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Invasive annual grasses destabilize plant communities in a northern mixed-grass prairie

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Abstract

Temporal community stability, here defined as temporal mean divided by temporal SD, plays an important role in predicting certain ecosystem services. However, temporal stability can change with invasion, with greater abundances of invasive species potentially having greater impacts on native community stability. The exact consequences of invasion for temporal stability are unclear and, in part, depend on the particular metric of stability measured. In rangeland ecosystems, predicable forage is important for livestock production but can be threatened by invasion. Therefore, using an observational field study conducted over three years in Wyoming, we assessed which metrics of plant community stability were altered by invasion and whether those effects were mediated by two environmental variables (light and soil moisture). *Bromus arvensis* and *Bromus tectorum* are two invasive annual weeds found across US rangelands, including the northern mixed-grass prairies of Wyoming. We established plots along natural invasion blocks of *B. arvensis* and *B. tectorum* abundance and collected plant species composition data over three growing seasons. We tested associations between seven different metrics of plant community stability and invasion by *B. arvensis* and *B. tectorum*. We found that species turnover increases with invasion by both species, while stability of forb (both brome species), C_4 grass (*B. arvensis* only), and C_3 grass (*B. tectorum* only) cover decreases with invasion. All metrics of stability associated with invasion supported the hypothesis of a destabilizing effect of invasion on the native plant community. Further, we found that light and soil moisture did mediate some associations between stability and invasion. Overall, our results align with previous work suggesting that invasive annual bromes can lead to decreased native plant stability, which has important implications for forage production and, thus, food security.

KEYWORDS
Bromus arvensis, *Bromus tectorum*, grassland, invasion, rangeland, stability

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INTRODUCTION

Temporal stability, defined here described as temporal mean divided by temporal SD (Lehman & Tilman, 2000), alters ecosystem dynamics (Ebel et al., 2022) and functioning (Loreau & de Mazancourt, 2013). Importantly, temporal stability can also impact provisioning of services, with temporally stable communities leading to better prediction of certain ecosystem services (e.g., consistent pollination leading to reliable crop yield; Montoya et al., 2019). Like most ecosystem properties, temporal community stability can be altered by invasive species (Valone & Balaban-Feld, 2018). Frequently, invasion is linked to decreased species richness, evenness, and diversity (Hejda et al., 2009; Xu et al., 2022), suggesting invasion should decrease stability, as high native diversity can increase community stability (Tilman et al., 2006). However, previous work is equivocal on the effects of invasion on temporal stability, and response may depend on the specific community and measure of stability (Pfisterer et al., 2004; Valone & Balaban-Feld, 2018). Further, the response of native communities to invasion depends on invasion degree, where increased dominance by invasives can lead to greater impacts on the native community (Brummer et al., 2016).

Grasslands, covering nearly 40% of Earth's terrestrial surface (Gibson, 2009), are commonly used as rangeland, providing natural grazing areas for livestock and supporting the livelihoods of billions around the world (Sayre et al., 2013). However, grasslands are threatened by global change, including widespread invasive plant species (DiTomaso, 2000; McCollum et al., 2017). While ecosystem heterogeneity in space and time is important for certain conservation objectives, such as wildlife habitat creation (Fuhlendorf & Engle, 2001), temporal stability also supports objectives associated with other ecosystem services. Stability of key palatable forage species on rangelands is critical for ranchers and land managers who rely on predictable forage abundance each year (Bonin & Tracy, 2012; Sasaki & Lauenroth, 2011), especially under natural (e.g., drought) and human-induced disturbances (e.g., grazing) (Haughey et al., 2018).

Across arid and semiarid regions of North America, invasive annual grasses have significantly altered the landscape, changing portions of many ecoregions such as the Great Basin and Great Plains from communities dominated by perennial grasses to dominance by invasive annual grasses (D'Antonio & Vitousek, 1992; Davies et al., 2021). This dominance shift has led to changes in rangeland productivity, including increased annual variability in herbaceous forage production (Bradley & Mustard, 2005; Clinton et al., 2010), as yearly abundance of invasive annual grasses tightly depends on resource availability (Bradley et al., 2016). Invasive annuals decrease native plant abundance and diversity, as invasive annuals outcompete native species by utilizing resources and growing rapidly earlier in the growing season (Davies, 2011; Melgoza et al., 1990). *Bromus arvensis* and *B. tectorum* are winter annual C_3 brome grasses that are well-established invasives throughout the North American Great Plains, especially in Northern mixed-grass prairies (Hulbert, 1955; Oja et al., 2003), which are biodiverse and essential as working rangeland (Samson et al., 2004). Though these annual brome species were introduced intentionally as forage for livestock and provide quality forage in spring, upon flowering in ~mid-June, they become very low-quality forage and decrease in protein percentage by ~97% after maturation (Chambers et al., 2007; Morrow & Stahlman, 1984). Because of this, for long-term stability of forage usage on rangelands and ultimately food security, it is important to understand how invasive annual bromes impact native plant community stability (Ziska et al., 2011).

