ANOVA) to compare selection frequency and tiller heights across treatments within years.

Patch contrast

Contrast in vegetation structure across patches (patch contrast) was determined by comparing the average visual obstruction between patches within each pasture. We recorded visual obstruction at 30 points per patch using a Robel pole (Robel et al. 1970), which is correlated with biomass (Ganguli et al. 2000, Vermeire and Gillen 2001). Each Robel pole measurement consisted of the mean of four readings taken per point, taken from a height of 1m above the ground, 4m away from the pole in each of the cardinal directions. Obstruction was defined as the highest value (1 dm increments) on the pole that was $\geq 50\%$ obscured by vegetation. Sampling occurred in mid July each year. To determine patch contrast in patch-burned pastures, we compared the visual obstruction between burned and unburned patches. We calculated contrast as

$$C = ((UB - B) / B) * 100, \hspace{2cm} [\text{Eq. 1}]$$

where C = contrast, UB = mean Robel height of the unburned patch, and B = mean Robel height of the burned patch. For control pastures in all three years, contrast was calculated by substituting the highest patch mean visual obstruction for UB in the contrast equation (Eq. 1) and substituting the lowest patch mean visual obstruction for B. This measure makes for a

conservative comparison against contrast in patch-burned pastures because it represents the highest possible contrast value for each control pasture. In 2007, when there were two unburned patches and one burned patch, the mean visual obstruction of the unburned patches was used as the UB term in the contrast equation.

We constructed multiple linear regression models to test for treatment effects across years. We also used a t-test to compare across treatments within years.

Animal performance

Animal performance was determined by comparing animal condition at the end of the grazing season to condition at the beginning of the grazing season. We used Body Condition Scoring (BCS), a nine-point scale used to index the condition of cows based on visual estimations of body fat (Edmonson et al. 1989). In this paper, we report the changes in mean BCS for each treatment over the 2007 grazing season. The changes in mean herd BCS for each treatment over the grazing season were compared with Analysis of Variance (ANOVA).

Tall fescue abundance

We monitored the effectiveness of patch-burn grazing in reducing the abundance of invasive tall fescue by comparing changes in tall fescue cover between patch-burned and control pastures. In mid July of each year, we visually estimated tall fescue canopy cover within a $0.5m^2$ quadrat using the Daubenmire (1959) scale: 0, <1% (1), 1-5% (3), 6-25% (16), 26-50% (38), 51-75% (63), 76-95% (86), 96-100% (98). Quadrats were placed at each Robel pole observation (see above) for a total of 30 quadrats per patch. Change in tall fescue abundance in control pastures and within the recent burned patch of patch-burned pastures in

2007 and 2008 was determined by comparing cover of tall fescue in each of these patches compared to 2006 pre-treatment abundance for each of those patches. We used pair-wise ANOVA to compare tall fescue abundance in the control pastures and recently-burned patches in 2007 and 2008 to tall fescue abundance in 2006.

Results

Tall fescue selectivity

There was no treatment effect over time for either tiller defoliation ($T = 0.15$, $p = 0.89$) or relative tiller length ($T = -1.57$, $p = 0.21$). In 2008, more tillers were grazed in the burned patches than both the unburned patches ($F = 14.63$, $p = 0.02$) and control pastures ($F = 22.53$, $p < 0.001$; fig. 1a). Also in 2008, the relative height of grazed tillers in the burned patches was less than those in both unburned patches ($F = 15.39$, $p = 0.02$) and control pastures ($F = 17.55$, $p < 0.01$).

Variance in these data was relatively low, indicating that across sites and across cattle herds, the burned patch was consistently effective in concentrating grazing (i.e., increasing patch-level selection) and reducing plant-level selection in 2008.

Patch contrast

There was no change in patch contrast over time for patch-burned pastures (Fig. 2). Multivariate regression indicated that the treatment effect was significant ($T = -2.19$, $p = 0.04$), which was explained by the nearly significant trend towards decreased patch contrast in the control pastures from 2006 to 2008 ($F = 4.12$, $p = 0.08$, $R^2 = 0.28$). Contrast in patch-burned pastures followed no trend ($F < 0.01$, $p = 0.92$). Variation in contrast for patch burned

pastures was very high in 2007 due to one burned patch that had higher visual obstruction than the unburned patches.

