



Range size, local abundance and effect inform species descriptions at scales relevant for local conservation practice

Erin K. Espeland¹ · Zachary A. Sylvain¹

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Abstract

Understanding species abundances and distributions, especially at local to landscape scales, is critical for land managers and conservationists to prioritize management decisions and informs the effort and expense that may be required. The metrics of range size and local abundance reflect aspects of the biology and ecology of a given species, and together with its per capita (or per unit area) effects on other members of the community comprise a well-accepted theoretical paradigm describing invasive species. Although these metrics are readily calculated from vegetation monitoring data, they have not generally (and effect in particular) been applied to native species. We describe how metrics defining invasions may be more broadly applied to both native and invasive species in vegetation management, supporting their relevance to local scales of species conservation and management. We then use a sample monitoring dataset to compare range size, local abundance and effect as well as summary calculations of landscape penetration (range size \times local abundance) and impact (landscape penetration \times effect) for native and invasive species in the mixed-grass plant community of western North Dakota, USA. This paper uses these summary statistics to quantify the impact for 13 of 56 commonly encountered species, with statistical support for effects of 6 of the 13 species. Our results agree with knowledge of invasion severity and natural history of native species in the region. We contend that when managers are using invasion metrics in monitoring, extending them to common native species is biologically and ecologically informative, with little additional investment.

Keywords Competitive outcomes · Fragmentation · Invasion · Plant community conservation · Species distribution

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✉ Zachary A. Sylvain
zach.sylvain@gmail.com

¹ USDA-ARS Pest Management Research Unit, 1500 N Central Avenue, Sidney, MT 59270, USA

Introduction

Species abundances and distributions are foundations of ecology (Andrewartha and Birch 1954; Brown 1984; Krebs 1985), and the causes and consequences of local abundance and geographic range are fundamental to many principles of community ecology, including neutrality (Volkov et al. 2003), competition (Grime 1977), and invasion (Parker et al. 1999). Because local abundance and geographic range often reflect aspects of individual species biology and ecology (Espeland and Emam 2011), these indices are often used as species descriptors. For rare species (Rabinowitz 1981), geographic range and local abundance help dictate coordinated management activities, policy, and reserve creation (IUCN 2012). Characterizations of geographic range and local abundance at the species level are mostly too coarse-grained to be of use in on-site management (Pearson and Dawson 2003; Thuiller et al. 2008; Thiele et al. 2010). This is especially true for plants, in part because vegetation management within conservation units requires an understanding of how plants affect one another (Thiele et al. 2010) in addition to metrics solely describing the distributions of individual species. These effects often vary spatially (see below), therefore associated indices may be appropriately constructed at the community level (e.g. Pearson et al. 2016). In this paper, we gather support for the contention that metrics calculated from vegetation monitoring data may be used to understand and manage the community-specific interactions of native and invasive species.

Parker et al. (1999) suggest quantifying species invasion severity through (1) a species' ability to penetrate the landscape, or, its invasiveness (geographic range multiplied by local abundance: density or cover) and (2) impact (invasiveness multiplied by per capita or per unit area effects on other species, such as through competition for resources or allelopathy). The quantitative framework presented by Parker et al. (1999) to describe invasive species has become widely accepted within the discipline, cited by over 1715 publications (Google scholar search performed 15 Aug 2018). The index of invasiveness directly applies to the effort required to find and control invasive populations (as in Mehta et al. 2007). Impact offers a single index by which to rank all invasive species in a community (Parker et al. 1999; Pearson et al. 2016) and provides a quantitative approach for deciding how to spend limited conservation dollars on invasive species control. An invasive species with high invasiveness score is widespread throughout the conservation unit, but when its effect is relatively low (resulting in low impact) a budget may be better spent on a species whose impact score is driven by high effects, even if it is less widespread.

