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Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems

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Summary

1. Ecosystem invasibility is determined by combinations of environmental variables, invader attributes, disturbance regimes, competitive abilities of resident species and evolutionary history between residents and disturbance regimes. Understanding the relative importance of each factor is critical to limiting future invasions and restoring ecosystems.

2. We investigated factors potentially controlling *Bromus tectorum* invasions into *Artemisia tridentata* ssp. *wyomingensis* communities across 75 sites in the Great Basin. We measured soil texture, cattle grazing intensity, gaps among perennial plants and plant cover including *B. tectorum*, biological soil crusts (BSCs) and bare soil. Using *a priori* knowledge, we developed a multivariate hypothesis of the susceptibility of *Artemisia* ecosystems to *B. tectorum* invasion and used the model to assess the relative importance of the factors driving the magnitude of such invasions.

3. Model results imply that bunchgrass community structure, abundance and composition, along with BSC cover, play important roles in controlling *B. tectorum* dominance. Evidence suggests abundant bunchgrasses limit invasions by limiting the size and connectivity of gaps between vegetation, and BSCs appear to limit invasions within gaps. Results also suggest that cattle grazing reduces invasion resistance by decreasing bunchgrass abundance, shifting bunchgrass composition, and thereby increasing connectivity of gaps between perennial plants while trampling further reduces resistance by reducing BSC.

4. *Synthesis and applications*. Grazing exacerbates *Bromus tectorum* dominance in one of North America's most endangered ecosystems by adversely impacting key mechanisms mediating resistance to invasion. If the goal is to conserve and restore resistance of these systems, managers should consider maintaining or restoring: (i) high bunchgrass cover and structure characterized by spatially dispersed bunchgrasses and small gaps between them; (ii) a diverse assemblage of bunchgrass species to maximize competitive interactions with *B. tectorum* in time and space; and (iii) biological soil crusts to limit *B. tectorum* establishment. Passive restoration by reducing cumulative cattle grazing may be one of the most effective means of achieving these three goals.

Key-words: bare ground, biological soil crusts, cattle grazing, disturbance, diversity, invasion, plant gaps

Introduction

Ecosystem invasibility is governed by a complex collection of biotic and abiotic factors including environmental conditions, disturbance regimes and responses of native species to those regimes, as well as the biotic resistance provided by the resident community (Lonsdale 1999; Richardson & Pysek 2006). Biotic resistance is especially important in limiting the magnitude of invasive species after they have established (Levine, Adler & Yelenik 2004). Changes that increase resource availability are likely to increase susceptibility to invasion (Davis, Grime & Thompson 2000). Further, the introduction of an exotic herbivore with which resident species have no

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evolutionary history may exacerbate the magnitude of non-native plant invasions if it reduces the competitive abilities of native plants and increases resource availability (Parker, Burkepile & Hay 2006). Developing a predictive understanding of invasibility requires that we develop an understanding of how the various factors work together to limit invasion (Agrawal *et al*. 2007).

Artemisia tridentata big sagebrush ecosystems of the Intermountain West, USA, evolved with little herbivore pressure until the introduction of livestock (Mack & Thompson 1982). Within these ecosystems, lower elevation, more arid, *A. tridentata* ssp. *wyomingensis* (henceforth *Artemisia*) communities are the most common, but least resistant to invasion by exotic annual plants and least resilient to disturbance (Miller *et al*. 2011). Even in the absence of fire, these communities are especially vulnerable to invasions by *Bromus tectorum* L, and under some circumstances, *B. tectorum* can dominate the herbaceous understorey community (Miller *et al*. 2011). Previous studies have demonstrated the importance of several factors in the invasion process (soil texture, landscape orientation, competition-driven biotic resistance from native bunchgrasses and biological soil crust (BSC) communities (Table 1). Livestock grazing has been implicated in the spread and dominance of *B. tectorum* via several mechanisms (Mack & Thompson 1982; Table 1). Nonetheless, we have a poor understanding of how these factors work together and their relative importance in determining the magnitude of *B. tectorum* invasions (Miller *et al*. 2011).

Once *B. tectorum* sufficiently dominates the understorey and fills interspaces among plants, it creates a continuous, highly flammable fuel that significantly increases the risk of fire (Pyke 2011). Once a fire occurs, *B. tectorum* increases the frequency of fires. This change in fire regime may lead to a 'catastrophic regime shifts' (Scheffer *et al*. 2009), whereby native shrub–steppe communities are transformed into annual grasslands dominated by *B. tectorum* and other invasives (Miller *et al*. 2011). For practical purposes, these shifts are irreversible because of the significant investments necessary to restore these systems (Pyke 2011).

Preventing such regime shifts will require a better understanding of the simultaneous interacting factors that determine the magnitude of *B. tectorum* invasion once it has established in pre-fire *Artemisia* communities (Miller *et al*. 2011). Managers would benefit from understanding the causal network of mechanisms by which these factors interact with each other and how they collectively influence *B. tectorum* dominance. They would also benefit from an early warning indicator that the cumulative resistance of the resident community has been compromised to the point that *B. tectorum* likely dominates the understorey and thereby potentially setting the stage for a regime shift with the next fire.

Using *a priori* knowledge, we developed a multivariate hypothesis of the invasibility of *Artemisia* ecosystems to *B. tectorum* invasion in the absence of fire based upon the findings of previous studies in this system. The model included abiotic (soil physical properties, landscape orientation), cattle grazing disturbance and biotic factors (resident community abundance, composition and structure), predicted to be important determinants of *B. tectorum* dominance (Fig. 1, Table 1). Our analyses addressed the following questions: (i) What combination of abiotic and biotic conditions limit the magnitude of *B. tectorum* dominance? (ii) Can shifts in community structure, measured by the size and connectivity of gaps between native plants, serve as an indicator of susceptibility to *B. tectorum*

Table 1. Components of hypothesis represented by initial metamodel (Fig. 1)

Path	Hypothesized mechanism
1	(−) Cattle herbivory decreases *Bromus tectorum* abundance (Hempy-Mayer & Pyke 2009). (+) Cattle increase abundance by dispersing seeds and increasing propagule pressure (Schiffman 1997)
2	Cattle trampling decreases biological soil crusts cover and increases safe sites for *B. tectorum* establishment (Ponzetti, McCune & Pyke 2007)
3	Cattle herbivory decreases bunchgrass abundance (Briske & Richards 1995)
4	Cattle herbivory alters bunchgrass community composition by favouring more grazing-resistant species (Briske & Richards 1995)
5	Higher heat loads and spring insolation increase *B. tectorum* abundance (Stewart & Hull 1949; Chambers *et al*. 2007)
6	Lower heat loads increase bunchgrass productivity (Davies, Bates & Miller 2007)
7	Deeper, coarser-textured soils increase *B. tectorum* abundance (Stewart & Hull 1949)
8	Changes in bunchgrass composition influence community structure because species have different life forms (Grime 1977; James *et al*. 2008)
9	Changes in bunchgrass composition influence invasibility because species have different competitive abilities (Goldberg & Barton 1992) and patterns of resource use (James *et al*. 2008)
10	Bunchgrass abundance is inversely related to the size of and connectivity between gaps in perennial vegetation (Herrick *et al*. 2005)
11	Native bunchgrass abundance decreases *B. tectorum* abundance by reducing resource availability (Chambers *et al*. 2007)
12	Safe sites increase *B. tectorum* establishment rates (Fowler 1988).
13	Sagebrush abundance may increase *B. tectorum* abundance via facilitation (Griffith 2010) or decrease abundance via competition (Reichenberger & Pyke 1990).
14	Increases in the size of and connectivity between gaps in perennial vegetation increase *B. tectorum* abundance by increasing general resource availability (James *et al*. 2008; Okin *et al*. 2009)

