

Biotic homogenization within and across eight widely distributed grasslands following invasion by *Bromus inermis*

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Abstract. Invasive species can alter the structure and function of the communities they invade, as well as lead to biotic homogenization across their invasive range, thus affecting large-scale diversity patterns. The mechanisms by which invasive species can lead to biotic homogenization are poorly understood. We argue that invasive species acting as strong, deterministic, and consistent filters within and across invaded communities are likely to cause biotic homogenization at multiple spatial scales. We studied *Bromus inermis* Leys. invasion into eight grasslands covering most of the grassland and parkland natural regions of Alberta (western Canada). Specifically, we tested whether *B. inermis* (1) has a strong impact on species richness and composition, (2) consistently alters resources (nutrients, light, and soil moisture), imposing the same ecological filter to species establishment and persistence across sites, and hence (3) whether it leads to biotic homogenization within and across sites. We recorded plant cover and resources across native-to-invaded transition areas combining space-for-time substitutions with time-series data analyses. *Bromus inermis* invasion was associated with rapid biotic homogenization of communities, within and among the eight grasslands. The sharp changes in species relative abundances following invasion was the initial driver of biotic homogenization, and species loss was delayed. Supporting the idea that biotic homogenization can occur when an invasive species presents a broad and consistent filter, resources modified by *B. inermis* invasion (particularly light and certain nutrients) were altered rather consistently within and across sites. The 50% reduction in light was likely the initial driver of biotic homogenization, and the increase in nutrient availability probably facilitates the displacement of species from the invaded areas and could lead to the establishment of self-reinforcing dynamics. Overall, our results support the idea that invaders acting as strong, deterministic, and consistent ecological filters are likely to cause biotic homogenization of the communities they invade.

Key words: beta diversity; biodiversity loss; biotic homogenization; invasion; light competition; nutrient availability; passenger-driver; smooth brome; species filtering; species turnover.

INTRODUCTION

Invasive plant species can alter community structure and function where they invade (Vilà et al. 2011). The impact of invasive species on diversity is, at least initially, only evident within invaded areas. However, local impacts can have important implications at broader scales (Gilbert and Levine 2013). Biotic taxonomic homogenization (hereafter biotic homogenization) is the increase in taxonomic similarity across habitats or regions (i.e., lower species turnover), generally associated with the loss of rare species and persistence and/or

spread of shared species (Olden and Poff 2003, Olden 2006, Smart et al. 2006). Biotic homogenization can also result in functional homogenization if only species with similar functional characteristics are able to persist across communities (Smart et al. 2006). Fragmentation and land-use change are known drivers of biotic homogenization (Lôbo et al. 2011, Arroyo-Rodríguez et al. 2013). Yet, whether invasive species can lead to the biotic homogenization of communities within and across invaded sites, and how, remains poorly studied (but see Qian and Ricklefs 2006, Price et al. 2017). We argue that invasive species that act as strong, deterministic, and consistent filters to species persistence and establishment, both within and across the communities they invade, are likely to cause biotic homogenization (Fig. 1). Understanding whether and how invasive plant species can homogenize communities is crucial, as biotic

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homogenization can lead to functional homogenization, increased species extinction risk, reduced ecosystem function, and decreased ecosystem resilience (Olden et al. 2004, Socolar et al. 2016, Hautier et al. 2018).

Biotic homogenization should occur when there are strong, deterministic ecological filters shaping species composition (Inouye and Tilman 1995, Chase 2003, 2007; Fig. 1). Filter strength can be estimated from the number of species excluded or the change in species composition. If the filter is weak (i.e., many species are able to overcome it), there is a larger species pool from which to draw species and assemble local communities. Consequently, different species combinations are possible and communities may remain distinct (Chase 2003, 2007). Invasive species generally act as strong filters, competitively excluding over half of the resident species from the communities they invade (Vilà et al. 2011, Stotz et al. 2017). However, biotic homogenization can also ensue from initial changes in species relative abundances, prior to species loss, and/or due to species replacements (Olden and Rooney 2006; Fig. 1). Independent of whether species are being excluded or replaced, strong ecological filters will only result in biotic homogenization if species filtering is deterministic, i.e., associated with species characteristics, thus leading to the exclusion of particular species (Chase 2007; Fig. 1). For example, invaders that alter vegetation structure and reduce light availability may exclude shade-intolerant species (Bennett et al. 2014, Molinari and D'Antonio 2014), likely resulting in biotic homogenization because only shade-tolerant species would persist in the invaded areas. If species are not excluded deterministically but at random (stochastic filter),

communities are more likely to remain distinct (Chase 2007).

The impact of invasive species on community structure may vary across sites not only in its strength (Vilà et al. 2006, Latzka et al. 2016), but also in terms of the mechanisms behind the species impact, depending on local conditions (Ehrenfeld 2003, Lankau et al. 2009). For example, the invader *Bromus tectorum* increases or decreases soil nitrogen availability depending on the ecosystem it invades (Ehrenfeld 2003), potentially filtering out different species across sites. Biotic homogenization is unlikely to occur when the ecological filter imposed on resident species is not consistent, varying in type and/or strength within and across sites (Tuomisto et al. 2003, Freestone and Inouye 2006; Fig. 1). On the other hand, invaders that modify conditions and/or resources consistently both within and across sites are likely to lead to biotic homogenization (Fig. 1). To our knowledge, it has not been shown whether a consistent impact of invasive species on resource availability is associated with biotic homogenization of previously distinct communities. Identifying the mechanisms behind biotic homogenization can help predict which species are more likely to be excluded, and the consequent loss of taxonomic and functional distinctiveness between communities (Keddy 1992, Olden et al. 2004).

In this study, we evaluated whether invasion by *Bromus inermis* Leys can lead to the biotic homogenization of communities within and across eight grasslands covering most of the grassland and parkland natural regions of Alberta, Canada (Appendix S1: Fig. S1). To this end, within each of the eight sites, we compared invaded, recently invaded, and uninvaded areas within 4-m