Because invasiveness and impact are informative descriptors for plant invasions, these indices may also provide insights into the importance of native plant species in the landscape (e.g. Bruno et al. 2004). Changes in the distributions of native plants and their effects on their neighbors are expected as a result of climate change, non-equilibrium dynamics, and changes in disturbance regimes (Thuiller et al. 2008; Tylianakis et al. 2008). Figure 1 shows two examples of how environmental change over space and time can increase or reduce a native species' effect on other plants. In the first example (Fig. 1a), an increase in rainfall ameliorates abiotic stress; this increase in rainfall could be due to a spatial environmental gradient or climate change. When conditions are abiotically stressful, competition is symmetrical and each plant gains resources in proportion to its size. With increased water availability, competition becomes asymmetrical, with the taller plant shading the smaller plant resulting in disproportional size differences (as in Schwinning and Weiner 1998). Less abiotic stress means the taller-statured plant has a greater effect on the smaller-statured plant. In the second example (Fig. 1b), ant granivory, or myrmecochory, drives a

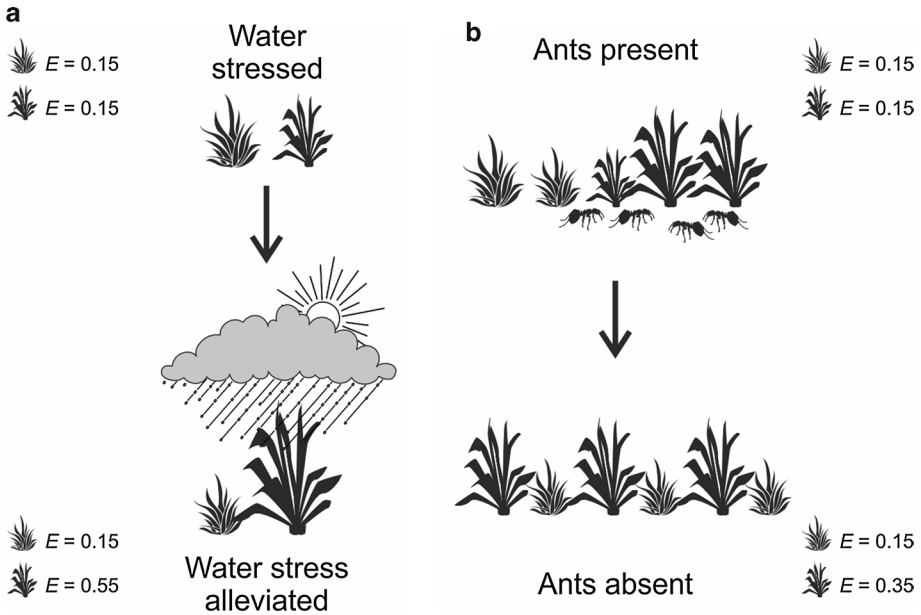


Fig. 1 Environmental change over space or time changes the symmetry of plant-plant interactions, altering the effect (E) of native species on one another. Examples include **a** abiotic stress (e.g., water limitation) driving symmetrical competition, which transitions to asymmetrical competition when water stress is alleviated; or **b** ant granivory (or myrmecochory) driving a clumped distribution of a particular plant species, resulting in a reduced effect of that species on its neighbors as compared to a greater effect observed when no granivory is present

clumped distribution in species A, so its effect on other species is small (as in Pringle and Tarnita 2017). When ants are not present, the distribution of species A becomes more even and the species has greater effect on other natives. Indices of invasiveness and impact may therefore be used in a comparative way to parse shifts in any species' dominance across space and time, separating effects on neighboring plants from changes in distribution.

A species' effect on its neighbors can be calculated from per capita or per unit area observations. While per capita and per unit area effects are not interchangeable (Saint-Germain et al. 2007; Morlon et al. 2009), they are often substituted for one another in vegetation research (Parker et al. 1999), particularly in systems dominated by perennial and/or clonal species where it may be difficult to tell individuals apart (Bullock 2006). As indicated by Fig. 1, plant size (cover or biomass) at the end of the growing season is a product of many factors, including intrinsic size of the species, nutrient acquisition, phenology, predation, and resource competition (e.g. Trinder et al. 2013). Therefore, per capita or per unit area effects of species will change in response to changing ecosystem processes (including competition) that drive community composition. Hierarchical sampling (e.g., sample units nested within blocks) enables a mixed-effects statistical approach that allows the inclusion of random factors (such as site or blocking effects) when calculating a species' effect metric score, accounting for abiotic differences among locations or non-equilibrium conditions in focal populations (Pearson et al. 2016). Using hierarchical sampling and calculating a species' effect on other plants overcomes the lack of ecological sophistication from which species distribution models often suffer (e.g. Austin 2007; Pearson and Dawson 2003).