Interestingly, variation in contrast was apparently greater in the control than treatment pastures in 2006, despite the random assignment of experimental units. Variation in contrast among all pastures in 2006 is probably best explained by high variability in grazing management (i.e., uniformity and severity of forage utilization) prior to the experiment. Consistent declines in variation in contrast in 2007 and 2008 likely reflects a response to moderated stocking rate across all treatment pastures.

Animal performance

There was no difference in the average change in Body Condition Scores between treatments over the course of the 2007 grazing season ($F = 0.16$, $p = 0.71$). Average fall BCS for patch-burned pastures was 6.1 (+/- 0.2 s.e.) and the average fall BCS for control pastures was 5.8 (+/- 0.1 s.e.).

Tall fescue abundance

Tall fescue abundance increased on the control pastures in 2007 ($F = 20.74$, $p < 0.001$) and 2008 ($F = 15.55$, $p = 0.001$) when compared to 2006 canopy cover (fig. 3). Tall fescue abundance in burned patches of patch-burned pastures, however, did not increase when compared to 2006 abundance in either year ($F < 0.001$, $p > 0.97$).

Variation across sites within each treatment (patch-burned or grazed control) is probably attributable to differences in tall fescue abundance, which is variable at several spatial scales, including within patches and within pastures (data not shown). Increased tall

fescue abundance in the 2007 burned patches of the patch-burn treatment pastures and in the control pastures in 2007 and 2008 is a function of either absolute abundance as a result of increased invasion, or relative abundance as the native community recovers more slowly than tall fescue from high levels of use in previous years.

Discussion

Patch contrast and tall fescue defoliation

We applied a patch-burn grazing treatment to native tallgrass prairie pastures to test the efficacy of the fire-grazing interaction in promoting selective defoliation of invasive tall fescue tillers. As predicted, selection for tall fescue tillers increased and the relative height of grazed tillers decreased in the most recently-burned patches, although tiller selection within burned patches did not differ from unburned patches within patch-burned pastures and control pastures until the second year of the study. Contrast decreased in control pastures as we would expect from moderated stocking following years of heavy use, but we did not observe the increase in patch contrast we predicted would develop as a result of the patch-burn grazing treatment. Thus, we cannot conclude that patch contrast as measured contributed to increased tall fescue defoliation in burned patches in 2008.

As predicted, patch-burning appeared to have a negative effect on tall fescue abundance. Also, animal performance did not vary between cattle on control and patch-burn grazed pastures, indicating that cattle were unaffected by tall fescue consumption. Animal condition was generally high from the beginning of the grazing season to the end across all pastures.

It is interesting that while we observed treatment differences in defoliation of tall fescue tillers in 2008, no difference was detected in the first year of patch-burning (2007). While the goal of reducing tall fescue abundance was accomplished, it was not the result of our predicted mechanism – contrast in vegetation structure between the burned and unburned patches. With the exception of tiller defoliation in 2008, variance in our data was quite high on account of many sources of ecological variation in the field. Table 1 lists sources of ecological and biological variability that might explain variance in defoliation of tall fescue by cattle across treatment pastures that might have dampened the influence of contrast. Here, we discuss how each might have affected our results and how their consideration affects the nature of our conclusions.

Variation within the plant community affects patch contrast

Perhaps the largest potential source of variance in the data arises from variability in pasture history. While we controlled for management as part of the experiment, our sites had previously been diversely managed: ownership was both public and private, and some had been grazed intensively for many years prior to inclusion in this study, whereas others had been moderately grazed, or not grazed at all. Unfortunately, most of our information of site histories are based on the recollection of past owners, managers, and neighbors. Observing man-made structures such as ponds and old terraces, it is likely that management history varies within sites, as well as between sites. Other elements of an agricultural history include fire suppression, herbicide application, and fertilization to promote introduced forage species over the native community.

Of forage species introduced to our sites, tall fescue is by far the most abundant and probably the most ecologically significant (McGranahan 2008). Thus, the extent to which it has invaded a particular patch – which can be variable within pastures – affects response of grazers to the experimental treatment. For example, tall fescue density will affect the rate at which grazers select for tall fescue tillers. In particular, interpretation of the change in tall fescue abundance over the course of this study is confounded by the fact that patch-burn grazed pastures had more tall fescue prior to treatment than control pastures (mean 29.5% ± 2.3 s.e. versus 18.5% ± 3.4 s.e., $p = 0.03$).