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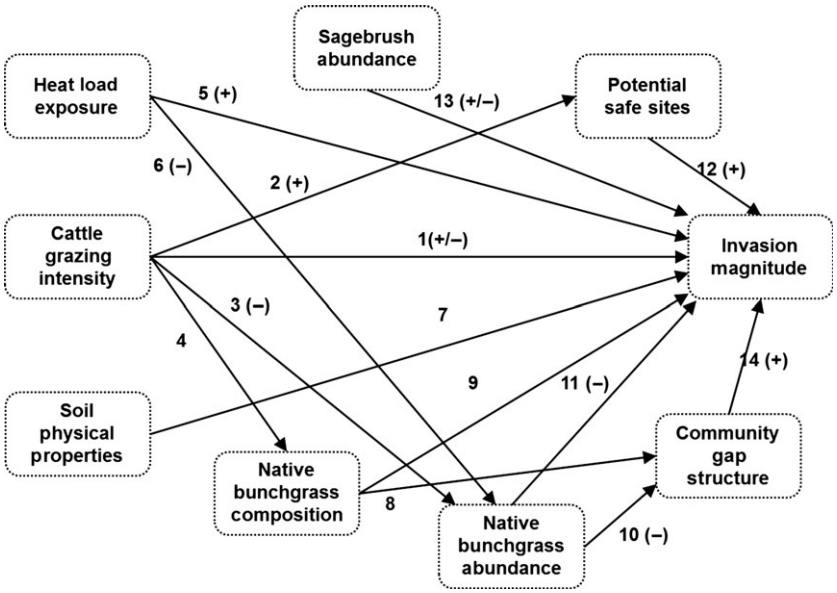


Fig. 1. Conceptual *a priori* multivariate model of *Artemisia* ecosystem susceptibility to *Bromus tectorum* dominance in the absence of fire. Dotted-line boxes represent conceptual variables hypothesized to influence invasibility. Components of the overall hypothesis are described in Table 1.

dominance and thereby vulnerability to a regime shift with the next fire?

We used structural equation modelling (SEM) to evaluate a multivariate hypothesis across 75 sites already invaded by *B. tectorum*. SEM provides a means of representing complex hypotheses about causal networks and testing for model data consistency (Grace 2006). It represents an advance over classical regression approaches (e.g. multiple regression) when used with observational data (Grace, Youngblood & Scheiner 2009). The advance provided by SEM comes partially from incorporating the associations among predictors into the overall hypothesis rather than to simply ignore or control for them. This is accomplished by extending the univariate model ($y = a + \beta x + \varepsilon$) to allow ys to depend on other ys and thereby represent networks of relationships in SEMs ($y = a + \beta x + \gamma y + \varepsilon$).

Because of this capability, SEM models can be used to specify hypotheses about mediating pathways and address questions, such as Can an association between A and C be explained by the factor B? This is achieved by evaluating a model such as $A \rightarrow B \rightarrow C$ and determining whether or not $r_{AC} = r_{AB} \cdot r_{BC}$. By assuming (and justifying based on prior information) that if A were manipulated, B could show a response, and similarly, if B were manipulated, C could show a response, then a test of the conditional independence of A and C in our example ($A \perp C|B$) could permit a result leading us to reject that possibility (A not independent of C when conditioned on B). SEMs thus build on causal assumptions to yield testable implications that can be evaluated with data. Estimated parameters obtained for a selected model then represent a set of predictions for further testing. The ultimate test of an SEM model is its ability to correctly predict future samples. For individual applications, the plausibility of causal assumptions (e.g. previous demonstrations that varying A can lead to response in B or known mechanisms whereby A can influence B) is often sufficient for reasonable inferences to be made.

Our results suggest that bunchgrass community structure, abundance and composition, and BSCs all play critical roles in limiting the magnitude of *B. tectorum* dominance. Cattle grazing may exacerbate the magnitude of invasion by reducing biotic resistance. Model evaluations imply that cattle grazing can reduce bunchgrass cover and shift bunchgrass community composition towards grazing-tolerant species and thereby increase the size and connectivity of gaps among perennial vegetation exacerbating invasion. Cattle trampling may also exacerbate invasion by reducing BSC cover. Ultimately, increases in the size and connectivity of gaps among native perennial vegetation may provide managers with an early warning indicator of increased susceptibility to *B. tectorum* dominance of *Artemisia* communities and thereby increased vulnerability to regime shifts in one of North America's most widespread but endangered ecosystems.

Materials and methods

STUDY AREA AND SAMPLING DESIGN

The study examined 75 *Artemisia* sites scattered across 4700 km^2 (roughly the size of state of Rhode Island) with elevations between 1265 and 1580 m across five *Artemisia*-dominated plant associations of the northern Great Basin floristic province of Oregon, USA. Natural Resource Conservation Service (NRCS) Ecological Site Descriptions and digital soil maps (http://websoilsurvey.nrcs.usda.gov) were used to ensure coverage of spatial variation in water stress driven by soil texture. Plant communities varied in dominant perennial tussock grasses and included the following ecological sites (ES): (i) loamy 254–308 mm precipitation zone (PZ) with *Pseudoroegneria spicata* and *Achnatherum thurberianum*; (ii) sandy loam 203–254 mm PZ with *Hesperostipa comata* and *P. spicata*; (iii) clayey 254–308 mm PZ with *A. thurberianum* and *Poa secunda*; and (iv and v) north slopes and south slopes 152–254 mm PZ with *P. spicata* and *A. thurberianum* co-dominating north and south slopes, respectively.

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Each ES was delineated into three landscape substrata using 10-m resolution US Geological Survey Digital Elevation Models (DEM) to ensure variation in heat loads and water stress associated with changes in landscape orientation: (i) northerly aspects (0–90°, 270–360°), (ii) southerly aspects (90–270°) or (iii) flat. Study plots were located at different distances from the nearest livestock watering locations to capture variation in cattle grazing intensity. Random points were selected and field verified to ensure that plots were located: (i) every 200–400 m, starting at 100 m and extending to >3200 m from the nearest water; (ii) in as many soil–landscape strata combinations as possible; and (iii) >200 m from the nearest road to minimize related effects. To reduce potential confounding effects of time since fire, all sites burned since 1930 were excluded using a fire perimeter data base (http://sagemap.wr.usgs.gov accessed 17/3/2008).

