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ORIGINAL PAPER

The hotter the better: high mean annual temperature, not seed predation, hastens the decline of invasive *Bromus tectorum*

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Abstract *Bromus tectorum* invasion degrades biodiversity and ecosystem functioning in the Great Basin Desert. To explain, predict, and manage *B. tectorum* invasion, we must understand the biotic and abiotic factors that influence its establishment and persistence. We explored interactions between two key constraints for invaders in general and *B. tectorum* in particular: post-dispersal seed predation and climate, including mean annual temperature, rainfall, snowfall, and aridity. At six study sites in undisturbed, climax *Artemisia tridentata* communities across northern Nevada and Utah, we performed one-time additions of 100 *B. tectorum* seeds to microsites outfitted with either a dummy ("open") cage that exposed seeds to rodent foraging, or a functional ("closed") cage that protected them from rodent foraging. Living *Bromus tectorum* plants within experimental cages were censused one and 5 years after seed additions. At both 1- and 5-years censuses, and regardless of climate, *B. tectorum* densities were similar in open and closed microsites, suggesting that rodent foraging did not affect *B. tectorum* establishment or persistence. Compared to 1-year censuses, *B. tectorum* counts declined by 47% across all sites after 5 years, but declines were sharpest at sites with the highest mean annual temperatures. Taken together, our findings suggest that undisturbed, climax *A. tridentata* communities can resist *B. tectorum* expansion, and this resistance increases with mean annual temperature, not rodent foraging. We suggest that controlling nascent populations of *B. tectorum* may be particularly urgent in intact climax *A. tridentata* communities in relatively cool climates, where community-level resistance against *B. tectorum* persistence is lowest.

Keywords *Bromus tectorum* · Biotic resistance · Environmental constraints hypothesis · Great Basin Desert · Granivory · Invasion resistance · Seed predation · Sagebrush steppe · Rodents

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Introduction

Invasive, non-indigenous plant species are important drivers of biodiversity loss around the world (Vilá et al. 2011), and despite efforts for their control,

continue to spread and impact native communities. Invasion success strongly depends on the introduced plant's ability to successfully establish and persist in recipient communities (Blackburn et al. 2011; Jeschke 2014). Thus, quantifying establishment and persistence in uninvaded environments has important implications for the ecology and management of invasive plant species and at-risk communities (Crystal-Ornelas and Lockwood 2020). For example, passive management strategies (Byun et al. 2018) may be viable when recipient communities are resistant enough to limit the establishment, persistence, and increase of invasive populations (Levine 2004), whereas active management may be required in native communities that are less resistant (Stanley et al. 2011; Assis et al. 2020). In this context, understanding which and to what extent biotic and abiotic factors contribute to community-level resistance against invasive plant species is essential.

Many investigations of biotic resistance have focused on the effects of native plant diversity, with species-rich communities tending to resist exotic invasion better than depauperate ones (Maron and Marler 2007, Mwangi et al. 2007; but see Smith and Côté 2018). For instance, experimental plant assemblages with high diversity (up to 16 species) effectively resisted *Centaurea maculosa* invasion under both low- and ambient-water resource availability (Maron and Marler 2007), whereas *C. maculosa* reduced native biomass by an average of 51% when introduced to native monocultures, regardless of water or nutrient availability (Maron and Marler 2008).

Abiotic factors also have strong effects on invasion success, and changes in temperature, precipitation, and aridity can alter the outcome of biotic interactions among exotics and natives (Har-Edom and Sternberg 2010; Lyseng et al. 2018; Giejsztowt et al. 2019; Lucero et al. 2022). For example, Van Dyke et al. (2022) observed that a 20% reduction in precipitation altered the outcome of competitive dynamics in favour of exotics in a California grassland community, while increasing aridity reduced the establishment and persistence of invasive *Erigeron (Conyza) canadensis* in a Mediterranean ecosystem (Har-Edom and Sternberg 2010; see also Leicht-Young et al. 2007). Understanding the effects of climate on plant invasions is vital because the large majority of exotic invasive plant species do not occupy the same climates in their native and non-native ranges, with some moving into entirely different biomes (Atwater et al. 2017).