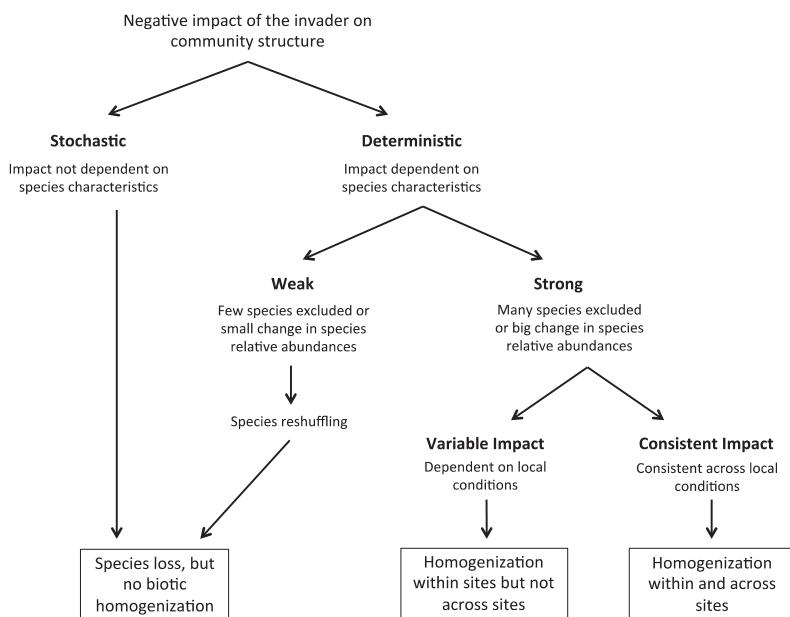


FIG. 1. Theoretical framework of the conditions under which invasive species are more likely to result in the biotic homogenization of communities, within and across sites.

transects, and tested for changes in community characteristics in areas that became invaded within the time frame of this study. *B. inermis* invasion has a negative impact on species richness (Mamet et al. 2017, Stotz et al. 2017), and this impact can be deterministic, with *B. inermis* more strongly suppressing shade-intolerant species (Bennett et al. 2014; Fig. 1). The latter study was performed only in one site (Bennett et al. 2014), so it remains to be tested whether the impact of *B. inermis* is strong and consistent within and across sites, and can, therefore, lead to biotic homogenization (Fig. 1). Furthermore, *B. inermis* tends to decrease light and soil moisture, and increase nutrient availability where it invades (Fink and Wilson 2011, Bennett et al. 2014, Piper et al. 2015a). Yet, again, whether *B. inermis* consistently alters these below- and aboveground resources within and across sites remains unknown. Here we test whether *B. inermis* invasion (1) has a strong impact on species richness and/or composition, (2) consistently alters below- and aboveground resources as it invades, and hence (3) whether it can lead to the biotic homogenization of communities within and across sites (Fig. 1).

METHODS

Study system

Many *Bromus* species are highly invasive, able to alter the structure and function of communities and ecosystems in North America (e.g., *Bromus tectorum*, *Bromus diandrus*; Brooks et al. 2016). *B. inermis* is a perennial grass intentionally introduced from Europe into North America as a forage crop in the late 1800s (Otfinowski et al. 2007). *B. inermis* is still being actively bred and planted across North America (Alderson et al. 1994, Coulman 2006, Otfinowski et al. 2007). *B. inermis* has escaped planted areas, invading natural and undisturbed grasslands (Grace et al. 2000, Otfinowski et al. 2007, Carrigy et al. 2016, Stotz et al. 2017). It is currently invading all Canadian provinces and most of the United States (Grace et al. 2000, Otfinowski et al. 2007, Ellis-Felege et al. 2013), and it continues to spread (Sinkins and Otfinowski 2012, Ellis-Felege et al. 2013). *B. inermis* establishes in grasslands, forest edges, and forest clearings, where it decreases species richness and suppresses forest regrowth or encroachment (Otfinowski et al. 2007). The introduction of multiple cultivars able to grow quickly and in high density under different environmental conditions (Cook 1943, Alderson et al. 1994) likely makes this species a successful invader across different sites (Jakubowski et al. 2011, Stotz et al. 2017). Where it establishes, *B. inermis* forms dense patches with a sharp edge, with its cover dropping from 60% to zero in less than a meter (Bennett et al. 2014). *B. inermis* disperses through seeds and through the vegetative growth of rhizomes, which is key to its invasiveness, increasing the density of patches and facilitating its expansion into adjacent uninvaded areas (Otfinowski et al. 2007, Otfinowski and Kenkel 2008).

This study took place in eight grassland sites distributed across the province of Alberta, Canada (Appendix S1: Fig. S1). These eight sites cover an area of about 170,000 km² and were chosen to be distributed throughout most of the grassland area of Alberta, where *B. inermis* is a serious invader (Otfinowski et al. 2007, Stotz et al. 2017). From south to north, the sites are: Police-Outpost provincial park (PP), Writing-on-Stone PP, the University of Alberta Mattheis ranch, Dry Island Buffalo Jump PP, Big Knife PP, the University of Alberta Roy Berg Kinsella ranch, Kleskun Hill Natural Area, and Saskatoon Island PP (see Stotz et al. 2017 for more information).

Sampling design

Within each of the eight sites we compared invaded, recently invaded, and uninvaded areas at small spatial scales (within 4-m transects) and over a relatively short time scale (from 2013 to 2014/2015; Fig. 2). Because *B. inermis* continuously and rapidly encroaches into adjacent uninvaded areas (Otfinowski and Kenkel 2008, Bennett et al. 2014) we were able to sample areas after 1 and 2 yr of invasion (Fig. 2) and quantify the immediate change in conditions following *B. inermis* invasion.

In 2013 we set up 15–20 transects per site, for a total of 133 transects across all sites. Each transect was 4 m long, running perpendicular to the invasion edge, starting 2 m into the *B. inermis* patch and ending 2 m into the native-dominated areas (Fig. 2a). The residence time of the invader in each site is unknown. We attempted to minimize the effect of possible differences in residence time among the sampled areas by standardizing the distance into the patch. Within each transect, we focused on four positions (Fig. 2): the area furthest into the *B. inermis* patch (invaded areas; Position 1: 0–50 cm), the area at the inner edge of the invasion front (recently invaded areas; Position 2: 150–200 cm), the area at the outer edge of the invasion front (uninvaded in 2013, became invaded by 2014/2015; Position 3: 200–250 cm), and the area farthest away from the *B. inermis* patch (uninvaded areas; Position 4: 350–400 cm). As *B. inermis* encroached from 2013 to 2014/2015 into the adjacent native-dominated areas, the area at the outer edge of the invasion front (Position 3) became invaded (Fig. 2). The percentage of bare ground in areas that became invaded from 2013 to 2015 (Position 3) was low (2% on average). Therefore, it is highly unlikely that *B. inermis* is establishing in open spaces: most likely it is displacing other species from the invaded areas. Transects where *B. inermis* invaded Position 3 (>5% *B. inermis* cover) prior to the initial sampling were removed from the analyses. Transects in which *B. inermis* invaded Position 4 by 2015 were also removed from the analyses because of a lack of an uninvaded area against which to compare the changes observed in *B. inermis*-invaded and recently invaded areas. This resulted in a total of 94 transects, with 8–14 transects per site. Initial differences in *B. inermis* cover among positions, and how it changed from 2013 to 2014 and 2015, was tested