SAMPLING

Thirty of the 0·39-ha study plots were sampled in 2008 and another 45 in 2009. Six 25-m transects were established in each plot using a spoke design, and herbaceous, shrub and BSC cover measured using line–point intercept (Herrick *et al.* 2005). All sampling occurred between 10 May and 15 July in both years to capture peak herbaceous biomass. Aspect and slope of each plot were calculated from DEM using Arc-GIS 13·0 and, with latitude, used to calculate potential heat loads for each plot (McCune 2007).

Potential variation in water stress was inferred by the following measurements: (i) soil texture at 0–15 cm soil depth; (ii) potential effective rooting depth, which was measured by digging a soil pit until bedrock, a restrictive layer (clay accumulation layer) or 2 m depth was reached; and (iii) amount and timing of precipitation for each study site derived from PRISM at 2-km^2 cell resolution (Daly *et al.* 2008). Sampling-year precipitation for all study plots was estimated for three seasons: 1 August to 31 October (fall), 1 November to 31 March (winter) and 1 April to 31 July (spring–summer).

Cattle grazing intensity was quantified by four measurements: field-verified distance from the nearest water; dung frequency and dung density from 12, 1 × 25 m belt transects; and bunchgrass (tussock) basal area. Basal circumference (C) of 30 randomly selected bunchgrasses was measured in each plot and used to calculate bunchgrass basal area (cm^2) using the following formula: Area = $\pi\,(C/2\pi)^2$.

Bare soil cover was calculated using line–point intercept data to represent exposed soil surface not covered by vegetation, visible BSC, dead vegetation, litter or rocks (Herrick *et al.* 2005). Soil surface aggregate stability was assessed in interspace microsites at 18 random sampling points along transects using soil from the upper 0–4 mm (Herrick *et al.* 2005). Two indicators of soil erosion resistance were calculated: mean soil stability and proportion of samples rated as extremely stable (Beever, Huso & Pyke 2006).

We assessed the structure of the native perennial community by quantifying the size of and connectivity of gaps between such vegetation using the basal gap intercept method (Herrick *et al.* 2005). We calculated mean gap length and the proportion of transects covered by large gaps (>200 cm in length).

MULTIVARIATE ANALYSIS

Species cover, distance from nearest water, dung density, bunchgrass basal area, heat loads, soil depth, precipitation, gap size and herbaceous biomass data were log-transformed to improve distributional properties, correlations with ordination axes and variation explained by ordinations (McCune & Grace 2002). Other variables were not transformed.

Non-metric multidimensional scaling (NMS) ordination was used to relate patterns in community composition to environmental gradients (PC-Ord™; McCune & Grace 2002). Joint plots and Pierson's correlations were used to describe relationships between environmental gradients and the strongest patterns of community composition.

We used nonparametric multiplicative regression (NPMR) in HyperNiche™ to quantify the relationship between species' cover and environmental gradients (McCune 2009). Predictors were scores of the three ordination axes. These scores represented an integrated measure of complex environmental gradients associated with dominant patterns of herbaceous community composition. Response variables were the cover of each species using a local mean estimator and Gaussian kernel function. To control for potential interactions between axes, response curves were generated using partial models and focal variables (McCune 2009). A final NPMR model was run using the three axes' scores as predictors. Final model fit was assessed with a cross-validated R^2 (McCune 2009).

Hierarchical agglomerative cluster analysis was used to identify groups of sites differing in community composition (McCune & Grace 2002). Multivariate differences in community composition between identified groups were tested using multiresponse permutation procedures (MRPP) ($\alpha = 0{\cdot}05$). Identified groups were overlaid onto ordinations to accentuate relationships between groups and environmental gradients. Multivariate differences in relativized environmental variables between groups were tested with MRPP. Differences in individual environmental variables between groups were assessed with ANOVA ($\alpha = 0{\cdot}10$), and Bonferroni-adjusted 90% confidence intervals were used to quantify differences between groups.

STRUCTURAL EQUATION MODELLING

In our study, an initial conceptual model was used as a SEM meta-model, representing a family of possible models (Fig. 1, Table 1). Our modelling process considered the available observed variables to identify 'indicator variables' (the observed variables that will serve as proxies for conceptual variables in the meta-SEM) using procedures described in Grace *et al.* (2012). Except for 'Potential Safe Sites', all model constructs were represented using single indicator variables. *Bromus tectorum* cover was selected as the indicator to measure 'Invasion Magnitude'. Bunchgrass and sagebrush cover were selected to measure their abundances. The three NMS ordination axes of bunchgrass species' cover data were used to develop an indicator of 'Bunchgrass Community Composition'. Distance from nearest water was selected as the indicator to measure cumulative 'Cattle Grazing Intensity'. Heat load was selected to measure 'Heat load Exposure', and percent sand content at 0–15 soil depth was selected to measure 'Soil Physical Properties'. The proportion of transects covered by large gaps (>200 cm in length) was selected as the measure of 'Community Gap Structure'. Two indicators were selected to represent 'Potential Safe Sites' – BSC and cover of bare soil.

All SEM analyses were conducted using AMOS 18.0 software (SPSS 2010). Maximum likelihood procedures were used for model evaluation and parameter estimation. Model fit was

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evaluated by sequentially evaluating likelihood ratios by using the single-degree-of-freedom chi-squared goodness-of-fit statistic. Modification indices were used to evaluate the need to include links or error correlations not in the original model. This process produced a final inferential model. The stability of the final model was evaluated by introducing other available indicators to determine whether they represented additional contributing information. For example, our initial indicator for cattle grazing intensity was 'distance from nearest water'. The three alternative potential indicators (cow pie frequency, cow pie density and bunchgrass basal area) for this construct did not improve model fit or amount of variation in cheatgrass dominance explained and were no longer included.

Results

PATTERNS OF INVASIBILITY – CONVENTIONAL MULTIVARIATE RESULTS

Nearly 92% of variation in community composition was explained by the final ordination (Fig. 2). Axis 1 was the dominant axis explaining 60·9% of variation in composition data. Axis 1 was a strong gradient of decreasing cattle grazing disturbance and heat stress (Fig. 2): dung density ($r = -0{\cdot}35$); dung frequency ($r = -0{\cdot}36$); distance from water ($r = 0{\cdot}41$); deep-rooted bunchgrass basal area ($r = 0{\cdot}71$); and heat loads ($r = -0{\cdot}44$). In addition, BSC cover, soil aggregate stability and proportion of soil aggregate stability values rated as highly stable increased along Axis 1 (Fig. 2). The size of and connectivity between gaps and amount of bare soil decreased strongly

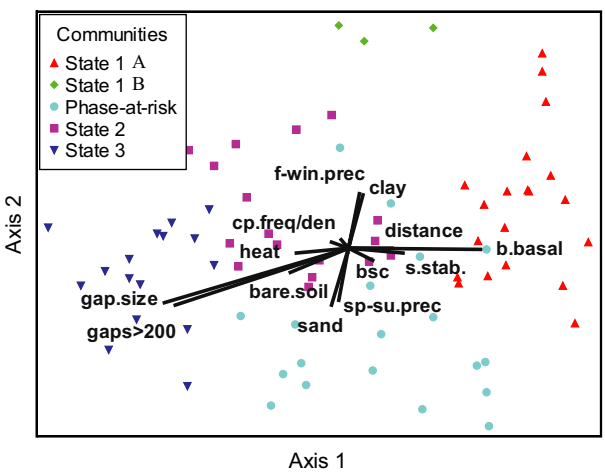


Fig. 2. Ordination of plots in community composition space. Non-metric multidimensional scaling ordination with final stress of 9·92; final instability of <0·01; Monte Carlo test *P*-value < 0·05. Vectors show the strength and direction of correlations between environmental variables and axes. Only variables with significant R^2 (>0·20) are shown. Different plot symbols show groups derived from cluster analysis that differ in composition and environmental factors. State 1A and 1B communities have understoreys dominated by native bunchgrasses; phase-at-risk communities are co-dominated by bunchgrasses and non-natives, and State 2 and State 3 communities are dominated by non-native species.

along Axes 1 and 2 (Fig. 2) (see Table S1, Supporting Information).