Consumer pressure can also resist invasions (Levine et al. 2004; Pearson et al. 2011; Kiss et al. 2022). This is somewhat counterintuitive because exotic invaders often encounter fewer or less potent consumers in their non-native ranges relative to their native ranges (Agrawal et al. 2005; Kulmatiski et al. 2008; Heger and Jeschke 2014; Sun et al. 2023). However, native consumers can mount strong biotic resistance against exotic invaders. For example, Pearson et al. (2011) showed that post-dispersal seed predation (granivory) by native rodents strongly reduced exotic *Tragopogon dubius* establishment in intermountain grasslands, which may at least partially explain why this species is rarely classified as "invasive" in the United States (Invasive Plants Atlas of the United States 2018). On the other hand, others report that native granivores predate on exotic seeds less frequently than coexisting native seeds (Maron et al. 2012). Thus, understanding how climate and consumers interact to resist invasion, or not, could help land managers focus their efforts where community-level resistance is low.

Bromus tectorum invasion in the Great Basin Desert presents opportunities for understanding how biotic and abiotic factors influence the establishment and persistence of invasive plant species. Sage-steppe communities throughout the Great Basin have suffered wide-scale degradation from the spread of *Bromus tectorum*, which currently dominates over a third of this system (Noss et al. 1995; Bradley et al. 2005; USDOI 2015; Bradley et al. 2018; Davies et al. 2021). As such, it imposes strong ecological and economic impacts (Knapp 1996; Crawford et al. 2004; Davies 2011; Sheley et al. 2014; Fantle-Lepczyk et al. 2021; Maher et al. 2023). Many biotic and abiotic factors contribute to *B. tectorum* invasion, including a highly plastic phenology allowing it to capitalize on favourable growth conditions (Ploughe et al. 2020), superior competitive ability relative to native neighbours (Harris 1967, Smith et al. 2008; Besaw et al. 2011), invasive grass-fire cycles (Brookes et al. 2004; Balch et al. 2013; Fenesi et al. 2016; Fernandez-Guisuraga et al. 2023), and positive associations with native shrubs that ameliorate environmental stress (Griffith 2010; Lucero et al. 2021). *Bromus tectorum* has likely experienced enemy release from the effects of granivorous rodents (Lucero et al. 2019), but not all rodent

communities have the same effects on *B. tectorum* establishment. On the one hand, several studies have shown that native rodents in the Great Basin have minimal effects on *B. tectorum* but strongly limit the establishment of native plant species (Connoly et al. 2014; Lucero and Callaway 2018a, b). In other cases, however, rodent communities can mount strong biotic resistance against *B. tectorum* invasion (St. Clair and Bishop 2019). Regardless, we know very little about the effects of granivorous rodents on the longer-term persistence of *B. tectorum* beyond initial establishment. This may be exceptionally important because, as an annual, *B. tectorum* recruits prolifically and exclusively from seed each year.

Climate has a strong effect on the outcome of biotic interactions that affect community-level resistance against invasion (Greenlee and Callaway 1996; Suttle et al. 2007; Schweiger et al. 2010), but little is known of how climatic factors limit *B. tectorum* invasion at regional spatial scales. Germination of *B. tectorum* is restricted by freezing temperatures and drought, while optimal temperature (20 °C) and sufficient available water can promote a germination response close to 100% (Dosdall et al. 2024). For our system, experiments at fine spatial scales suggest that *B. tectorum* performs better under more mesic conditions (Prevéy and Seastedt 2015), but nothing is known about the extent to which climate mediates granivore effects on *B. tectorum*. While geospatial models have predicted likely areas for future *B. tectorum* expansion across the western United States (McMahon et al. 2021), we know relatively little about the climatic controls of biotic resistance against *B. tectorum* establishment and persistence. Indeed, failure to account for climatic variables may help explain divergent reports of rodent effects on *B. tectorum* in local communities (e.g., Lucero and Callaway 2018a, b vs. St. Clair and Bishop 2019). Addressing this gap is important for understanding invasions, and for informing management decisions on controlling emerging *B. tectorum* populations across heterogeneous landscapes and changing climates.