When land managers and conservationists monitor and describe invasions using metrics of invasiveness and impact (Parker et al. 1999; Pearson et al. 2016), concurrently collected data on native species may also be useful, as the abundance, range or effect of a native species on other members of the community may change as environmental conditions shift. Changes in any of these three metrics can influence the overall impact of a given species, which can have important management implications. For example, under current conditions a common (high range and abundance) native plant may have a low effect (and hence low impact) on other plants, while a rarer (low range and abundance) plant may have greater effect on its neighbors (but a low overall impact; Fig. 2a). High effect coupled with relative rarity may be a consequence of natural selection (see Rabenowitz 1981) or of restrictions imposed by environmental conditions. In this latter case, it is possible that changes to environmental conditions could relax the limits to a species' range and/or abundance, as is the case with shrub encroachment into grasslands (e.g., Van Aucken 2000; Briggs et al. 2002). These changes to a species' abundance and range can in turn influence soil properties (e.g., C, N and pH) and grass cover (and consequently forage availability on rangelands; Eldridge et al. 2011). Invasion can also influence the range and abundance of native plants (Fig. 2b), which can reduce their impact within the community and disrupt the dynamics of ecosystems. To illustrate the utility of these metrics for management, we use an observational dataset collected from 1196 plots on 120 transects across 40 undisturbed sites that span a management unit (approximately 400,000 hectares) of mixed grass prairie in western North Dakota, USA. These sites were measured in 2015 to form a baseline dataset from which to assess changes in plant communities via increasing fragmentation (e.g. Saunders et al. 1991; Ewers and Didham 2006) and other forms of disturbance due to energy development in the region. Because it is somewhat confusing to refer to the “invasiveness” of a native species, we use the functionally equivalent term “landscape penetration” for clarity, to reflect that the metric represents a species' ability to increase in abundance across the landscape. We consider results of (1) impacts of invasive

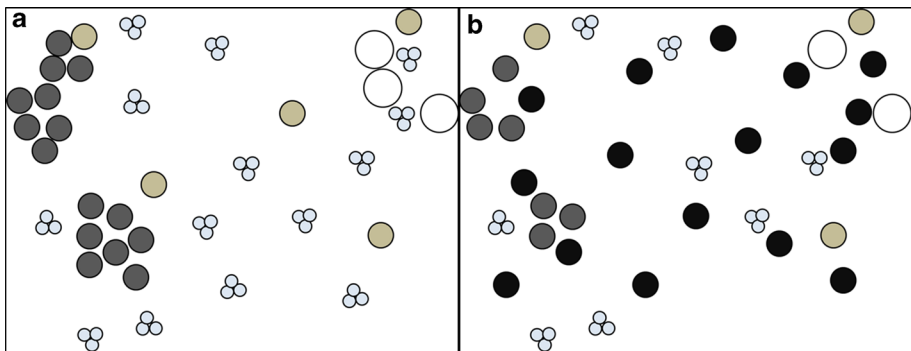


Fig. 2 Conceptual diagram depicting metrics of abundance (A), range (R), and effect (E) for a community of **a** native plants alone and **b** the same community invaded by an exotic plant. Abundance of each plant species is depicted by numbers of adjacent circles (each circle of similar size and color represents an individual species), range of each plant species is depicted by the distribution within each panel (i.e., plants with higher ranges are located more broadly across the panel) and the effect size of each species is depicted by the area of each circle. Small, light colored circles represent *Bouteloua gracilis* (high A, high R, low E); medium, dark grey circles represent *Schizachyrium scoparium* (high A, low R, moderate E); medium, light colored circles represent *Pascopyrum smithii* (low A, high R, moderate E); large, open circles represent *Nasella viridula* (low A, low R, high E); medium, black circles represent *Poa pratensis* (moderate A, high R, moderate E)

species greater than native species, and (2) landscape penetration and impact of native species reflecting what we know about their natural history as support of the concept.