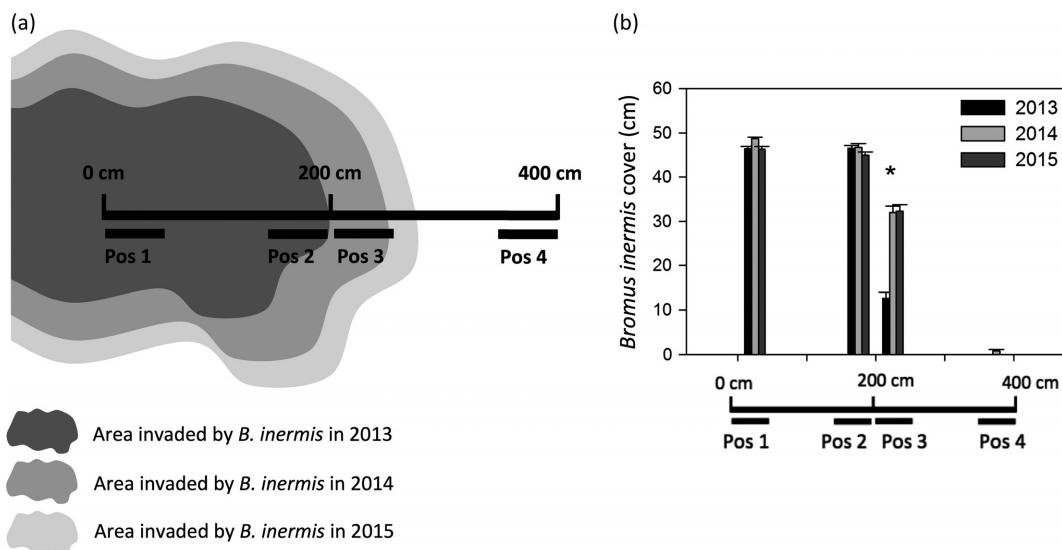


FIG. 2. Sampling design. (a) Transects were designed to encompass the transition between *Bromus inermis*-invaded areas (gray areas) to native-dominated areas (in white). Transects were divided into four areas of interest, which we refer to as positions (or Pos, in the diagram (a)): Position 1 is the area furthest inside *B. inermis* patches (invaded areas), Position 2 is the area at the inner edge of the invasional front (recently invaded areas), Position 3 is the area at the outer edge of the invasional front (areas invaded from 2013 to 2014 and 2015), and Position 4 is the area outside the smooth brome patch (uninvaded areas). (b) *B. inermis* cover across positions in 2013, 2014, and 2015. Position 3 became invaded by smooth brome between 2013 and 2014 and 2015, as evidenced by a significant increase in *B. inermis* cover.

using linear mixed models, with transect within site as a random factor.

Community structure and resource availability

In each position, we used the line-intercept method to assess species richness and estimate abundance of all species present in 2013 and 2015. Cover of *B. inermis* was also monitored in 2014. The line-intercept method was specifically designed to quantify changes in cover over time and has been found to be an efficient method in grassland communities (Mueller-Dombois and Ellenberg 1974, Caratti 2006). Species were identified at every 1 cm in each position (50 cm per position). Abundance was estimated as the added number of centimeters at which each species was found at each position along the transect.

The availability of nutrients (ammonium, nitrate, calcium, magnesium, potassium, phosphorus, iron, manganese, copper, zinc, boron, sulphur, lead, aluminum, and cadmium) was measured using Plant Root Simulator probes (PRSTM, Western Ag Innovation, Saskatoon, Saskatchewan, Canada), which are ion-exchange resin membranes. Nutrient availability was measured in 2013 and 2014 (nutrient data are not available for 2015) in a subset of transects (10 transects per site) at three sites (Mattheis [Mat], Roy Berg Kinsella University of Alberta research station [Kin], and Dry Island Buffalo Jump PP [DI]) because of the limited availability of nutrient probes. These three sites span the grassland and parkland Natural Regions of Alberta (Appendix S1: Fig. S1). Transects in these three sites were set up in

May 2013 to allow resins to absorb nutrients for 2 months. In both 2013 and 2014, PRSTM probes were set up at the end of May and retrieved at the end of July.

Light transmission was estimated by measuring photosynthetically active radiation (PAR) above and below the canopy with a linear PAR sensor (Decagon Devices Inc., Pullman, Washington, USA) and calculated as the proportion of light above the canopy able to penetrate below the canopy. Measures were taken in June and July within ~2.5 h of solar noon on clear, sunny days, in all sites, transects, and positions.

Soil moisture was measured using ECH2O EC-TM moisture and temperature sensors, attached to Em50 ECH2O Loggers (Decagon Devices). Sensors were installed in each position (10 cm deep) and set to record every 2 h. Measures were taken from 1 June through 10 July in 2013 and 2015. Soil moisture was measured in six to nine transects per site, in the same three sites where nutrient availability was measured (see above).

Changes in species richness and composition following *B. inermis* invasion

To test whether biotic homogenization is driven by species loss, we (1) evaluated differences in species richness among positions, and (2) evaluated differences in the number of species lost and gained from 2013 to 2015, among positions. Differences between positions were tested using linear mixed models with position as a fixed effect and transect within site as a random factor, using the *lme* function in the *nlme* package in R (Pinheiro et al.

2016). Pairwise differences between positions were evaluated through Tukey contrasts using the *ghlt* function from the *multcomp* package in R (Hothorn et al. 2008).

To determine whether species composition in *B. inermis*-invaded areas differed from native-dominated areas, we tested for differences in species composition along the invasion gradient (i.e., among positions). More importantly, to assess whether *B. inermis* was the driver of the differences observed between invaded and uninvaded areas, we evaluated how species composition changed over time in each position. Differences in composition were assessed with a perMANOVA (permutational multivariate analysis of variance) using the *adonis* function in the *vegan* package in R, with site as *strata* to account for the nested structure of the data (Oksanen et al. 2016). Analyses were done using a Bray-Curtis distance matrix. Pairwise differences between positions were also assessed. Changes in species composition in each position from 2013 to 2015 were tested using the same analyses as above.

Changes in resource availability following B. inermis invasion

To evaluate the differences in nutrient availability due to *B. inermis* invasion, we tested for differences along the invasion gradient (i.e., among positions), as well as how nutrient availability changed over time in each position. Differences were assessed with a perMANOVA, using the *adonis* function in the *vegan* package in R, with site as *strata* to account for the nested structure of the data (Oksanen et al. 2016). Cadmium was not included in the analyses, as its concentration was always below the detection limit, and copper was not included because of a very strong correlation with lead ($r^2 = 0.90$, $t_{117} = 22.42$, $P < 0.001$). Two very high nitrate values (outliers) were found in the uninvaded areas (Position 4) in 2014 (values 7 and 11 times higher than the average for the position). Excluding these two outliers from the analyses did not change the overall results (Appendix S1: Section 1). Importantly, to assess whether the differences and changes in nutrient availability among positions were consistent within and across sites, we tested for their interaction (position * transect and position * site). A significant position * site interaction would indicate that differences in resource availability between *B. inermis*-invaded areas and native areas vary in magnitude and/or direction across sites. Likewise, a significant position * transect interaction would indicate that differences in resources availability between *B. inermis*-invaded areas and native areas vary in magnitude and/or direction within sites. We also tested for differences among positions for each individual nutrient in both years (2013, 2014) using linear mixed models with transect within site as a random factor. Tukey contrasts were used, as above, to assess pairwise differences between positions.