Using an observational field study conducted over three growing seasons, we assessed changes in plant community stability with invasion. We used blocks of invasion abundance to study the effects of two invasive annual grasses (*B. arvensis* and *B. tectorum*), as impacts of invasion on native plants vary depending on invasion abundance (Brummer et al., 2016). Further, while there are many definitions of stability, such as those associated with constancy, resilience, and resistance (Grimm et al., 1992), here we assess several metrics of temporal stability of the plant community, as well as synchrony and species turnover, to determine which aspects of community stability change with invasion. We hypothesized that invasive bromes would associate with instability in the plant community, but that increasing brome invasion would result in higher species turnover. Invasive plants increase native plant species turnover by hindering reappearance of resident native species (Somodi et al., 2008), while negatively impacting community stability (Walker & Smith, 1997). Second, we assessed whether patterns of community stability associated with invasion were mediated by stability of environmental factors (light transmittance to the soil surface and soil moisture). Invasive annual bromes can decrease light at the soil surface (Vinton & Goergen, 2006) and deplete soil moisture early in the growing season (Souther et al., 2020). Thus, we explored the direct and indirect (via light and soil moisture) effects of invasion on community stability.

METHODS

Site description

Northern mixed-grass prairies cover 38% of grassland area in North America (Lauenroth, 1979) and are

important regions for biodiversity and livestock production, with up to 50% used for livestock grazing (Holechek et al., 2011). We conducted our study in Converse County in northeastern Wyoming (43.30° N, −105.05° W) on privately owned, working rangeland within the Thunder Basin ecoregion, a 7000-km^2 region centered on the United States Forest Service-managed Thunder Basin National Grassland (Porensky et al., 2018). Climate in this shrubland-grassland ecotone is semiarid (30-year mean annual precipitation = 363 mm/year, with 40%–50% of precipitation in April–June; mean temperature ranges from −5°C in December to 22°C in July; elevation = 1097–1585 m above sea level) (Connell et al., 2019; NOAA National Centers for Environmental Information, 2022). During this study, annual precipitation in Converse County, WY, was 390.7 mm (2019), 216.4 mm (2020), and 341.6 mm (2021) (Appendix S1: Figure S1, NOAA National Centers for Environmental Information, 2022). Common native plant species include *Artemisia tridentata* (Wyoming big sagebrush), *Bouteloua gracilis* (blue grama), *Carex filifolia* (threadleaf sedge), *Hesperostipa comata* (needle-and-thread grass), *Pascopyrum smithii* (Western wheatgrass), *Plantago patagonica* (wooly plantain), *Sphaeralcea coccinea* (scarlet globemallow), and *Opuntia polyacantha* (Plains prickly pear) (Porensky et al., 2018).

Study design

Data collection and study design were consistent across all three study years from 2019 to 2021. In July 2019, we established blocks of plots varying in invasion abundance in Wyoming. Each block consisted of five permanent, 1 × 1 m plots with different levels of invasion (assigned visually as 0%, 25%, 50%, 75%, and 100% relative cover) of each respective invasive species grouped together in space (Figure 1). Invasion levels represent approximate categorized aerial cover of the invasive annual brome, but actual cover was assessed through plant species composition (Figure 1). *B. tectorum* and *B. arvensis* each had five blocks (50 plots total). Each year in late June/early July, we collected all data. At each plot, we measured plant species composition across the plot by visually estimating foliar cover (i.e., calibrated to estimates generated by a 100 pinpoint intercept frame) for each species to the nearest percent; species overlap, including by shrubs, was accounted for as each species cover was estimated independently. Thus, theoretically, total cover could have been over 100%. Additionally, we measured photosynthetically active radiation (PAR) below and above the plant canopy using an AccuPAR LP-80 Ceptometer to calculate percent transmittance of light to the soil surface. Last, we collected soil moisture (percentage volumetric water content [VWC]) from the center of each plot. We measured all abiotic variables (PAR and soil moisture) from all plots within a 2-h period centered around mid-day to account for daily variability.

Stability metric calculations

For the stability of richness, total cover (a measure of abundance and a proxy for total biomass; Mahood et al., 2021; Ónodi et al., 2017), C_4 grass cover, C_3 grass cover, forb cover, light, and soil moisture, we calculated stability as the temporal mean divided by temporal SD across all three study years. Essentially, higher stability numbers indicate, in comparison with the mean value, the metric does not vary much from year to year. We used the codyn package to calculate stability (of all variables), as well as two additional metrics (Hallett et al., 2016): synchrony (how populations covary over time; Valencia et al., 2020), calculated with the synchrony function from the codyn package (Loreau & de Mazancourt, 2008) and species turnover (proportion of species gained or lost over time in relation to the total number of species), calculated with the turnover function from the codyn package (Cleland et al., 2013). A low synchrony value indicates a stable community, and a high turnover value indicates an unstable community. Because annual bromes are part of the plant community, we assessed how turnover, synchrony, and stability of richness, total cover, and C_3 grass cover changed in association with annual brome invasion using two methods: without (Table 1) and with (Table 2) brome data included (i.e., with and without *B. arvensis* data included in *B. arvensis* blocks and *B. tectorum* data included in *B. tectorum* blocks). For ease, we refer to the non-brome plant community as the native plant community. However, our plant composition data also included low cover of several introduced annual forbs (*Alyssum desertorum*, *Camelina microcarpa*, *Lactuca serriola*, *Logfia arvensis*, *Polygonum aviculare*, and *Tragopogon dubius*).

