AN ABSTRACT OF THE DISSERTATION OF

Michael D. Reisner for the degree of Doctor of Philosophy in Forest Resources presented October 18, 2010.

Title: Drivers of Plant Community Dynamics in Sagebrush Steppe Ecosystems: Cattle Grazing, Heat and Water Stress.

Abstract approved:

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Sagebrush steppe ecosystems are one of the most widespread but endangered ecosystems in North America. A diverse array of human-related stressors has gradually compromised these ecosystems' resilience to disturbance and invasion by *Bromus tectorum* (cheatgrass). The role of the foundational shrub *Artemisia* as a driver of herbaceous community structure and dynamics during this degradation process is poorly understood. Many of the individual factors driving *B. tectorum* invasions are well documented. However a predictive understanding of the relative importance of complex, interacting factors in the causal network of simultaneously occurring processes determining invasibility has proven elusive.

I examined these issues at the landscape level across 75 sites capturing a range of soil and landscape properties and cattle grazing levels similar to those found across the

Great Basin. Cumulative cattle herbivory stress levels were a predominant component of both the overlapping heat and water stress gradients driving the structure of *Artemisia* interactions with herbaceous species. Consistent with the stress gradient hypothesis, *Artemisia* facilitation of herbaceous species was most frequent and strongest at the highest stress levels, and competition was most frequent and strongest at the lowest stress levels. The two species with the highest competitive response abilities, *Elymus elymoides* and *Poa secunda*, showed the strongest facilitation at the upper limits of their stress tolerances. The structure of *Artemisia* interactions with the invasive *B. tectorum* was strikingly different than those with native bunchgrasses. *Artemisia* interactions with native bunchgrasses shifted from competition to facilitation with increasing heat, water, and herbivory stress, but its interactions remained competitive with *B. tectorum* along the entire stress gradient.

Shifts in the structure of interactions between *Artemisia* and native bunchgrasses were associated with both an increase and decrease in community compositional and functional stability. I report the first evidence of native species facilitation decreasing community invasibility. *Artemisia* facilitation increased native bunchgrass composition, which reduced the magnitude of *B. tectorum* invasion in under-shrub compared to interspace communities. This decreased invasibility did not translate into lower invasibility at the community level because of the limited spatial scale over which such facilitation occurs. *Artemisia* facilitation increased community compositional and functional stability at intermediate stress levels but decreased community stability at high stress levels. Facilitation became a destabilizing force when native bunchgrass species became “obligate” beneficiaries, i.e. strongly dependent on *Artemisia* facilitation for their continued persistence in the community.

Structural equation modeling assessed the structure of the causal network and relative importance of factors and processes predicted to drive community invasibility. The linchpin of ecosystem invasibility was the size of and connectivity between basal gaps in perennial vegetation, driven by shifts in the structure and spatial aggregation of the native bunchgrass community. Landscape orientation and soil physical properties determined inherent risk to invasion. Resident bunchgrass and biological soil crust communities provided biotic resistance to invasion by reducing the size of and connectivity between basal gaps and thereby limiting available resources and reducing safe sites for *B. tectorum* establishment. High levels of cattle grazing reduced ecosystem resilience by reducing native bunchgrass and biological soil crust abundance and altering bunchgrass community composition and facilitated *B. tectorum* invasion.

Conserving and restoring resilience and resistance of these imperiled ecosystems will require reducing cumulative stress levels. As global climate change increases heat and water stress, reducing cumulative cattle grazing intensities by altering utilization rates and/or seasons of use may be the only effective means of accomplishing these goals.

Drivers of Plant Community Dynamics in Sagebrush Steppe Ecosystems: Cattle Grazing, Heat and Water Stress

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorized release of my dissertation to any reader upon request.

Michael D. Reisner, Author

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Dr. Paul S. Doescher and David A. Pyke assisted in experimental design, interpretation of results and manuscript preparation for Chapters 2, 3, and 4. Dr. Bruce McCune contributed to the statistical analyses and data interpretation for Chapters 2, 3, and 4. Dr. James B. Grace contributed to the statistical analyses and manuscript preparation for Chapter 4.

