



Stress-gradient hypothesis explains susceptibility to *Bromus tectorum* invasion and community stability in North America's semi-arid *Artemisia tridentata wyomingensis* ecosystems

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Keywords

Artemisia; Caespitose bunchgrass; Cattle; Cheatgrass; Competition; Disturbance; Facilitation; Heat stress; Sagebrush; Water stress

Abbreviations

Artemisia = *Artemisia tridentata* subsp. *wyomingensis*; BLM = U.S. Department of the Interior, Bureau of Land Management; ISA = indicator species analysis; MRPP = multi-response permutation procedures; NMS = non-metric multidimensional scaling; NPMR = non-parametric multiplicative regression; NRCS = U.S. Department of Agriculture, Natural Resources Conservation Service; SGH = stress-gradient hypothesis; SIR = severity–interaction relationship.

Nomenclature

United States Department of Agriculture, Natural Resources Conservation Service, Plants Database

Received 3 July 2014

Accepted 20 May 2015

Co-ordinating Editor: Richard Michalet

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Abstract

Questions: (1) What combinations of overlapping water and heat stress and herbivory disturbance gradients are associated with shifts in interactions between *Artemisia tridentata* subsp. *wyomingensis* (*Artemisia*) and herbaceous beneficiary species? (2) Do interactions between *Artemisia* and beneficiaries shift from competition to facilitation with increasing stress-disturbance where facilitation and competition are most frequent and strongest at the highest and lowest levels, respectively? (3) Do such relationships differ for native and non-native beneficiaries? (4) What are the implications of any observed shifts in interactions between community compositional stability in space and susceptibility to invasion?

Location: North American *Artemisia* communities.

Methods: We tested the stress-gradient hypothesis (SGH) in an observational study consisting of 75 sites located along overlapping water and heat stress and disturbance gradients. We used spatial patterns of association among *Artemisia* and six native and two non-native beneficiary species; including the invasive annual grass *Bromus tectorum*, representing a diverse array of life history strategies, to infer whether the net outcome of interactions was facilitation or competition. We assessed implications for community stability by examining shifts in community composition in space and resistance to invasion.

Results/Conclusions: Cattle herbivory, a novel disturbance and selective force, was a significant component of two overlapping stress gradients most strongly associated with observed shifts in interactions. Facilitation and competition were strongest and most frequent at the highest and lowest stress levels along both gradients, respectively. Contrasting ecological optima among native and non-native beneficiaries led to strikingly different patterns of interactions. The four native bunchgrasses with the strongest competitive response abilities exhibited the strongest facilitation at their upper limits of stress tolerance, while the two non-natives exhibited the strongest competition at the highest stress levels, which coincided with their maximum abundance. *Artemisia* facilitation enhanced stability at intermediate stress levels by providing a refuge for native bunchgrasses, which in turn reduced the magnitude of *B. tectorum* invasion. However, facilitation was a destabilizing force at the highest stress levels when native bunchgrasses became obligate beneficiaries dependent on facilitation for their persistence. *B. tectorum* dominated these communities, and the next fire may convert them to annual grasslands.

Introduction

Plant interactions (Tilman 1996; Callaway 2007) and stress (Grime 1977) are fundamental drivers of community composition and structure. Stress is defined broadly as a combination of stress, consisting of all phenomena that limit photosynthesis either directly (e.g. extreme temperatures) or indirectly (e.g. water availability) and disturbance, consisting of all phenomena that reduce biomass (e.g. herbivory; *sensu* Brooker & Callaghan 1998). The stress-gradient hypothesis (SGH) predicts that facilitation and competition vary inversely along stress gradients, with facilitation more frequent and stronger when stress is high and competition more frequent and stronger when stress or disturbance is low (Bertness & Callaway 1994; Brooker & Callaghan 1998). Recent studies have highlighted the context-dependence of shifts in interactions along overlapping stress and disturbance gradients (Maalouf et al. 2012; Le Bagousse-Pinguet et al. 2014) and revealed a complex set of other important factors (Michalet 2007; Michalet et al. 2014).

Interactions among the type of stress, life-history strategy and location of beneficiary species relative to their ecological optimum strongly influence the severity interaction relationship (SIR; Choler et al. 2001; Liancourt et al. 2005). Stress can be resource-based (water, nutrients) or non-resource-based (heat; Michalet 2007). If the *only* stress is non-resource based, facilitation is likely to be more frequent and stronger because the only prerequisite to such an outcome is benefactor amelioration of stress (Callaway 2007; Maestre et al. 2009). However, if the *only* stress is resource-based and that resource is a limiting factor for both species, facilitation is likely to be less frequent and weaker because such an outcome can only occur if the benefactor increases resource availability (Maestre et al. 2009). Along a given stress gradient, species with the strongest competitive responses, defined as the ability to avoid being suppressed by a neighbour, are likely to exhibit the strongest facilitation when they are located at the upper limits of their tolerance to that stress (Liancourt et al. 2005; Le Bagousse-Pinguet et al. 2012). Under these circumstances, such species are best able to minimize the impacts of competing with the benefactor and maximize benefits of stress amelioration provided by the benefactor.

Despite well-documented support for the SGH at the individual level (He & Bertness 2014), our knowledge concerning the importance of facilitation and shifts in interactions as drivers of community composition and diversity is incomplete. This gap is especially large along overlapping stress and disturbance gradients (Le Bagousse-Pinguet et al. 2013). Facilitation can increase taxonomic diversity within benefactor canopies compared to open spaces

(Michalet et al. 2006; Le Bagousse-Pinguet et al. 2014) and increase site-level species richness and phylogenetic diversity (Valiente-Banuet & Verdú 2007; Butterfield et al. 2013) by ameliorating stress or reducing disturbance on species otherwise intolerant of such conditions. However, co-occurring high levels of stress and disturbance may reduce the ability of facilitation to enhance diversity (Le Bagousse-Pinguet et al. 2014), lead to rapid local extinctions, and hasten critical degradation transitions in arid systems (Verwijmeren et al. 2013). Furthermore, conceptual models predict that facilitation will only increase community compositional stability up to intermediate levels of stress and decrease stability at high stress (Butterfield 2009). A shift to obligate facilitation where many species only persist beneath a benefactor is predicted to be the tipping point between facilitation stabilizing vs destabilizing a community (Butterfield 2009). No studies have tested these predictions by examining the consequences of facilitation on community stability along overlapping stress-disturbance gradients.