Data analysis

To analyze relationships between stability and invasion, we used linear mixed-model regressions with invasion abundance as a fixed effect, block as a random effect, and metrics of stability of as the response variable (lmerTest package (Kuznetsova et al., 2017). Each metric of stability (nine in total) was assessed in a separate model. We assessed fixed effect significance using Type III ANOVA

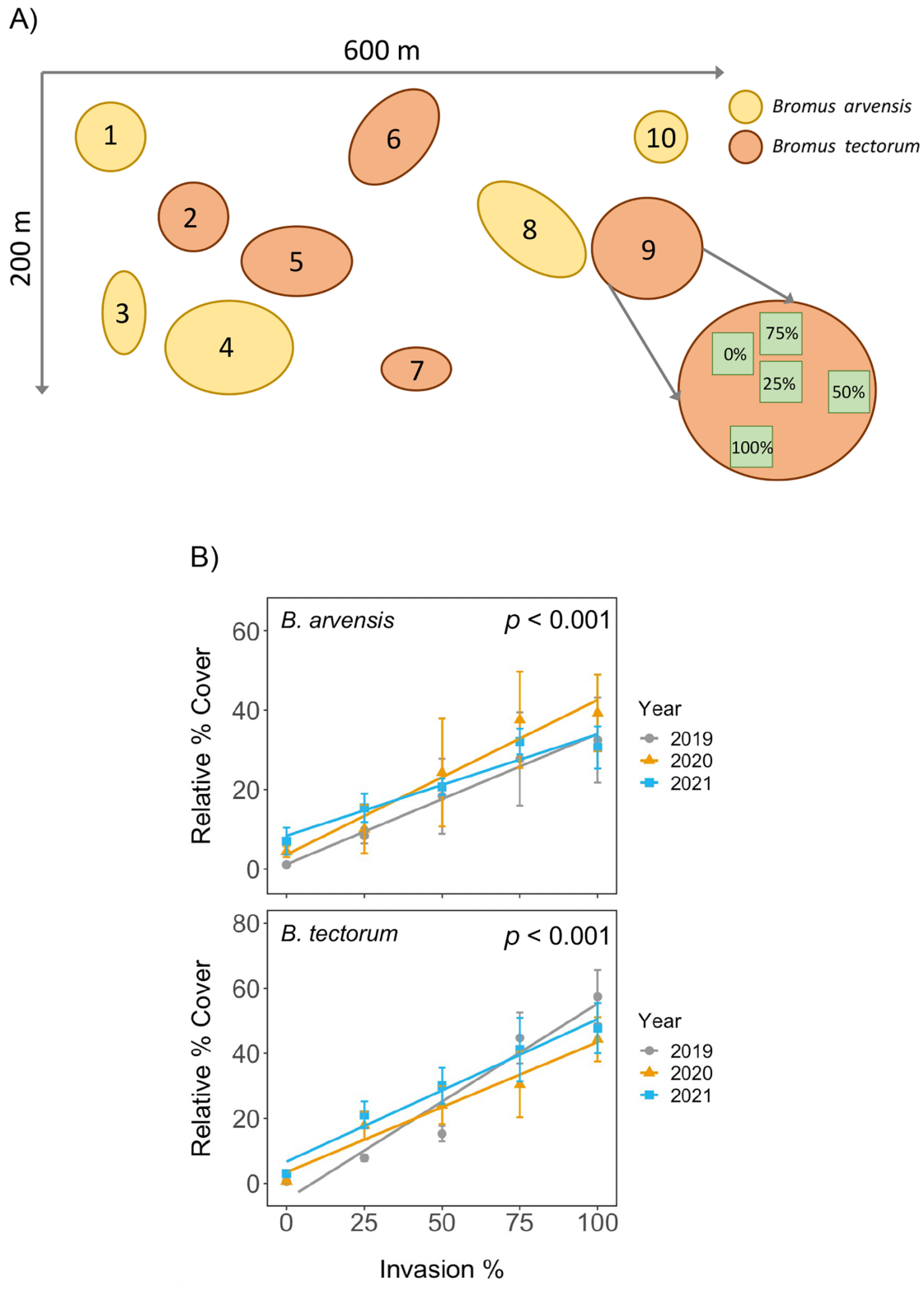


FIGURE 1 (A) Approximate plot layout. Blocks were selected randomly across the landscape by identifying areas that had a high abundance of the two target invasive species. From there, five plots were established by selecting plots that fit into the five categories of invasion abundance. If a plot could not be found within 10 m of another plot in a block, that block was abandoned, and a new block established. This created blocks of varying geographic extent, ranging from 200 m × 600 m. (B) Relative percent cover of *Bromus arvensis* and *Bromus tectorum* across categorized invasion levels from 2019 to 2021 (mean ± SE). Solid lines indicate significant relationships between invasion level and relative invasion cover ($p < 0.05$). The p values are for the main effect of invasion level from repeated measures mixed-model ANOVAs.

TABLE 1 Linear mixed-model ANOVA for the response of stability metrics to invasion by annual bromes.

	Bromus arvensis				*Bromus tectorum*			
Metric	**Log transformation**	**df**	***F***	**Adjusted *p***	**Log transformation**	**df**	***F***	**Adjusted *p***
Synchrony	No	1, 23.00	0.16	0.692	No	1, 23.00	0.66	0.566
Species turnover	No	1, 22.97	6.25	**0.080***	No	1, 19.579	16.16	**0.003****
Richness stability	Yes	1, 22.24	2.15	0.312	No	1, 20.00	7.03	**0.031****
Cover stability	Yes	1, 23.00	0.95	0.453	Yes	1, 23.00	0.13	0.726
C_4 grass stability	Yes	1, 18.22	6.01	**0.037****	Yes	1, 20.00	0.03	0.874
C_3 grass stability	Yes	1, 22.56	1.30	0.266	No	1, 19.62	13.84	**0.001****
Forb stability	Yes	1, 21.52	6.71	**0.037****	Yes	1, 16.04	3.85	0.101
Light stability	Yes	1, 23.00	42.51	**<0.001*****	Yes	1, 23.00	25.75	**<0.001*****
Soil moisture stability	Yes	1, 20.85	0.26	0.614	No	1, 20.75	1.41	0.249
Average light availability	No	1, 22.14	45.32	**<0.001*****	No	1, 20.88	75.34	**<0.001*****
Average soil moisture	No	1, 20.10	1.93	0.240	No	1, 20.10	1.59	0.249

Note: Stability of richness, total cover, and C_3 grass cover, as well as turnover and synchrony, were calculated without respective brome data for each block type. Significant values are shown in boldface type, with *$p < 0.1$; **$p < 0.05$; ***$p < 0.001$. The p values were adjusted for multiple comparisons using Benjamini–Hochberg's correction.