The rate of infection by the fungal endophyte might affect the frequency at which grazers can return to tall fescue: higher infection rates might require longer or more frequent abstention periods to maintain low toxin levels in the animals' systems (Pfister 1997). On the other hand, endophyte infection rates might not account for variability so much as generally low rates of selection for tall fescue tillers across sites, as the infection rate was consistently high (mean 78% ± 6% s.e., Rebecca McCulley, personal communication).

In the context of this study, site history – especially those elements that promote invasion by tall fescue – is probably most important in affecting the rate at which patch contrast develops. A landscape can retain ecological memory from previous processes that affect patterns within that landscape through time (Peterson 2002). In this system, the generally slow rate of contrast development, as well as the wide variation in contrast across treatment pastures, is likely a vestige of variable rates of vegetation recuperation from overgrazing.

As defined in this paper, contrast is composed of the absolute difference between two elements: the average visual obstruction across unburned patches and the average visual

obstruction in the most recently burned patch. Contrast begins with a successful fire in the burned patch: the succulent regrowth attracts grazers, and repeated herbivory maintains the low sward height and high forage quality of the grazing lawn as described by Fuhlendorf and Engle (2004). This interaction, however, is dependent on a successful fire, which depends on sufficient fuel. Here again, tall fescue creates variability. Tall fescue has been implicated as an "anti-pyric" invasive species (McGranahan et al., unpublished manuscript), which is a reference to traits that limit fire in tall fescue-dominated fuelbeds. When invasive in native, fire-adapted grasslands, tall fescue can limit fire spread in three ways: (1) by increasing the amount of live, green material in the fuelbed to the point that that fires fail to propagate (Jolly 2007); (2) by outcompeting native vegetation that would otherwise contribute dormant-season fuel (Clay 1993, Rudgers et al. 2004, Rudgers et al. 2005); and (3) through rapid decomposition of its own otherwise combustible litter (Mayer et al. 2005). Thus, accumulating enough fuel to successfully carry a fire is the first step in creating a grazing lawn in which grazers are not adverse to consuming tall fescue, and the rate of fuel accumulation (as measured by visual obstruction) might be hampered by slow vegetation recovery from an ecological memory of overgrazing.

The contribution of the burned patch to patch contrast, however, cannot increase further once the fire has consumed fuel entirely and evenly throughout the patch. In other words, there is a maximum degree to which managers can rely on the "magnet effect" to attract grazers and drive the fire-grazing interaction. Grazers must perceive an advantage to grazing in the burned patch, and thus perceive a disincentive to foraging in the other patches. Here, ecological memory – specifically, temporal distance from severe grazing – is perhaps at its peak importance. The amount of biomass in the unburned patches is determined by the

species composition of the patch, and their productivity. Evidence that the unburned patches

have not sufficiently recovered is apparent in the lack of difference in visual obstruction

between burned and unburned patches, and the lack of difference in total canopy cover in the

Daubenmire frames between the patches (McGranahan et al, unpublished data). We predict

that as we continue with moderate stocking, these grasslands will continue to recover and

accumulate standing necromass and a deep litter layer that contribute to structural and

nutritional deterrents from grazing in these patches. These deterrents will continue to

concentrate grazing in the burned patch and further force selection for tall fescue tillers. In

this manner, the unburned patches are nearly limitless in their contribution to patch contrast.

Through 2008, however, any interest by cattle in tall fescue in the burned patch has been a

function of the fire's magnet effect, rather than structural deterrents in the unburned patches.

Variation among grazers affects selection for targeted species

Unlike mechanical and chemical methods of control that can be expected to perform

in a uniformly predictable manner, any grazing system has an inherent degree of variability

due to the inclusion of living organisms with a complex suite of needs. Herbivores are

constantly making decisions, including foraging decisions, at several spatial scales (Senft et

al. 1987, Stuth 1991), and are constantly re-evaluating their forage options along a dynamic

scale of nutritional needs (Stuth 1991, Launchbaugh et al. 2001). As such, managers must

appreciate the varied needs of herbivores and learn how to manipulate the landscape in which

foraging decisions are made in order to achieve management goals.