Methods

Sampling was conducted on undisturbed public lands within the northern half of the Little Missouri National Grassland (between 47°N and 47°42'N and 103°15'W and 104°W), a wheatgrass-needlegrass mixed-grass prairie (Barker and Whitman 1988) in western North Dakota. We identified forty 0.75 km² sites on public land using ArcGIS (v. 10.2.1, ESRI, Redlands, California, USA) to create map layers buffered from the locations of oil wells and pipelines (active, inactive and reclaimed, obtained from the website of the North Dakota Industrial Commission Oil and Gas Division) by 1.5 km, with 200 m buffers around other infrastructure (e.g. gravel roads, fences and power transmission lines) and tilled lands (obtained from a US Forest Service shapefile of Little Missouri National Grassland broken lands). We included a soil layer based on the USDA NRCS SSURGO database (Soil Survey Staff 2015) to ensure replication within six soil associations common throughout the sampling region: Sen-Cabba-Brandenburg, Rhoades-Cabba-Amor, Golva-Chama-Cabba, Rhoades-Moreau-Belfield, Fleak-cherry-Cabbart-Badland, and Cherry-Cabbart-Badland. We imported map layers into Google Earth Pro (v. 7.1.4.1529, Google Inc., Mountain View, California, USA), selecting sites separated from each other by a minimum distance of 1.5 km and possessing < 15% slope. We chose sites where cattle tanks, cattle tracks and prairie dog towns visible in Google Earth were absent. Ungulate grazers were not excluded.

We sampled between 13 July and 11 September 2015. At each site, we established three parallel 150 m transects separated by 200 m. Plant cover was determined using 0.1 m² Daubenmire frames (or, plots) placed every 15 m along the transect totaling 10 plots per transect (one transect was shortened to 6 plots due to rapid expansion of a nearby prairie dog town into the sampling area), resulting in 30 plots per site and 1196 total plots. We recorded species cover in plots via the intercept method: identifying and tallying plants at 12 sample points along each frame including the four corners and 8 points along the frame sides. We identified vascular plants to species using Johnson and Larson (2007), Larson and Johnson (2007) and Stubbendieck et al. (1997). We ascertained name changes, native status, and life history group (Table 1) with the USDA-NRCS PLANTS database.

Each species present in > 1% of plots was considered a focal species when subject to independent analysis. We calculated geographic range, R , as the total area of sampling plots in which each species occurred and the local abundance, A , of each species as the average cover in plots where it was found: the number of frame intercepts (noted above) divided by 12 (the total possible number of intercept points). We estimated E , the effect per unit cover of each focal species on native plant species cover, using a linear mixed effects model approach in R v.3.2.4 (R core development team 2016) with the 'lme4' package (Bates et al. 2015). We use % cover as our response variable because it integrates plant abundance and plant size into a single metric that helps to standardize differences between species (Thiele et al. 2010; Pearson et al. 2016). We calculated associated F-statistics (using the Kenward-Roger approximation) and P-values with the 'lmerTest' package (Kuznetsova et al. 2016). For the non-native species models, we used total percent cover of native plants as the response variable, with percent cover of focal non-native species and total percent cover of all non-focal non-native species as fixed effects to account for additive effects from multiple invasive species. For native species models we used the total

Table 1 Penetration, impact, and effect scores for the most commonly sampled monocots, in order of penetration score