TABLE 2 Linear mixed-model ANOVA for the response of stability metrics to invasion by annual bromes.

	Bromus arvensis				*Bromus tectorum*			
Metric	**Log transformation**	**df**	***F***	**Adjusted *p***	**Log transformation**	**df**	***F***	**Adjusted *p***
Synchrony	No	1, 23.00	0.92	0.463	No	1, 20.28	1.60	0.293
Species turnover	No	1, 22.97	5.50	0.112	No	1, 19.54	13.18	**0.007****
Richness stability	Yes	1, 22.31	1.81	0.769	No	1, 20.00	5.03	**0.073***
Cover stability	Yes	1, 23.00	0.18	0.679	Yes	1, 19.90	0.14	0.711
C3 grass stability	Yes	1, 23.00	1.21	0.283	Yes	1, 20.12	2.32	0.143

Note: Here, each metric was calculated with respective brome data included for each block type (as opposed to results in Table 1). Of note, we found less significant results overall when including annual brome data in analyses. The positive relationship between *B. tectorum* abundance and species turnover is consistent, while the negative relationship between *B. tectorum* abundance and richness stability is now marginally significant. Significant values are shown in boldface type, with *$p < 0.1$, **$p < 0.05$. The p values were adjusted for multiple comparisons using Benjamini–Hochberg's correction.

with Satterthwaite's method; Satterthwaite, 1941). We also examined how average soil moisture and light availability changed with invasion abundance using the same model structure. To ensure the blocks of invasion abundance held over time, we used repeated measures mixed-model ANOVAs. Predictors were invasion levels (categorical), year (categorical), and the interaction between invasion level and year; the response variable was the actual percent brome cover (*B. arvensis* in *B. arvensis* blocks and *B. tectorum* in *B. tectorum* blocks), and a random effect of block was included (Figure 1). For all analyses, we adjusted for multiple comparisons using Benjamini–Hochberg's correction (Benjamini & Hochberg, 1995).

Then following Duchardt et al. (2021), we tested hypotheses about mediation of the effects of *B. arvensis* and *B. tectorum* on metrics of plant community stability by light availability and soil moisture. Specifically, we assessed hypotheses that the effect of each brome species on each stability metric was mediated by (1) light availability and (2) soil moisture. We assessed evidence for direct versus indirect effects of bromes on stability via full mediation (i.e., the effect of bromes on stability was fully mediated by light or soil moisture; meaning evidence of indirect effects only where brome abundance correlated with stability responses), partial mediation (i.e., the effect of bromes on stability was partially mediated by light or soil moisture; meaning evidence of both direct and indirect effects where brome abundance correlated with stability responses; partial mediation also implies that other, unmeasured factors may be influencing the relationship

between invasion and stability metrics), or no mediation (i.e., the effect of bromes on stability was not mediated by light or soil moisture; meaning evidence of direct effects only where brome abundance correlated with stability responses). We used structural equation modeling (lavaan package; Rosseel, 2012) to build a model including all links and assessed whether each link was fully, partially, or not mediated by light or soil moisture (Grace, 2006). We tested for evidence of full ($A \rightarrow B \rightarrow C$), partial ($A \rightarrow B \rightarrow C$; $A \rightarrow C$), and no ($A \rightarrow C$) mediation both by comparing path coefficients in the partial mediation models and assessing difference in corrected Akaike information criterion between models for small sample size (ΔAIC_c Burnham & Anderson, 2002) between full, partial, and no mediation models. Here, A represents annual brome abundance, B represents light or soil moisture, and C represents the stability metric (e.g., richness stability). We used a ΔAIC_c cutoff of 5 in combination with path coefficient strength to determine if we had support for one model over another. Where no consensus could be made (i.e., conflict between ΔAIC_c cutoff and path coefficient strength), we determined no conclusion could be drawn based on our data. We conducted two separate mediation analyses—one with stability of light and soil moisture as mediators and the other with average light and soil moisture as mediators. Average light/soil moisture does not directly account for dispersion around the mean (SD), which is more robustly demonstrated by stability metrics. However, because stability of light and soil moisture may be less familiar, in our analyses, we demonstrate both can be mediators, as results were largely the same for each. We used Chi-square goodness-of-fit tests to assess model fit of each model. Of note, we found no evidence against good model fit ($p > 0.1$ in every case).

We conducted all calculations and analyses in R version 3.6.2 (R Core Team, 2019) ($\alpha = 0.05$, but we report results with $0.05 < p < 0.1$ as marginally significant). We visually assessed plots of the residuals and Autocorrelation Function/Partial Autocorrelation Function to look for evidence of nonlinearity and autocorrelation, respectively, but we did not find evidence of violations of either assumption in any of our results. To test the assumption of homoscedasticity, we used Levene's test for equality of variances (Levene, 1960). We assessed normality of the residuals of all response variables using Shapiro–Wilk, Anderson–Darling, Cramer–von Mises, and Kolmogorov–Smirnov tests from the Olsrr package (Hebbali, 2020). We log-transformed data when necessary to achieve approximate normality and homoscedasticity (Table 1). We conducted all analyses for blocks of *B. arvensis* and *B. tectorum* separately.