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CHAPTER 1

General Introduction

From the 1940s into the 1970s, big sagebrush (*Artemisia tridentata*) was eradicated from millions of acres throughout the western United States (Suring et al. 2005). The explicit goal of these efforts was to increase herbaceous production for livestock and wildlife. These removal efforts assumed that competition was the primary determinant of community organization and predicted that eliminating sagebrush would increase herbaceous species performance. Although many studies reported that removals significantly increased perennial grass productivity (Blaisdell 1953; Hedrick et al. 1966; Sneva 1972; Harniss and Murray 1973), additional studies showed that removals had no measurable effect (Blaisdell 1953; Peek et al. 1979) or that such removals reduced productivity and diversity (Pechanec and Stewart 1944; West and Hassan 1985; Cook et al. 1994; Watts and Wambolt 1996; Wambolt et al. 2001). These eradication efforts combined with a diverse array of human land uses, introduction of invasive species and altered fire regimes have caused loss, fragmentation, and degradation of millions of hectares of shrub-steppe ecosystems (Leu et al. 2008; Knick et al. 2009; Knick et al. 2010).

Consequently, semi-arid *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) (henceforth "*Artemisia*") ecosystems are currently one of North America's most widespread, but endangered ecosystems (Noss et al. 1995; Miller et al. 2010). The keystone species for these ecosystems, the Greater Sage-Grouse (Suring et al. 2005), was recently listed as a warranted but precluded species under the Endangered Species Act. *Artemisia* ecosystems of the Great Basin are especially vulnerable to additional losses and degradation because of their susceptibility to invasion by *Bromus tectorum* (cheatgrass), an exotic annual grass (Suring et al. 2005; Bradford and Lauenroth 2006). B. tectorum currently dominates 7% of the Northern Great Basin (Bradley and Mustard 2005; Bradley and Mustard 2006), and Suring et al. (2005) recently estimated that 50% of the Great Basin Ecoregion has a moderate or high probability of B. tectorum dominance in the herbaceous understory. Fire is considered to be the dominant historical disturbance driving community phase transitions in the reference state of this ecosystem. In the presence of B. tectorum, fire is increasingly triggering “catastrophic regime shifts,” (Scheffer et al. 2001; Scheffer et al. 2009) whereby diverse native shrub-steppe communities are transformed into annual grasslands dominated by B. tectorum and other non-native species (Billings 1990; D'Antonio and Vitousek 1992; Knapp 1996; Pyke and Brooks 2001; Knick et al. 2010).

These catastrophic landscape-level conversions have rippling effects on other ecosystem processes and functions including: (1) altering fire disturbance regimes by increasing the size and frequency of fires (Miller et al. 2010); (2) altering the energy balance by converting such communities from a carbon sink to a significant new source (Prater et al. 2006); (3) altering wildlife habitat functions by reducing sagebrush cover required by sagebrush-obligate species, such as the Greater Sage Grouse, for prolonged periods of time (Knick et al. 2009; Miller et al. 2010); and (4) and potentially transforming conservative decomposition and nutrient cycles dominated by immobilization to more open cycles dominated by mineralization (Austin et al. 2004; Norton et al. 2004; Hooker et al. 2008; Norton et al. 2008).

These catastrophic regime shifts and associated disruptions of ecological processes and functions indicate that a combination of disturbances and stressors has compromised the functional stability, i.e. increased the invasibility, of these communities (McNaughton 1977; Tilman 1996; Foster et al. 2002; Scheffer et al. 2009).

Invasibility is an emergent property of an ecosystem and thus under the control of multiple operating factors connected simultaneously by a causal network of underlying mechanisms (Lonsdale 1999). Successful invasion depend on: (1) characteristics of invading species or species invasiveness (Daehler 2003) and (2) community invasibility. Community invasibility is determined by: (a) the type and amount of disturbances and the relative resilience of natives and non-native species to such disturbance regimes, (b) biotic resistance to invasion that is determined by the competitive abilities of resident native species, (c) community structure and (d) propagule pressure (Hobbs and Huenneke 1992; Williamson and Fitter 1996; Lonsdale 1999; Richardson and Pysek 2006; Rilov et al. 2009). All of these factors determine source availability and the timing of this availability relative to the interacting organisms.