Axes 2 and 3 represented weaker relationships explaining 19·3% and 11·6% of the variation, respectively. Axis 2 showed a strong gradient of decreasing sand, increasing clay and increasing fall and winter precipitation (Fig. 2). Axis 3 demonstrated a weaker gradient of decreasing cattle grazing associated with decreasing dung density and frequency and increasing deep-rooted bunchgrass basal area (see Table S1, Supporting Information).

Nonparametric multiplicative regression model sensitivities indicate that Axis 1 was the best predictor of non-native species. The strength of the relationship between cover of native species and these three axes varied considerably (Fig. 3; see Table S2, Supporting Information). *P. spicata*, *A. thurberianum*, *P. secunda* and forbs had strong positive relationships with Axis 1, *P. secunda* and forbs had strong positive relationships with Axis 2, and *Elymus elymoides* had a strong positive relationship with Axis 3 (Fig. 3).

Cluster analysis identified five distinct groups of communities with 0% of the information remaining (MRPP using species data: $A = 0{\cdot}33$, $P < 0{\cdot}01$; Fig. 4; See Tables S3 and S4, Supporting Information). Several species were uniquely associated with one or more groups (Fig. 4; See Table S3, Supporting Information). Combined heat loads, soil physical properties, BSC cover, bare soil cover, soil stability, community gap structure and cattle grazing intensity differed significantly among groups (MRPP using environmental data: $A = 0{\cdot}59$, $P < 0{\cdot}0001$; Fig. 5; See Table S4, Supporting Information).

State 1 consisted of two groups (1A and 1B) of communities with an intact herbaceous understorey dominated by native bunchgrasses and forbs (Fig. 4). Thirty-one percentage of study plots were in one of these groups. State 1 also contained phase-at-risk communities (communities at risk of crossing a biological threshold to being dominated by *B. tectorum*; 25% of study plots) with an understorey co-dominated by native species and *B. tectorum*. States 2 (23% of study plots) and 3 (21% of study plots) consisted of communities that have crossed a biological threshold and had understories dominated by *B. tectorum* and the non-native annual forb, *Lepidium perfoliatum*.

Communities in Groups 1A and 1B had the lowest levels of cattle grazing combined with the smallest and least connected gaps between perennial vegetation (Fig. 5). Group 1B communities had higher heat loads and finer-textured soils compared to those of Group 1A. Communities comprising phase-at-risk communities were characterized by intermediate levels of cattle grazing, heat loads, water stress and size of and connectivity between gaps (Fig. 5).

State 2 communities were characterized by intermediate to high levels of cattle grazing and intermediate levels of heat loads and water stress. State 3 communities had the highest levels of cattle grazing and bare soil cover, largest and most connected gaps and lowest soil aggregate stability (Fig. 5).

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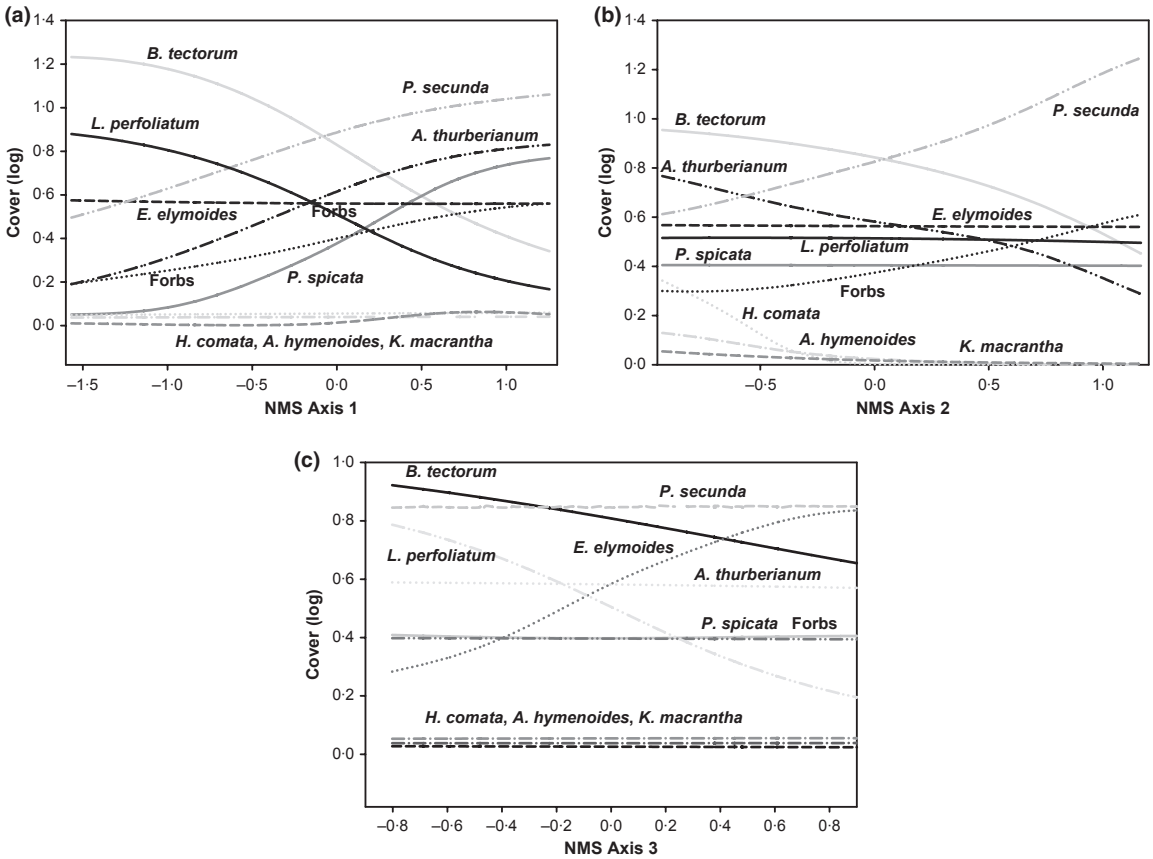


Fig. 3. Nonparametric multiplicative regression response curves showing relationship between species cover and gradients represented by non-metric multidimensional scaling ordination axes. Axis 1 is a gradient of decreasing cattle grazing intensity and heat load exposure (a), Axis 2 is a gradient of decreasing water stress (b), and Axis 3 is a gradient of decreasing cattle intensity (c).