Our objective was to observe the individual and combined influence of native granivorous rodents and climate (annual rainfall, annual snowfall, aridity, and mean annual temperature) on the establishment and persistence of experimentally introduced *B. tectorum* populations 1- and 5-years post seed addition. We predicted that rodent foraging would have variable, site-specific effects on *B. tectorum* (Lucero and Callaway 2018a; Lucero et al. 2019, St. Clair and Bishop 2019), though we had no clear a priori predictions for how environmental context might mediate those effects. However, independently of rodent foraging, we predicted that *B. tectorum* establishment and persistence would be highest where growing conditions were most favourable, i.e., under the most mesic and least arid conditions (Prevéy and Seastedt 2015).

Materials and methods

Site description

The study took place at six sites located on public land in the Great Basin Desert, USA. Sites were located near Elko, NV; Golconda, NV; Jackpot, NV; McGill, NV; Vernon, UT; and Wheeler, NV (Fig. 3). The vegetation at all sites represented an undisturbed sagebrush community, with *Artemisia tridentata* as the dominant shrub species and native forbs and bunchgrasses occurring relatively sparsely across common patches of bare ground. Rodent communities were not directly surveyed, but we observed signs of rodents (burrows, tracks, etc.) at all sites. Importantly, previous work near our study sites has detected robust small mammal communities with strong potential to influence plant community organization through foraging (Lucero et al. 2015, St. Clair et al. 2016, Bowman et al. 2017, Lucero and Callaway 2018a). Invasive species at the sites were visually estimated to be 5% cover or less using an ocular method (Helm and Mead 2004). To assure spatial independence of study sites, was all sites were separated by at least 120 km. For each site, we recorded GPS coordinates, elevation (m), mean annual rainfall (mm), mean annual snowfall (mm), mean annual temperature (°C), and aridity over the 6-years period (2015–2020) of the study. We focused on climatic values for the study period, not long-term averages, because long-term climatic trends are less relevant than current trends to the life history of annual species like *B. tectorum*. We estimated aridity with de Martonne's (1920) index (A_dM):

$$A_dM = \frac{P}{MAT + 10}$$

where P is total annual precipitation (rain and snowfall combined) for a given year, and MAT is the mean annual air temperature over that same year. Thus, low A_dM values indicate high aridity. This widely used index is without units. Climate data were obtained from the National Oceanic and Atmospheric Administration (NOAA) database, sourced from the NOAA weather station closest to each site. GPS, elevation, and climate data are summarised in Table 1.

Experimental setup

Bromus tectorum seeds were collected by hand in July 2010 in Rush Valley and Skull Valley, UT, USA. Cylindrical rodent exclusion cages (30 cm in diameter × 30 cm in height) were constructed of 1 cm mesh hardware cloth and included a floor and roof to prevent rodents from climbing or burrowing into the cages. The cages were installed by removing 4 cm of topsoil and then placing the cage into the shallow pit. The cages were then secured to the ground using 13 cm-long sod staples, and once secured, the excavated soil was replaced on top of the cage floors. The cages were installed in August 2015, and simultaneously 100 *B. tectorum* seeds were sown in each cage by hand scattering and patting the seeds into the top 5 mm of the soil profile. This method was selected as lightly buried seeds are relatively inaccessible to invertebrate and avian granivores, while rodents can still find and remove buried seeds via olfaction (Kamil and Balda 1985). The cages were randomly selected to be functional (closed cages that effectively excluded granivores) or non-functional (open cages that admitted granivores through one 7 × 7 cm hole cut into the cage wall). Additionally, a control treatment was installed using a functional (closed) cage and no seed addition, in order to monitor recruitment from the seedbank. Collectively, a closed, open, and control cage each spaced approximately 1 m from one another comprised a subplot. We replicated five subplots per study site, and sub-plots were separated by 50 m.

Data collection

Following the installation of the cages and seed sowing in August 2015, sites were left undisturbed leaving *B. tectorum* to complete its annual life cycle under wild conditions. Living *B. tectorum* individuals were counted in August 2016 (Lucero and Callaway 2018a, b) and again in August 2020.