Mechanistically, invasibility may be linked to increases in resource availability (Davis et al. 2000). Communities are predicted to be more vulnerable to invasion when there is an increase in the amount of unused resources because resident species are satiated, resource supplies increase faster than they can be utilized, or both (Stohlgren et al. 1999; Davis et al. 2000). Recent studies predict that grazing and associated disturbances caused by non-native herbivores will exacerbate the magnitude of non-native invasions by decreasing the abundance of native species compared to non-native species (i.e. invasional meltdown) (Parker et al. 2006; Simberloff 2006; Nunez et al. 2008; Nuñez et al. 2010).

Recommendations for landscape-scale restoration to reverse this degradation have grown exponentially in the last decade (Meinke et al. 2008; Pyke 2010). These initiatives include a renewed interest in selective sagebrush removal to restore native herbaceous communities for wildlife habitat and to restore ecosystem resistance to invasion and resilience in to disturbance (McIver and Starr 2001; McIver et al. 2009). While the objective of such removals has changed, the underlying premise remains resolute; *Artemisia* competition with herbaceous species is the dominant driver of community composition, and its removal will result in a release of herbaceous species (McIver et al. 2009). At this turning point for these ecosystems, we need to heed the cautionary words of Mark Twain, "What gets us into trouble is not what we don't know, it's what we know for sure that just ain't so."

Contrary to this dominant paradigm and conventional wisdom, biotic interactions are mechanistically comprised of simultaneously occurring positive and negative interactions (Hunter and Aarssen 1988; Holmgren et al. 1997; Holzapfel and Mahall 1999). Negative interactions involve competition for different resources (Grime 1976; Tillman 1987), while positive interactions may involve enhancement of resources or amelioration of stress (Callaway 2007; Maestre et al. 2009). Stress plays a pivotal role in determining interaction outcomes because it strongly influences the strength of underlying positive and negative interactions. Stress is defined as any external abiotic (heat, water) or biotic (herbivore) constraint that limits the rate of photosynthesis and reduces a plant's ability to convert energy to biomass (Grime 1977). The strength of positive interactions increases with increasing stress except at the most extreme levels (Brooker et al. 2008; Maestre et al. 2009). In contrast, the strength of negative interactions is either unrelated to stress and remains consistently high (Tillman 1988; Wilson and Tillman 1991; Reader 1994; Wilson and Tillman

1995), or alternatively, decreases with increasing stress (Grime 1976; Wilson and Keddy 1986; Twolan-Strutt and Keddy 1996; Goldberg et al. 1999; Gaucherand et al. 2006).

Changes in strength of these underlying processes drive shifts between competition and facilitation. 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 is low. The SGH also predicts that the strongest facilitation should occur with competitive species at the upper limits of their stress tolerance while the strongest competition should occur with stress tolerant species located at their ecological optimum (Bertness and Callaway 1994; Liancourt et al. 2005).

Shifts in the structure of interaction outcomes, i.e. a shift from competition to facilitation, along stress gradients are likely to have profound implications for community stability (Tilman 1996; Callaway 2007; Ives and Carpenter 2007; Butterfield 2009). The structure of species interactions is a critical determinant of community compositional stability (McCann et al. 1998; Lehman and Tilman 2000; McCann 2000; Fargione and Tilman 2005). Community compositional instability can be defined as changes in species abundances that drive directional changes in community composition (Collins 2000; Baez and Collins 2008). There is growing evidence that changes in the structure of species interactions can reduce such stability (McCann 2000; Baez and Collins 2008; Villarreal-Barajas and Martorell 2009). Compositional stability is likely one of the mechanisms by which community functional stability, the ability to resist changes in aggregate properties or process (i.e. invasibility), is maintained (Tilman 1996; Hooper et al. 2005; Krushelnycky and Gillespie 2008).

Facilitation may increase or decrease community stability (Bruno et al. 2003; Brooker et al. 2008; Butterfield 2009). Facilitation is predicted to increase stability at intermediate levels of stress but decrease stability at high stress levels (Butterfield 2009). A shift to obligate facilitation, where many species only persist next to their benefactor, is predicted to be the tipping point between facilitation stabilizing versus destabilizing a community (Butterfield 2009). Facilitation is predicted to increase functional stability, i.e. decrease community invasibility, by increasing resistance when one resident native species increases the abundance and/or diversity of other native species, which in turn reduce the magnitude of an invasion (Zavaleta and Hulvey 2004; Fargione and Tilman 2005; Brooker et al. 2008).