Plant species	R	A	Penetration	Impact	R'	Penetration'	Impact'	E	F	df	P
<i>B. gracilis</i>	39.2	22	862.4	77.6	32.9	723.8	65.1	-0.09	10.27	11, 173.90	0.0014
<i>P. pratensis</i>	30.3	14.7	445.4	178.1	25.3	371.9	148.8	-0.4	39.09	11, 189.20	<0.0001
<i>C. filifolia</i>	19.7	15.3	301.4	66.3	16.5	252.5	55.5	-0.22	9.25	11, 192.90	0.0024
<i>P. smithii</i>	22.9	11	251.9	60.5	19.1	210.1	50.4	-0.24	5.48	11, 173.20	0.019
<i>S. scoparium</i>	7.9	21.8	172.2	68.9	6.6	143.9	57.6	-0.4	28.18	11, 126.50	<0.0001
<i>H. comata</i>	13.4	11.2	150.1	49.5	11.2	125.4	41.4	-0.33	6.38	11, 166.90	0.012
<i>A. purpurea</i>	3.9	13.7	53.4	-	3.3	45.2	-	-0.22	2.04	11, 151	0.15
<i>A. cristatum</i>	4.5	11.5	51.8	-	3.8	43.7	-	-0.38	3.27	11, 177.40	0.07
<i>N. viridula</i>	5	9.3	46.5	37.2	4.2	39.1	31.2	-0.8	9.69	11, 151.40	0.002
<i>B. curtipendula</i>	2.2	19.7	43.3	-	1.8	35.5	-	-0.21	1.74	11, 159	0.19
<i>D. spicata</i>	2.6	13.1	34.1	-	2.2	28.8	-	-0.19	0.98	11, 148.80	0.32
<i>K. macrantha</i>	1.7	10.3	17.5	-	1.8	18.5	-	-0.1	0.087	11, 133.80	0.77
<i>M. cuspidata</i>	1.3	11.5	14.9	-	1.1	12.7	-	-0.64	3.18	11, 154.30	0.07

R = total area of plots where the species occurred, A = per plot cover, penetration score = $R \times A$, E = per unit area effect of species on other (native) species, impact score = $R \times A \times |E|$, R' represents the standardized range (percentage of sampling plots occupied); Penetration' and Impact' represent values calculated using R'. Non-native species are in bold. Note degrees of freedom for the F test statistic are calculated using the Kenward-Roger approximation. Impact and impact' are not reported when E is non-significant

percent cover of non-focal native plants per plot as the response variable, and percent cover of the focal species as a fixed effect to test the effects of individual species on other native species within the community. Models included transect nested within site as random effects. Following Pearson et al. (2016) we tested additional mixed models for effects of non-native species including an interaction term between cover of the focal non-native species and cover of all non-focal non-native species combined (to test for possible synergistic effects such as invasional meltdown) or a second-order polynomial term for focal non-native species cover to test for potential non-linear relationships; the simplest base model was selected following AIC comparisons. Once an appropriate model was selected, E was determined as the slope parameter estimate from the model output. When no significant relationship was found between cover of a focal species and its effect on the cover of native plants, E was considered to be equivalent to 0 and no impact score was calculated.

We determined landscape penetration (invasiveness in Pearson et al. 2016) as $R \times A$ and impact as $R \times A \times E$. To standardize R and to compare our results to other sampling efforts, we also calculated R' as the percentage of plots where a species occurred. Standardizing R in this manner helps to control for sampling artifacts arising from different sampling effort to area ratios and facilitates comparisons between studies differing in sampling effort. To determine how penetration reflects abundance at the four scales we measured, we checked for correlations among R , A , and transect and site occurrence using Pearson's correlation coefficient in the base R package (R core development team 2016). We used R' in place of R to calculate standardized landscape penetration' and impact'. We found no substantial deviations from normality when testing model residuals using Q–Q plots and the Shapiro–Wilk test.

Results

We recorded 56 plant species, of which eight were non-native and none were short-lived annuals (see Table S1.1). Monocots had different patterns in the landscape than dicots (Fig. 3), with monocots found in more plots (Fig. 3a) and with higher cover (Fig. 3b). Because dicots tended to be rare, we focused further analyses on common monocot species.