A key element in the management of the fire-grazing interaction, as with grazing

management in general (Vallentine 1990), is stocking rate. Establishment and maintenance of

an effective grazing lawn requires the proper balance of burn area and herbivore population: too few grazers or too large of a burned area will not sufficiently concentrate grazing to create a grazing lawn, while too many grazers or too small of a burned patch will force animals to forage in the less-nutritious unburned areas (Fuhlendorf et al. in press). Table 1 shows potential sources of variation in stocking rate, including herd demographics (age, sex, etc.) and animal type. For example, calves born in the spring might increase stocking rate of a pasture compared to fall-calving cows that spend the grazing season gestating rather than lactating.

A final source of variation is attributable to the experience of the individual animals. Grazers introduced to new sites with potentially unfamiliar forage are forced to explore and experiment, and the rate at which the animals learn and familiarize themselves with new surroundings is critical not only to the effectiveness of the grazers in achieving management goals, but also to the animals' health and condition (Provenza and Launchbaugh 1999). Thus, in our experiment, variation in the responses of each herd to patch-burn grazing, as measured by their utilization of tall fescue, might be partially attributable to different levels of experience with the landscape and the forage matrix, in addition to the characteristics of the vegetation community as discussed above.

Conclusions

Despite the lack of support for patch contrast as a primary mechanism behind patch-burn grazing in invasive species control, the fact remains that we observed higher levels of grazing on tall fescue tillers in the patch-burn grazing treatment. Thus, we conclude that pyric-herbivory – the single disturbance that results from the interaction of fire and grazing

within a heterogeneously-managed landscape – shows promise as an effective method of managing tall fescue invading tallgrass prairie. Conclusions about the mechanisms behind increased grazer selection for an otherwise unpreferred species, however, are more tenuous. The magnet effect certainly appears to have been a factor in the patch-burned pastures in 2008, even though patch contrast was not achieved. Persistent ecological memory resulting from a recent history of heavy stocking rate in the plant community was most likely responsible for accumulated biomass in the unburned patches below that necessary to contrast with the burned patches. We predict that, as sites respond to moderated stocking rate and lose ecological memory and returning herds carry over their experiences with grazing lawns, the effects of pyric-herbivory will intensify and the mechanisms that drive the fire-grazing interaction will play an increasingly efficacious role in selective herbivory of tall fescue.

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Level of consideration		Sources of variation
Vegetation		
	Tall fescue	
		extent of invasion
		endophyte infection rate
		composition of plant matrix
	Disturbance history	
		agricultural activity
		grazing intensity
		fire suppression
Herbivores		
	Class	
		age
		sex
		reproductive status
	Kind	
		breed
	Experience	
		familiarity with site
		previous exposure to forage types

