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Research Article

Patterns of Smooth Brome, Kentucky Bluegrass, and Shrub Invasion in the Northern Great Plains Vary with Temperature and Precipitation

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ABSTRACT

Biological diversity and ecological integrity in native prairies of the northern Great Plains are substantially modified from pre-Euro-American settlement. About 90,000 ha of native mixed-grass and tallgrass prairie are managed by the US Fish and Wildlife Service (Service) in North Dakota, South Dakota, and northeastern Montana. We used belt transects to classify floristic composition of all Service-owned prairies in the Dakotas and northeastern Montana. Prairies were significantly degraded, mainly by invasion of introduced grass and forb species and by native shrubs. In general, floristic integrity of Service-managed prairies was most compromised by smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*). The degradation was, in part, an unintended outcome of long-term management by the Service. The degree of degradation varied spatially across the broad geographic area defined by our study and was invader-specific, corresponding to geographic patterns in precipitation and temperature. Within the study area, floristic quality was relatively high on prairies toward the north and west, where plant growth sites generally were cooler and drier, based on long-term averages. In contrast, growth sites to the south and east generally were warmer, moister, and characterized by lower floristic quality, primarily because they were substantially invaded by smooth brome. Kentucky bluegrass was the most widespread invader of Service-owned prairies, with less frequent occurrence only in prairies dominated by smooth brome, especially in South Dakota or by native grass–forbs, especially in northwestern North Dakota and northeastern Montana. Improved knowledge of geographic and climate-related patterns of plant invasion enhances decision making for protecting northern mixed-grass and tallgrass prairies by focusing restoration efforts where probability of success is greater.

Index terms: invasive species; Kentucky bluegrass; northern Great Plains; prairie; smooth brome

INTRODUCTION

Grasslands are imperiled worldwide, ranking as the most converted and least protected of Earth's major biomes (Hoekstra et al. 2005). The vast Great Plains is North America's most altered major ecosystem, primarily modified during Euro-American settlement by conversion to agriculture. Conversion of prairie continues at an alarming rate in North Dakota and South Dakota (GAO 2007; Stephens et al. 2008; Gage et al. 2016; Wimberly et al. 2017). Biological diversity of remaining grasslands is adversely affected by urbanization, energy development, invasive plants, suppression of fire, certain grazing practices, and likely climate change (Samson and Knopf 1994; Askins et al. 2007; Duell et al. 2016). Invasive plant species are implicated in loss of biological diversity in prairies, but specific mechanisms underlying ecological change are poorly understood (Samson et al. 2004; Grant et al. 2009; DeKeyser et al. 2013). Degradation of prairies has broader and mostly negative implications for important ecosystem services and processes such as ecological integrity, wildlife species and habitats, important pollinators, nutrient cycles, and hydrologic systems (Grant et al. 2009; Ellis-Felege et al. 2013; Toledo et al. 2014).

Roughly 90,000 ha of native mixed-grass and tallgrass prairie (hereafter "prairie") are managed by the US Fish and Wildlife Service (Service) north and east of the Missouri River in North Dakota, South Dakota, and northeastern Montana (Figure 1). Service prairies are scattered across a vast landscape and range from isolated 16 ha Waterfowl Production Area (WPA) tracts within agricultural settings to >15,000 ha National Wildlife Refuges (NWR) occurring in grassland-dominated landscapes. Conservation of biological diversity and ecological integrity and management of habitats for migratory birds are primary functions of most Service lands (Dixon et al. 2019).

Major anthropogenic disruptions in ecological processes that shaped the Great Plains have occurred since Euro-American settlement. Historically widespread grazing by native herbivores coupled with frequent fires all but stopped following settlement (1880–1915). Extending into the 1930s, conversion of grassland for agriculture and grazing of remaining prairies by domestic livestock predominated across much of the northern Great Plains. After acquisition by the Service (mainly 1930s–1950s), Service-owned prairies generally were managed with a combination of no grazing or season-long grazing at low stocking rates; wildfires were quickly suppressed (Murphy and Grant 2005; Grant et al. 2009; Dixon et al. 2019). Beginning in the 1960s,

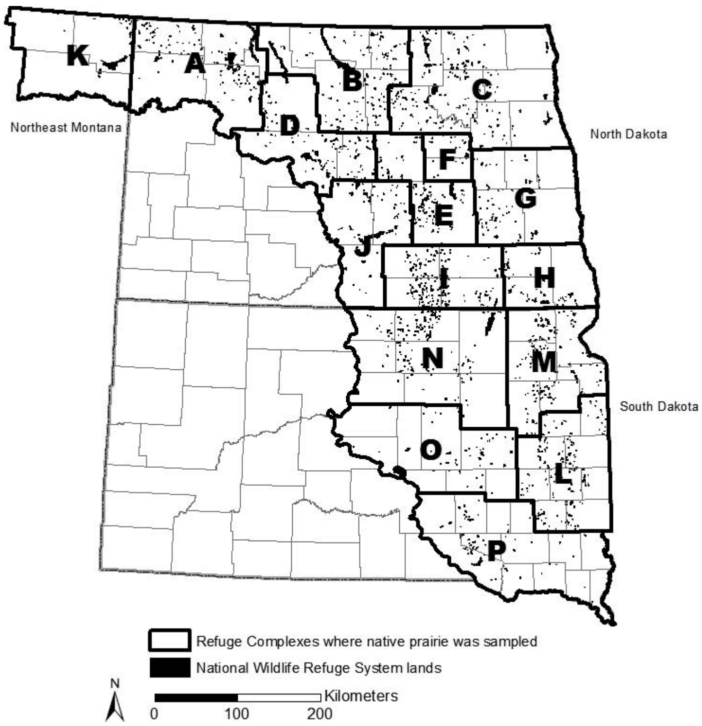

Figure 1.—National Wildlife Refuge System lands (shaded in black) located east and north of the Missouri River in North Dakota and South Dakota and northeastern Montana. Service-owned prairies were inventoried within National Wildlife Refuge Complexes (bold outline) that often include one or more large National Wildlife Refuges and many widely scattered Waterfowl Production Areas, including (A) Des Lacs, (B) J. Clark Salyer, (C) Devils Lake, (D) Audubon, (E) Chase Lake, (F) Arrowwood, (G) Valley City, (H) Tewaukon, (I) Kulm, (J) Long Lake, (K) Northeast Montana, (L) Madison, (M) Waubay, (N) Sand Lake, (O) Huron, and (P) Lake Andes.

grazing of Service-owned prairies was deferred with increasing frequency to emphasize undisturbed nesting cover for prairie ducks and upland game birds. Suppression of wildfires continued and prescribed fire was infrequent during the 1970s and 1980s. Since the early 1990s, prescribed fire has been more frequently and extensively applied, although this convention was not universal across Service-owned prairies. In summary, Service-owned prairies north and east of the Missouri River have collectively experienced decades of deferment from grazing and fire disturbances, a significant departure from presettlement conditions. More recently, the extent and frequency of prescribed grazing has increased, mainly in response to unforeseen increases and consequences of invasive plant species (Grant et al. 2009).