STRUCTURAL EQUATION MODELLING RESULTS

The final SEM model ($\chi^2 = 18{\cdot}88$; $P = 0{\cdot}54$; 20 d.f.) showed very close fit between model and data. A number of the initially hypothesized relationships (Table 1) were not supported by data. Sagebrush abundance did not help explain invasion magnitude, either directly or indirectly. As a result, that variable was removed from the final model. Heat load exposure, cattle grazing intensity and native bunchgrass cover were indirect predictors of invasion magnitude in the final model (Fig. 6). Unanticipated in the initial model was dependence of safe sites on heat loads and sand, and dependence of bunchgrass composition on sand content. The final model explained 72% of the variation in the magnitude of invasions among sites.

Concerning strengths of linkages in the final model, changes in community gap structure, that is, increases in the size of and connectivity between gaps among native plants, were predictive of higher levels of *B. tectorum* cover ($r = 0{\cdot}83$). Native bunchgrass cover and composition were not direct predictors of *B. tectorum* cover, rather they were indirect predictors through their relationship to gaps. Gaps characterized by bare soil had a strong positive association with *B. tectorum* cover ($r = 0{\cdot}38$), whereas gaps characterized by BSC cover had a strong negative association with *B. tectorum* cover ($r = -0{\cdot}26$).

Cattle grazing intensity was positively associated with *B. tectorum* cover through three independent pathways. Because distance from water is inversely related to cattle grazing levels, positive path coefficients indicate a negative relationship between cattle grazing and the response variable in the model (Fig. 6). Thus, model results imply that pathways from cattle grazing to *B. tectorum* cover propagate through (i) negative influences on bunchgrass abundance (0·34), (ii) negative influences on BSC abundance (0·29) and (iii) impacts on bunchgrass community composition (Axis 2) (0·22). There was no evidence that cattle grazing directly decreased or increased *B. tectorum* cover independent of these stated routes.

High levels of heat load exposure were associated with lower levels of bunchgrass (−0·46) and BSC (−0·36) abundance. Coarser-textured soils were more likely to have higher levels of *B. tectorum*, regardless of the other factors (i.e. a direct linkage of 0·48). Coarser-textured soils also had an indirect path through effects on bare soil cover and bunchgrass community composition (Axis 3) that increased *B. tectorum* cover.

By adding up the path strengths, it is possible to compute what is referred to as 'total effects' of predictors on

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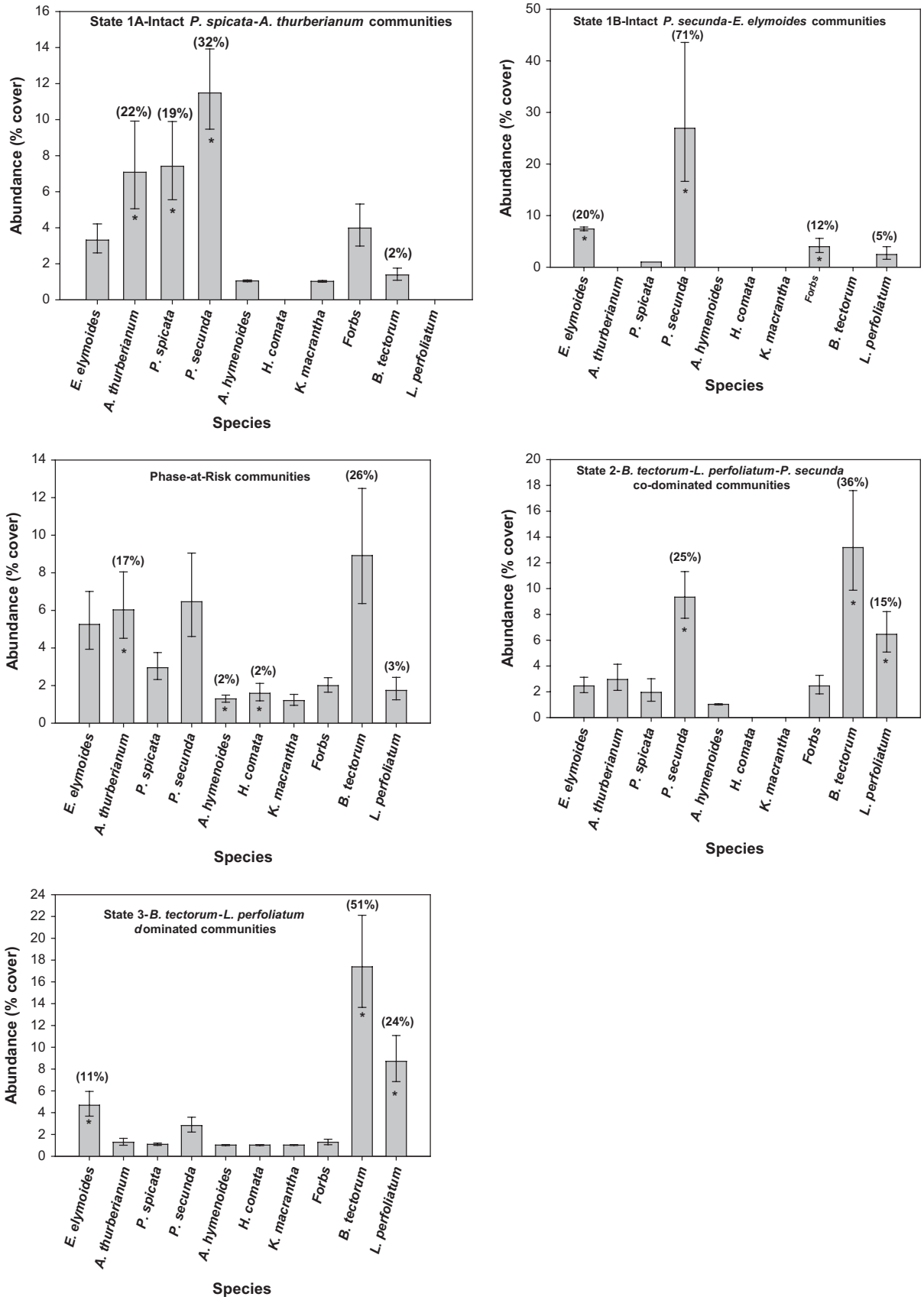


Fig. 4. Community composition of five groups derived from cluster analysis. *Denotes species with highest three indicator values for the group from indicator species analysis. Reported values are back-transformed means, and error bars are 90% Bonferroni-adjusted confidence intervals. (%) is the relative abundance of the species calculated as the proportion of total cover of the group.