Artemisia communities are characterized by strong resource-based (water) and non-resource-based (heat and herbivory) stress gradients (West 1983; Chambers et al. 2007; Davies et al. 2007). Annual variation in amount and timing of precipitation interacts with soil properties to determine plant available water, which in turn produce spatial water stress gradients (Noy-Meir 1973; Passey et al. 1982; Bates et al. 2006). Across these water stress gradients, changes in landscape orientation (aspect and slope) create gradients of heat stress (Hironaka et al. 1983; Jensen 1989; Jensen 1990; Davies et al. 2007). Cattle grazing produces strong gradients of herbivory stress that radiate outward from the nearest source of water (Andrew 1988; Adler and Hall 2005; Brooks et al. 2006). Cattle grazing is a novel disturbance in the Intermountain West where most native bunchgrasses are highly sensitive to such herbivory (Mack and Thompson 1982) and remains a predominant land use across *Artemisia* communities (Noss 1994; Knick et al. 2010; Crawford et al. 20004).

The overarching goal of Chapters 2 and 3 was to gain a better understanding of the role of *Artemisia* as a driver of species abundances and community compositional and functional stability (invasibility) across stress gradients. I examined these issues at the landscape level across 75 sites capturing a range of soil and landscape properties and cattle grazing levels similar to those found across the Great Basin.

In Chapter 2, spatial patterns of association between the foundational shrub *Artemisia* and eight focal herbaceous, six native species and two non-native species, were used to infer interaction outcomes, i.e. competition and facilitation, by comparing focal species cover beneath *Artemisia* canopies and in adjacent interspaces.

Greater focal species cover under *Artemisia* (under-shrub) compared to interspace microsites, i.e. positive spatial association, was interpreted as facilitation. Greater cover in interspace compared to under-shrub microsites, i.e. negative spatial association, was interpreted as competition (Greenlee and Callaway 1996; Holzapfel and Mahall 1999; Callaway 2007). The six native species were *Pseudoroegneria spicata* (bluebunch wheatgrass), *Achnatherum thurberianum* (Thurber’s needlegrass), *Hespirostipa comata* (needle-and-thread grass), *Achnatherum hymenoides* (Indian ricegrass), *Poa secunda* (Sandberg bluegrass), and *Elymus elymoides* (bottlebrush squirreltail). The two non-native species were *B. tectorum*, and *Lepidium perfoliatum* (clasping pepperweed).

This study had three objectives. The first was to quantify spatial patterns of association between *Artemisia* and the eight focal herbaceous species and use patterns to infer interaction outcomes. The second was to describe the stress gradients driving spatial patterns of association. The third was to use this information to test several recent predictions derived from the SGH.

The primary goal of Chapter 3 was to determine whether findings observed at the species-level in Chapter 2 translated into ecologically meaningful effects on community compositional and functional stability. The study had three objectives. The first was to examine whether pronounced shifts in the structure of interactions between *Artemisia* and bunchgrasses, a shift from competition/neutral to facilitation/strongly facilitation, reduced community compositional and functional stability. The second was to examine whether *Artemisia* facilitation of native bunchgrasses would increase stability at intermediate stress levels but decrease stability at high stress levels. The third was to assess whether *Artemisia* facilitation of native bunchgrasses would increase functional stability, i.e. decrease invasibility, by maintaining greater bunchgrass composition, which in turn would reduce non-native composition of under-shrub compared to interspace communities.

Given the complex, context-dependent nature of community invasibility, accurately characterizing effects of one factor or mechanism requires taking into account potential effects of others. Not surprisingly, untangling and understanding such complexity has proven elusive to ecologists. In Chapter 4, structural equation modeling (SEM) was used to evaluate a complex, multivariate hypothesis of a causal network of factors and processes predicted to control community invasibility. SEM was used to accomplish three objectives. The first was to evaluate the numerous causal mechanisms by which cattle grazing and associated disturbances influence the susceptibility of these communities to B. tectorum invasion. The second objective was to place the role of cattle grazing in context by controlling and accounting for influences of other factors known to be important determinants of the composition, structure, and invasibility of these communities (i.e. to partition relationships). The third objective was to assess the relative importance of these inter-correlated factors and processes (Grace 2006).