Shifts in the structure of interactions along stress gradients may influence community compositional and functional stability (Collins 2000). These effects are predicted to be especially pronounced in communities where a single species strongly influences the structure of interactions or other processes and when a disturbance or invasion fundamentally alters the structure of those interactions (Baez & Collins 2008; Villarreal-Barajas & Martorell 2009). Community compositional instability can be defined as changes in species abundances over time or space that drive directional changes in community composition (Baez & Collins 2008; Krushelnycky & Gillespie 2008). Compositional stability is likely one of the mechanisms by which community functional stability, defined as the ability to resist changes in aggregate properties or process (e.g. N cycling, invasibility, etc.), is maintained (Zavaleta & Hulvey 2004; Krushelnycky & Gillespie 2008).

Invasibility, defined as the susceptibility to exotic invasion, is one measure of functional stability, with lower invasibility associated with higher community stability (Chambers et al. 2013). Competition from resident species often limits the magnitude of invasions because it reduces resources available to potential invaders (Levine et al. 2004). Facilitation is predicted to increase this competition-induced resistance and reduce invasibility when one resident native species increases the abundance of other natives, which then reduce the invasion magnitude (Brooker et al. 2008); however, no studies have tested this prediction. On the contrary, several studies have shown that facilitation can increase invasibility by ameliorating stress on invaders (Cavieres et al. 2005; Griffith 2010; Saccone et al. 2010; Cushman et al. 2011).

We examined whether the SGH can explain on-going shifts in community stability and susceptibility to invasion by the grass *Bromus tectorum* within North America's semi-arid *Artemisia tridentata* subsp. *wyomingensis* (*Artemisia*) sagebrush ecosystems. These ecosystems are one of North America's most widespread yet endangered ecosystems because of their vulnerability to *B. tectorum* invasion (Miller et al. 2010). Abundant, diverse and spatially dispersed (both beneath *Artemisia* canopies and interspaces among shrubs), they play a pivotal role in minimizing *B. tectorum* dominance by limiting the size and connectivity of gaps among native perennials (Reisner et al. 2013). Once *B. tectorum* sufficiently dominates the understorey, it creates a continuous, highly flammable fuel that increases fire risk, frequency and severity (Pyke 2011). This change in fire regime may irreversibly transform native shrub-steppe communities into *B. tectorum*-dominated annual grasslands (Miller et al. 2010; Pyke 2011).

We incorporated recent recommendations to more robustly test the SGH including: (1) conducting the study at the landscape scale across 75 study sites to capture a complete severity gradient, i.e. sites ranging from the lowest to highest levels of stress, where *Artemisia* and the beneficiary species co-occurred; (2) capturing overlapping heat and water stress and herbivory disturbance gradients; (3) examining interactions between a benefactor and six native and two non-native beneficiary species representing a range of life-history strategies and differing ecological optima along the gradients; and (4) examining whether shifts in interactions observed at the species level translated into meaningful effects on community stability and susceptibility to exotic invasion. Incorporating these recommendations necessitated an observational approach examining spatial patterns of association between *Artemisia* and beneficiary species to infer whether the net outcome of interactions was facilitation (positive association) or competition (negative association; Michalet 2007; Shultz et al. 2007). We acknowledge that such an approach precludes making definitive inferences concerning the causal mechanisms driving such patterns.

We also acknowledge that our findings are limited to the patch-scale (interspace–undershrub areas) at which such spatial associations were observed because vegetation patterns are scale-dependent. We examined the consequences of facilitation for community compositional stability and invasibility in space (interspace–undershrub microsites). The 2-yr duration of our study precluded assessing the implications on compositional stability and invasibility over time. Despite these limitations, our findings have far reaching implications because of the vital role heterogeneity generated by interspace–undershrub patches play in community assembly and diversity (Davies et al. 2007; Hoover & Germino 2012), resistance to

B. tectorum invasion (Chambers et al. 2007), resilience to fire (Davies et al. 2009) and other disturbances (Chambers et al. 2013) in *Artemisia* communities.

Using this approach, we sought answers to the following questions:

- 1 What combination of overlapping water and heat stress and herbivory disturbance gradients are associated with shifts in interactions between *Artemisia* and herbaceous beneficiary species?
- 2 Do interactions between *Artemisia* and beneficiaries shift from competition to facilitation with increasing stress-disturbance with the most frequent and strongest facilitation and competition at the highest and lowest stress-disturbance levels, respectively? Do such relationships differ for native and non-native beneficiaries?
- 3 What are the implications of any observed facilitation and shifts in interactions for community stability and susceptibility to invasion in space?

Methods

Artemisia communities, benefactor and beneficiary species

Artemisia communities are characterized by strong resource-based (water) and non-resource-based (temperature) stress and herbivory disturbance gradients (Chambers et al. 2007). Annual variation in the amount and timing of precipitation plays a pivotal role in determining water availability within the soil profile (Chambers et al. 2007). This temporal variability in the amount and timing of precipitation interacts with soil properties to determine plant available water. Coarser texture soils are characterized by substantially higher water stress and lower herbaceous productivity compared to loamier or finer-textured soils (Davies et al. 2006). Across these water stress gradients, changes in landscape orientation (aspect and slope) create gradients of heat stress (Davies et al. 2007). Compared to north aspects, south aspects are characterized by higher heat loads (McCune 2007) that increase evapotranspiration demand, which increases stress and significantly lowers herbaceous productivity (Davies et al. 2007). Finally, livestock grazing produces strong herbivory and trampling-induced disturbance gradients that radiate outward from the nearest source of water (Andrew 1988).

The foundational shrub species *Artemisia*, the benefactor, is stress-tolerant (*sensu* Grime 1977; Miller & Shultz 1987). *Artemisia* competes with herbaceous species (Caldwell et al. 1987), but may also facilitate herbaceous species (Davies et al. 2007, 2009). The eight beneficiary herbaceous species used to investigate pair-wise interactions with *Artemisia* represent a wide range of *relative* competitive response abilities and tolerances to water and heat

stress and herbivory disturbance (Appendix S1). The eight species (*Pseudoroegneria spicata*, *Achnatherum thurberianum*, *Hesperostipa comata*, *Achnatherum hymenoides*, *Poa secunda*, *Elymus elymoides*, *Lepidium perfoliatum* and *B. tectorum*) co-occur in the study area, but their ecological optima, point of maximum abundance along the stress gradients, differed. Collectively, these species comprised >90% of the herbaceous cover in the study area.