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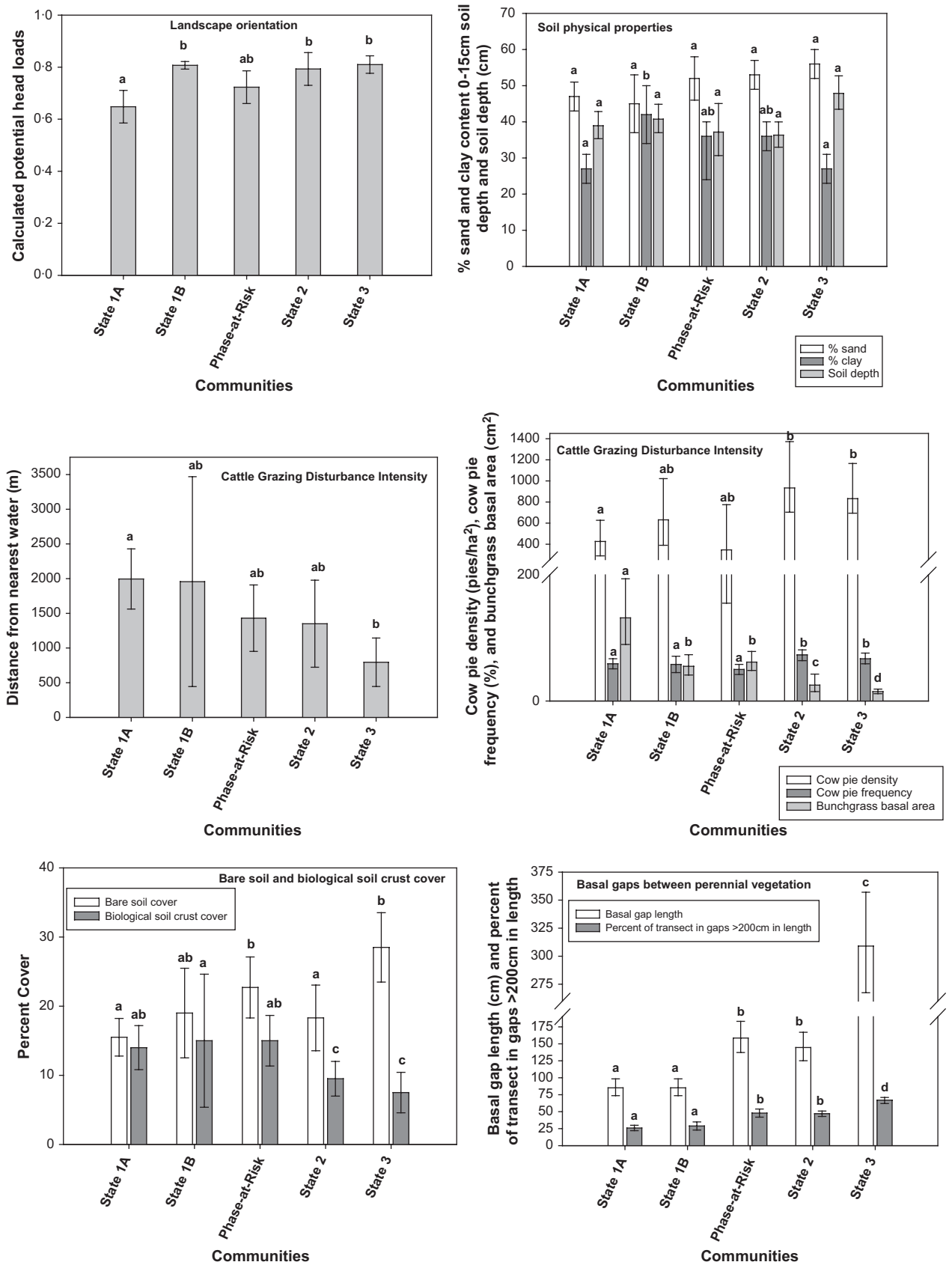


Fig. 5. Differences in heat loads, soil physical properties, biological soil crusts, bare soil cover, soil stability, community gap structure and cattle grazing intensity of five groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different lower-case letters above bars indicate significant differences between groups ($\alpha = 0{\cdot}10$).

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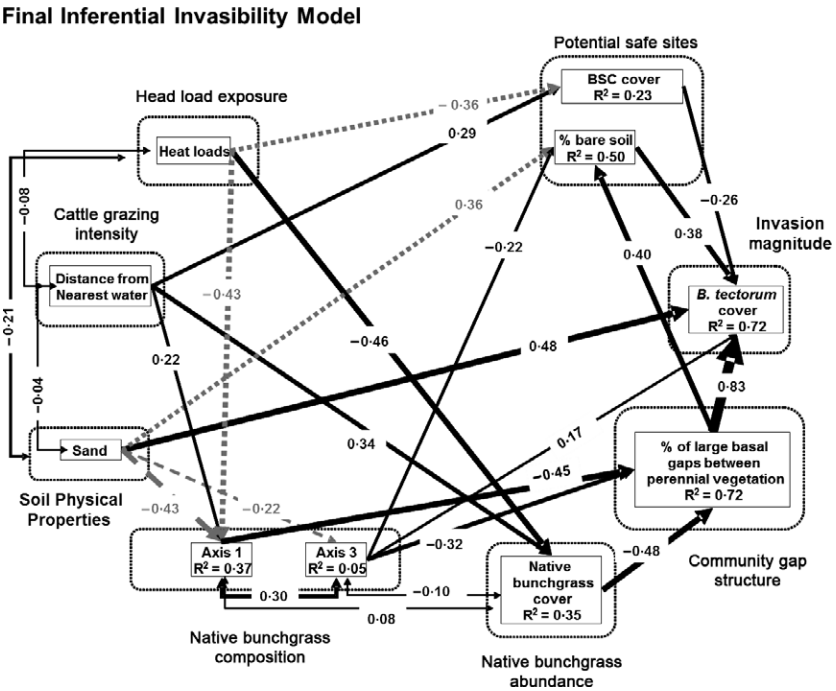


Fig. 6. Final inferential model of *Artemisia* ecosystem invasibility. Single-headed arrows represent significant linkages ($\alpha = 0{\cdot}05$). Double-headed arrows indicate significant correlations between variables and their residuals. The magnitudes of standardized path coefficients are represented by line thicknesses. Dotted grey lines are unanticipated significant paths. Because distance from water is inversely related to cattle grazing intensity (i.e. grazing intensity increases with decreasing distance), positive path coefficients and correlations between grazing intensity and variables indicate an inverse relationship (i.e. increasing cattle grazing intensity decreases bunchgrass abundance). R^2 values depict the proportion of variation of endogenous variables explained by the model. The dotted boxes depict conceptual variables of the meta-structural equation modelling (Fig. 1).

downstream responses. Computed total effects of predictor variables on *B. tectorum* in order of importance were as follows: (i) community gap structure (0·68), (ii) soil physical properties (0·42), (iii) safe sites (bare soil cover, 0·38), (iv) heat load exposure (0·37), bunchgrass community composition (NMS#1, −0·31), (v) safe sites (BSC cover, −0·26), (vi) cattle grazing disturbance (−0·26), (vii) bunchgrass abundance (−0·24) and (viii) bunchgrass community composition (NMS#3, 0·04).