An inventory of prairies on two refuges in North Dakota (data collected 1999–2004) revealed significant invasion by introduced cool-season grasses, especially smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.), and native species of low shrub (e.g., western snowberry [*Symphoricarpos occidentalis* Hook.] and silverberry [*Elaeagnus commutata* Bernh.] Murphy and Grant 2005). During 2005–2006, inventories were expanded to prairies within five National Wildlife Refuge Complexes (i.e., administrative groupings) of Service-owned lands in North Dakota and South Dakota (Grant et al. 2009). In that study, native grasses and forbs were common (mean frequency of occurrence 47–54%) on two complexes but uncommon (4–13%) on two others. Results from Grant et al. (2009) corroborated significant invasion described by Murphy and Grant (2005) and further indicated that degradation of Service-owned prairies may be more widespread in the region than previously known. Recent studies confirmed similar loss of floristic diversity in prairies elsewhere in the Dakotas, driven by invasion of Kentucky bluegrass and smooth brome (DeKeyser et al. 2009, 2015; Toledo et al. 2014; Printz and Hendrickson 2015; Stotz et al. 2017).

In this study, we completed assessments begun by Murphy and Grant (2005) and Grant et al. (2009) to include all Service-owned prairies in North Dakota, South Dakota, and northeastern Montana. Our primary objectives were twofold. First, we comprehensively described the floristic composition of prairies across all Service lands in the region (i.e., our final product includes data from Murphy and Grant 2005 and Grant et al. 2009). Specifically, we assessed the composition of Service-owned prairies and quantified the spatial extent and degree of invasion by undesirable plants (e.g., Kentucky bluegrass) or plant groups (e.g., introduced weedy forbs) that compromise the floristic integrity of prairies. The potential for restoration or maintenance of native plant communities on prairies undoubtedly depends on the degree and effects of invasion by undesirable plant species. Secondly, we looked for broad-scale geographic patterns in invasion by smooth brome, Kentucky bluegrass, and low shrubs. We then examined if spatial heterogeneity in floristic composition might be related to temperature and precipitation that also varied across our study area. Invasion by undesirable plants and climate effects are important anthropogenic factors implicated in reduced floristic diversity in prairies, although little empirical evidence is available to link these factors (Duell et al. 2016). Discernable spatial patterns in degree of invasion or invader-specific attributes may suggest opportunities to focus prairie restoration at a local or regional scale where probability of restoration success is greater.

METHODS

Study Area

Our focus area was the glaciated plains north and east of the Missouri River (Bluemle 2000). We inventoried native prairies within 16 complexes of Service-owned lands in North Dakota, South Dakota, and northeastern Montana (Figure 1). We define complexes as administrative units that include several counties, often consisting of one or more large NWRs, several smaller NWRs, and many smaller WPAs (Figure 1). Earliest assessments of floristic composition were completed in 1999–2004 (include portions of two refuges described in Murphy and Grant 2005) and expanded to five complexes in 2005–2006 (Grant et al. 2009). We completed the remaining complexes in 2007–2008. Collectively the data set included all Service-owned prairies $\geq$4.1 ha occurring within 16 complexes.

Native prairie throughout the area occurs mainly on soils dominated by gravel-loam and clay-loam glacial tills, and sandy-loam glacial outwash. Native vegetation is northern mixed-grass prairie, except in the eastern-most portions of North Dakota and

South Dakota, where it is northern tallgrass prairie (Coupland 1992; Bragg 1995). Flora include several species of cool-season graminoids, mainly needlegrasses (*Hesperostipa* spp., *Nassella* spp.) and wheatgrasses (*Pascopyron* spp., *Elymus* spp.), but also others such as Junegrass (*Koeleria macrantha* Ledeb. Schult.), native bluegrasses (*Poa* spp.), and sedges (*Carex* spp.); several warm-season grass species, mainly gramma grasses (*Bouteloua* spp.) and bluestems (*Andropogon* spp., *Schizachyrium* spp.); low shrubs, mainly western snowberry and silverberry; and many forb species, dominated by Asteraceae and Fabaceae. Climate of our study area is semi-arid to subhumid continental, characterized by long cold winters and moderately warm summers. Annual precipitation varies across the study area with long-term averages of 40–50 cm, two-thirds of which occurs during the growing season, although droughts are common.

Field Methods and Spatial Analysis

We measured vegetation composition of native sod tracts (i.e., never cultivated) ≥4.1 ha, following methods described by Murphy and Grant (2005) and Grant et al. (2009). In summer 1999–2008, we used belt transects to record relative frequency of plant species or species groups on prairies within each Service complex (Grant et al. 2004). Transects were 25 m long except on some sites with very steep slopes (such as choppy sandhills at J. Clark Slayer NWR), where we used 8- or 10-m transects. We distributed one transect per 1–4 ha of prairie. Sampling intensity was consistent within each complex but varied among complexes based on the perceived heterogeneity in vegetation, needs for ancillary data, and logistical considerations (Grant et al. 2009). We summarized data separately for each complex to avoid unequal weighting due to different sampling intensities. We selected transects randomly but constrained them to be ≥50 m from adjacent transects (except for earliest areas inventoried), also avoiding, to the extent possible, seasonal and semipermanent wetlands, woodlands, roads, trails, rock outcroppings, etc. Selection included a random starting point and azimuth orientation (1–360°). We classified the dominant plant species group at each of 50 contiguous 0.5 × 0.1 m belts along each 25-m transect (16 belts for an 8-m transect), using a plant species group classification system specific to the region (e.g., Appendix A in Grant et al. 2004). We summarized transect data by percent frequency of occurrence according to specific plant genera or species categories, certain functional groups (e.g., warm-season native grasses), or life form groups (e.g., low shrub; Grant et al. 2004; Murphy and Grant 2005).