To evaluate whether *B. inermis* caused changes in light availability and soil moisture we tested for differences

among positions, within and across sites, and how they changed over time. Differences across positions in both years (2013, 2015) were tested using linear mixed models, with transect within site as a random factor. Tukey contrasts were used, as above, to assess pairwise differences between positions. To assess whether the differences and changes in light availability and soil moisture among positions were consistent within and across sites, we tested for their interaction (position * transect and position * site). The interaction between position and transect could not be tested for soil moisture, because of the low sample size.

Last, to further assess whether *B. inermis* is driving the increase in resources (light, moisture, and nutrients), we tested for the effect of *B. inermis* cover on resource availability in the areas invaded between 2013 and 2014/2015. We used linear mixed effect models, with *B. inermis* cover as a fixed effect and transect within site as a random factor.

Biotic homogenization within and across sites following B. inermis invasion

To test for biotic homogenization of communities following *B. inermis* invasion, we evaluated differences in beta diversity among positions, within and across sites, and how it changed over time. Beta diversity was estimated as the multivariate dispersion in species composition within each position (Anderson et al. 2006). This approach evaluates the distances of each replicate within a group (in this case, within position) to the group's centroid, as a measure of dispersion (Anderson et al. 2006), with shorter distances to the centroid indicating lower beta diversity (i.e., greater biotic homogenization). We used the group spatial median as the group centroid, as it is a more conservative approach than using the actual centroid (Oksanen et al. 2016).

We used the *betadisper* function in the *vegan* package to obtain the distances of each replicate to each group's centroid and then used a linear (mixed) model to test for differences among positions. To test for differences within site, we calculated the distance of each transect to the position's centroid, per site, and then used a mixed model, with site as a random factor, to evaluate differences among positions in their multivariate dispersion. To test for differences in beta diversity across sites, we pooled species in each position per site, calculated the distance of each site to the position's centroid, and then used a linear model to evaluate differences in dispersion among positions. We tested for differences in dispersion among positions in both years, as well as whether the dispersion changed from 2013 to 2015 in each position, at both spatial scales (within and across sites).

RESULTS

We identified a total of 129 vascular plant species in invaded (Position 1) and uninvaded (Position 4) areas

(Fig. 2) across all sites, with 14 species present only in *B. inermis*-invaded areas (present in Position 1, but not in Position 4), and 44 species (34%) present only in non-invaded areas (present in Position 4, but not in Position 1; Appendix S1: Table S1). *B. inermis* cover differed among positions ($F_{3, 279} = 933.38$, $P < 0.001$) and increased over time (2013–2014/2015) in the areas immediately outside the *B. inermis* patch ($F_{2, 185} = 114.98$, $P < 0.001$; Fig. 2). Specifically, in Position 3 *B. inermis* cover in both 2014 ($Z = 12.99$, $P < 0.001$) and 2015 ($Z = 13.26$, $P < 0.001$) was higher than in 2013.

Changes in species richness and composition following *B. inermis* invasion

Species richness was lower in *B. inermis*-invaded areas than in uninvaded areas in both years (2013: $F_{3, 279} = 30.64$, $P < 0.001$; 2015: $F_{3, 279} = 34.14$, $P < 0.001$; Fig. 3). However, there was no evidence of species richness decreasing in the areas invaded by *B. inermis* between 2013 and 2015 (i.e., Position 3; Fig. 3a). Consistently, we did not find a greater number of species being lost in those areas (Fig. 3c) from 2013 to 2015 (Position 2). However, *B. inermis*-invaded areas (Position 1) had lower species turnover than recently invaded and uninvaded areas, with fewer species gained ($F_{3, 279} = 9.66$, $P < 0.001$, Fig. 3b) and lost ($F_{3, 279} = 5.91$, $P < 0.001$; Fig. 3c).

Species composition was significantly different among positions in both years (2013: $F_{3, 372} = 23.66$, $P = 0.001$; 2015: $F_{3, 372} = 24.68$, $P = 0.001$; Fig. 4). In 2013 the greatest difference was between invaded and recently invaded areas (Positions 1 and 2) and still uninvaded areas (Position 3) and uninvaded areas (Position 4; Fig. 4; Appendix S1: Table S2). Areas on either side of the invasion front differed in species composition (Fig. 4) in spite of being spatially adjacent to each other on the inner and outer edges of the *B. inermis* patch (Fig. 2), indicating a sharp transition from uninvaded (Positions 3 and 4) to *B. inermis*-invaded and recently invaded areas (Positions 1 and 2). Further, the area that was invaded between 2013 and 2015 (Position 3) became different from the native-dominated areas and more similar in species composition to *B. inermis*-invaded areas (Fig. 4; Appendix S1: Table S2). Consistent with results above, areas invaded by *B. inermis* did not change between 2013 and 2015 (Position 1: $F_{1, 186} = 0.66$, $P = 0.614$; Position 2: $F_{1, 186} = 0.97$, $P = 0.174$) whereas areas invaded during 2013–2015 and uninvaded areas did change (Position 3: $F_{1, 186} = 7.45$, $P = 0.001$; Position 4: $F_{1, 186} = 2.39$, $P = 0.001$). Although species composition in uninvaded areas changed from 2013 to 2015, they remained significantly different from invaded areas (Fig. 4).

Changes in resource availability following *B. inermis* invasion

Nutrient availability was different between invaded and uninvaded areas in 2013 ($F_{3, 114} = 1.48$, $P = 0.019$;