RESULTS

Effectiveness of brome blocks

Invasion abundance held across time for both *B. arvensis* and *B. tectorum* blocks (Figure 1). Percent cover of *B. arvensis* and *B. tectorum* increased with categorical invasion level (percent) within each year across all three years of the study (for *B. arvensis*, invasion level, $F_{1,67} = 88.3$, $p < 0.0001$; for *B. tectorum*, invasion level, $F_{1,67} = 132.5$, $p < 0.0001$). In the *B. arvensis* blocks, we also found a significant effect of year on percent cover of *B. arvensis* (year, $F_{1,67} = 5.5$, $p < 0.0001$, $p = 0.022$) but saw no interaction between invasion level and time (invasion level × year, $F_{1,67} = 2.3$, $p = 0.132$). In the *B. tectorum* blocks, we found no significant effect of year (year, $F_{1,67} = 0.9$, $p = 0.345$) or interaction between invasion level and year on percent cover of *B. tectorum* (invasion level × year, $F_{1,67} = 2.6$, $p = 0.113$).

Associations between invasion and stability metrics

In *B. tectorum* blocks, native plant species turnover significantly increased with invasion (44.4% increase), while in *B. arvensis* blocks, turnover marginally increased with invasion (17.0% increase; Figure 2). In the *B. arvensis* blocks, stability of C_4 grass and forb cover decreased with invasion cover (47.7% and 73.2% decrease, respectively; Figure 3, Table 1). In the *B. tectorum* blocks, native plant species richness stability decreased with invasion (12.0% decrease) and C_3 grass cover stability significantly decreased with invasion (32.1% decrease; Figure 3, Table 1). We found no significant impact of either annual brome species on synchrony or total cover stability (Figure 2, Table 1). When including *B. arvensis* and *B. tectorum* data in each species' respective analyses, we found that species turnover significantly increased with invasion in *B. tectorum* blocks only (Table 2).

Stability of light and average light availability significantly decreased with invasion by both annual bromes, while soil moisture stability and average soil moisture were not related to brome invasion (Table 1; Appendix S1: Figures S2 and S3, Table S1).

Abiotic mediation of invasion-stability relationships

In the *B. arvensis* blocks, we found strong evidence that stability of light availability fully or partially mediated the effects of invasion on stability of C_4 grass cover, and