Based on geographical differences in floristic composition observed among five Service-owned complexes reported in Grant et al. (2009; table 1), we predicted that geographic differences in prairie composition were likely to occur when examined across our study area. Therefore, we developed a process to describe large-scale spatial patterns in floristic composition. We measured the floristic composition (based on relative frequency of occurrence for each plant species or functional group) of 862 units of various sizes that were irregularly spaced across the study area (Figure 1). Size of units and sampling intensity were variable; measurements were made on 1–2145 transects per unit. Unit-specific estimates of floristic composition were obtained by averaging across transects of a given unit. Precision of unit-specific estimates varied markedly because of the wide range in number of transects per unit, making broad spatial patterns somewhat difficult to discern based on mean values. We addressed this issue by developing a two-dimensional spatial model that smoothed observed values in composition, giving more weight to units with larger sample sizes. Response variables were unit-specific mean values, averaged across transects for native grass–forb (all groups of native grasses and forbs combined), smooth brome, Kentucky bluegrass, and low shrub. Predictor variables were the first (PC1) and second (PC2) principal component scores of Universal Transverse Mercator (UTM; zone 14) coordinates (EASTING and NORTHING). We used PC1 and PC2 instead of EASTING and NORTHING because our study area was irregularly shaped and we desired predictors to be uncorrelated. The response variable was not strictly a binomial proportion; however, its expected value (μ) was bounded by 0 and 1. We used a generalized linear model and the GLIMMIX procedure of SAS software version 9.3 (SAS Institute 2011) to model the proportion as a pseudo-binomial variable with logit link function, via quasi-likelihood estimation (McCullagh and Nelder 1989). Residual plots showed evidence that data were under-dispersed relative to the binomial distribution. We therefore specified a variance function in which the variance equaled $\mu^{1/3} * (1 - \mu)^{1/3}$. Residuals from this model showed an adequate distribution, and the number of outlying residuals was greatly reduced compared to a model with standard binomial variance. We explored various functional forms for the spatial model and settled on two-dimensional regression splines. We considered first- (linear), second- (quadratic), and third-degree (cubic) splines with anywhere from three to seven equally spaced knots in each direction. We fit models with all combinations of degree and number of knots and ranked models on the basis of the quasi-likelihood information criterion (*QIC*; Pan 2001; SAS Institute 2011). We also considered linear spline models that included interactions between PC1 and PC2. We used the model with lowest *QIC* to produce smoothed estimates of proportion composition. We graphically evaluated residuals from the model to ensure that remaining variation appeared random. To quantify the proportion of variation accounted for by the model, we computed

$$R^2 = 1 - \frac{\sum n_i (p_i - \widehat{p}_i)^2}{\sum n_i (p_i - \overline{p})^2},$$

where

p_i is the observed proportion composition for unit i,
$\widehat{p}_i$ is the model-estimated proportion for unit i,
$\overline{p}$ is the mean of observed proportions,
n_i is the number of transects for unit i.

Summation and averaging was across all 862 units. We completed separate analyses for native grass–forbs, smooth brome, Kentucky bluegrass, and low shrub categories, graphically displaying spatial results for all prairie units across our study area.

Table 1.—Floristic composition of Service-owned prairies in North Dakota, South Dakota, and northeastern Montana. $n =$ number of prairie units (number of transects) for estimated Mean and SE. Data for understory of low shrubs are the percent of the understory dominated by either Kentucky bluegrass, smooth brome, crested wheatgrass, or native grass–forbs (not available for South Dakota).

	Full study area $n = 862$ (15,144)		North Dakota $n = 419$ (9538)		South Dakota $n = 376$ (4229)		NE Montana $n = 67$ (1377)	
Plant group/species	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Native grass–forb	24.8	0.2	24.7	0.3	14.6	0.4	49.2	1.0
Smooth brome	29.2	0.3	27.1	0.3	40.7	0.5	14.6	0.7
Kentucky bluegrass	25.4	0.2	25.5	0.3	34.0	0.5	4.7	0.4
Crested wheatgrass	3.4	0.1	0.5	0.1	1.7	0.1	23.3	0.8
Low shrub	10.3	0.1	14.7	0.2	1.5	0.1	5.7	0.4
Bluegrass understory	53.1	23.3	56.8	26.9	NA		30.3	15.8
Brome understory	30.7	23.7	32.6	27.2	NA		18.9	22.2
Native understory	12.6	11.8	8.8	13.0	NA		36.4	26.4
Crested understory	1.7	2.7	< 0.1	< 0.1	NA		12.2	19.5
Weedy forbs	4.2	0.1	3.9	0.1	0.2	1.3	1.3	0.1
Canada thistle	1.1	< 0.1	0.9	< 0.1	1.8	0.1	0.6	0.1
Leafy spurge	1.1	0.1	1.7	0.1	0.1	< 0.1	0.1	< 0.1
Sweet clover	1.5	0.1	1.0	0.1	3.1	0.2	0.3	0.1

Geographic Patterns in Precipitation and Temperature

We investigated whether anticipated geographic variability in floristic composition might be related to 30-y average precipitation or temperature that varied across our study area. In general, temperature varies along a north–south gradient, with northern latitudes being relatively cooler. Precipitation varies along an east–west gradient, with higher values in more easterly longitudes. We selected the climate normal period of 1961–1990 to use in our analysis, primarily because substantial invasions of Service-owned prairies by smooth brome, Kentucky bluegrass, and woody plants reportedly occurred during this period, and because it preceded our period of data collection (1999–2008). We obtained spatially explicit long-term averages for two temperature metrics (mean temperature in the warmest month [MTWM] and mean maximum temperature in the warmest month [MMAX]) and two precipitation (mean annual precipitation [MAP] and growing season [i.e., April–September] precipitation [GSP]) metrics (Rehfeldt 2006). Because these metrics were strongly correlated, we performed a principal components analysis and derived two new metrics (CLIMATE1 and CLIMATE2) that were uncorrelated. We then compared quadratic-response surface models derived from CLIMATE1 and CLIMATE2 to models obtained with PC1 and PC2. Models for native grass–forb, smooth brome, Kentucky bluegrass, and low shrub were compared and ranked on the basis of *QIC* and R^2.