Study area and sampling design

The study examined 75 sites located in the Northern Great Basin floristic province of Oregon ranging in elevation from 1265 to 1580 m. We employed a stratified random sampling design to include strata for soils, landscape orientation and cattle grazing intensity using ArcGIS 13.0 (ESRI, Redlands, CA, US). Natural Resource Conservation Service (NRCS) digital soil maps were used to ensure coverage of spatial variation in water stress driven by differences in soil texture (<http://websoilsurvey.nrcs.usda.gov>). Soil map unit components were matched with corresponding NRCS Ecological Sites (ES) to identify five *Artemisia*-dominated sites that varied in co-dominant perennial bunchgrasses (Appendix S2). Each of five ESs were delineated into three landscape substrata using 10-m resolution U.S. Geological Survey Digital Elevation Models (DEMs) to ensure we sampled variation in heat loads associated with changes in landscape orientation: (1) northerly aspects (0–90°, 270–360°), (2) southerly aspects (91–271°) or (3) flat. Study sites were located at different distances from the nearest livestock watering location using a BLM database to capture variation in cattle herbivory disturbance. Study sites were selected from random points generated for each of the soil–landscape–livestock strata combinations.

Sampling

Thirty of the 0.39-ha study sites were sampled in 2008 and another 45 in 2009. To measure the abundance of each species, six, 25-m transects were established in each plot using a spoke design, and herbaceous cover was measured using line-point intercept. All sampling occurred between 10 May and 15 Jul each year to capture peak herbaceous biomass. Three measures of cover were calculated for each of eight beneficiary species: (1) undershrub cover (all pin intercepts of herbaceous species when the pin intersected *Artemisia* as the ‘top canopy’), (2) interspace cover (all pin intercepts of herbaceous species when herbaceous species were the ‘top canopy’), and (3) plot-level cover (all pin contacts of species regardless of the ‘top canopy’ species).

Cumulative stress was quantified by measuring herbaceous biomass in 20 (0.5 m × 1.0 m) quadrats, ten located

in the interspace and ten located in undershrub microsites. Potential variation in water stress was estimated by using soil texture (percentage sand, silt and clay) at 0–15 cm soil depth. Potential effective rooting depth was measured by digging a soil pit until bedrock, a restrictive confining layer, or 2-m depth was reached. To quantify potential temporal variation in water stress, the amount and timing of precipitation for each study site was derived from PRISM at 2 km² cell resolution for three seasons 1 Aug to 31 Oct (autumn), 1 Nov to 31 Mar (winter), and 1 Apr to 31 Jul (spring–summer; Daly et al. 2008; Appendix S3). Potential heat stress for each site was calculated using the aspect, slope and latitude of the site and the method described in McCune (2007).

Cattle herbivory disturbance was quantified through four measurements: field-verified distance from the nearest watering location (stress increasing with decreasing distance); cow pie frequency and density from 12.1 m × 25-m belt transects placed parallel to line-point intersect transects; and mean bunchgrass basal area from 30 randomly selected bunchgrasses (stress increasing with decreasing basal area; Briske & Richards 1995).

The difference between undershrub and interspace cover was calculated separately for each beneficiary species for each study site. Results were combined into a ‘difference in cover’ matrix (8 beneficiary species × 75 study sites). The measures used to quantify heat, herbivory, water and cumulative stress levels were combined into a second matrix (13 stress variables × 75 study sites). Plot-level cover was used to estimate beneficiary species abundance and evaluate the status of the beneficiary species relative to their ‘ecological optimum’, defined as a species’ point of maximum abundance along the stress-disturbance gradient (Liancourt et al. 2005).

All measures of beneficiary species cover, distance from nearest water source, cow pie density, bunchgrass basal area, heat loads, soil depth, precipitation and herbaceous biomass were log-transformed to improve distributional properties, correlations with ordination axes and amount of variation explained by the ordinations (MjM Software Design, Gleneden Beach, OR, US).

A combination of multivariate and bivariate techniques was used to analyse the resulting data set. Hierarchical agglomerative cluster analysis (Euclidean distance and flexible β linkage, $\beta = -0.25$) of the ‘differences in cover’ matrix was used to identify groups of study sites differing in spatial patterns of association (MjM Software Design). Multivariate differences in spatial patterns of association and combined levels of heat stress, water stress, herbivory disturbance among the identified groups were tested using multi-response permutation procedures (MRPP, $\alpha = 0.05$). Significance was assessed at a P -value $\alpha = 0.05$. This pro-

cess identified three easily interpretable groups: low, intermediate and high stress-disturbance communities.

Non-metric multidimensional scaling (NMS) was used to ordinate study sites in 'patterns of spatial association' space using the 'difference in cover' matrix (PC-ORD; MjM Software Design). This approach related patterns of spatial association between *Artemisia* and the beneficiary species to the overlapping stress-disturbance gradients. NMS ordination was performed using Euclidean distances to accommodate negative values in the 'difference in cover' matrix. To improve interpretability, the ordination was rotated to load the non-resource-based stress (heat loads) on Axis 1. Joint plots and Pearson's correlations were used to describe the relationship between gradients and strongest patterns of spatial association represented by the ordination axes. The three groups of communities identified by cluster analysis were classified for depiction on the NMS ordination.

Non-parametric multiplicative regression (NPMR) in HyperNiche was used to quantify the SIR for beneficiary species because it provides the flexibility to fit complex non-linear response curves (McCune 2006). Predictors were the axes 1 and 2 ordination scores. These scores represented an integrated measure of complex stress gradients associated with the dominant patterns of spatial association extracted by the ordination. Response variables were the 'difference in cover between undershrub and interspace' for each of the beneficiary species. To control for potential interactions between axes, response curves were generated using partial models and focal variables (MjM Software Design).

Final model fit was assessed with a cross-validated xR^2 , a conservative approach that excludes each data point when calculating the residual sum of squares for the response at that point and estimating the amount of variation explained by the model (McCune 2006). Because there are no coefficients or slopes to compare in NPMR, sensitivity analysis was used to evaluate the relative importance of model predictors. In ecological terms, a higher sensitivity to one of the predictor axes translated into more pronounced shifts in SIR compared to shifts along the stress disturbance gradient represented by the other ordination axis (McCune 2006). We similarly constructed response curves for plot-level cover data for the beneficiary species, an estimate of abundance, to quantify their 'ecological optimum' along stress-disturbance gradients.