Discussion

By combining SEM with an observational approach, we were able to gain important new insight into the relative importance of the numerous factors determining the magnitude of *B. tectorum* invasions of *Artemisia* ecosystems and gain valuable insight into potential underlying mechanisms. Our results provide strong support for some *a priori* hypothesized mechanisms (i.e. cattle trampling reduces bunchgrass and BSC abundance) and no support for others (i.e. cattle reduce invasions by grazing *B. tectorum*). Our SEM findings should help prioritize future experiments to test our inferences regarding underlying mechanisms and more landscape-scale observational studies to further evaluate and refine the model and construct predictive models (Grace 2006).

In this study, model results support the idea that a complex causal network of simultaneously operating factors and mechanisms are driving invasion of *B. tectorum* in *Artemisia* ecosystems. Based upon the SEM results, shifts in community structure, as measured by the size of and connectivity of gaps between native plants, exert a strong positive effect on the magnitude of *B. tectorum* invasion. This finding is consistent with growing evidence in semi-arid and arid ecosystems showing that increases in gap connectivity (Busso & Bonvissuto 2009; Okin *et al.* 2009) and changes in how species abundance is distributed in a community (James *et al.* 2008) are associated with a loss of ecosystem resistance to invasion (Scheffer *et al.* 2009). We define resistance as the collective ability of the resident sagebrush community to limit *B. tectorum* dominance in the face of invasion (Chambers *et al.* 2007). Increases in the connectivity of these gaps were associated with a dramatic increase in the magnitude of such invasions (Okin *et al.* 2009). This loss of resistance to invasion probably increases the magnitude of *B. tectorum* dominance after subsequent disturbances and may set the stage for a regime shift to *B. tectorum*-dominated grasslands with the next fire (Scheffer *et al.* 2009).

Our research suggests that two environmental factors influence the inherent resistance of *Artemisia* ecosystems to *B. tectorum* invasion. Communities located on coarser-textured soils or characterized by higher potential heat loads (Stewart & Hull 1949) were inherently least resistant to *B. tectorum* invasion. These communities are characterized by higher levels of water stress and lower productivity. The inherent structure of these communities that consists of larger and more connected gaps among perennial vegetation and higher amounts of bare soil may make them vulnerable to other disturbances that increase the size of gaps.

Consistent with other studies, biotic resistance from resident bunchgrass and BSC communities played pivotal roles and appears to limit the magnitude of *B. tectorum* invasion (Richardson & Pysek 2006). Water availability is the primary controlling factor of seedling establishment in these ecosystems (Schupp 1995). Several studies have found a strong negative association between BSC community integrity and *B. tectorum* abundance (Ponzetti, McCune & Pyke

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2007; Ponzetti & McCune 2008) and showed that BSCs reduce *B. tectorum* germination and establishment rates by impeding root penetration and growth (Serpe *et al.* 2008). Our findings suggest that BSC communities are especially important in limiting the magnitude of *B. tectorum* invasions in gaps between perennial vegetation by minimizing potential safe sites for establishment.

Consistent with other studies, we found that bunchgrasses reduced the magnitude of *B. tectorum* invasions most likely by reducing water and nutrient availability (Chambers *et al.* 2007; Prevéy *et al.* 2010). Our findings provide important insight into this mechanism. Nearly all the biotic resistance effect was indirect through a strong direct effect of bunchgrass abundance and composition on community structure. By limiting the size and connectivity of gaps, bunchgrasses likely minimize resources available to *B. tectorum* spatially. Further, three species, *P. spicata*, *A. thurberianum* and *P. secunda,* appear to be especially important determinants of such resistance. *P. spicata* and *A. thurberianum* are dominant deep-rooted bunchgrasses with most active growth in later spring, whereas *P. secunda* is a shallow-rooted bunchgrass that is active in late winter and early spring. This combination of differing structure and phenology reflects their differing abilities to acquire resources at different soil depths (James *et al.* 2008) and seasons and thereby provide continuous interaction with *B. tectorum* and collectively limit available resources temporally and at different soil depths.

By controlling for several potentially confounding factors (Knick *et al.* 2011), we gained important insights into the role of cattle grazing as a determinant of ecosystem resistance to *B. tectorum* invasion. We found no evidence that cattle grazing, even at the high intensities 100 m from the nearest water development, reduced *B. tectorum* cover. To the contrary, we found strong evidence that increasing cattle grazing intensity indirectly promotes an increase in the magnitude of *B. tectorum* dominance. Cattle herbivory was found to be associated with reduced native bunchgrass abundance, shifts in bunchgrass composition to only the most grazing-tolerant species and aggregated bunchgrasses beneath protective sagebrush canopies (Reisner 2010). These collective cattle-induced changes thus appear to ripple through the community by increasing the size and connectivity of gaps between perennial vegetation. As gaps get bigger and more connected, both live and dead (litter) herbaceous soil cover decreases and the amount of bare soil increases. Cattle trampling reduced resistance within these larger gaps by reducing BSC cover.

Changes in community structure and how species' abundance is distributed in the community may increase general resource availability (James *et al.* 2008). As cattle grazing increased, *P. spicata*, *A. thurberianum* and *P. secunda* cover decreased, *E. elymoides* cover did not change, and *B. tectorum* cover increased. These shifts parallel the relative differences in grazing avoidance and tolerance mechanisms among these species. Cattle grazing introduced a novel disturbance regime into this system where most bunchgrasses are highly sensitive to herbivory (Mack & Thompson 1982). To the contrary, *B. tectorum* exhibits a collection of grazing avoidance and tolerance attributes that makes it extremely tolerant of even highly intensive grazing (Vallentine & Stevens 1994; Hempy-Mayer & Pyke 2009). Because of its attributes (Chambers *et al.* 2007), *B. tectorum* is well positioned to take maximum advantage of this window of invasion opportunity by exploiting larger and more connected gaps.

If the goal is to conserve and restore resistance of these systems to invasion, managers should consider focusing their efforts on maximizing the pre-emption of resources provided by BSC and bunchgrasses. We suggest three priorities: first, maintain and/or restore high overall bunchgrass cover and community structure characterized by spatially dispersed bunchgrasses in interspaces and small gaps between such individuals to maximize the capture of resources; second, maintain and/or restore a diverse assemblage of bunchgrass species with different spatial and temporal patterns of resource use to maximize capture of resources at different soil depths and times; third, maintain and/or restore a BSC community to limit safe sites for *B. tectorum* establishment within gaps.

Our findings suggest that multiple factors (bunchgrass cover, BSC cover, cattle grazing, etc.) may influence the susceptibility of these ecosystems to *B. tectorum* invasion. Importantly, many of these influences are mediated by the size and connectivity of gaps, as well as the conditions of gaps. Thus, gaps in perennial vegetation may serve as an important early warning indicator of when cattle grazing or other stressors are compromising resistance of these systems to *B. tectorum* invasion. Our findings raise serious concerns regarding proposals to use cattle grazing to control *B. tectorum* in these systems where remnant bunchgrass communities persist (Vallentine & Stevens 1994). In contrast, our findings support recent guidance for passively restoring resistance of these systems by reducing grazing levels (Pyke 2011). Future research should focus on gathering information concerning the size of and connectively of such gaps across a range of ES consistent with maintaining resistance. These data could be used to develop indicators for adaptive management frameworks to conserve and restore these endangered systems.