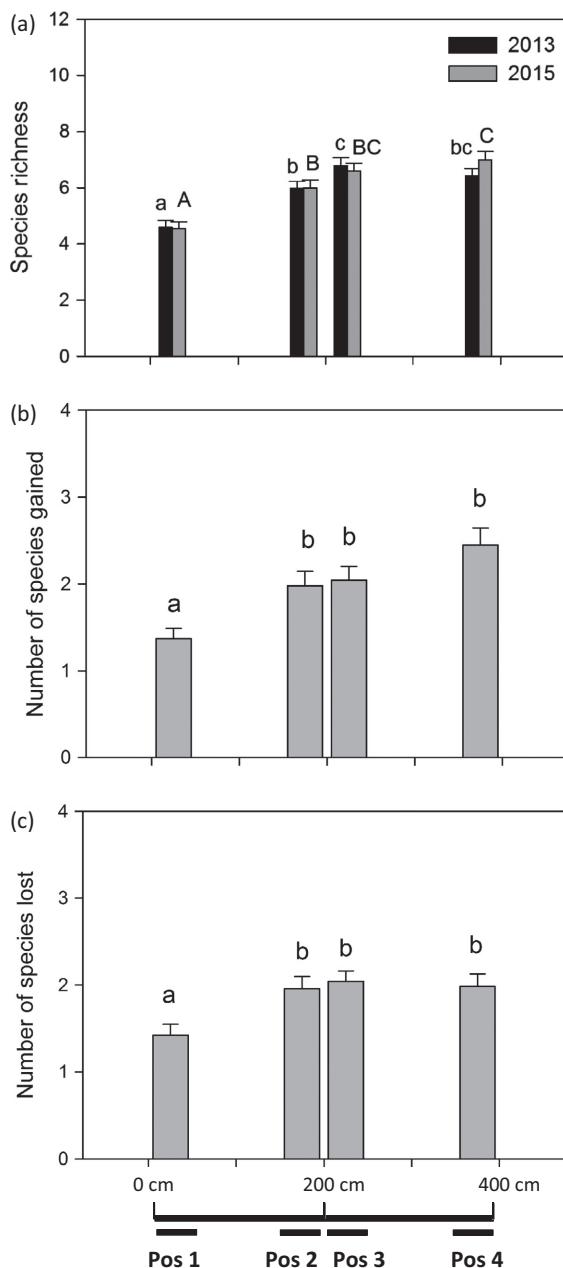


FIG. 3. (a) Species richness in 2013 and 2015 and the number of species (b) gained and (c) lost from 2013 to 2015 as a function of position along a *Bromus inermis*-invaded to native-dominated transition area. A line-intercept method was used, identifying species at each centimeter along a 50-cm line at each position, both years. Position 1 (Pos 1) is farther into the *B. inermis*-invaded area, Position 2 (Pos 2) is a more recently invaded area, Position 3 (Pos 3) got invaded between 2013 and 2015, and Position 4 (Pos 4) remained uninvaded (see Fig. 2 for more details). Columns sharing a letter are not statistically different ($P > 0.05$). Bars indicate mean \pm SE.

Fig. 5) and the differences between invaded and uninvaded areas were consistent across sites and transects (site * position: $F_{6, 107} = 0.02$, $P = 0.986$; transect * position: $F_{3, 111} = 0.01$, $P = 0.907$). Individual nutrients

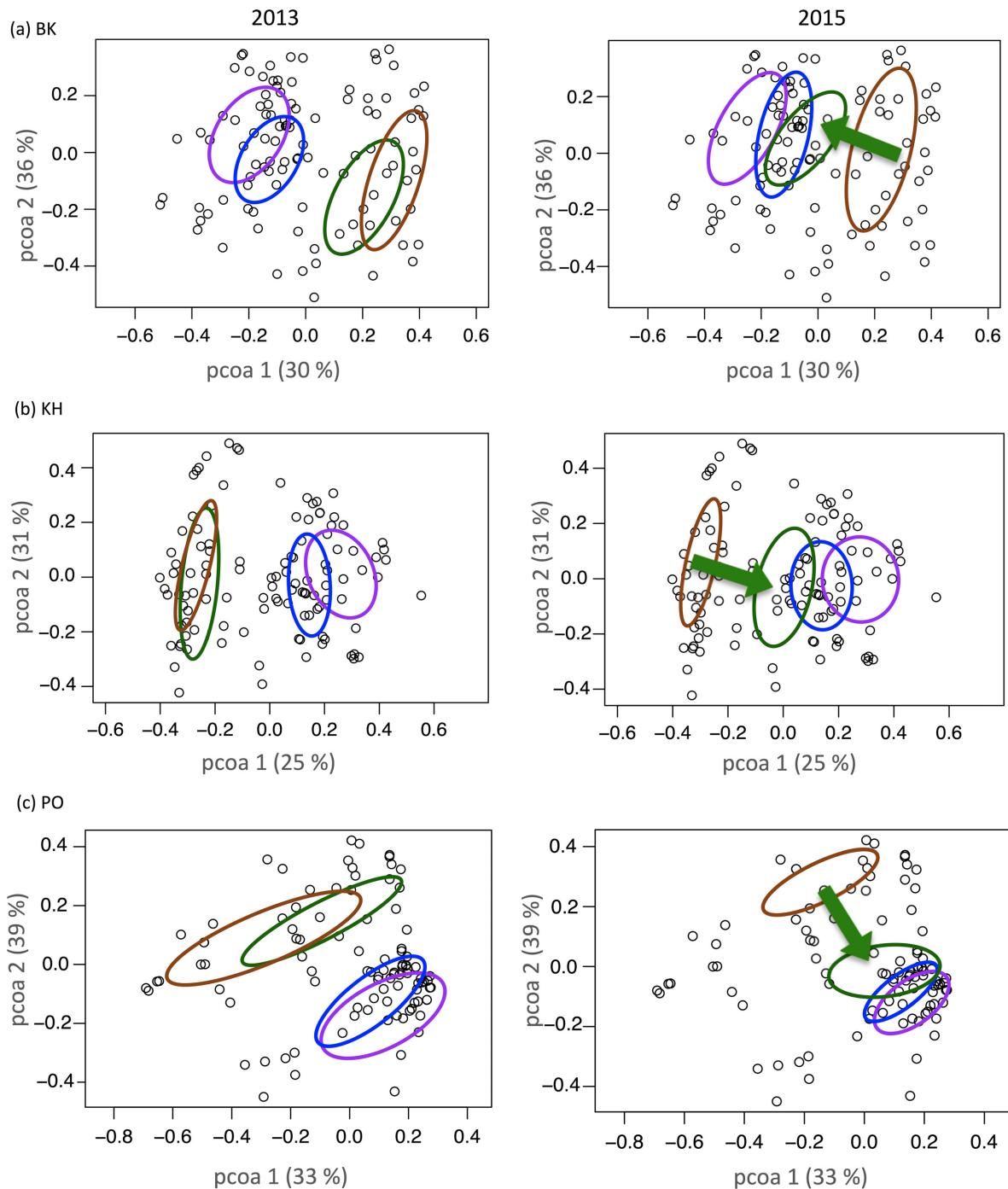


FIG. 4. Change in species composition as a function of position along a *Bromus inermis*-invaded to native-dominated transition area in 2013 and 2015. The ordinations for three sites are shown: (a) Big Knife provincial park (BK), (b) Kleskun Hill natural area (KH), and (c) Police-Outpost provincial park (PO). The green arrow indicates the direction of movement of the community following *B. inermis* invasion. Position 1 (shown in purple) is farther into the *B. inermis*-invaded area, Position 2 (shown in blue) is a more recently invaded area, Position 3 (shown in green) got invaded between 2013 and 2015, and Position 4 (shown in brown) remained uninvaded (see Fig. 2 for more details).