Differences in individual stress-disturbance variables between the low, intermediate and high stress-disturbance communities were assessed with ANOVA ($\alpha = 0.10$), and Bonferroni-adjusted 90% confidence intervals were used to quantify differences between groups. For log-transformed variables, back-transformed medians and 90% confidence intervals were reported. Spatial patterns of association between *Artemisia* and beneficiaries were used

to infer interactions by comparing beneficiary undershrub and interspace cover. The relative interaction index (RII; Armas et al. 2004) was used to quantify interactions for the beneficiary species with *Artemisia* at each site. $RII = (P_{+N} - P_{-N}) / (P_{+N} + P_{-N})$, where P is the performance of the beneficiary species in the presence (undershrub cover, +N) and absence (interspace cover, -N) of *Artemisia*. This index represents interaction outcomes as a continuum from competition to facilitation. Values between 0 and 1 indicate facilitation, while values between 0 and -1 indicate competition. The mean RII for each beneficiary species was calculated for the low, intermediate and high stress-disturbance communities. Differences in the mean RII for each beneficiary species among the three groups were assessed with ANOVA ($\alpha = 0.10$), and Bonferroni-adjusted 90% confidence intervals were used to quantify differences in RIIs among groups. Indicator species analysis (ISA) was used to quantify community composition using species abundance (cover) data among the low, intermediate and high stress-disturbance communities and determine whether any of the beneficiary species were uniquely associated with one of them.

Within the low, intermediate and high stress-disturbance communities, MRPP was used to quantify differences in composition of the undershrub and interspace herbaceous communities using species abundance (cover) data. Blocked indicator species analysis (ISA) in PC-ORD was used to elucidate whether any of the beneficiary species were uniquely associated with the undershrub or interspace communities. This approach differs from traditional ISA because it emphasizes within-block (low, intermediate and high stress-disturbance communities) differences between undershrub and interspace communities (MjM Software Design). A Mantel test using Sørensen's distance was used to evaluate overall community similarities using species abundance (cover) data between undershrub and interspace communities within low, intermediate and high stress-disturbance communities. Significant positive Mantel statistics (R) indicate that communities are compositionally similar in space, and non-significant statistics indicate communities are compositionally unrelated.

Results

Cluster analysis identified three distinct groups: low, intermediate and high stress-disturbance communities that were characterized by different combined levels of herbivory disturbance and heat and water stress (MRPP: $A = 0.21$, $P < 0.0001$; Appendix S4). High stress-disturbance communities had greater combined stress levels compared to low stress (MRPP, $A = 0.38$, $P < 0.001$) and intermediate stress ($A = 0.12$, $P < 0.0001$) ones. Although

low and intermediate stress-disturbance communities had similar combined stress levels (MRPP, $A = 0.03$, $P = 0.33$), low stress communities were located further from water compared to intermediate stress ones (Appendix S4).

The NMS ordination explained 91% of the variation in spatial patterns of association between *Artemisia* and beneficiary species (Fig. 1: $P = 0.004$; stress = 10.6). Axis 1 and axis 2 explained 27% and 56% of the variation, respectively (Fig. 1, Appendix S5). Axis 1 is a gradient of increasing herbivory disturbance and heat stress. Heat loads had a moderate positive relationship with the axis (0.38). All measures of herbivory disturbance showed significant relationships with the axis: distance to the nearest water (-0.38) and bunchgrass basal area (-0.41) had moderate negative correlations, while cow pie frequency (0.21) and density (0.31) had positive correlations with the axis. Axis 2 is a gradient of increasing herbivory disturbance and water stress. Distance to the nearest water (-0.41) and bunchgrass basal area (-0.47) had strong negative correlations with the axis. Autumn (-0.49) and winter (-0.56) precipitation had strong negative correlations with axis 2. Soil sand content (0.37) had a moderate positive correlation, whereas clay content (-0.53) had a strong negative correlation with axis 2.

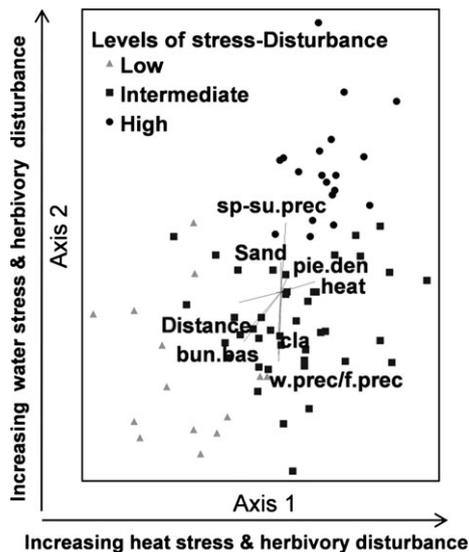


Fig. 1. Non-metric multidimensional scaling (NMS) ordination of study sites in patterns of spatial association between *Artemisia* and beneficiary species (difference in undershrub and interspace cover) space. Axes represent complex gradients in patterns of spatial association across the beneficiary species. Vectors show the strength and direction of correlations between the stress indicators and the axes. Only variables with a significant Pearson correlation (>0.20) are shown. Different plot symbols show the low, intermediate and high stress-disturbance communities (groups) derived from a cluster analysis that differ in patterns of spatial association between *Artemisia* and beneficiary species and combined stress levels.

The shape and strength of the SIR varied depending on the life-history strategy of the beneficiary species and gradient (Fig. 2, Appendix S6). The native beneficiaries with the strongest competitive response ability, *E. elymoides* ($xR^2 = 0.56$, P -value 0.004; sensitivity = 0.59 to axis 1 and 0.74 to axis 2) and *P. secunda* ($xR^2 = 0.41$, P -value 0.004; sensitivity = 0.44 to axis 1 and 0.76 to axis 2) had strong positive monotonic relationships of increasing facilitation along both gradients (Fig. 2). *A. thurberianum* SIR exhibited a strong positive monotonic relationship with axis 2 ($xR^2 = 0.44$, P -value 0.004; sensitivity = 1.2) but no relationship with axis 1. *P. spicata* SIR exhibited a strong plateau-shaped relationship, with increasingly strong facilitation with increasing stress until being constrained at the highest stress levels along both gradients ($xR^2 = 0.44$, P -value 0.004; sensitivity = 0.52 to axis 1 and 0.94 to axis 2). On the contrary, the SIR for the non-natives *L. perfoliatum* ($xR^2 = 0.47$, P -value 0.004; sensitivity = 1.15) and *B. tectorum* ($xR^2 = 0.52$, P -value 0.004; sensitivity = 1.11) exhibited a negative relationship of increasing competition along axis 2. The consistently low cover values ($<2\%$) for *H. comata* and *A. hymenoides*, the most water stress-tolerant natives, precluded assessing their interactions with *Artemisia*.