RESULTS

We quantified floristic composition (based on frequency of occurrence) for 15,144 transects located within 862 prairie units. Collectively, native grasses and forbs accounted for 24.8% frequency of occurrence (Table 1). Smooth brome (29.2%) and Kentucky bluegrass (25.4%) were the most common invader species, with both occurring at higher frequency in South Dakota than North Dakota or Montana. Crested wheatgrass (*Agropyron cristatum* L.) accounted for 3.4% frequency of occurrence across all units but was a significant invader only in Montana (23.3%). Weedy forbs accounted for 4.2% frequency of occurrence, dominated by sweet clover (*Melilotus* spp.; 1.5%), leafy spurge (*Euphorbia esula* L.;1.1%), and Canada thistle (*Cirsium arvense* Scop.; 1.1%). Low shrub accounted for 10.3% frequency of occurrence and was most prevalent in North Dakota. The understory of low shrubs was dominated by Kentucky bluegrass (53.1%) and smooth brome (30.7%) rather than native grasses and forbs.

Geographic Variation in Prairie Composition

Linear spline models best described geographic distribution of native grass–forb, smooth brome, Kentucky bluegrass, and low shrub (Appendix 1). A linear spline model with five knots in the PC1 direction (oriented approximately southeast to northwest), six in the PC2 direction (oriented approximately southwest to northeast), and that included interactions had lowest *QIC* for both native grass–forb and smooth brome. The model for native grass–forb explained 65% of the spatial variation in observed values (Figure 2A). Native grass–forb frequency was greater in northwest and north-central North Dakota and northeastern Montana, and, to a lesser extent, in northeastern South Dakota. The frequency of native grass–forb was lowest in the southern half of North Dakota and most of South Dakota, averaging <30%.

The model for smooth brome accounted for 50% of the spatial variation in observed values (Appendix 1). The spatial pattern for smooth brome (Figure 2B) was nearly a mirror image of that for native grass–forb. Brome was most prevalent in regions of South Dakota where it accounted for >60% mean frequency of cover. South-central North Dakota was also a hotspot for brome where frequency of occurrence was ≥50%. Smooth brome was much less prevalent across the northern tier of our study area, especially in north-central and northwestern North Dakota.

A linear spline model with four knots in the PC1 direction, three in the PC2 direction, and that included interactions had lowest *QIC* for Kentucky bluegrass (Appendix 1). This model explained the lowest percent (44%) of spatial variation relative to observed values of our four dependent variables. Kentucky bluegrass was the most ubiquitous of the four variables across