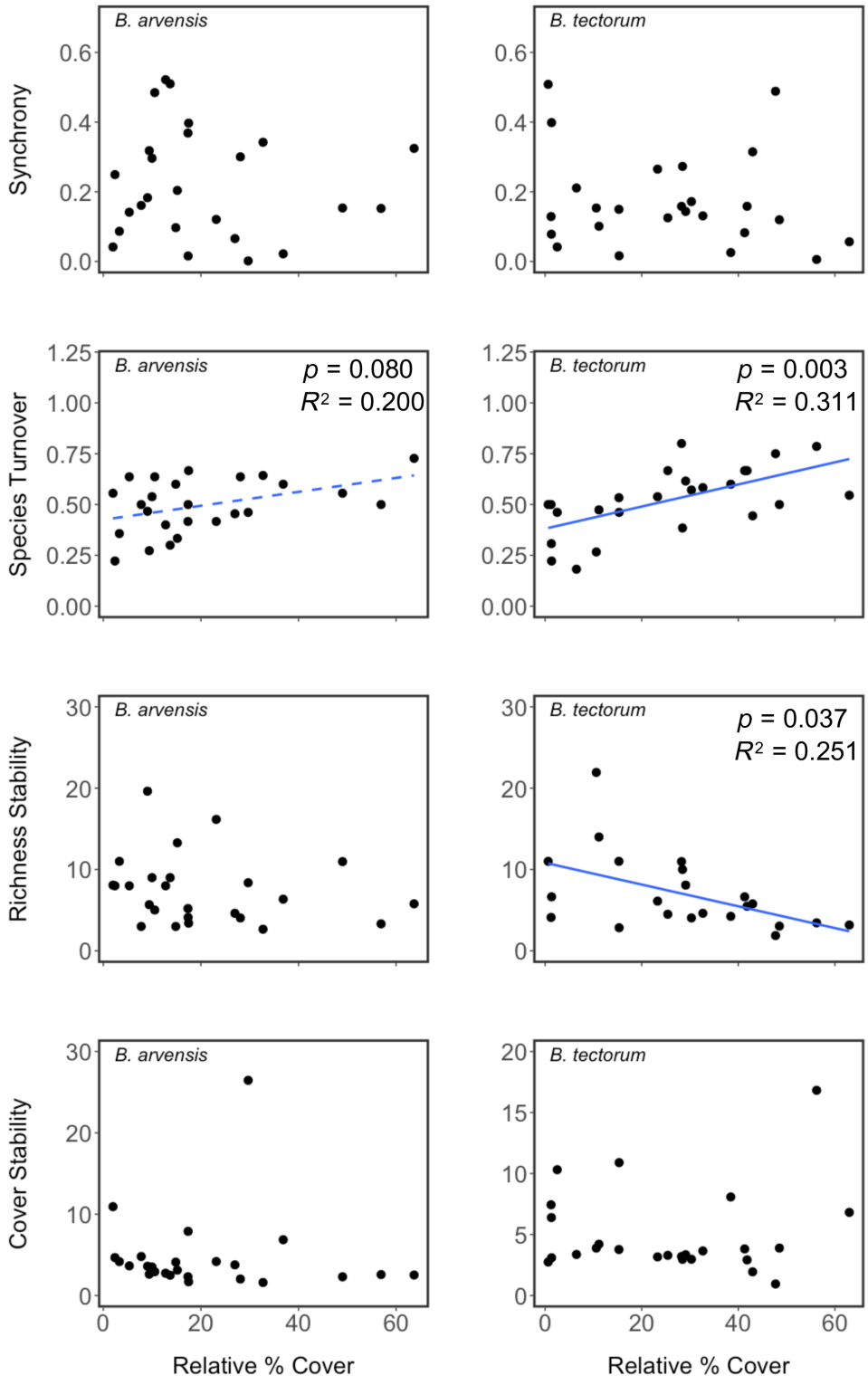


FIGURE 2 Changes in plant species synchrony, species turnover, richness stability, and total cover stability with relative invasion cover by *Bromus arvensis* and *Bromus tectorum*. Stability of richness and total cover, as well as turnover and synchrony, were calculated without respective brome data for each block type. The *p* values and marginal R^2 values for significant (solid lines) or marginally significant (dashed line) effects of invasion on stability metrics are shown according to results from mixed-model ANOVAs (Table 1).

weak evidence of this mediation on stability of forb cover. We also found weak support that soil moisture stability fully or partially mediated the effects of *B. arvensis* on stability of plant species richness. In the *B. tectorum* blocks, soil moisture stability strongly mediated the effects of invasion on stability of C_4 grass cover and

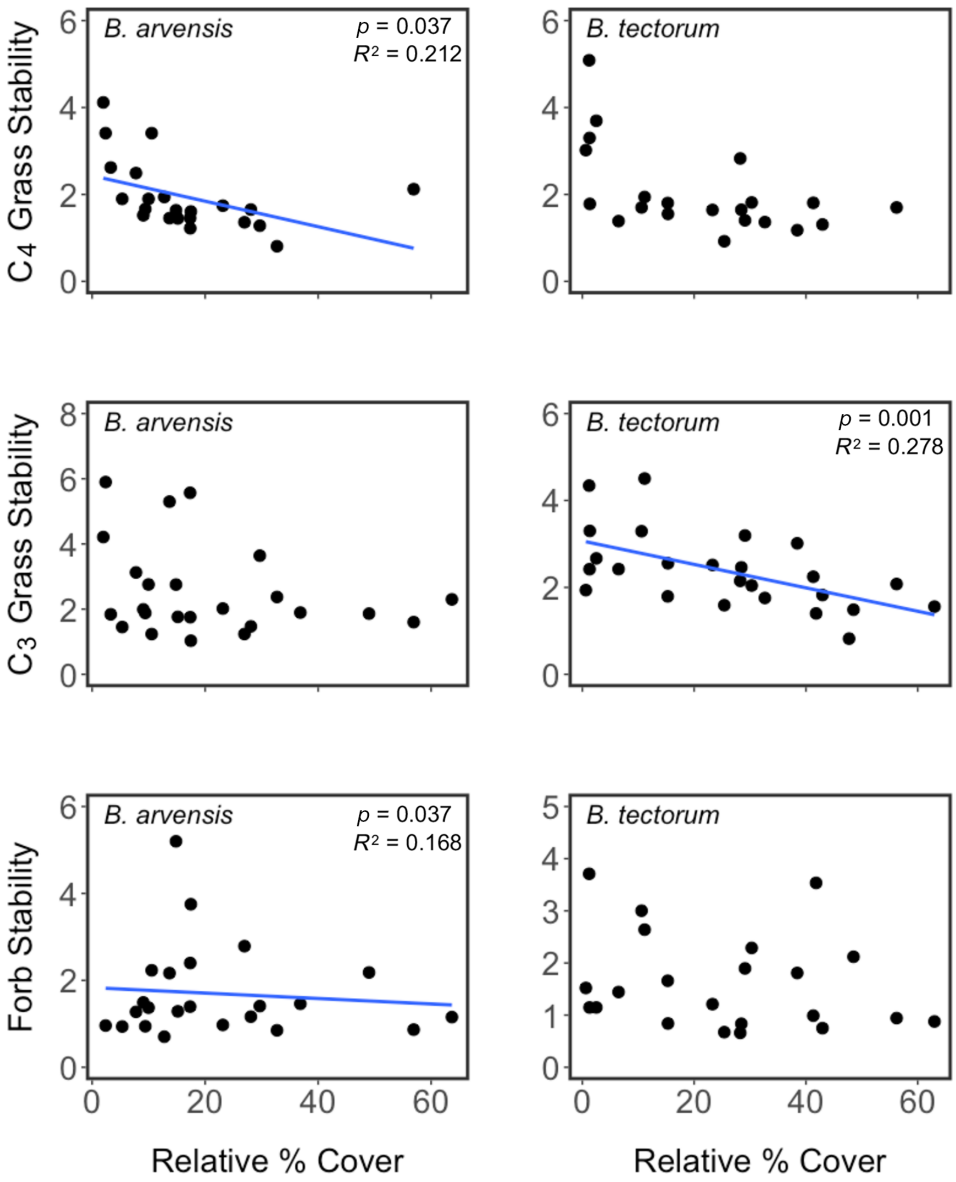


FIGURE 3 Changes in stability of C_4 grass, C_3 grass, and forb cover with relative invasion cover by *Bromus arvensis* and *Bromus tectorum*. Stability of C_3 grass cover was calculated without respective brome data for each block type. C_4 grass cover was largely dominated by one species, *Bouteloua gracilis*. The *p* values and marginal R^2 values for significant (solid lines) or marginally significant (dashed line) effects of invasion on stability metrics are shown according to results from mixed-model ANOVAs (Table 1).

weakly mediated the effects of invasion on forb cover stability (Table 3; Appendix S1: Table S2).