To prevent new *B. tectorum* populations establishing outside of cages, at both the 2016 and 2020

Table 1 Latitude, longitude, elevation (m), mean annual rainfall (mm) (MAR), mean annual snowfall (mm) (MAS), mean annual temperature (°C) (MAT), and de Martonne aridity (AdM; see Methods for formula) for each site during the study period (2015–2020)

Site	Lat.	Long	Elevation (m)	MAR (mm)	MAS (mm)	MAT (°C)	A_dM
[a]Elko	41.06274	− 115.82829	1891	349 (31)	1179 (195)	8.78 (0.09)	18.6
[b]Golconda	40.91317	− 117.39893	1584	249 (24)	623 (118)	10.75 (0.12)	12.0
[c]Jackpot	41.93206	− 114.73369	1679	195 (19)	517.652 (120.607)	7.30 (0.24)	11.3
[d]McGill	39.62455	− 114.72939	1959	210(33)	879.348 (149.738)	9.300 (0.299)	10.865
[e]Vernon	40.12452	− 112.51788	1692	441.096 (34.227)	1871.98 (243.076)	11.461 (0.178)	20.553
[f]Wheeler	39.02270	− 114.44784	1801	347.624 (19.984)	1825.752 (274.262)	9.1663 (0.126)	18.137

Values in parentheses indicate SE. Superscripts give the source of climate data, all accessed July 3, 2020. See Fig. 3 for a map of the study sites

[a]https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00262570/detail

[b]https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USW00024128/detail

[c]https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00264016/detail

[d]https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00264950/detail

[e]https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00428771/detail

[f]https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00263340/detail

Table 2 Results of independent one-sample t-tests and linear mixed-effects models that tested for differences in *B. tectorum* counts in 2020 versus 2016 at each site (t-tests) and across all ("All") sites (linear mixed-effects models) (see Table 2 for formula)

Site	Treatment	Δ *B. tectorum* (2020–2016)	SE	df	*t*-value	*P*-value
Elko	Closed	−1.000	3.647	4	−0.274	0.796
	Open	0.000	4.359	4	0.000	1.000
	Control	0.600	0.400	4	1.500	0.208
	Total	−0.400	7.891	4	−0.051	0.962
Golconda	Closed	−10.000	0.707	4	−14.142	< 0.001
	Open	−9.600	1.249	4	−7.686	0.002
	Control	0.000	0.000	4	N/A	N/A
	Total	−19.600	1.661	4	−11.798	< 0.001
Jackpot	Closed	0.600	2.561	4	0.234	0.826
	Open	−2.600	2.040	4	−1.275	0.271
	Control	1.200	1.200	4	1.000	0.374
	Total	−0.800	4.800	4	−0.167	0.876
McGill	Closed	−7.400	0.400	4	−18.500	< 0.001
	Open	−7.800	0.374	4	−20.746	< 0.005
	Control	0.000	0.000	4	N/A	N/A
	Total	−15.200	0.583	4	−26.068	< 0.001
Vernon	Closed	−5.600	1.965	4	−2.850	0.046
	Open	−5.200	1.281	4	−4.061	0.015
	Control	2.000	1.049	4	1.907	0.129
	Total	−8.800	3.734	4	−2.357	0.048
Wheeler	Closed	−3.800	2.154	4	−1.764	0.153
	Open	−5.800	0.970	4	−5.982	0.004
	Control	0.000	0.000	4	N/A	N/A
	Total	−9.600	1.327	4	−7.236	0.002
All	Closed	−4.533	1.619	5	−2.800	0.038
	Open	−5.167	1.417	5	−3.645	0.015
	Control	0.633	0.336	5	1.883	0.118
	Total	−9.067	3.122	5	−2.904	0.034

censuses, we hand collected and destroyed any *B. tectorum* plants growing within 2m of the cages. This method has prevented *B. tectorum* invasion following other seed addition experiments in the Great Basin (Lucero et al. 2015).