For common monocots (present in >1% of plots), abundance was highly correlated across the landscape: presence in plots was correlated with presence across

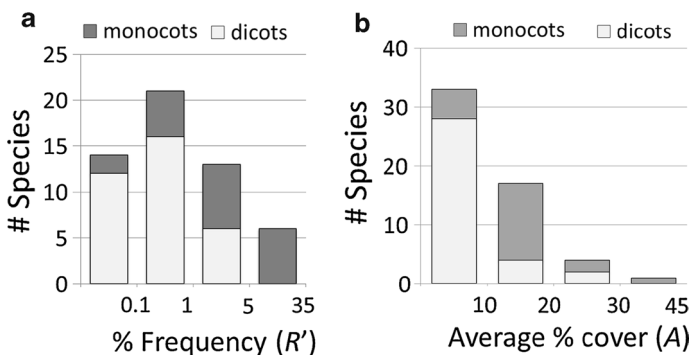


Fig. 3 Distribution patterns of monocot and dicot species: **a** number of species present in plot percentages (frequency classes), **b** number of species in cover classes

transects ($r=0.97$, $t_{17}=16.45$, $p<0.0001$) and across sites (or, range size, $r=0.9$, $t_{17}=8.66$, $p<0.0001$). However, these presence measures were poorly correlated with percent cover inside plots (or, local abundance, $r=0.32$ and $r=0.31$, respectively, neither significant). Table 1 shows R (geographic range), R' (standardized geographic range), and A (local abundance). Variance across soil associations was low: all common monocot species were present in at least five of the six soil associations, except *Agropyron cristatum* (three soil associations).

Values of R , R' , A , and E (effect on native plant neighbors) were comparable between common native and non-native monocots (Table 1). Penetration for *Poa pratensis* (445.4) was large, but not the largest we observed. However, impact of *P. pratensis* at 148.8 was over twice that of the next most impactful species (*Bouteloua gracilis* at 65.1). Otherwise, the rank of impact of each common grass species largely matched its penetration rank, except for *Nassella viridula*, which had relatively large effect (E), and *Schizachyrium scoparium*, which had large local abundance (A). As would be expected, standardizing scores had no effect on species ranks.

Discussion

Monitoring data are used to calculate metrics such as range size, abundance and the effect of a species on other members of an ecological community and incorporated into summary metrics of invasiveness and impact. This approach is commonly used for invasive species, but has not been applied more broadly to describe native species. We compared how well these metrics described both invasive and native species, finding that the resulting metrics for native plants were comparable to those for invasives and reflected what we know of the biology and ecology of native plant species. The most common native plant in our study, *Bouteloua gracilis* had nearly twice the penetration score but less than half the impact of the most common invasive (*Poa pratensis*), highlighting the threat this species poses to native rangeland communities. Applying these metrics to native plants also showed that *Nasella viridula* had an outsized impact on other native plants relative to its penetration throughout the landscape, illustrating the utility these metrics provide for understanding native plant dynamics. Given that altered disturbance regimes or climate change can influence native species dynamics, such metrics can benefit land management or conservation decisions by providing additional insight into plant community dynamics using existing data. Our results support the utility of extending this approach to native plants, given the availability of monitoring data.

We found that one invasive species, *P. pratensis*, had the greatest impact, which was multiple times greater than that of any native species. Similar to work in other grasslands, the majority of species we recorded were infrequent with very low cover, and these species were largely dicotyledonous (e.g. Eriksson and Jakobsson 1998). We were not able to calculate impact for six of the eleven native grass species because E was not statistically significant. Therefore, impact measurements are only applicable to the most common species in communities.