Gaining a predictive understanding of the complexity driving an ecosystem's susceptibility to invasion requires placing the effect of one factor or mechanism in context relative to the importance of others operating simultaneously. Understanding the relative importance of these controlling factors, instead of factoring some of them out, is vital to predicting and managing ecosystem responses (Grace 2006). Knowledge of this causal network gained by SEM could be used to develop better predictive models (Marcot 2006). Models capable of accurately predicting ecosystem responses to different management scenarios or changes in circumstances, i.e. climate change, changes in disturbance regime, etc., are urgently needed to conserve and restore resilience of these highly endangered ecosystems (Suring et al. 2005; Meinke et al. 2008; Connelly et al. 2010).

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CHAPTER 2

A test of the stress gradient hypothesis along overlapping gradients of novel herbivory, water, and heat stress: shifts in interactions between a foundational shrub and native and non-native herbaceous species

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ABSTRACT

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 is low. We tested this hypothesis across 75 sites in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities designed to capture a resource--based water and two non-resource-based heat and herbivory stress gradients. We inferred competition and facilitation by examining spatial patterns of association between the foundational shrub *Artemisia* and 6 native and 2 non-native species. The focal species co-occurred, but differed in their ecological optimums and competitive response abilities and stress tolerances. *Poa secunda* and *Elymus elymoides* are the most competitive, but sensitive to heat and water stress. *Hespirostipa comata* and *Achnatherum hymenoides* are the least competitive, sensitive to herbivory stress, but highly tolerant of heat and water stress. *Pseudoroegneria spicata* and *Achnatherum thurberianum* have intermediate life history strategies but are sensitive to herbivory stress. *Bromus tectorum* and *Lepidium perfoliatium*, the non-natives, avoid water and heat stress and are extremely tolerant of or avoid herbivory.

Overlapping gradients of novel cattle herbivory, heat, and water stress drove spatial patterns of association between *Artemisia* and the focal species. Facilitation was most frequent and strongest at the highest combined levels of heat, water, and herbivory stress, and competition most frequent and strongest at the lowest combined stress levels. The two species with the highest competitive response abilities, *E. elymoides* and *P. secunda*, showed the strongest facilitation at the limits of their stress tolerances. Contrasting ecological optimums among the natives and non-natives, including the highly invasive *Bromus tectorum*, led to strikingly different patterns. For the most stress tolerant natives, competition was strongest and most frequent at the lowest stress levels, but for the stress avoiding non-natives, competition was strongest and most frequent at the highest stress levels. These findings suggest that the relationship is both species and stress gradient specific.

INTRODUCTION

Biotic interactions are critical drivers of species abundance and community composition (Clements 1916; Gleason 1926; Grime 1976; Tillman 1988; Bruno et al. 2003; Callaway 2007). Interactions are mechanistically comprised of simultaneously occurring positive and negative interactions (Hunter and Aarssen 1988; Holmgren et al. 1997; Holzapfel and Mahall 1999). Negative interactions involve competition for different resources (light, water, nutrients) (Grime 1976; Tillman 1987), while positive interactions may involve enhancement of resources or amelioration of stress (heat, herbivory) (Callaway 2007; Maestre et al. 2009). The balance of the strength of these underlying processes determines whether the interaction outcome is competition, neutral, or facilitation (Malkinson and Tielbörger 2010).

Stress plays a pivotal role in determining interaction outcomes because it influences the strength of underlying positive and negative interactions. Stress is defined as any external abiotic (heat, water) or biotic (herbivore) constraint that limits the rate of photosynthesis and reduces a plant's ability to convert energy to biomass (Grime 1977). 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 is low. The original SGH predicted that facilitation would increase and competition would decrease in frequency with increasing stress (Bertness and Callaway 1994). Subsequent refinements have focused on shifts in pair-wise species interactions, which collectively determine the community-level frequency of facilitation, and predict a shift from competition to facilitation with increasing stress, (Brooker and Callaghan 1998; Callaway 2007; Maestre et al. 2009).

One approach to testing the SGH involves observational studies that infer interaction outcomes, i.e. competition and facilitation, from spatial patterns of association among species. These studies compare the abundance of a focal species beneath nurse plants and adjacent open areas. Greater under-shrub abundance and greater interspace abundance are interpreted as evidence of facilitation and competition, respectively (Greenlee and Callaway 1996; Tewksbury and Lloyd 2001; Arroyo et al. 2003; Holzapfel et al. 2006; Michalet 2007; Sthultz et al. 2007).