Table 1: List of several factors that potentially contribute to variation in the effects of the patch-burn grazing treatment on herbivore selection of tall fescue.
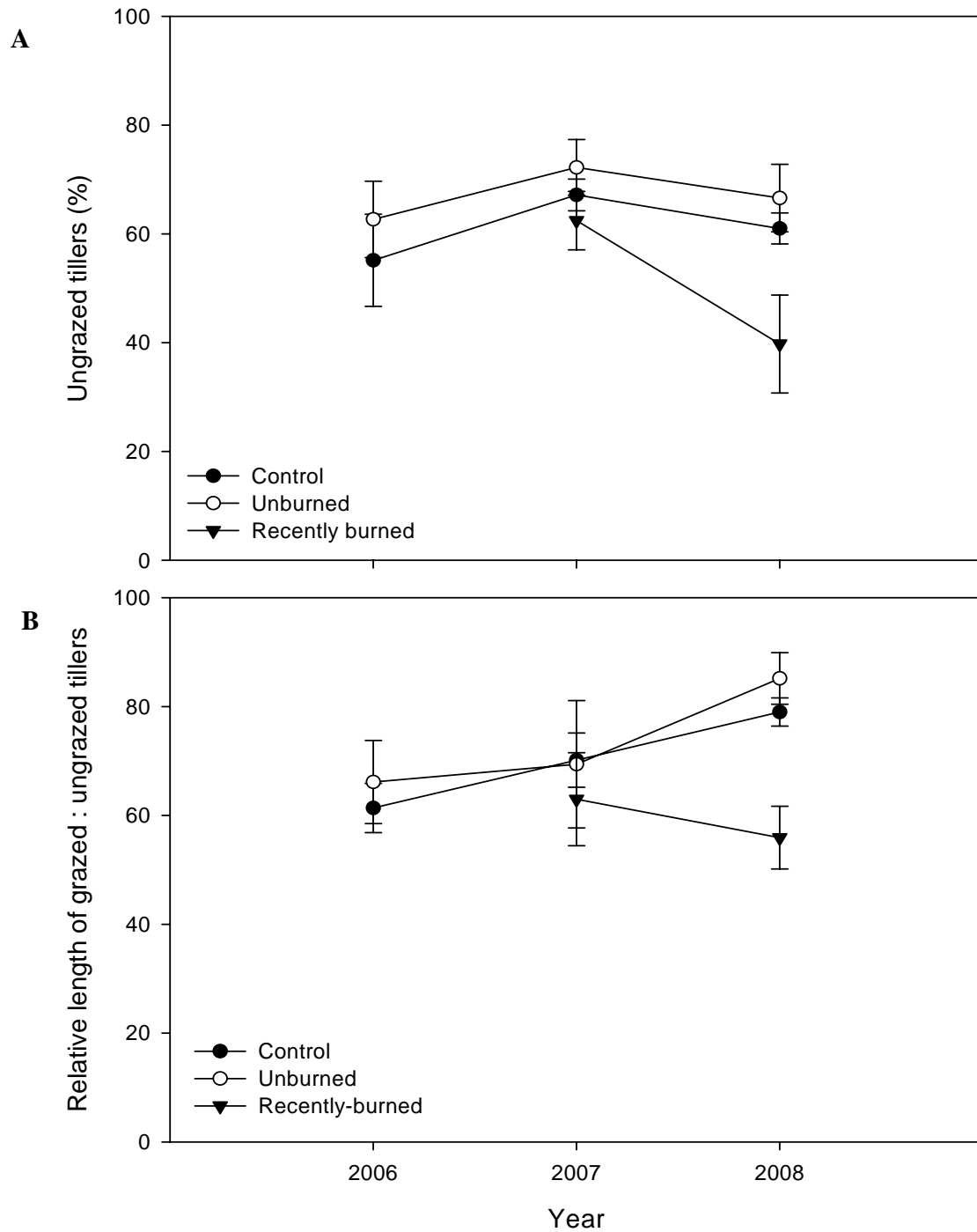
Fig. 1: Tall fescue tillers (%) left ungrazed (A) and relative height (%) of grazed to ungrazed tall fescue tillers (B) within burned and unburned patches in patch-burn treatment pasturesand within grazed control pastures.
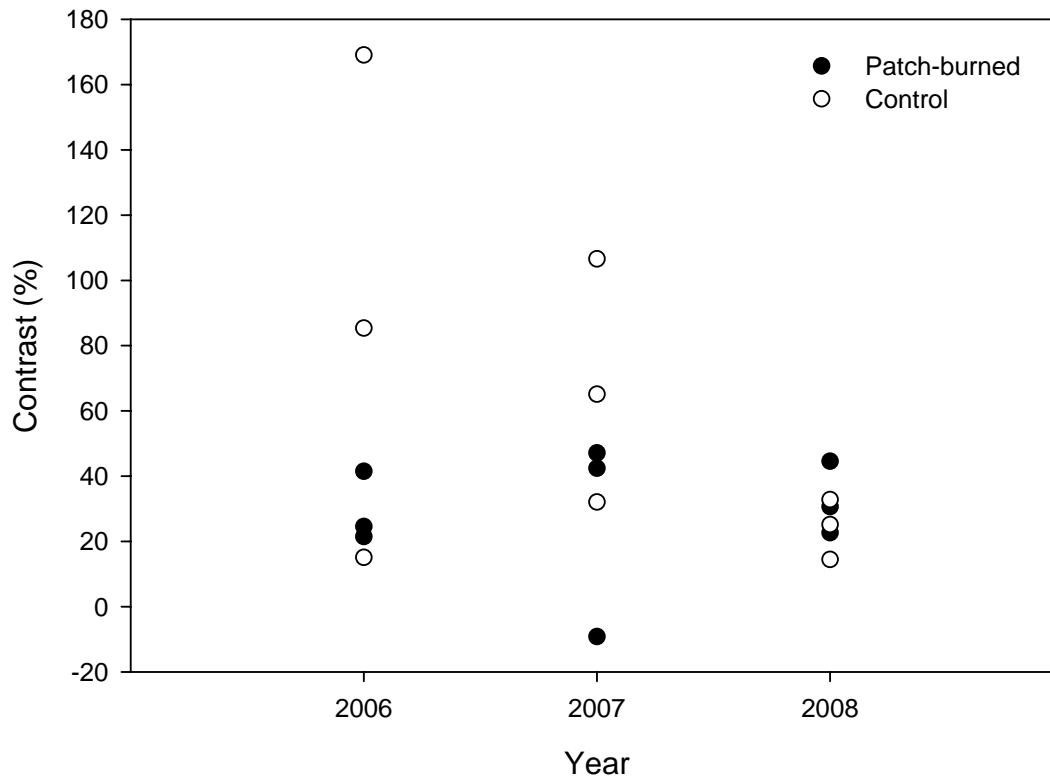