Per unit area effects of *A. cristatum* and *P. pratensis* on other species are similar to those of common native perennial grass species in this landscape. An E of -0.40 for *P. pratensis* in western North Dakota (this paper) means this species has less effect in western North Dakota than in west-central Montana ($E=-0.64$, Pearson et al. 2016). Although the effect of *P. pratensis* reported by Pearson and others is high, the impact' they report

(36.9) is quite low compared to the impact we measured in North Dakota (148.8). In effect (E) or local abundance (A), *P. pratensis* did not appear to differ substantially from native perennial grass species. Greenhouse studies support the finding that *P. pratensis* does not have larger competitive effects than native cool season grasses (Ulrich and Perkins 2014). DeKeyser et al. (2015) report *P. pratensis* frequency in private rangelands of North Dakota at 82%. We found the species in only 25% of our plots, but it occurred in 74% of transects and 95% of sites. Even though site- and transect- level data were not part of impact calculation, site, plot, and transect occurrence were highly correlated. Our data show that *P. pratensis* exhibits high landscape penetration and impact. It is not known if the *P. pratensis* invasion has reached its maximal extent in this landscape: assessing landscape penetration over time will determine if the species is still spreading. The importance of this invasion to plant community dynamics in the Little Missouri National Grasslands is supported by its high impact score and by other work (DeKeyser et al. 2015; Preston 2015; Toledo et al. 2014).

Although *A. cristatum* is sometimes invasive (Williams et al. 2017), it has relatively poor landscape penetration across our sites. Non-native grasses *Poa compressa* and *Bromus inermis* also had poor landscape penetration; this together with a negligible abundance of the noxious weed *Euphorbia esula* (Table 1) indicates that these intact lands are relatively uninvaded.

Penetration and impact for native species generally aligns with abundance at regional scales (R), but not at local scales (A). A notable exception is *S. scoparium*, whose large local abundance (A) gives it a greater impact score than the more regionally common species *Pascopyrum smithii* and *Carex filifolia*. High cover but low effect for *S. scoparium* aligns with our qualitative observation that it tends to occur in monospecific stands. Another exception where penetration and impact ranks are mismatched is *N. viridula*, whose large effect (E) places it just below the impact of the far more common species *Hesperostipa comata*. Our somewhat low penetration score supports the literature that states that *N. viridula* is a minor component of the mixed grass prairie (NRCS 2005), however the high effect size may partly explain why *N. viridula* often performs very well in restoration plantings (Rinella et al. 2016) and suggests that this species may be seed- or dispersal-limited. Our results indicate that penetration and impact ranks can reflect native species' importance in determining (or reflecting) plant community dynamics.

We expect that increasing landscape fragmentation in these grasslands will alter resident species distributions and may introduce new species. In the future, we should be able to use the metrics of penetration, effect, and impact for the species listed in Table 1 to detect modifications in ecosystem function that significantly alter plant–plant relationships and to observe changes in species' ability to colonize the landscape. We will be able to monitor the *P. pratensis* and *A. cristatum* invasions and determine if the invasion is increasing in scope (penetration) or severity (impact) over time. With further surveys in other plant community types in the region, we may be able to determine if different invasion management strategies might be appropriate in different locations (as in Thiele et al. 2010; Gomola et al. 2017) that would be indicated by diverging impact values. While we are unable to provide an empirical test of how these metrics reflect change over time, we have some support for the utility of these summary statistics created from a baseline monitoring dataset.

Because of the support for invasion metrics of penetration and impact and their strongly quantitative nature, we suggest that they be used to describe species distributions for common native plants as well. Dominant native species are used to define vegetation types (e.g. Egler 1954; Daubenmire 1966; NRCS 2005), and using observational techniques coupled with metrics of landscape penetration and impact to define species roles within the

community could greatly increase our power to detect species responses to landscape-level change (Fig. 1), in turn informing management and conservation activities. Ranking invasive species penetration and impact is a supportive decision making tool to prioritize invasive species control efforts. Ranks of species penetration and impact, informed by the constituent metrics of abundance and effect, may adequately reflect the roles of common native plant species within communities. We contend that when managers are already using invasion metrics in vegetation monitoring, calculating these metrics for common native species is biologically and ecologically informative, with very little additional investment.

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Data Availability We intend to archive our data on the Ag Data Commons repository operated by the United States Department of Agriculture National Agricultural Library (<https://data.nal.usda.gov>).

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