show an almost twofold increase in phosphorus, potassium, and iron, and a ~30% increase in manganese, zinc, and sulphur in invaded areas, relative to native areas

(Appendix S1: Fig. S2). The differences in nutrient availability observed between invaded and uninvaded areas were not found in 2014. The changes between years were

independent of *B. inermis* invasion (i.e., were observed in all positions; Position 1: $F_{1, 57} = 2.65$, $P = 0.011$; Position 2: $F_{1, 56} = 3.34$, $P = 0.003$; Position 3: $F_{1, 57} = 3.71$, $P = 0.001$; Position 4: $F_{1, 57} = 4.13$, $P = 0.001$). When looking at differences in particular nutrients in 2014, differences between invaded and uninvaded areas only remained for phosphorus and sulphur. Differences also appeared in calcium, with invaded areas having greater availability of calcium compared to uninvaded areas (Appendix S1: Fig. S2). Only phosphorus was found to increase slightly (not yet becoming different from uninvaded areas) in the areas invaded during 2013–2014 (Position 3; Appendix S1: Fig. S2).

Light penetration was significantly lower in *B. inermis*-invaded areas (Position 1), compared to uninvaded areas in 2013 (Positions 3 and 4; $F_{3, 279} = 22.14$, $P < 0.001$) and 2015 ($F_{3, 277} = 29.48$, $P < 0.001$; Fig. 6a). These differences among positions were consistent across sites and transects, as evidenced by the lack of significant interaction between position and site ($F_{21, 312} = 0.62$, $P = 0.905$) and position and transect ($F_{3, 312} = 2.34$, $P = 0.074$). The areas that were invaded from 2013 to 2015 (Position 3) became significantly different from noninvaded areas in 2015 (Fig. 6a).

Soil moisture was higher in 2015 compared to 2013, yet it did not differ along the *B. inermis*-invaded to native-dominated transitions (i.e., among positions) in 2013 ($F_{3, 72} = 0.67$, $P = 0.576$) or 2015 ($F_{3, 75} = 1.37$, $P = 0.258$; Fig. 6b). The lack of difference between positions was consistent across sites (position * site: $F_{6, 66} = 0.99$, $P = 0.437$).

Consistent with the results above, we found *B. inermis* cover to be associated with a decrease in light availability (Appendix S1: Fig. S3). Aluminum was also found to decrease with increasing *B. inermis* cover, but all other resources were not associated with *B. inermis* cover (Appendix S1: Fig. S3).

Biotic homogenization within and across sites following *B. inermis* invasion

Bromus inermis-invaded and recently invaded areas were more homogeneous (i.e., more similar in terms of species composition) compared to native areas, as evidenced by a lower beta diversity (Appendix S1: Table S3; Fig. 7a, b). Beta diversity did not change from 2013 to 2015 in *B. inermis*-invaded and recently invaded areas (Position 1: $F_{1, 179} = 0.16$, $P = 0.693$; Position 2: $F_{1, 179} = 0.001$, $P = 0.972$) but it decreased in the areas invaded from 2013 to 2015 and uninvaded areas (Position 3: $F_{1, 179} = 9.45$, $P = 0.002$; Position 4: $F_{1, 179} = 7.64$, $P = 0.006$). Across sites, the areas invaded from 2013 to 2015 (Position 3) became as homogeneous as invaded areas in terms of species composition (Fig. 7b), indicating a rapid change following *B. inermis* invasion. Within sites, the areas invaded from 2013 to 2015 (Position 3) also became more homogeneous, but their beta diversity was not as low as that of invaded areas (Fig. 7a). Beta diversity in the uninvaded areas (Position 4) also decreased over time, but it remained significantly higher than that of invaded areas at both scales (Fig. 7a, b).

DISCUSSION

We found strong differences between *B. inermis*-invaded and uninvaded areas in terms of species composition across small spatial scales (within 4-m transects), and rapid changes following invasion (Fig. 4). Although occurring at local, small spatial scales, these patterns were highly consistent within and across sites and, hence, can have significant implications at broader spatial scales (Gilbert and Levine 2013). *B. inermis* led to the biotic homogenization of communities within as well as

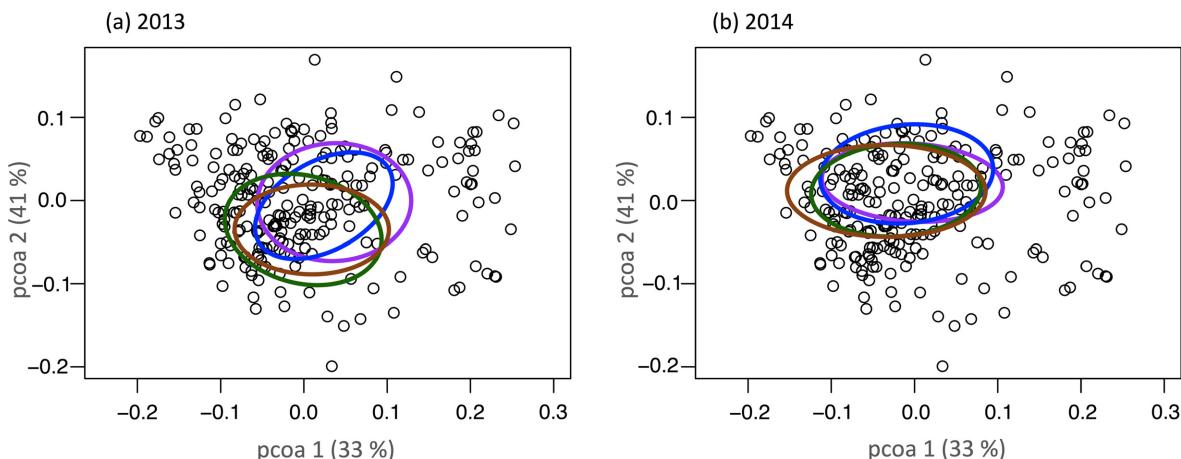


FIG. 5. Nutrient availability as a function of position along a *Bromus inermis*-invaded to native-dominated transition area in (a) 2013 and (b) 2014. Position 1 (shown in purple) is farther into the *B. inermis*-invaded area, Position 2 (shown in blue) is a more recently invaded area, Position 3 (shown in green) got invaded between 2013 and 2015, and Position 4 (shown in brown) remained uninvaded (see Fig. 2 for more details).

across sites (Fig. 7). Biotic homogenization can have important consequences for conservation, such as increased species extinction risk, reduced ecosystem function, and lower ecosystem resilience (Olden et al. 2004, Socolar et al. 2016, van der Plas et al. 2016, Hautier et al. 2018). Consequently, there is a need to understand the mechanisms behind invader-driven biotic homogenization. Bennett et al. (2014) reported that *B. inermis* has a deterministic impact on community composition by more strongly suppressing shade-intolerant species from invaded areas (Fig. 1). We found *B. inermis* to alter species composition within only 2 yr of invasion (Fig. 4), which suggests that it acts as a strong filter in the invaded communities (Fig. 1). Moreover, *B. inermis* acts as a consistent filter: regardless of whether resources were altered or not following *B. inermis* invasion, the change (or lack thereof) was consistent within and across sites (Figs. 5, 6), thus likely filtering out similar functional groups across sites (Bennett et al.