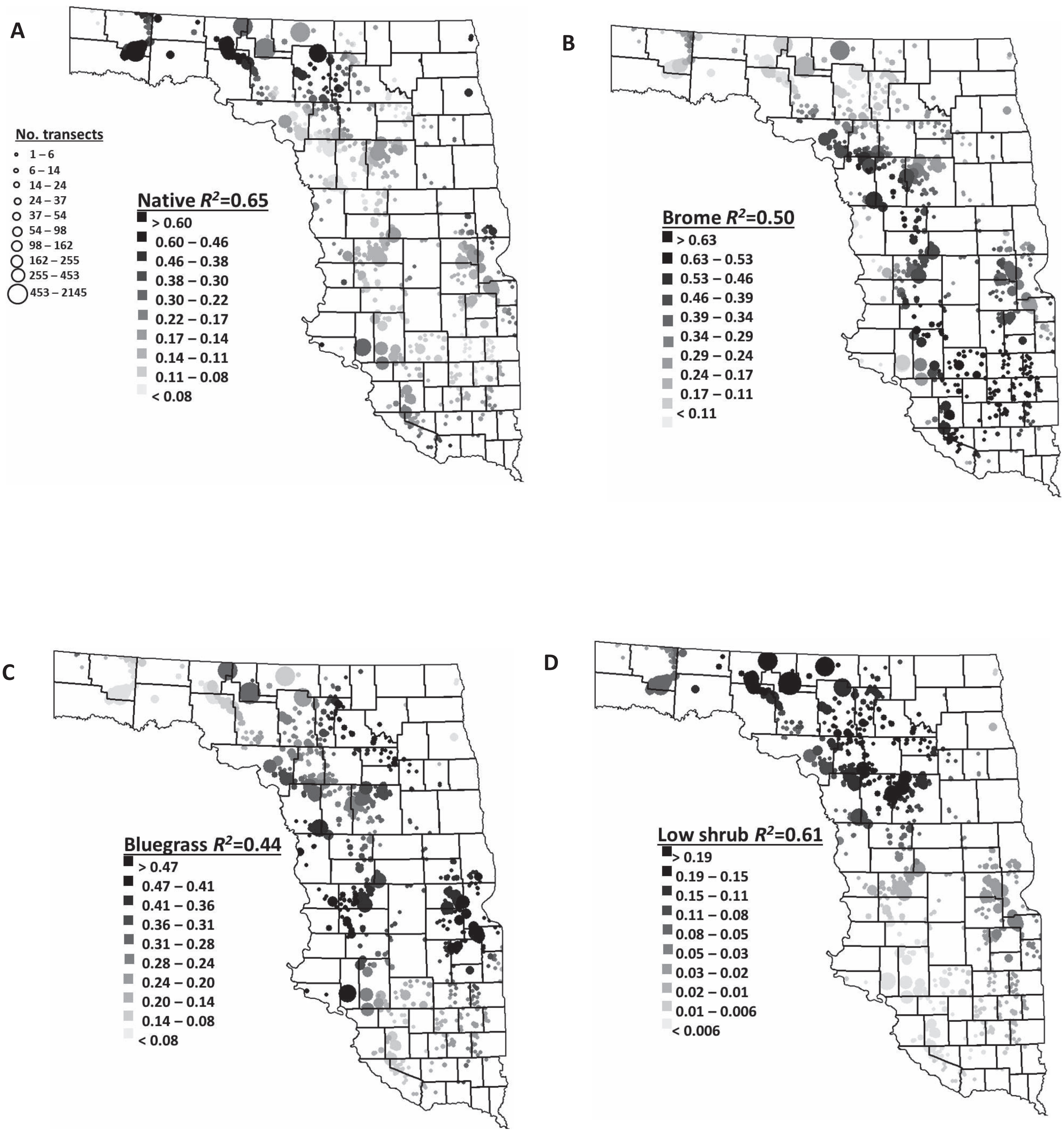

Figure 2.—Relative frequency of occurrence for native grass–forb, smooth brome, Kentucky bluegrass, and low shrub categories occurring on Service-owned prairies in North Dakota and South Dakota and northeastern Montana. Increasingly darker shading reflects an increasing frequency of occurrence. Increasingly larger circles reflect increasing size (ha) of prairie units composed of a greater number of transects. R^2 is the amount of variation accounted for by each model relative to observed values.

the region but appeared slightly more prevalent in eastern to northeastern North Dakota and in the northern third of South Dakota, where it comprised ≥40% mean frequency of occurrence (Figure 2C). Kentucky bluegrass was least common in extreme northwestern North Dakota and northeastern Montana and, to a lesser degree, the southern third of South Dakota.

The linear spline model with five knots in the PC1 direction and three knots in the PC2 direction, without interaction terms, had the lowest *QIC* for the low shrub category, accounting for 61% of the spatial variation relative to observed values (Appendix 1). Low shrub had a strong north–south pattern and was far more prevalent in central, north-central, and northwestern North Dakota prairies, but was clearly a minor component of South Dakota prairies (Figure 2D).

Geographic Variation Related to Temperature and Precipitation

Correlations among climate variables ranged from 0.46 to >0.99, and the first two principal components captured >99% of the total variation. The first principal component CLIMATE1 (0.532*MTWM + 0.451*MMAX + 0.511*MAP + 0.502*GSP) accounted for 79% of the variation and represented a continuum from warmer, wetter conditions in the southeast region to cooler, drier conditions in the northwest portion of the study area (Figure 3A). The second principal component CLIMATE2 (0.345*MTWM + 0.657*MMAX − 0.455*MAP − 0.492*GSP) captured an additional 20% of the variation and represented a continuum from warmer, drier conditions in the southwest region to cooler, wetter conditions in the northeast portion of the study area (Figure 3B).

We predicted that differences in climate across our study area would partially explain the geographic variation in floristic composition we observed. We found CLIMATE1 to be a strong surrogate for PC1 ($r = 0.92$, $P < 0.001$) and CLIMATE2 to be a weaker but useful surrogate for PC2 ($r = -0.63$, $P < 0.001$). Furthermore, quadratic response surface models derived from CLIMATE1 and CLIMATE2 were superior to those derived from PC1 and PC2 in predicting both native grass–forb and Kentucky bluegrass frequency of occurrence and were almost as good for smooth brome and low shrub (Table 2). Our results suggest that temperature and precipitation influenced floristic composition across the Dakotas and northeastern Montana. More floristically intact prairies composed of higher frequencies of native grass–forb species occurrence, as well as greater frequency of low shrub, occurred under relatively cooler, drier conditions in the northwest portion of the study area. In contrast, significant smooth brome invasion was associated with relatively warmer and wetter conditions in the southeast region of our study area (e.g., Figure 3C). Although ubiquitous in distribution, Kentucky bluegrass appeared to dominate in the geographical area between climate extremes and the higher frequencies of native grass–forb and smooth brome.

DISCUSSION

Invasion by smooth brome, Kentucky bluegrass, and low shrubs is a significant threat to floristic diversity of Service-owned prairies in the northern Great Plains. Our data confirmed results of Murphy and Grant (2005) and Grant et al. (2009), concluding that Service-owned prairies no longer collectively represent the region's prairie heritage at the scope and scale previously assumed to occur on lands administered by the Service within the region. Other protected natural areas where fire and grazing have been reduced or excluded are similarly degraded, especially by Kentucky bluegrass and smooth brome (Larson et al. 2001; DeKeyser et al. 2009; Fink and Wilson 2011; Sinkins and Otfinowski 2012; DeKeyser et al. 2013). Ecological effects of smooth brome and Kentucky bluegrass invasion have been underestimated by managers and researchers until recently (Dillemuth et al. 2009; Grant et al. 2009; Printz and Hendrickson 2015). Both species remain widely cultivated and neither is recognized formally as invasive, a designation that normally stimulates research and management actions to address invasion issues. Frequencies of low shrub, particularly in north-central and northwestern North Dakota, occur well above the range of natural variability estimated for the region prior to Euro-American settlement (Murphy 1993; Murphy and Grant 2005).

Smooth brome and Kentucky bluegrass have autecological characteristics that allow them to alter key processes (e.g., nutrient cycling) within grasslands in ways that afford them with distinct competitive advantages over native plants. Low shrub invasion can modify site characteristics such that shrub patches become susceptible to subsequent invasion by tall woody plants, Kentucky bluegrass, and smooth brome (Pelton 1953; Murphy 1993; Manske 2006; this study). Recent reviews on the individual biology of smooth brome (Otfinowski et al. 2007; Salesman and Thomsen 2011), Kentucky bluegrass (DeKeyser et al. 2013; Toledo et al. 2014; Printz and Hendrickson 2015), and low shrubs (primarily western snowberry; Manske 2006; Hauser 2007) do not adequately discuss effects of smooth brome, Kentucky bluegrass, and low shrubs as codominant invaders, an occurrence too often observed on many Service-owned prairies. Next, we discuss key factors implicated in susceptibility of Service-owned prairies to invasions by smooth brome, Kentucky bluegrass, and woody shrubs.

Does Geographical Variation in Temperature and Precipitation Explain Patterns of Invasion in Service-Owned Prairies?