Statistical analysis

Analyses were conducted using R-Studio software. We used relative interaction indices (RIIs; Armas et al. 2004) as an effect size measure to estimate the sign and intensity of rodent effects on *B. tectorum* counts. We calculated RIIs as follows:

$$RII = \frac{B_o - B_c}{B_o + B_c}$$

where B_o was the count of *B. tectorum* individuals in non-functional cages open to rodent foraging, and B_c was the count of *B. tectorum* individuals in functional cages closed to rodent foraging. We subtracted the number of *B. tectorum* plants in control cages from the number in open or closed cages to account for seed bank recruitment. RII values range from −1 to +1. Negative RII values would indicate negative effects of rodent foraging on *B. tectorum* counts, positive values would indicate positive effects, and

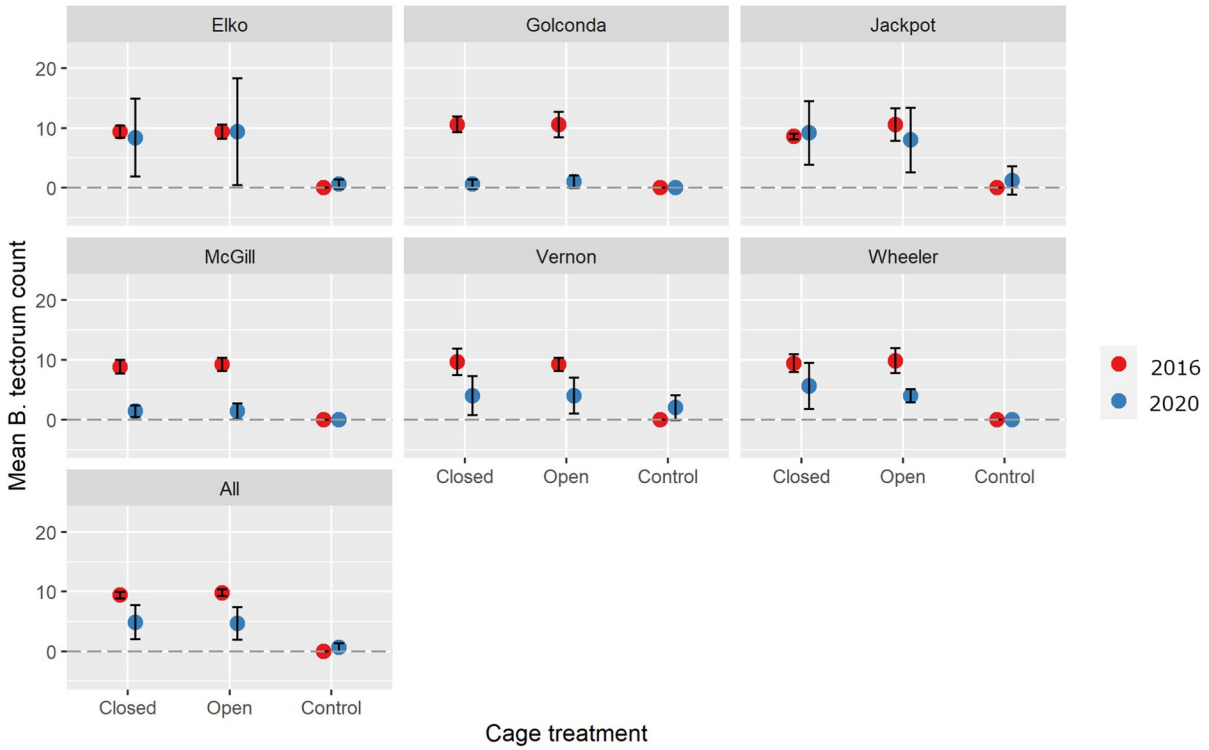

Fig. 1 Mean ± 95% CI for *Bromus tectorum* counts (no. living individuals) in closed, open, and control cage treatments at each study site and across all sites combined ("All") in 2016 (see also Lucero and Callaway 2018a, b) and 2020

a value of 0 would indicate no effect. We used one-sample *t*-tests with RII (adjusted for seed banks) as the response variable to test whether rodent effects on *B. tectorum* counts differed from zero at each site and across all sites for 2016 and 2020.