Although beneficiary species co-occurred across study sites, their points of maximum abundance, i.e. ecological optima, differed along the two stress-disturbance gradients (Appendix S7, Appendix S6). *A. thurberianum*, *P. secunda* and *P. spicata* abundance was highest at the lowest stress and disturbance levels, and decreased strongly with increasing stress and disturbance along both gradients. In contrast, *B. tectorum* and *L. perfoliatum* abundance was largest at highest stress and disturbance levels.

Beneficiary species' RIIs (Fig. 3) and points of maximum abundance, i.e. ecological optima, (Fig. 4) differed among the low, intermediate and high stress-disturbance communities. With the exception of *P. secunda* (Fig. 3b), native beneficiaries had the strongest negative RIIs (competition) in the low stress-disturbance communities and strongest positive RIIs (facilitation) in the high stress-disturbance communities (Fig. 3a,c,d). For all native species, RII increased along the gradient with strong positive RIIs (facilitation) in the high stress-disturbance communities (Fig. 3a,c,d). The strongest negative RIIs and strongest positive RIIs for all native beneficiaries coincided with their ecological optima and limits to stress-disturbance (lowest abundance), respectively (Figs. 3a–d and 4a–d). In contrast, RII values for the non-native beneficiary species, *B. tectorum* and *L. perfoliatum*, were consistently negative regardless of stress-disturbance levels (Fig. 3e,f). *B. tectorum* and *L. perfoliatum* had the strongest negative RII in the high stress-disturbance communities, which coincided with their maximum abundance, i.e. ecological optima (Fig. 4e,f).

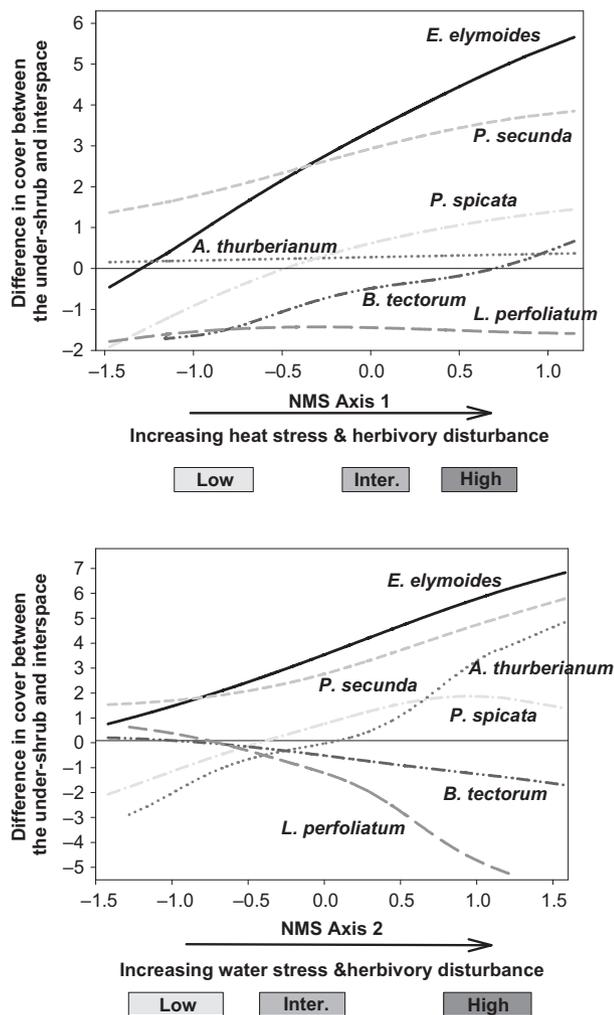


Fig. 2. Non-parametric multiplicative regression (NPMR) response curves showing relationships of patterns of spatial association, measured by the difference in cover between the undershrub and interspace, between *Artemisia* and beneficiary species and the gradients. Values <0 indicate that interspace cover was greater than undershrub cover, and values >0 indicate that that undershrub cover was greater than interspace cover. Rectangles below their respective x-axis depict the locations of the low, intermediate and high stress-disturbance communities. The width of the rectangle equals 90% confidence interval of mean ordination scores for the community along the axis.

Low, intermediate and high stress-disturbance communities were characterized by different levels of interspace and undershrub composition and community similarity (MRPP: $A = 0.12$, $P < 0.001$; Appendix S8). In low stress-disturbance communities, undershrub and interspace community composition was similar (MRPP, $A = 0.01$, $P = 0.349$), the communities were positively related ($R = 0.42$, $P = 0.003$), and none of the beneficiary species were uniquely associated with undershrub or interspace communities (Appendix S8). In intermediate stress-distur-

bance communities, composition of the undershrub and interspace communities differed (MRPP, $A = 0.03$, $P < 0.001$), but only one species, *E. elymoides*, was uniquely associated with the undershrub community [Blocked ISA, Indicator value (IV) = 37]. Importantly, the positive relationship between undershrub and interspace communities ($R = 0.71$, $P < 0.001$) increased in strength compared to the low stress communities ($R = 0.51$). In high stress-disturbance communities, differences in composition of undershrub and interspace communities were strongly evident (MRPP, $A = 0.28$, $P < 0.001$), and the communities were unrelated ($R = 0.24$, $P = 0.328$). Native beneficiaries *P. secunda*, *E. elymoides*, *P. spicata* and *A. thurberianum* (IV = 56, 56, 45 and 24, respectively) were uniquely associated with and dominated undershrub communities; whereas the non-natives *B. tectorum* and *L. perfoliatum* (IV = 42 and 33, respectively) dominated interspace communities.

Composition of low, intermediate and high stress-disturbance communities differed (MRPP: $A = 0.12$, $P < 0.001$; Fig. 4, Appendix S9). Differences in composition were especially pronounced between low and high stress-disturbance ($A = 0.21$; MRPP: $P < 0.001$) and intermediate and high stress-disturbance communities (MRPP: $P < 0.001$; $A = 0.11$) compared to low and intermediate stress-disturbance communities (MRPP: $P = 0.040$; $A = 0.02$). *P. spicata*, *A. thurberianum* and *P. secunda* were uniquely associated with and dominated low (ISA IV = 45, 37, respectively) and intermediate (ISA IV = 26, 33, respectively) stress-disturbance communities, where *B. tectorum* and *L. perfoliatum* composition was low. In contrast, *B. tectorum* and *L. perfoliatum* were uniquely associated with and dominated high stress-disturbance communities (ISA IV = 51, 50, respectively) where bunchgrass composition was low.