Our most compelling findings show that degradation of Service-owned prairies is not only spatially variable, but also invader-specific. Our results also suggest spatial variation (based on EASTING and NORTHING) in floristic composition is likely a proxy for geographic variability in precipitation and temperature across the Dakotas and Montana. Cooler and drier sites occurring farther to the north and west had higher relative frequencies of native grasses and forbs compared to warmer and wetter areas located to the south and east, primarily because these latter prairies were substantially invaded by smooth brome. Stotz et al. (2017) described a pattern for smooth brome whereby plant species richness and biomass were more adversely affected in warmer, wetter, and more productive sites in Alberta, Canada. Other reviews describe local or regional sites invaded by Kentucky bluegrass or smooth brome, but these studies did not consider the implications of spatial–climate variation we

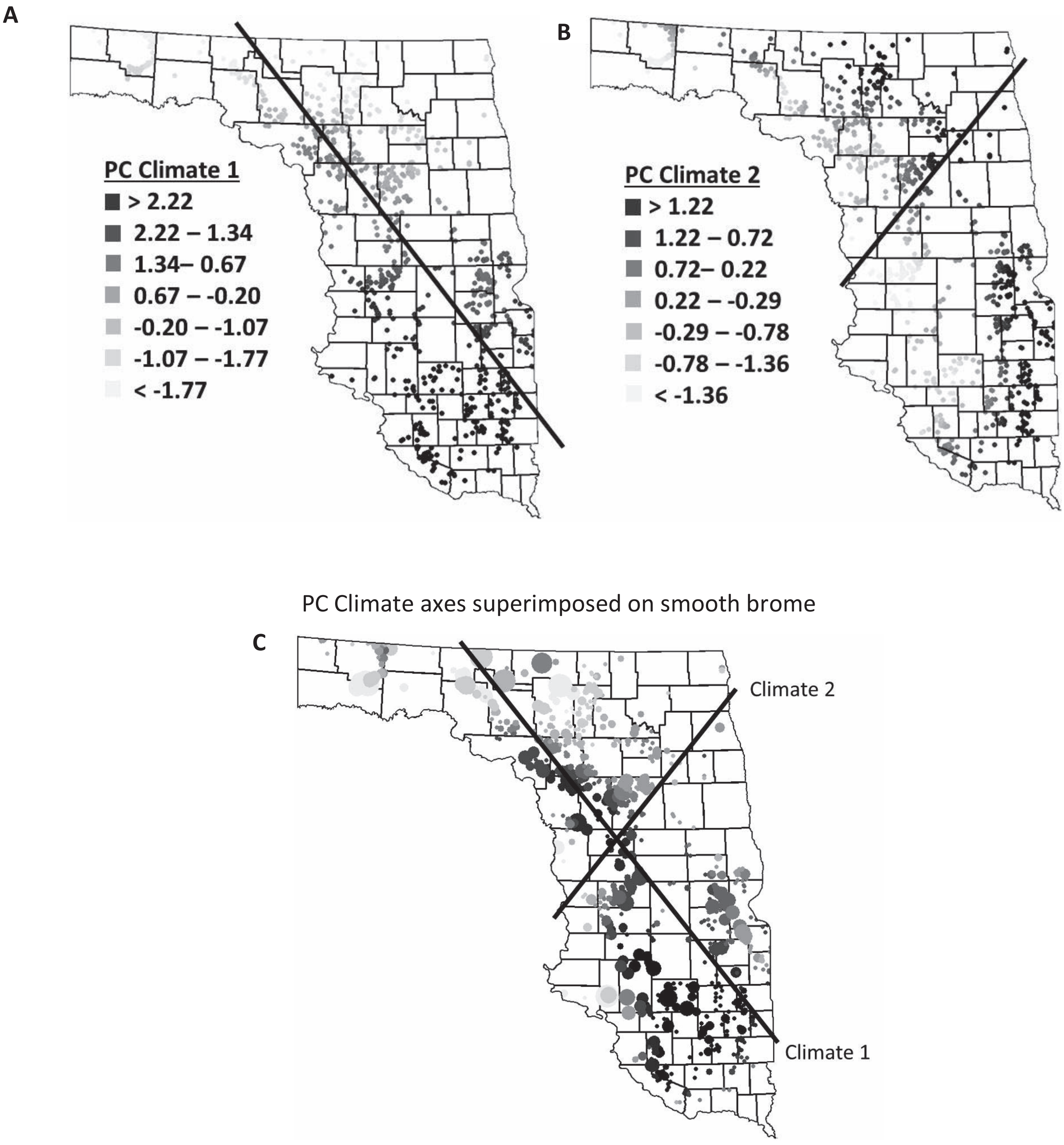

Figure 3.—Principal component axes and scores (relative values indicated by shading from light to dark) for CLIMATE1 (A) and CLIMATE2 (B), which are derived from two temperature and two precipitation metrics. CLIMATE1 represented a continuum from warmer, wetter conditions in the southeastern region to cooler, drier conditions in the northwest portion of the study area. CLIMATE2 represented a continuum from warmer and drier conditions in the southwest to cooler and wetter conditions in the northeast portion of the study area. To illustrate (C), we superimpose CLIMATE1 and CLIMATE2 axes on frequency of smooth brome derived from Figure 2. Increasingly darker shading in (C) reflects an increasing relative frequency of smooth brome occurrence. Greater smooth brome invasion was associated with relatively warmer and wetter conditions occurring for prairies located further to the south and east.

Table 2.—Comparison of quadratic response surface models derived from climate variables to those obtained with a spatial analysis of Universal Transverse Mercator (UTM) Coordinates. CLIMATE1 and CLIMATE2 are first and second principal components of two temperature and two precipitation metrics. PC1 and PC2 are first and second principal components of UTM coordinates. PC1 and CLIMATE1 represent axes that align southeast to northwest, while PC2 and CLIMATE2 represent axes that align southwest to northeast. *QIC* is the quasi-likelihood information criterion (smaller is better). R^2 is the proportion of variation in vegetation composition explained by either PC1 and PC2 or CLIMATE1 and CLIMATE2. Temperature and precipitation vary across the study area and may be causal in explaining spatial variation in vegetation composition.