Fig. 2: Contrast between patches in patch-burned and grazed control pastures over three years. Year effect was not significant. Contrast between patches in patch-burned pastures (i.e., recently burned patch contrasted with unburned patch) did differ from contrast between patches in the control pastures in any year.
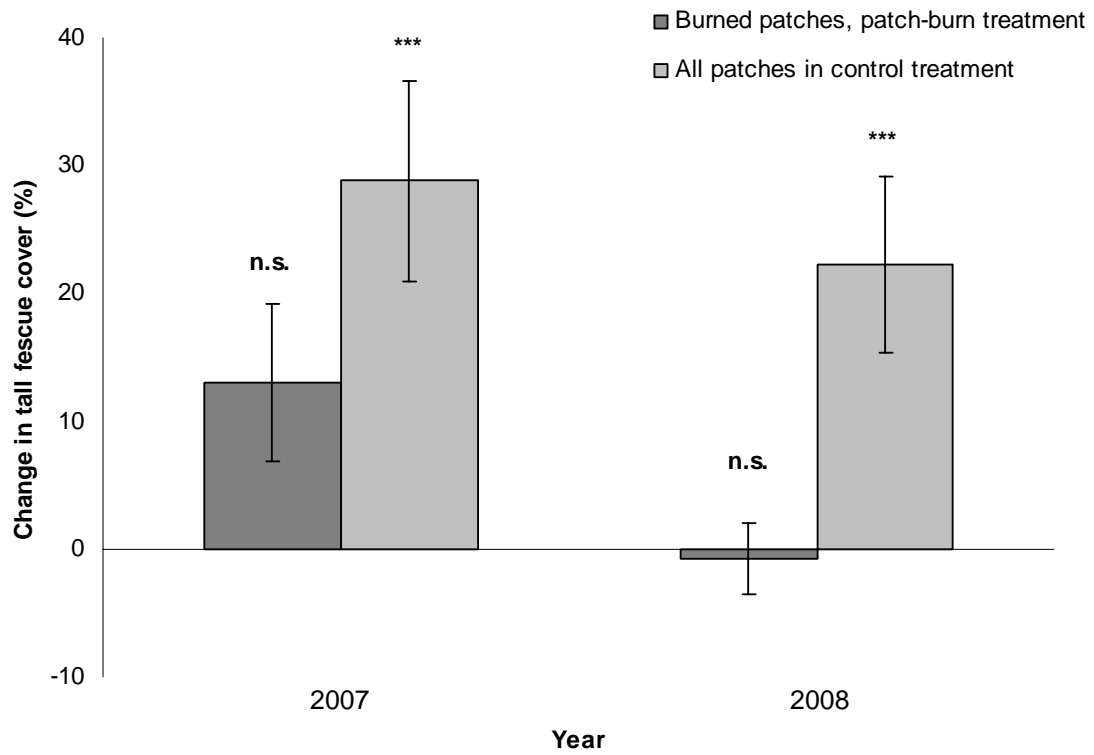
Fig. 3: Relative change in tall fescue cover in the patch-burned treatment patches and across 3 control patches for 2007 and 2008, each compared to the same patch in 2006. Three stars (***) represent significance at p < 0.001.