2014). Overall, these results support the proposed theoretical framework, strongly suggesting that invaders able to act as strong, deterministic, and consistent ecological filters are likely to result in the biotic homogenization of the communities they invade (Fig. 1; Tuomisto et al. 2003, Chase 2003, Freestone and Inouye 2006, Chase 2007).

Species richness was lower in *B. inermis*-invaded areas (Position 1; Fig. 3), but we found no evidence of species loss within the first 2 yr of invasion (i.e., in Position 3; Fig. 3), likely due to a time lag for species exclusion (Crooks 2005). Similarly, in 2013 species richness in the recently invaded areas (Position 2) was not as low as that of invaded areas (Position 1; Fig. 3). Nonetheless, rapid changes in species composition were observed following *B. inermis* invasion (Fig. 4). The rapid and consistent impact of *B. inermis* on species composition across sites may be related to its agronomic history: it was bred to grow fast and at high density under different conditions (Cook 1943, Wilkins and Humphreys 2003, Coulman 2006). The rapid changes in species composition following invasion highlight the need for early detection and timely management strategies to prevent the impact of invasive species, as restoration efforts in later invasion stages (i.e., after the time lag to species loss) can be more costly and ultimately unsuccessful (Rejmánek and Pitcairn 2002, Norton 2009, Simberloff et al. 2013). Biotic homogenization was driven mainly by a change in species relative abundances, and potentially later reinforced by species loss (Olden and Rooney 2006), as biotic homogenization was evidenced in the recently invaded areas (Fig. 3) where species richness was still high (Fig. 3). This stresses the importance of assessing biodiversity changes beyond species richness (Hillebrand et al. 2018), especially considering that severe consequences, such as biotic homogenization, may ensue even before species are displaced from invaded areas (Olden and Poff 2003, Olden et al. 2004). Identifying the drivers of the change in species composition and hence of biotic homogenization can help prevent further biodiversity losses (Olden and Poff 2003).

Resources that changed following *B. inermis* invasion showed consistent changes within and across sites. Light availability changed within the first 2 yr of invasion and tended to decrease as *B. inermis* cover increased (Appendix S1: Fig. S3). This pattern suggests that light is likely the main driver of biotic homogenization following *B. inermis* invasion (Fig. 6a). *B. inermis* decreased light availability by ~50% (Fig. 6a), which is consistent with earlier findings that shade tolerance is a key attribute determining species persistence in *B. inermis*-invaded areas (Bennett et al. 2014). However, biotic homogenization was already evident in the recently invaded areas (Position 2) in 2013 (Fig. 7), but light was not yet as low as in the invaded areas (Position 1; Fig. 6). This suggests that although light was reduced by ~50%, the species tolerance threshold is likely lower, as homogenization was already evident after a ~20–30% reduction

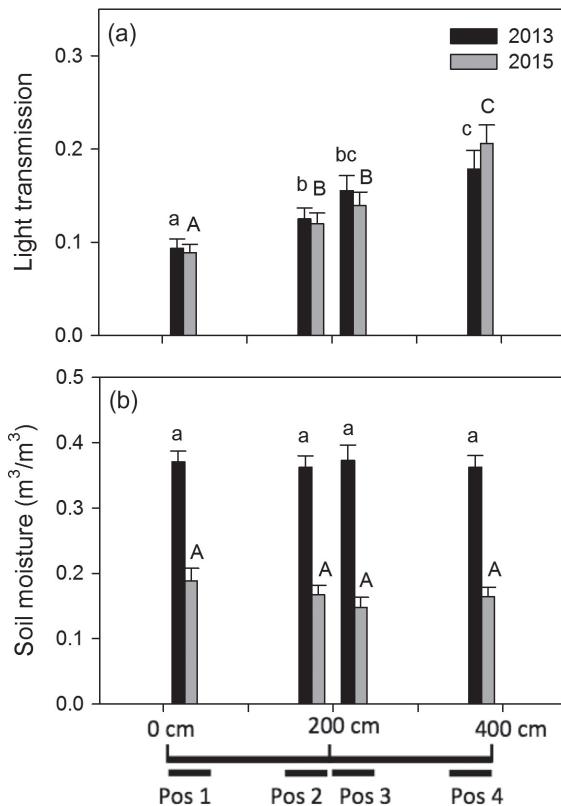


FIG. 6. (a) Light transmission (proportion of light above the canopy/light below the canopy) and (b) soil moisture (water volume/soil volume) as a function of position along a *Bromus inermis*-invaded to native-dominated transition area, and year (2013, black bars, 2015, gray bars). Position 1 (Pos 1) is farther into the *B. inermis*-invaded area, Position 2 (Pos 2) is a more recently invaded area, Position 3 (Pos 3) got invaded between 2013 and 2015, and Position 4 (Pos 4) remained uninvaded (see Fig. 2 for more details). Columns sharing a letter are not statistically different ($P > 0.05$). Bars indicate mean \pm SE.

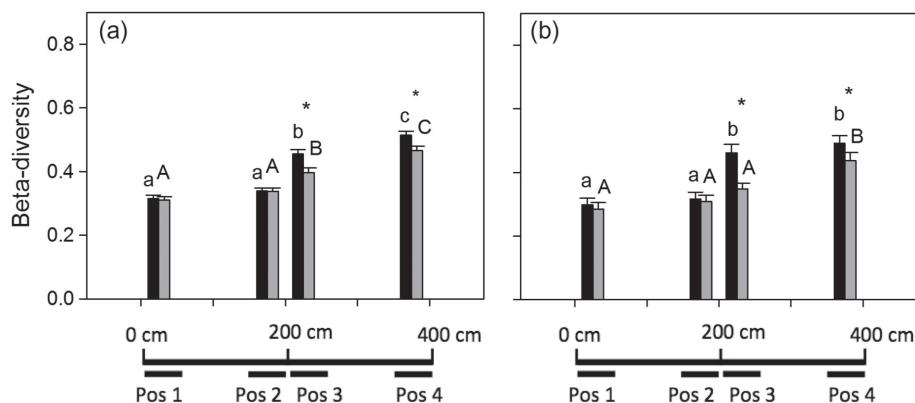


FIG. 7. Beta diversity (calculated as the average distance from the group centroid), (a) within and (b) across sites in 2013 (black bars) and 2015 (gray bars) along a *Bromus inermis*-invaded to native-dominated transition area. Position 1 (Pos 1) is farther into the *B. inermis*-invaded area, Position 2 (Pos 2) is a more recently invaded area, Position 3 (Pos 3) got invaded between 2013 and 2015, and Position 4 (Pos 4) remained uninvaded (see Fig. 2 for more details). Columns sharing a letter are not statistically different ($P > 0.05$). The asterisks indicate statistical difference ($P < 0.05$) between years. Bars indicate mean \pm SE.