	PC1 and PC2		CLIMATE1 and CLIMATE2	
Response variable	*QIC*	R^2	*QIC*	R^2
Native grass–forb	813.0	0.33	749.8	0.39
Smooth brome	896.1	0.30	901.4	0.29
Kentucky bluegrass	662.5	0.24	633.3	0.28
Low shrub	180.8	0.54	192.3	0.51

described (e.g., Toledo et al. 2014; Murphy and Grant 2005). For example, a strong east–west pattern in Kentucky bluegrass invasion is apparent from National Resources Inventory data from non-federal rangelands of the United States (USDA-NRCS 2014, figure 7). In our study, Kentucky bluegrass was the most widespread invader of Service-owned prairies, with a lower frequency of occurrence only in prairies dominated either by smooth brome in South Dakota or by native grass–forbs in northwestern North Dakota and northeastern Montana. Kentucky bluegrass may be the predominant contemporary grass species within the region, occurring on 82% and 61% of private rangeland sites sampled in North Dakota and South Dakota, respectively (USDA-NRCS 2014; DeKeyser et al. 2015). Kentucky bluegrass invasion has increased both in spatial extent and in a westward direction during the past 20–30 y, coinciding with higher precipitation recorded during the same period (Toledo et al. 2014; DeKeyser et al. 2015). In North Dakota, the length of the growing season has increased by 12 d in the past 120 y resulting in an extended period of growth in spring and fall (Badh et al. 2009). An extended growing season may disproportionately favor growth and spread of Kentucky bluegrass and smooth brome primarily because some native grass species are dormant during early spring and late fall but invaders are not, although empirical evidence for this effect is limited (DeKeyser et al. 2013, 2015).

Low shrub invasion was greater on Service-owned prairies that occur in cooler and drier locations, mainly in north-central and northwestern North Dakota. Prairies in this region occur near the southern boundary of the Aspen Parkland Ecoregion, a transition zone between grassland and woodland habitats. Low shrubs dominated >20% (observed values) of the plant community on many Service-owned prairies in north-central and northwestern North Dakota. This frequency of low shrub is greater than 1–5% coverage estimated prior to Euro-American settlement for that area (Coupland 1950, 1961; U.S. Soil Conservation Service 1975; Murphy 1993). Low shrub species (especially western snowberry) spread by rhizomes; established clonal patches can outcompete herbaceous plants for soil moisture and light (Pelton 1953; Manske 2006). Western snowberry proliferates with fire suppression or infrequent fire and may increase with grazing (Manske 2006; Hauser 2007). In our study, Kentucky bluegrass and smooth brome were far more prevalent components of the low shrub understory than were native grasses and forbs, suggesting that low shrub encroachment may facilitate subsequent bluegrass and brome invasion. Indeed, low shrub invasion appears to alter grassland soil moisture and nutrients, thereby creating conditions conducive for subsequent invasion by taller woody plants as well as Kentucky bluegrass and smooth brome (Murphy 1993; Grant and Murphy 2005; Murphy and Grant 2005; Manske 2006). Ironically, woody plant invasion is most severe within the same area where native grasses and forbs reach their highest frequency of occurrence on Service-owned prairies.

Is Long-Term Management Implicated in Prairie Degradations?

Grasslands of the northern Great Plains developed through the interactions of frequent disturbance, principally fire, grazing, and periodic drought as long-term ecological drivers (Samson et al. 2004). Our data support the contention that long-term deferment or infrequent defoliations (i.e., "rest") facilitate rapid conversion of prairies to brome- or bluegrass-dominated communities (Murphy and Grant 2005; DeKeyser et al. 2009, 2013; Grant et al. 2009; Printz and Hendrickson 2015). Our results suggests that smooth brome may be the more pervasive threat under a "rest-dominated" scenario, potentially replacing most herbaceous species over time, particularly on sites with loamy soils characteristic of much of the Dakotas (Murphy and Grant 2005; Dekeyser et al. 2009). Even short-term rest intended to increase plant vigor especially after drought, extensive grazing, or wildfire, can be problematic where brome and bluegrass are already present (Printz and Hendrickson 2015).

Kentucky bluegrass, smooth brome, and low shrubs differ in their documented responses to management, especially fire and grazing. Kentucky bluegrass is exceptionally grazing tolerant, with growing points much closer to the soil surface than most native grasses (DeKeyser et al. 2013). Summer grazing in the absence of fire can increase cover of Kentucky bluegrass (Patton et al. 2010; DeKeyser et al. 2013) and western snowberry (Pelton 1953; Manske 2006). Smooth brome may be sensitive to repeated grazing because meristematic tissues occur well above the soil surface, making plants susceptible to damage. Defoliation during smooth brome tiller elongation when root carbohydrate reserves are lowest appears most effective in reducing the plant's vigor and thus competitive ability (Willson and Stubbendieck 2000; Otfinowski et al. 2007).

During 1960–1990s, grazing by cattle was reduced or in many cases eliminated on Service-owned prairies within our study area, primarily to increase duck and upland game bird nest densities associated with increased height and density of vegetation (Naugle et al. 2000; Grant et al. 2009; Dixon et al. 2019). When grazing did occur, turnout of livestock typically was deferred until after 1 June, based on the belief that ducks and other birds may avoid nesting in prairies where cattle occur during the nest initiation period (i.e., April and May; Bowen and Kruse 1993; Kruse and Bowen 1996). On private rangelands, grazing has been similarly delayed under the concept of "range readiness" to allow cool-season grasses the opportunity to establish enough leaf surface area to replenish carbohydrate reserves and provide sufficient green growth before defoliation begins (Perryman et al. 2005; Printz and Hendrickson 2015). Smooth brome and Kentucky bluegrass are cool-season grasses that mature more quickly than all warm- and many cool-season native grass species (DeKeyser et al. 2015; Printz and Hendrickson 2015). This proclivity for early growth likely favors smooth brome and Kentucky bluegrass when grazing is delayed until after 1 June; palatability of brome and bluegrass is lower during summer relative to later-maturing native species, often resulting in overutilization of native species (Printz and Hendrickson 2015). Grazing before 1 June may be a strategy for reducing smooth brome and bluegrass, because these early-maturing species are more available and palatable than many native species during this period, although empirical data are lacking. Similarly, fire during spring–early summer tiller elongation may reduce competition by smooth brome, especially when warm-season grass species are present (Willson and Stubbendieck 2000). Because the northern mixed-grass prairie region is dominated by cool-season perennial species, timing of management (e.g., fire and grazing) to reduce cool-season invaders may have limited effectiveness (Murphy and Grant 2005; Grant et al. 2009; Toledo et al. 2014).