In the *B. arvensis* blocks, we also found evidence that average light availability fully mediated invasion effects on C_4 grass stability and fully or partially mediated the effect of invasion on forb stability, though support for this was weaker. Further, we found strong support that average soil moisture fully or partially mediated invasion effects on richness stability. In *B. tectorum* blocks, we found strong support that average soil moisture fully or partially mediated the effects of invasion on C_4 grass stability and forb stability (Table 3; Appendix S1: Table S2).

DISCUSSION

Overall, we found multiple metrics of plant community stability to be associated with brome invasion. Importantly, when any stability metric was altered, invasion was associated with a destabilizing effect on the plant community. This is consistent with prior research, where greater dominance by bromes produces less stable native plant abundance (Germino et al., 2016). Richness stability was associated with *B. tectorum* invasion. Richness is often associated with a stable, negative relationship with invasion, though there is evidence that the effect of invasion on native richness is declining across certain taxa,

TABLE 3 Mediation tests to assess support for direct and indirect effects of invasive annual bromes on plant community stability (see also Appendix S1: Table S2).

Question	Metric	Conclusion
(A) Is the effect of *Bromus arvensis* invasion on X mediated by abiotic variables (light **stability**, soil moisture **stability**)?	Synchrony	No conclusion
	Species turnover	No conclusion
	Richness stability	Fully or partially mediated by soil moisture stability
	Cover stability	No conclusion
	C4 grass stability	Fully or partially mediated by light stability
	C3 grass stability	No conclusion
	Forb stability	Fully or partially mediated by light stability
(B) Is the effect of *Bromus tectorum* invasion on X mediated by abiotic variables (light **stability**, soil moisture **stability**)?	Synchrony	No conclusion
	Species turnover	No conclusion
	Richness stability	No conclusion
	Cover stability	No conclusion
	C4 grass stability	Fully mediated by soil moisture stability
	C3 grass stability	No conclusion
	Forb stability	Fully or partially mediated by soil moisture stability
(C) Is the effect of *B. arvensis* invasion on X mediated by abiotic variables (**average** light, **average** soil moisture)?	Synchrony	No conclusion
	Species turnover	No conclusion
	Richness stability	Fully or partially mediated by soil moisture
	Cover stability	No conclusion
	C4 grass stability	Fully mediated by light
	C3 grass stability	No conclusion
	Forb stability	Fully or partially mediated by light
(D) Is the effect of *B. tectorum* invasion on X mediated by abiotic variables (**average** light, **average** soil moisture)?	Synchrony	No conclusion
	Species turnover	No conclusion
	Richness stability	No conclusion
	Cover stability	No conclusion
	C4 grass stability	Fully or partially mediated by soil moisture
	C3 grass stability	No conclusion
	Forb stability	Fully or partially mediated by soil moisture

Note: Mediator variables are (A, B) stability of light availability and soil moisture and (C, D) average light availability and soil moisture. Stability of richness, total cover, and C_3 grass cover, as well as turnover and synchrony, were calculated without respective brome data for each block type. The words stability and average were bolded to more clearly point out the differences between Questions A and B from Questions C and D.

including invasive plants (Crystal-Ornelas & Lockwood, 2020). The variation seen in stability changes could also indicate that at even low levels of invasion, we can predict changes to native plant stability, emphasizing the importance of near-total control of invasive annual bromes under certain management plans. However, not all measured metrics of plant community stability were altered by annual bromes. In some cases, temporal stability is not necessarily altered by changes to diversity, especially where the invasive species is dominant and shows high stability itself (Valone & Balaban-Feld, 2018). This could help partially explain our results, as annual brome cover stayed consistent throughout the study (Figure 1). Further, some results differed between species. In general, measures of stability were more strongly associated with invasion in *B. tectorum* blocks, suggesting that this species may be more disruptive to stability. While research comparing *B. arvensis* to *B. tectorum* is lacking, we suspect this species difference is partially due to the greater influence of *B. tectorum* on light availability preventing native species dominance. *B. tectorum* creates a dense, thick layer of vegetation, essentially blocking out most light available to lower lying vegetation. While *B. arvensis* is similar in blocking most light (Appendix S1: Figures S2 and S3) at the plot level, it does not create the same dense vegetation layer, allowing more light between

individual plants and lower lying species to coexist. While both species are managed actively in the Northern Great Plains region, *B. tectorum* is commonly considered one of the most problematic invasive species in the Western United States (DiTomaso et al., 2010).