While many studies support the general predictions of the SGH, conflicting studies have highlighted the context-dependency of the relationship between interaction outcomes and stress gradients and revealed several factors driving such complexity (Bruno et al. 2003; Callaway 2007; Brooker et al. 2008; Maestre et al. 2009). Although the original SGH predicted a monotonic, linear increase in the strength of facilitation with increasing stress (Bertness and Callaway 1994; Brooker and Callaghan 1998), current evidence suggests more complex, non-linear relationships are possible (Kawai and Tokeshi 2007; Maestre et al. 2009; le Roux and McGeoch 2010; Malkinson and Tielbörger 2010).

Although level of stress is the overriding factor, interactions between the type of stress and life history strategy and location of focal species relative to their ecological optimum strongly influence the relationship between interaction outcomes and stress gradients (Choler et al. 2001; Liancourt et al. 2005; Brooker et al. 2008; Wang et al. 2008; Maestre et al. 2009). Stress can be resource-based (water, nutrients) or non-resource-based (heat, herbivory) (Maestre et al. 2009). If the *only* stress is non-resource based, facilitation is likely to be more frequent and stronger because the only prerequisite to such outcome is benefactor amelioration of stress (Callaway 2007; Maestre et al. 2009). 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 outcome can only occur if the benefactor increases resource availability (Maestre and Cortina 2004; Maestre et al. 2009).

Along a given stress gradient, species with strongest competitive response abilities, the ability to minimize the inhibitory effects of neighbors (Goldberg and Landa 1991), are likely to exhibit the strongest facilitation when they are located at the upper limits of their tolerance to that stress (Choler et al. 2001; Liancourt et al. 2005; Brooker et al. 2008). These species should best be able to minimize costs of competition for resources with and maximize benefits of stress amelioration by neighbors (Brooker and Callaghan 1998; Maestre et al. 2009).

The overall goal of this study was to test the SGH in the semi-arid *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) (hereafter "*Artemisia*") communities of the Northern Great Basin. Spatial patterns of association between the foundational shrub *Artemisia* and eight focal herbaceous species, six native and two non-native, were used to infer interaction outcomes, i.e. competition and facilitation, by comparing focal species cover beneath *Artemisia* canopies (hereinafter “under-shrub microsites”) and in adjacent interspaces (hereinafter “interspace microsites”). Greater focal species cover in the under-shrub compared to interspace microsite was interpreted as facilitation. Greater cover in the interspace compared to under-shrub microsite was interpreted as competition. No difference in cover was interpreted as a neutral outcome (Greenlee and Callaway 1996; Holzapfel and Mahall 1999; Callaway 2007). The magnitude of the difference in cover was used to infer the strength of the interaction outcome. The number of focal species exhibiting a particular interaction outcome was used to infer the frequency of that interaction at the community-level.

The foundational shrub species *Artemisia*, the benefactor, is characterized by numerous adaptations that make it extremely stress tolerant (Depuit and Caldwell 1973; Miller and Shultz 1987; Donovan and Ehleringer 1994). *Artemisia* competes with herbaceous species for water (Sturges 1977) and nutrients (Caldwell et al. 1987; Miller et al. 1991). Simultaneously, *Artemisia* may facilitate herbaceous species by ameliorating heat stress (Pierson and Wight 1991; Davies et al. 2007), increasing water availability by hydraulic lift or shade-induced reductions in evapo-transpiration demand (Caldwell and Richards 1989; Davies et al. 2007), enhancing nutrient availability (Doescher et al. 1987), or protecting against herbivory (Hazlett and Hoffman 1975; France et al. 2009). Compared to adjacent interspaces, *Artemisia* canopies are associated with greater tree herbaceous seedling establishment (Hazlett and Hoffman 1975; Wirth and Pyke 2003) and greater abundance of some herbaceous species (Davies et al. 2007).