To evaluate 5-years persistence of experimental *B. tectorum* populations, we used *t*-tests and linear mixed effects models to test whether *B. tectorum* counts changed from 2016 to 2020. For each cage treatment (open, closed, control) and across all cage treatments, we calculated 5-years changes in *B. tectorum* counts (Δ *B. tectorum*) as follows:

$$\Delta B.\,tectorum = B.\,tectorum_{2020} - B.\,tectorum_{2016}$$

where *B. tectorum*$_{2020}$ was the count of *B. tectorum* plants in 2020 and *B. tectorum*$_{2016}$ was the count in 2016. Thus, positive Δ *B. tectorum* values indicate a 5-years increase and negative values indicate a 5-years decrease. We used one-sample *t*-tests to test whether Δ *B. tectorum* values differed from zero within a study site, and we used linear mixed effects models to test whether Δ *B. tectorum* values differed from zero across all sites. *T*-tests and linear mixed-effects models (lme4 package in R; Bates et al. 2015) fit Δ *B. tectorum* in closed, open, control, or totaled across all cage treatments as the response variable. Linear mixed-effects models fit study site as a random effect.

We used linear mixed-effects models to examine the effects of climatic variation on 5-years changes in *B. tectorum* counts. These models fit Δ *B. tectorum* across all cage treatments as the response variable; annual rainfall, annual snowfall, de Martonne aridity, and mean annual temperature as fixed effects (each averaged at the site level over the study period); and study site as a random factor.

Results

Rodent foraging did not have a significant effect on *B. tectorum* establishment or persistence (Table 2). RII

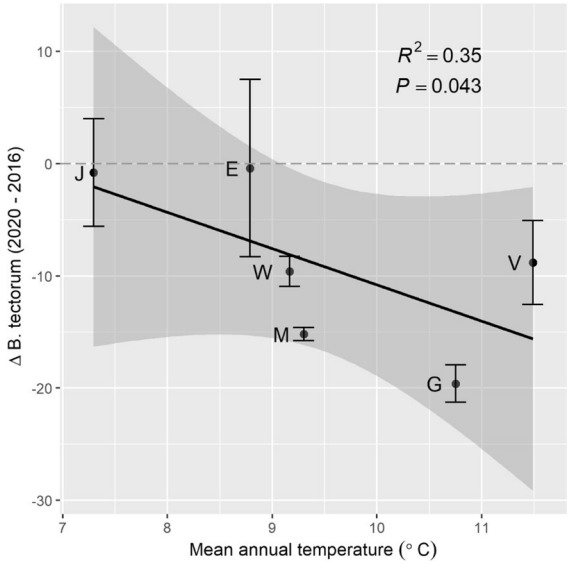

Fig. 2 Δ *B. tectorum* (see Table 2 for formula) regressed against the mean annual air temperature of each study site during the study period. Y-values below zero indicate that total *B. tectorum* counts were lower in 2020 than in 2016; the more negative, the greater the difference. Points and error bars show the mean (±95% CI) difference at each site. Letters identify study sites (see Fig. 3 for full names). The 95% confidence band for the regression is shaded; test statistics refer to the regression

Table 3 Results of a linear mixed effects model that regressed Δ *B. tectorum* against environmental covariates

Environmental factor	Df	F-value	*P*-value
Mean annual rainfall	1, 25	1.683	0.206
Mean annual snowfall	1, 25	1.819	0.189
Mean de Martonne aridity	1, 25	0.858	0.363
Mean annual temperature	**1, 25**	**4.553**	**0.043**

All models used Δ *B. tectorum* (Δ *B. tectorum* = [*B. tectorum* count in 2020] – [*B. tectorum* count in 2016]) for each cage treatment (closed, open, control) and summed across all treatments ("Total") as the response variable, and linear mixed-effects models used site as a random effect. "N/A" values are due to zero 5-years variation in *B. tectorum* counts. Δ *B. tectorum* was the response variable; mean annual rainfall, mean annual snowfall, mean de Martonne aridity, and mean annual temperature were fixed factors (each averaged over the study period); and study site was a random factor. Numerator and denominator degrees of freedom ("Df") are separated by commas. The significant regression appears in bold

values did not differ from zero at any site or across all sites in 2016 or 2020 (Table 2; note that all $P \geq 0.20$).