Historically in the northern Great Plains, fires were frequent and recurrent, e.g., 5- to 10-y return intervals for northern mixed-grass prairies (Wright and Bailey 1982; Bragg 1995). This range is corroborated by observations that fire return intervals greater than 5–6 y in the mesic mixed-grass region of North Dakota appear insufficient to control the spread of woody vegetation into Service-owned prairies (Grant and Murphy 2005; Grant et al. 2010). In our region, natural and anthropogenic fires have been suppressed for >100 y. Prescribed fires have been too infrequently applied, poorly timed (e.g., dormant season only), or applied repeatedly during the same phenological period (Grant and Murphy 2005; Printz and Hendrickson 2015; Kobiela et al. 2017). Many effects of fire on plant structure and composition are short-lived, with metrics returning to preburn conditions within 3–4 y; single or very infrequently applied fires are particularly ineffective (Higgins et al. 1989; Grant et al. 2010). Historically, fire and grazing were ecologically linked, with herbivores attracted to recently burned areas when given freedom of selection (Fuhlendorf et al. 2009; Gates et al. 2017). Contemporary fire and grazing are often decoupled as management applications, with one or several growing seasons of post-fire deferment recommended before grazing (Naugle et al. 2000). This approach may be ineffective when ecological restoration is an objective (Grant et al. 2010; Printz and Hendrickson 2015). Less fire results in excess plant litter and thus increased shading and cooling of the soil surface. These conditions may favor Kentucky bluegrass and low shrubs over native species, especially native warm-season grasses (Smith 1985; Manske 2006; Toledo et al. 2014; Printz and Hendrickson 2015). A greater frequency of ecologically linked fire and grazing may be necessary to effectively restore ecological processes that maintain grasslands, especially in cases where invasive plant species are already established (Collins and Barber 1986; Grant et al. 2010; Allred et al. 2011; Gates et al. 2017; Powell et al. 2018).

MANAGEMENT IMPLICATIONS

Native prairies of the northern Great Plains are imperiled, primarily by conversion for agriculture. However, despite 50–80 y of protection from the plow, the ecological integrity of many prairies held in public trust by the Service continues to decline, mainly because of increasing prevalence of invasive plants. Our study further demonstrated the pitfalls in managing a disturbance-dependent ecosystem as relatively static, late-successional grasslands over many decades. Furthermore, our study comprehensively captures the scope and scale of this dilemma, augmenting results from other studies that primarily document invasion at more local scales. Prairies in relatively cooler and drier northwestern North Dakota and northeastern Montana may be more resilient to invasion by smooth brome and Kentucky bluegrass but appear susceptible to invasion by woody vegetation. Prairies substantially invaded by smooth brome, Kentucky bluegrass, or woody vegetation may be extremely difficult to restore, regardless of effort expended, in part because the mechanisms of invasion are poorly understood by grassland ecologists. Because smooth brome, Kentucky bluegrass, and woody vegetation each respond differently to management (e.g., grazing and fire) as well as the timing of defoliation, the reduction in one undesirable species may inadvertently result in replacement by other invasive species rather than by desired native grass and forb species (Murphy and Grant 2005; Hendrickson and Lund 2010; Kobiela et al. 2017; Slopek and Lamb 2017).

Based on our results, the most promising long-term approach for the Service to retain at least some modicum of floristically intact native prairie on lands it manages in the northern prairie region would be to focus efforts on the restoration and maintenance of indigenous plant communities on select tracts in the cooler, drier, north and west locales. In this vein, new acquisitions (either via fee-title ownership or long-term easements) of prairies by the Service would focus on specific tracts (higher native composition) or regions (north and west) where prairies occur that are more floristically intact or more likely to be maintained long term. Alternatively, geographic variation in smooth brome and Kentucky bluegrass invasion may be a substitute for time, in the sense that invasion levels we observed in warmer and wetter locales to the southeast may have occurred decades ago; invasion into cooler and drier environments north and west may either be more recent and/or proceeding at a slower rate. This second scenario has clear implications for potential regional climate change, although speculative evaluations are beyond the scope of our paper. The geographic heterogeneity we observed would suggest that climate scenarios forecasting increasing temperatures coupled with higher precipitation may accelerate the rate of Kentucky bluegrass and smooth brome invasions into Service-owned prairies that currently are more floristically intact. Displacement/replacement of native species by smooth brome and Kentucky bluegrass in response to a changing climate requires immediate attention by the scientific community.

It remains unclear if invasion levels and patterns we observed are representative of non-Service-owned prairies in North Dakota, South Dakota, and northeastern Montana. Management of Service-owned prairies was probably similar (i.e., annual grazing and no fire) to that of privately owned prairies until the 1950s, after which they diverged. From 1960 to 1990, Service-owned prairies (as well as other natural protected areas) were mostly rested, with varying degrees of prescribed fire and grazing occurring only in recent decades. Under this "rest-dominated" scenario, we observed codominant invasions by Kentucky bluegrass, smooth brome, and in North Dakota, woody species (Murphy and Grant 2005; DeKeyser et al. 2009; Sinkins and Otfinowski 2012; this study). In northern prairies managed primarily for livestock production (e.g., privately owned pastures or other public lands where economics emphasize grazing), defoliation by cattle has been annual and often season-long, deferment is minimal, and fire is almost nonexistent. Under this scenario, Kentucky bluegrass is the primary invasive species threat (DeKeyser et al. 2013; Toledo et al. 2014; Printz and Hendrickson 2015). We propose a floristic comparison of Service-owned prairies to that of nearby private pastures (e.g., Murphy and Grant 2005) using data available from USDA-NRCS, National Rangeland Inventory, adjusted for geographic patterns identified in our study. Differences in degree of invasion and species-specific invasion patterns may offer additional insights into mechanisms of smooth brome, Kentucky bluegrass, and low shrub invasion, given the disparity in long-term management paradigms evident between Service-owned and privately owned prairies.

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