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References

Agrawal, A.A., Ackerly, D.A., Adler, F., Arnold, B., Cáceres, C., Doak, D.F., Post, E., Hudson, P., Maron, J., Mooney, K.A., Power, M., Schemske, D., Stachowicz, J.J., Strauss, S.Y., Turner, M.G. & Werner,

13652664, 2013, 4, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.12097, Wiley Online Library on [08/05/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

E. (2007) Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment*, **5**, 145–152.
Beever, E.A., Huso, M. & Pyke, D.A. (2006) Multi-scale responses of soil stability and invasive plants to removal of non-native grazers from an arid conservation reserve. *Diversity and Distributions*, **12**, 258–268.
Briske, D.D. & Richards, J.H. (1995) Plant responses to defoliation: a physiological, morphological, and demographic evaluation, pp. 625–710. *Wildland Plants: Physiological Ecology and Development Morphology* (eds D.J. Bedunah & R.E. Sosebee), pp. 710. Society for Range Management, Denver, CO.
Busso, C. & Bonvissuto, G. (2009) Structure of vegetation patches in northwestern Patagonia, Argentina. *Biodiversity and Conservation*, **18**, 3017–3041.
Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E. & Whittaker, A. (2007) What makes great basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, **77**, 117–145.
Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J. & Pasteris, P.P. (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the United States. *International Journal of Climatology*, **27**, 935–969.
Davies, K.W., Bates, J.D. & Miller, R.F. (2007) Environmental and vegetation relationships of *Artemisia tridentata* ssp. *wyomingensis* alliance. *Journal of Arid Environments*, **70**, 478–494.
Davis, M.A., Grime, J.P. & Thompson, J.N. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
Fowler, N.L. (1988) What is a safe site? Neighbor, litter, germination date, and patch effects. *Ecology*, **69**, 947–961.
Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific interaction competition in natural communities: a review of field experiments with plants. *The American Naturalist*, **139**, 771–801.
Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, UK.
Grace, J.B., Youngblood, A. & Scheiner, S.M. (2009) Structural equation modeling and ecological experiments. *Real World Ecology: Large-Scale and Long-Term Case Studies and Methods*, Chapter 2 (S. Miao, S. Carstenn & M. Nungesser), pp. 19–45. Springer Verlag, New York.
Grace, J.B., Schoolmaster Jr, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M. & Schweiger, E.W. (2012) Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, **3**, article 73.
Griffith, A.B. (2010) Positive effects of native shrubs on *Bromus tectorum* demography. *Ecology*, **91**, 141–154.
Grime, J.P. (1977) Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1182.
Hempy-Mayer, K. & Pyke, D.A. (2009) Defoliation effects on *Bromus tectorum* seed production: implications for grazing. *Rangeland Ecology & Management*, **61**, 116–123.
Herrick, J.E., Van Zoo, J.W., Havstad, K.M., Burkett, L.M. & Whitford, W.G. (2005) *Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems*, Vol 1. US Department of Agriculture, Agriculture Research Station, Jornada Experimental Range, Las Cruses, NM, pp. 42.
James, J., Davies, K., Sheley, R. & Aanderud, Z. (2008) Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. *Oecologia*, **156**, 637–648.
Knick, S.T., Hanser, S.E., Miller, R.F., Pyke, D.A., Wisdom, M.J., Finn, S.P., Rinkes, E.T. & Henny, C.J. (2011) Ecological influence and pathways of land use in sagebrush. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology*, Vol. 38 (eds S.T. Knick & J.W. Connelly), pp. 203–251. University of California Press, Berkeley, CA.
Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of exotic plant invasions. *Ecology Letters*, **7**, 975–989.
Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
Mack, R.N. & Thompson, J.N. (1982) Evolution in steppe with few large, hooved mammals. *The American Naturalist*, **119**, 757–773.
McCune, B. (2007) Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. *Journal of Vegetation Science*, **18**, 751–754.
McCune, B. (2009) *Nonparametric Multiplicative Regression for Habitat Modeling*. Oregon State University, Corvallis, OR.
McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MJM Software Design, Gleneden Beach, OR.
Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J. & Hild, A.L. (2011) Characteristics of sagebrush habitats and limitations to long-term conservation. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology*, Vol. 38 (eds S.T. Knick & J.W. Connelly), pp. 145–184. University of California Press, Berkeley, CA.
Okin, G.S., Parsons, A.J., Wainwright, J., Herrick, J.E., Bestelmeyer, B.T., Peters, D.C. & Fredrickson, E.L. (2009) Do changes in connectivity explain desertification? *BioScience*, **59**, 237–244.
Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459–1461.
Ponzetti, J.M. & McCune, B.P. (2008) Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. *The Bryologist*, **104**, 212–225.
Ponzetti, J.M., McCune, B. & Pyke, D.A. (2007) Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington. *The Bryologist*, **110**, 706–722.
Prevéy, J., Germino, M., Huntly, N. & Inouye, R. (2010) Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecology*, **207**, 39–51.
Pyke, D.A. (2011) Restoring and rehabilitating sagebrush habitats. *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and its Habitats. Studies in Avian Biology*, Vol. 38 (eds S.T. Knick & J.W. Connelly), pp. 531–548. University of California Press, Berkeley, CA.
Reichenberger, G. & Pyke, D.A. (1990) Impact of early root competition on fitness components of four semiarid species. *Oecologia*, **85**, 159–166.
Reisner, M.D. (2010) *Drivers of plant community dynamics in sagebrush steppe ecosystems: cattle grazing, heat and water stress*. Dissertation, Oregon State University, Corvallis, OR, pp. 286.
Richardson, D.M. & Pysek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409–431.
Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M. & Sugihara, G. (2009) Early-warning signals for critical transitions. *Nature*, **461**, 53–59.
Schiffman, P.M. (1997) Animal-mediated dispersal and disturbance: driving forces behind alien plant naturalization. *Assessment and Management of Plant Invasions* (eds J.O. Luken & J.W. Thieret), pp. 87–94. Springer-Verlag, New York, NY.
Schupp, E.W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399–409.
Serpe, M., Zimmerman, S., Deines, L. & Rosentreter, R. (2008) Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. *Plant and Soil*, **303**, 191–205.
SPSS (2010) *Amos 18.0*. SPSS, Chicago, IL.
Stewart, G. & Hull, A.C. (1949) Cheatgrass (*Bromus Tectorum* L.): an ecologic intruder in southern Idaho. *Ecology*, **30**, 58–74.
Vallentine, J.F. & Stevens, A.R. (1994) Use of livestock to control cheatgrass-a review. *Proceedings of Symposium on Ecology, Management, and Restoration of Intermountain Rangelands*, Boise, ID, May 18–22, 1992, pp. 202–206.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Relationships between environmental variables and ordination axes.

Table S2. Relationships between species abundance and ordination axes.

Table S3. Indicator species analysis of groups.

Table S4. Pairwise MRPP comparisons of groups.

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