Discussion

Consistent with the SGH, community-level facilitation was most frequent and strongest at the highest stress-disturbance levels; however, contrasting ecological optima among native and non-native beneficiaries led to strikingly different patterns of interactions with the foundational shrub *Artemisia*. The four native bunchgrasses exhibited the strongest facilitation at their upper limits of stress-disturbance tolerance, while the two non-natives exhibited the strongest competition at the highest stress-disturbance levels, which coincided with their ecological optima. These observed differences at the species level had profound implications for community stability and susceptibility to non-native invasions in the face of a novel selective disturbance force.

The two native beneficiaries with the strongest competitive response abilities, *E. elymoides* and *P. secunda*, showed

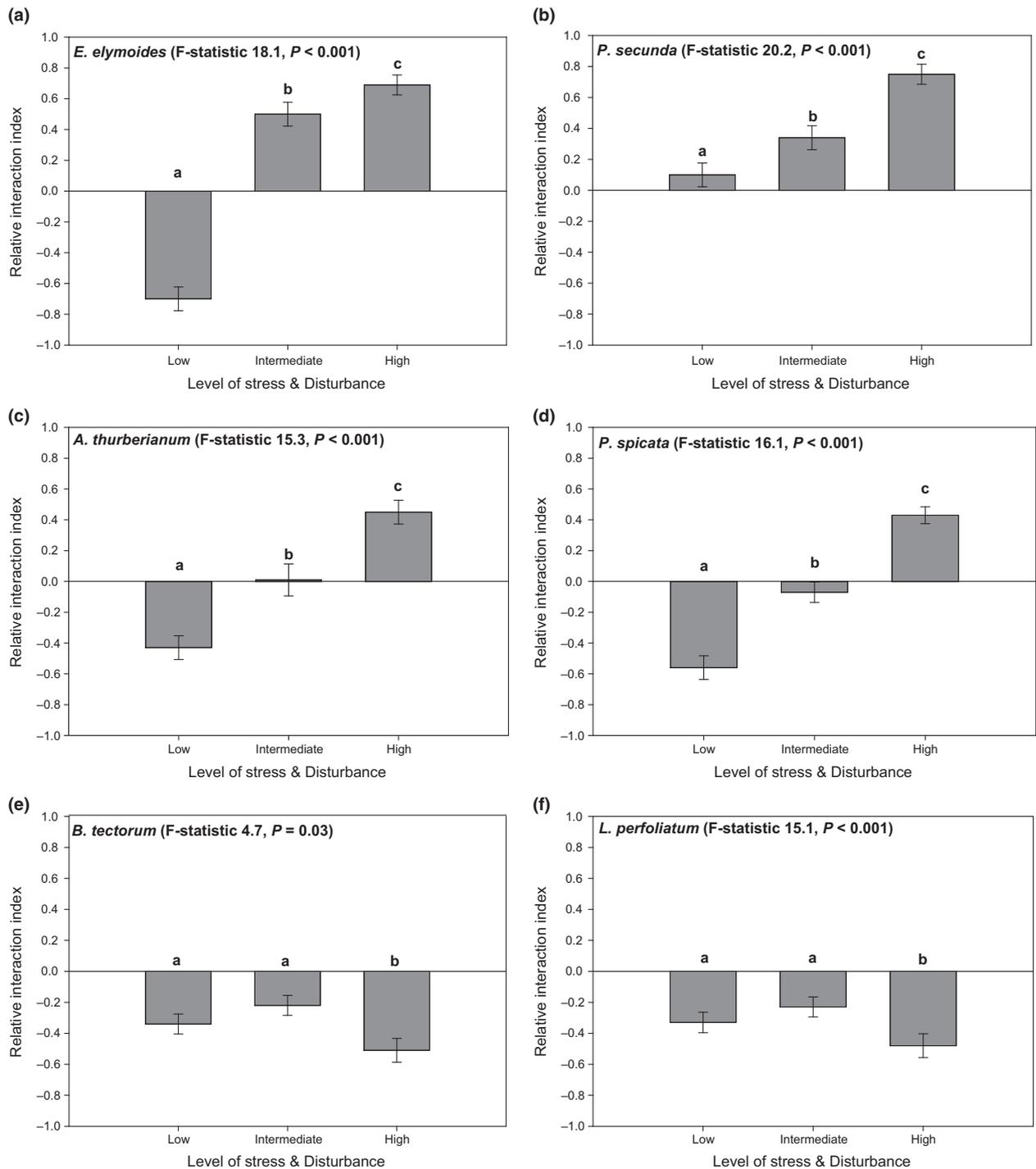


Fig. 3. Comparison of RII for beneficiary species calculated using undershrub and interspace cover among the low, intermediate and high stress-disturbance communities. Values higher or lower than 0 indicate facilitation (positive spatial associations) or competition (negative spatial associations) effects of *Artemisia*, respectively. Values are means, and error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above the bars indicate differences between the three communities ($\alpha = 0.10$).

the strongest facilitation. Both species have an early phenology and shallow roots that minimize overlap with *Artemisia*'s most active growth period and root system (Miller

& Shultz 1987), but their shallow roots make them vulnerable to water stress. Consequently, these species likely minimize competition costs with *Artemisia* for resources