In both *B. arvensis* and *B. tectorum* blocks, species turnover was related to brome abundance, demonstrating that even in the short term, invasion can shape community structure (Leibold et al., 1997). High species turnover can lead to deregulation of trophic structures (Leibold et al., 1997) and functional traits (Lepš et al., 2011). Decreases in C_4 grass (*B. arvensis* blocks), C_3 grass (*B. tectorum* blocks), and forb (*B. arvensis* blocks) cover stability with invasion suggest possible increases in variability of forage and pollination availability, as high abundances of native grasses and forbs improve forage production and pollinator diversity respectively on disturbance-adapted rangelands (Drobney et al., 2020; Shaw et al., 2005). In the *B. tectorum* blocks, decreases in richness stability could indicate that invasion is associated with greater variability in biodiversity. Dominance by invasive bromes can lead to differences in plant community composition, compared with native dominated communities, causing consequences for both above- and belowground properties of rangeland ecosystems (Duncan et al., 2004; Gasch et al., 2013). These increases in variability are important for rangeland utility, as ranchers rely on native forage to graze livestock (Haferkamp et al., 2001). Further, the linear relationships found between stability and invasion abundance may serve as a target reference point for managers to implement control strategies.

In several cases, our mediation tests showed that relationships between invasion and plant community stability were mediated by abiotic factors. For example, in both brome blocks, C_4 grass cover stability and forb cover stability were mediated by light (*B. arvensis* blocks) or soil moisture (*B. tectorum* blocks). Annual bromes can alter microclimatic conditions, in turn affecting plant community composition (Ogle, 2000). C_4 grass success often depends on moderate-high light (Still et al., 2003) and is influenced by soil moisture (Nie et al., 1992). Similarly, forb success is related to soil moisture (Fay & Schultz, 2009) and light (Turner & Knapp, 1996), so it is expected that the relationship between invasion and stability of C_4 grass cover and forb cover is mediated by soil moisture and light. Understanding direct and indirect responses to invasion is important, as resistance and response to invasion are highly related to the environment (including climate and soil properties) (Chambers et al., 2014). Generally, higher native species stability, especially that of dominant forage species, corresponds to higher resistance to invasive annuals, even on disturbed rangelands (DiTomaso et al., 2010). Conversely, continued spread and impact of invasion on native communities are also related to environmental factors. For instance, high summer precipitation can increase resistance to brome invasion, but high variability in soil moisture with low perennial cover can lead to further invasion (Chambers et al., 2007). Further, brome dominance is related to high light availability, while low irradiance hinders brome establishment (Bookman & Mack, 1983; Pierson et al., 1990).

For other stability metrics, we were unable to draw conclusions about the direct or indirect effects of invasion on plant community stability. In particular, we were unable to attribute the relationship between invasion and C_3 grass stability to light or soil moisture, possibly because other, unmeasured variables more strongly contribute to this relationship, such as soil nitrogen availability (Vasquez et al., 2008). Nevertheless, it is also notable that we did not find strong evidence of direct effects (unmediated by abiotic factors) for any metric. Conflict in AIC_c values and estimate significance suggests that there is not enough evidence in a particular pathway to determine direct versus indirect effects. Biologically, this is likely due to confounding, unmeasured factors that more strongly influence each stability metric. Full versus partial mediation implies whether the mediator (light or soil moisture) fully explains the association between stability and invasion, or if other factors also need to be considered. Because these exploratory analyses were conducted with an observational field study, a more controlled experimental manipulation would be useful to tease apart the direct and indirect effects of invasion on stability. We also acknowledge that these analyses represent a first attempt at exploring mediation between stability and annual brome invasion. Additional factors, such as increased sample size, sampling from different time points (especially moisture through time), and addition of other environmental mediators such as soil nitrogen, would likely be beneficial in deciphering how stability is influenced by bromes. Despite these limitations, mediation analyses may allow us to better predict forage and biodiversity under given environmental conditions.

Interestingly, over this 3-year study, the blocks of invasion abundance held, suggesting *B. arvensis* and *B. tectorum* abundance in each plot was relatively constant. The first year of the study, 2019, was a relatively wet year, while year two, 2020, was a relatively dry year, and year three, 2021, had near average precipitation (Appendix S1: Figure S1). Yearly brome abundance tends to be greatly associated with precipitation (Bradley et al., 2016), so it is somewhat surprising that invasion abundance held so constant given these differences in yearly precipitation. However, bromes tend to be more heavily influenced by fall/winter/spring precipitation

(Bradley et al., 2016), which had less variability over the course of the study than later spring/summer precipitation (Appendix S1: Figure S1).

To our knowledge, this study is the first to explore possible influences of annual bromes, especially the understudied *B. arvensis*, on stability metrics. This study also addresses both familiar and novel metrics of stability, including a first attempt to understand how environmental variables mediate annual bromes' influence on stability. Understanding how temporal stability changes with invasion has important consequences for ecosystem services like food security, and even restoration potential of invaded range. Native plant production is critical to range-fed livestock. The forage quality of invasive annual bromes is known to peak early in the growing season and decline rapidly relative to native vegetation, which can negatively impact livestock performance and animal mass gain (Haferkamp et al., 2001). In addition, invasion by annual species, coupled with year to year variability in climate, can impact restoration success, as unstable native cover may lead to long-term changes in soil properties (Mahood et al., 2022). In general, we found that annual bromes were associated with destabilization of plant communities, including metrics associated with native forage (stability of C_3 grass, C_4 grass, and forb cover). Therefore, annual brome invasion may increase the need for adaptive management to cope with increased interannual variability in forage quantity and quality (Monaco et al., 2016), as this may have unforeseen consequences for the livelihoods of billions of people worldwide who depend on working rangeland (Sayre et al., 2013).

AUTHOR CONTRIBUTIONS

Morgan D. T. Frost and Sally E. Koerner designed the study. Morgan D. T. Frost conducted the study and all analyses. Morgan D. T. Frost wrote the manuscript, and all authors advised on analyses and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code and data (Frost et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.13760295.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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