Across all sites, *B. tectorum* counts declined from 2016 to 2020, but declines were sharpest at the hottest sites (Fig. 1). More specifically, across all sites, *B. tectorum* declined 4.5 ± 1.6% in closed cages, 5.2 ± 1.4% in open cages, and 9.1 ± 3.1% across all cage treatments in 2020 relative to 2016 (Table 2). *Bromus tectorum* counts did not change from 2016 to 2020 in control cages at any site (Fig. 1, Table 2). As the mean annual air temperature for a site increased, Δ *B. tectorum* decreased ($P = 0.043$) (Fig. 2). We found no significant relationships between Δ *B. tectorum* and annual rainfall, annual snowfall, or de Martonne aridity (Table 3).

Discussion

High relative temperature, not rodent foraging, hastened the decline of *B. tectorum* counts in undisturbed sage-steppe communities across the Great Basin. Our results are consistent with others showing that granivorous rodents have no effects on initial *B. tectorum* establishment (Connolly et al. 2014; Lucero and Callaway 2018a; Lucero et al. 2019), but extends these findings to longer-term persistence and potential for expansion. Encouragingly, we found no evidence of *B. tectorum* population expansion—*B. tectorum* counts declined across all sites combined over 5 years, and there was no expansion at any site. The largest population decline was observed at Golconda ($P = 0.043$) where mean annual temperature was amongst the highest of the study sites, whereas there was no significant decline (or increase) in counts over the 5 years at Elko and Jackpot, which were the two coolest sites. These results confirm reports that climax sage-steppe communities can mount strong resistance against *B. tectorum* expansion in the absence of disturbance (St. Clair et al. 2016, St. Clair and Bishop 2019). The success of *B. tectorum* in cooler climates has been attributed to its exceptional frost tolerance and early seasonal growth (Bykova and Sage 2012), which gives this weed priority access to resources (Morrow and Stahlman 1984).

Our cage treatments operated on all effects of rodents and could not distinguish between

granivory or folivory, but we found similar *B. tectorum* counts in open and closed cages at both the one- and 5-years censuses, suggesting no effects of rodents on either initial establishment or 5-years persistence. Thus, the 5-years declines in *B. tectorum* counts relative to first-year counts cannot be attributed to rodent foraging. In our mature *A. tridentata* communities, previous work has shown that rodents preferentially consume and impose stronger negative impacts on native grass species, including *Festuca idahoensis*, *Pseudoroegneria spicata*, *Elymus elymoides*, and *Achnatherum hymenoides*, than on *B. tectorum* (Lucero et al. 2015, 2019; Lucero and Callaway 2018a, b). However, these native species may not have been sufficiently rare at our study sites to incentivize rodents to switch to less-preferred *B. tectorum* seeds. In this context, disturbance—as an agent of native plant mortality—could have altered our results (St. Clair et al. 2016, St. Clair and Bishop 2019). Other studies have reported that native rodents in the Great Basin can, in fact, consume the aboveground biomass of *B. tectorum*, which can lead to reduced seed production (Pyke 1986). Newingham et al. (2007) found that herbivory reduced *B. tectorum* biomass and survival to a modest degree.

Our results suggest that intact sage-dominated systems free of recent disturbance can resist *B. tectorum*, at least at the scale of this study, and that this resistance may be greatest where mean annual temperature is highest. However, changes in the severity of disturbance events are likely to weaken community-level resistance and facilitate *B. tectorum* dominance (Bradford and Lauenroth 2006; Kroel-Dulay et al. 2015). Fire is of particular concern, as *B. tectorum* can rapidly establish following fire and then substantially increase fire frequencies afterwards (Balch et al. 2013; Davies and Nafus 2013; Bradley et al. 2018; Mahood and Balch 2019). Climate change-mediated increases in drought severity are also projected to reduce biotic resistance from native perennial grasses, potentially facilitating *B. tectorum* dominated state (Bradley 2009). If so, our data suggests that such effects may be most pronounced where native resistance is currently strongest—i.e., where mean annual temperatures are lowest. Therefore, it is critical to consider how climate change parameters may alter a community's ability to resist *B. tectorum* in order to prevent the further spread and impact of this invader (Kroel-Dulay et al. 2015).