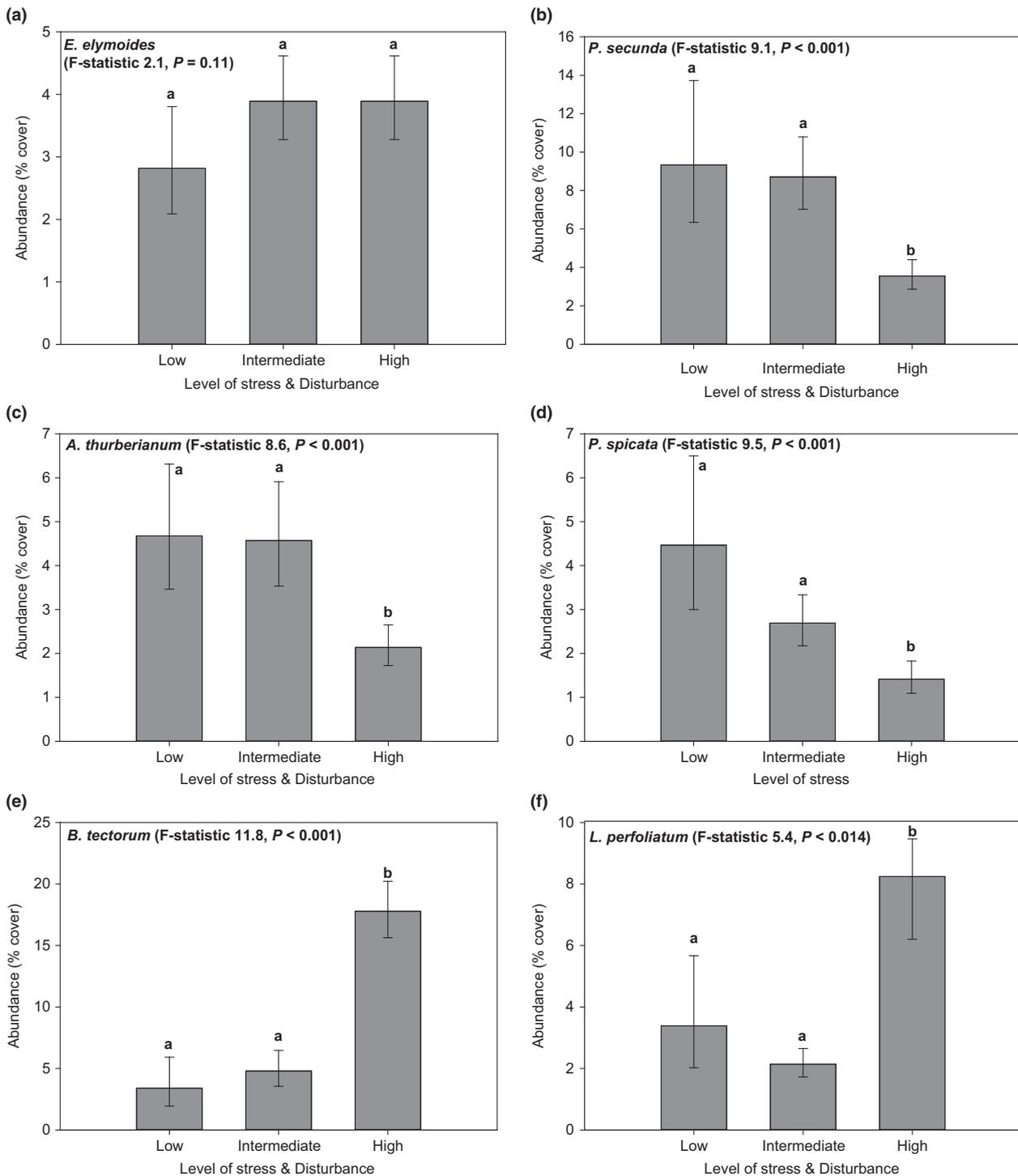


Fig. 4. Comparison of beneficiary species abundance calculated using plot-level cover among the low, intermediate and high stress-disturbance communities. Values are means, and error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above the bars indicate differences between the three communities ($\alpha = 0.10$).

while maximizing benefits derived from its amelioration of heat stress (Davies et al. 2007) and protection from herbivory (France et al. 2009). The two beneficiaries with

intermediate life history strategies, *P. spicata* and *A. thurberianum*, exhibited the next strongest facilitation at the upper limits of their stress-disturbance tolerance. These

water stress-tolerant species also exhibited the strongest competition at low stress levels that coincided with their ecological optima (Liancourt et al. 2005). Both species probably benefit from *Artemisia* amelioration of herbivory disturbance because of their grazing sensitivity. However, their weaker competitive ability likely precludes them from realizing the full benefits of herbivore protection because they incur higher costs competing with *Artemisia*.

In striking contrast, the non-native beneficiary species, *B. tectorum* and *L. perfoliatum*, exhibited the strongest competition at the highest stress levels, which coincided with their ecological optima. Because of their strong herbivory tolerance and avoidance of water stress, both species may derive few benefits from *Artemisia* facilitation but incur the costs of competition. These strikingly different patterns of interaction suggests that a shift in the relative importance of selective forces has fundamentally altered the structure of *Artemisia* interactions with herbaceous species. We contend that prior to cattle introduction, competition between *Artemisia* and bunchgrasses was likely one of the most important selective forces (Caldwell et al. 1987). The strong competition between *Artemisia* and non-natives observed in this study evidences these past interactions and forces (Brooker et al. 2008). Historically, facilitation was probably limited to *Artemisia* amelioration of heat stress and water stress (Davies et al. 2007).

With the introduction of cattle as a novel selective force (Mack & Thompson 1982), *Artemisia* protection from herbivory likely increased in importance because of the grazing sensitivity of most bunchgrasses (France et al. 2009). The consistently strong *Artemisia* facilitation of native bunchgrasses at high stress-disturbance levels provides convincing evidence for the strength of this current selective force (Brooker et al. 2008). Similarly, this novel selective force may also explain the extremely low abundance of the most stress-tolerant beneficiary species, *H. comata* and *A. hymenoides*, across the study area; these two bunchgrasses are extremely sensitive to herbivory (Rickard et al. 1975). Lacking strong competitive responses, these two species are probably least able to minimize the costs of competing with *Artemisia* for resources and thus have a limited ability to realize the benefits of *Artemisia* protection from herbivory (Villarreal-Barajas & Martorell 2009; Maestre et al. 2009). We speculate that persistently high disturbance levels from high cattle stocking rates in the early 1900s (Miller et al. 2010), when combined with these species' sensitivity to herbivory and inability to tolerate *Artemisia* competition, likely substantially reduced these two species. Like the many Mediterranean species lineages that evolved under more mesic climatic conditions than current ones now dependent on facilitation for their persistence (Valiente-Banuet et al. 2006), some native bunchgrass species may now be dependent on *Artemisia*

facilitation for their continued persistence under otherwise unsuitable combined levels of disturbance and stress. These changes in selective forces and structure of interactions between *Artemisia* and many bunchgrass species has profound implications for community stability and susceptibility to *B. tectorum* invasion.