(Figs. 6, 7). Decreased light availability did not appear to have resulted in decreased evapotranspiration, as no differences in soil moisture were observed along the invasion gradient (Fig. 6b). The lack of difference in soil moisture could be partly explained by the low statistical power resulting from the small sample size. Nevertheless, although small differences among treatments may remain undetected, large differences are likely to be apparent even with low sample sizes. Moreover, increased sample size should decrease data dispersion around the mean but is not likely to modify mean values. Fig. 6b suggests that mean values across positions are very similar, so it is improbable that increased sample size would modify the outcome. By limiting light availability, *B. inermis* likely shifted competition in these grasslands from being mainly belowground (Lamb et al. 2007) to mainly aboveground. Evidence and theory suggest that plant competition for light is likely to result in competitive exclusion (Lamb and Cahill 2008, Hautier et al. 2009), because it tends to be size asymmetric, i.e., taller plants get a disproportionate advantage over smaller ones (Weiner 1986, Schwinning and Weiner 1998, DeMalach et al. 2017). Phosphorus was also found to increase following *B. inermis* invasion (Appendix S1: Fig. S2), which could enhance *B. inermis* growth and hence further decrease light availability (Fig. 6a; DeMalach et al. 2017). Increased phosphorus could alter species composition (Bennett and Cahill 2016) by way of disruption of mycorrhizal associations (Johnson et al. 1997, 2015). Although a clear trend of change following *B. inermis* invasion (in recently invaded areas) was only observed for phosphorus (Appendix S1: Fig. S2), the role of other nutrients in driving biotic homogenization cannot be ruled out.

Nutrients (specifically phosphorus, potassium, manganese, zinc, and sulphur) were higher in *B. inermis*-invaded areas, although none (except phosphorus) increased in the recently invaded areas (from 2013 to

2014; Fig. 5; Appendix S1: Fig. S2), and none (except aluminum) were associated with *B. inermis* cover (Appendix S1: Fig. S3). These patterns are generally consistent with previous studies (Fink and Wilson 2011), except that other studies also found nitrogen to be higher in invaded areas (Piper et al. 2015a, Carrigy et al. 2016, Stotz et al. 2018). Collectively, these results suggest that *B. inermis* tends to increase nutrients as it invades, rather than invade high-nutrient areas (i.e., driver rather than passenger of the change in nutrient availability, MacDougall and Turkington 2005). Other studies have also found that although *B. inermis* easily invades resource-rich areas, it is able to invade and remain a strong competitor across a broad range of conditions (Nernberg and Dale 1997, Gendron and Wilson 2007, Carrigy et al. 2016). Although some of the nutrients may not be involved in the initial changes in community composition, an overall greater nutrient availability may increase *B. inermis* performance, persistence, and subsequent impact (Gendron and Wilson 2007, DiAllesandro et al. 2013). The increase in nutrient availability generally results in species loss in grasslands (Gough et al. 2000, Clark and Tilman 2008) and thus the time lag to the increase in nutrient availability may be associated with the time lag to species loss (Fig. 3). Further, greater nutrient availability can help establish self-reinforcing dynamics (Ehrenfeld 2003, Suding et al. 2004), which increase invader resistance to restoration efforts (Hobbs and Harris 2001, Suding et al. 2004).

We found strong differences in species composition (Fig. 4) and resource availability (Figs. 5, 6) between adjacent invaded and uninvaded areas, and important differences appearing within only 2 yr of *B. inermis* invasion (Figs. 4, 6). Sharp and rapid changes in conditions are generally associated with alternative stable states, which are generally characterized by alternative combinations of state variables, such as community structure and abiotic conditions (Suding et al. 2004) and rapid changes

between states (Scheffer et al. 2001, Schröder et al. 2005). Other studies have found evidence of rapid, yet reversible, transitions between invaded and uninvaded community states (Brownstein et al. 2014, Stein et al. 2016). It remains to be tested whether the *B. inermis*-invaded community state in these grasslands is stable or reversible. *B. inermis* may be establishing self-reinforcing dynamics by increasing nutrient availability, yet negative plant–soil feedbacks have also been found (Sherrard and Maherali 2012, Stotz et al. 2018), likely driven by the accumulation of soil pathogens (Myhr et al. 1966). Further, although soil conditions in invaded areas do not appear to prevent the recruitment of native species in invaded areas (Stotz et al. 2018), the high aboveground biomass and litter accumulation may prevent their establishment (Facelli and Pickett 1991, Stotz et al. 2017). Some studies suggest that *B. inermis* is generally persistent, being highly resistant to restoration efforts, persisting and even increasing in abundance over time (Salesman and Thomsen 2011, Sinkins and Otfinowski 2012).

Biotic homogenization of communities, or the establishment of similar alternative community states across previously distinct communities, can have important consequences for local and regional biodiversity (Olden et al. 2004, Socolar et al. 2016, Hautier et al. 2018). By reducing the available habitat for native species, invasive species can decrease native species' long-term persistence (Gilbert and Levine 2013). Although species exclusion and biotic homogenization are currently restricted to invaded patches within a broader community, *B. inermis* patches were found to be continuously expanding. If *B. inermis*, a widely distributed species across North American grasslands (Otfinowski et al. 2007), is consistently excluding certain species from the areas it invades, it might increase those species' extinction risk. Further, if *B. inermis* is consistently excluding certain functional groups (e.g., shade-intolerant species), it may not only result in the taxonomic homogenization, but also in the functional homogenization of communities (Olden and Rooney 2006). Moreover, the loss in plant species alpha and beta diversity can cascade to further losses of diversity in associated guilds (Zak et al. 2003, Horner-Devine et al. 2004). Piper et al. (2015b) found microbial communities to be more homogeneous among *B. inermis*-invaded areas, compared to uninvaded areas. However, at least within patches, the soil biotic quality experienced by plants appears to be equally variable within and outside *B. inermis*-invaded areas (Chagnon et al. 2018). The consequences of biotic homogenization within and across sites due to *B. inermis* invasion should be further investigated, as they could lead to losses in ecosystem function (Zak et al. 2003, Lamb et al. 2011, Hautier et al. 2018) and increase the vulnerability of these communities to large-scale disturbances (Olden et al. 2004).

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