Bromus tectorum is currently widely distributed throughout the Great Basin Desert where it has established dominant populations across a wide gradient of temperatures (Zeidali et al. 2021). Substantial ecotypic variation has arisen due to adaption to local conditions, which could facilitate ongoing persistence of particular ecotypes (Beckstead et al. 1996; Dosdall et al. 2024). This was supported by climate modelling conducted by Boyte et al. (2016), which suggested that areas that are currently most impacted by *B. tectorum* will continue to be the most problematic areas under projected future climate conditions in the Great Basin Desert.

Conclusion

Undisturbed, climax *A. tridentata* communities can resist *B. tectorum*, and this resistance increases with mean annual temperature and was not affected by rodents. As this study was limited in identifying broad, community-level biotic interactions that could contribute to *A. tridentata* community resistance, further experimental research on biotic resistance and abiotic covariates is needed. As it is anticipated that mountainous environments will warm by an estimated 2.5 °C within the next 20 years as a consequence of climate change (IPCC 2019), our findings provide insight and can contribute to climate-ready management strategies. We suggest that controlling nascent populations of *B. tectorum* may be particularly urgent for climax *A. tridentata* communities located at the cooler limits of *B. tectorum's* current invasive range, where community-level resistance against *B. tectorum* persistence is lowest.

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Availability of data and material The data that supports this study will be shared upon reasonable request to the corresponding author.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent to publication Not applicable.

Appendix

See Figs. 3 and 4.

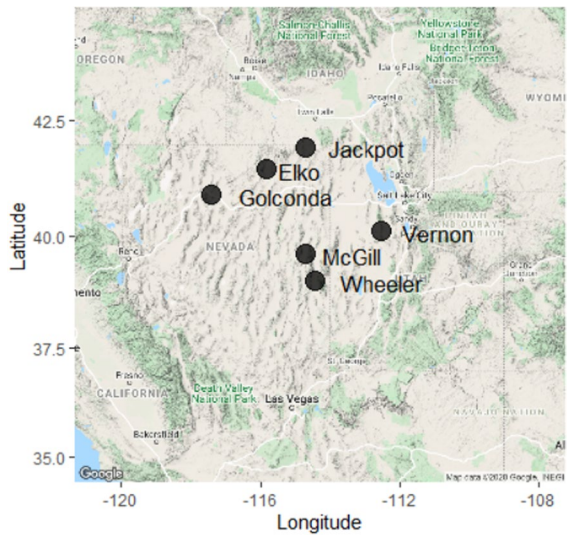

Fig. 3 Six sites used to experimentally test the potential for undisturbed shrub communities and vertebrate granivores in particular to provide biotic resistance against *Bromus tectorum* expansion

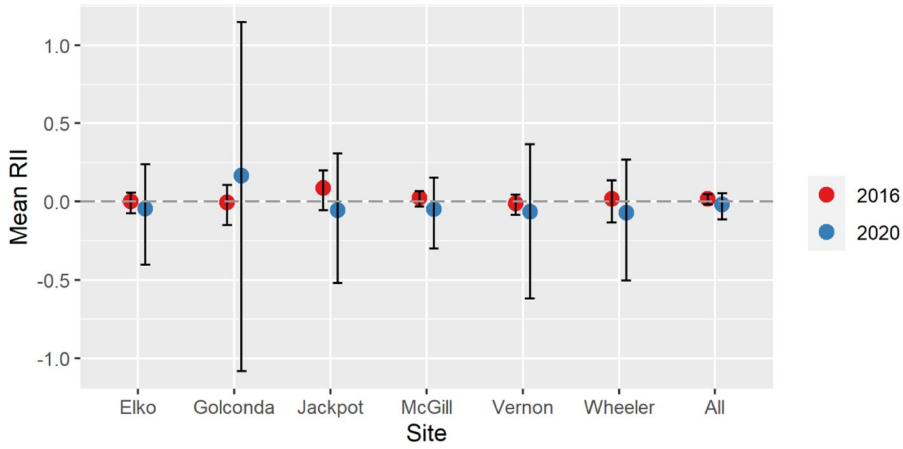

Fig. 4 Mean ± 95% CI for granivory (RII, adjusted for seed banks; see Methods) on *Bromus tectorum* counts at each site and across all sites ("All") in 2016 and 2020

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