Our study reports the first evidence suggesting that facilitation by a foundational shrub reduces susceptibility to exotic invasion by maintaining the abundance of other natives, which in turn could indirectly limit the magnitude of non-native invasion (Brooker et al. 2008). In high stress-disturbance communities, native beneficiaries dominated undershrub communities, at least in part, because of strong *Artemisia* facilitation. In contrast, *B. tectorum* and *L. perfoliatum* exclusively dominated interspace communities. Although not an absolute barrier to invasion, the bunchgrasses directly facilitated by *Artemisia* likely out-competed the two invasives beneath shrubs and limited the magnitude of the invasion in undershrub communities (Michalet et al. 2015). Unfortunately, this facilitation-mediated resistance to invasion at the undershrub-interspace scale may not translate into higher resistance at the community scale because of the limited spatial scale over which facilitation occurs. *Artemisia* cover ranged between 9% and 30% across the study sites, which leaves between 70% to 91% of these communities beyond the influence of *Artemisia* facilitation-increased resistance to *B. tectorum* dominance.

We also report the first evidence suggesting that facilitation increases community stability in space at intermediate stress levels, but decreases stability at higher stress levels (Butterfield 2009), adding to growing evidence that disturbance-mediated shifts from competition to facilitation may reduce community stability (Baez & Collins 2008). Our low stress-disturbance communities were analogous to 'low severity' environments described by Butterfield (2009). Undershrub and interspace communities had the same composition. This high compositional stability was associated with high functional stability, at least to the extent measured by lower susceptibility to invasion (Krushelnycky & Gillespie 2008). Despite some differences in composition between undershrub and interspace communities in intermediate stress-disturbance environments, the strength of the positive relationship between these communities increased compared to those in low stress environments. Although *E. elymoides* was clearly associated with the undershrub community, it was still a significant component of the interspace communities, and none of the native beneficiaries were entirely dependent on facilitation for their continued persistence.

These findings suggest that *Artemisia* facilitation increased compositional stability through what Butterfield (2009) referred to as 'facultative' facilitation. This high compositional stability was again associated with high

functional stability at the community level where non-native composition remained low. However, Butterfield (2009) predicted that facilitation would destabilize communities if species became 'obligate' beneficiaries of facilitation such that a larger proportion of the population can only persist next to a benefactor. We found convincing evidence of this critical tipping point where *Artemisia* facilitation became a destabilizing force in the high stress-disturbance communities. All the native beneficiaries persisted in the undershrub communities, while their composition was strikingly lower in the interspace communities. This aggregation of bunchgrasses beneath *Artemisia* likely increased the size and connectivity of gaps among perennial vegetation and increased general resource availability in interspaces (Chambers et al. 2007; Reisner et al. 2013). *B. tectorum* and *L. perfoliatum* dominated these communities.

A perfect storm of factors likely explain the destabilizing effects associated with shifts in the structure of interactions between *Artemisia* and herbaceous species. First, *Artemisia* could control the structure of interactions because it simultaneously competes with herbaceous species for resources (Caldwell et al. 1987) and facilitates them by protecting them from herbivory (France et al. 2009), ameliorating heat stress and enhancing resource availability (Davies et al. 2007). Second, cattle herbivory disturbance, a novel type of disturbance in these ecosystems, could be a predominant driver of shifts in the structure of *Artemisia*-bunchgrass interactions, given that most native bunchgrass species are sensitive to such herbivory (Mack & Thompson 1982). This sensitivity likely makes bunchgrasses especially vulnerable to destabilizing 'obligate' *Artemisia* facilitation. Third, the structure of *Artemisia* interactions with the invasive *B. tectorum* seems to be fundamentally different than those with native bunchgrasses. Further, *B. tectorum*'s rapid growth, nutrient uptake and reproduction rates allow it to exploit increased resource availability when bunchgrass abundance declines in interspaces (Chambers et al. 2007).

Increasing spatial aggregation of vegetation is an indicator that ecosystem resilience has been compromised and that future disturbances may trigger a 'catastrophic regime shift' (Scheffer et al. 2009). Verwijmeren et al. (2013) proposed that declines in facilitation at the severe ends of a stress gradient may serve as an early warning for critical degradation transitions in arid ecosystems, and that consumer pressure may accelerate such transitions. The obligate destabilizing facilitation we observed between *Artemisia* and bunchgrasses may play a similar indicator role, with novel disturbances associated with cattle grazing potentially accelerating the degradation process by reducing ecosystem resilience. Once bunchgrasses persist only beneath shrubs, they are likely more

susceptible to fire-induced mortality since fires burn more intense under woody vegetation (Whelan 1995). Consequently, fires, which are natural disturbances in *Artemisia* ecosystems but occur more frequently with *B. tectorum* invasion (Pyke 2011), are increasingly likely to trigger a catastrophic regime shift, converting perennial-dominated shrub steppe to *B. tectorum*-dominated grasslands (Miller et al. 2010). Our findings suggest that reducing cattle-related disturbances may be one of the most effective means of limiting the risk of such regime shifts.

Acknowledgements

We thank our field assistants and families. We give special thanks to Dr. Bruce McCune and Dr. James Grace for statistical advice. This is contribution #73 from the Sagebrush Steppe Treatment and Evaluation Project, funded by the US Joint Fire Sciences Program and by the Coordinated Intermountain Restoration Project, US Geological Survey Forest and Rangeland Ecosystem Science Center and Oregon State University. The use of any trade, product or firm name is for descriptive purposes only and does not imply endorsement by the US Government.

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Supporting Information

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

Appendix S1. Beneficiary species' life-history strategies and relative competitive response abilities and stress tolerances.

Appendix S2. Description of ecological sites.

Appendix S3. Temporal variation in precipitation amount and timing.

Appendix S4. Differences in individual stress and disturbance variables between the low, intermediate and high stress-disturbance communities.

Appendix S5. Relationship between heat, herbivory, water and cumulative stress and NMS ordination.

Appendix S6. Relationships between difference in beneficiary species cover between the undershrub and interspace microsites and beneficiary species' plot-level cover (community composition) and the NMS ordination axes.

Appendix S7. Relationships between beneficiary species' abundance (plot-level cover) and the NMS ordination axes.

Appendix S8. Blocked indicator species analysis comparing composition of undershrub and interspace communities within the low, intermediate and high stress-disturbance communities.

Appendix S9. Indicator species analysis comparing community composition (plot-level cover) of the low, intermediate and high stress-disturbance communities.

Graphical Abstract

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We found that facilitation enhanced stability at intermediate stress levels by providing a refuge for native bunchgrasses from cattle herbivory and stress, which in turn reduced the magnitude of *Bromus tectorum* invasion. However, facilitation was a destabilizing force at the highest stress levels when bunchgrasses became obligate beneficiaries dependent on facilitation for their persistence. *B. tectorum* dominated these communities.