The eight focal herbaceous species used to investigate pair-wise interactions with *Artemisia* represent a wide range of *relative* competitive response abilities and tolerances to water, heat, and herbivory stress. The eight species co-occur in the study area, but their ecological optima, location of maximum community composition along the stress gradients, differed. *Poa secunda* (Sandberg bluegrass) and *Elymus elymoides* (bottlebrush squirreltail) have high competitive response abilities (Hironaka and Tisdale 1963; Humphrey and Schupp 2004), are sensitive to heat and water stress (Link 1990; Johnson and Aguirre 1991), but tolerant to herbivory stress (Trilica and Cook 1971). *Hespirostipa comata* (needle-and-thread grass) and *Achnatherum hymenoides* (Indian ricegrass) are long-lived, deep-rooted bunchgrasses, highly tolerant of heat and water stress (Platou et al. 1986), but highly sensitive to herbivory stress (Rickard et al. 1975). *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Achnatherum thurberianum* (Thurber’s needlegrass) are relatively tolerant of heat and water stress (Passey et al. 1982) but are sensitive to herbivory stress (Blaisdell and Pechanec 1949; Mueggler 1975; Ganskopp 1988). The two non-natives, *Bromus tectorum* (cheatgrass), a highly invasive annual grass, and *Lepidium perfoliatum* (clasping pepperweed), an annual forb, are ruderal species that avoid water and heat stress by senescing. Both species exhibit grazing avoidance and tolerance mechanisms that make them extremely tolerant of herbivory stress (Archer and Pyke 1991; Hempy-Mayer and Pyke 2009).

This study had two objectives. The first was to quantify spatial patterns of association between *Artemisia* and the eight focal herbaceous species and use those patterns to infer interaction outcomes. The second was to describe stress gradients driving spatial patterns of association. The following specific hypotheses regarding the SGH were tested:

1. Interaction outcomes between *Artemisia* and the focal species would shift from competition to facilitation with increasing stress. However, the precise shape of the relationship between interaction outcomes and the stress gradients would be variable and species-specific.
2. *P. secunda* and *E. elymoides*, the native species with strongest competitive response abilities would exhibit the strongest facilitation at the upper limits of their stress tolerance (Liancourt et al. 2005; Brooker et al. 2008). The other six species would exhibit less pronounced facilitation; however facilitation would still occur at the upper limits of each species tolerance to a stress gradient.
3. At the community-level, facilitation would be most frequent and strongest at the highest stress levels and competition most frequent and strongest at the lowest stress levels.

STUDY AREA AND SAMPLING DESIGN

Artemisia communities are excellent systems in which to test the SGH because they are characterized by strong resource-based (water) and non-resource-based (heat and herbivory) stress gradients (West 1983; Chambers et al. 2007; Davies et al. 2007). Annual variation in the amount and timing of precipitation plays a pivotal role in determining water availability within the soil profile (Noy-Meir 1973; Passey et al. 1982; Bates et al. 2006). This temporal variability in the amount and timing of precipitation interacts with soil properties to determine plant available water, which in turn produce spatial water stress gradients. Coarser-texture soils are characterized by substantially higher water stress and lower herbaceous productivity compared to loamier or finer-textured soils (Passey et al. 1982; Hironaka et al. 1983; Davies et al. 2006).

Across these water stress gradients, changes in landscape orientation (aspect and slope) create gradients of heat stress (Hironaka et al. 1983; Jensen 1989; Jensen 1990; Davies et al. 2007). Compared to north aspects, south aspects are characterized by higher heat loads (McCune 2007) that increase evapo-transpiration demand, which increases water stress (Burkhardt and Tisdale 1969; Hinds 1975; Pierson and Wight 1991; Chambers 2001; Davies et al. 2007), and significantly lower herbaceous productivity (Hinds 1975; Passey et al. 1982; Davies et al. 2007).

Finally, livestock grazing is a predominant land use across *Artemisia* communities (Brussard et al. 1994; Noss 1994; Knick et al. 2010; Crawford et al. 2004). Livestock grazing produces strong gradients of herbivory and trampling-induced disturbance stress that radiate outward from the nearest source of water (Andrew 1988; Adler and Hall 2005; Brooks et al. 2006).

The study consisted of 75 study sites located in the Northern Great Basin floristic province of central Oregon (Miller et al. 2010) on three Bureau of Land Management (BLM) federal grazing allotments in the Burns District, Three Rivers Resource Area. We employed a stratified random sampling design with two objectives: (1) to capture a complete severity gradient, i.e. sites ranging from the lowest to highest levels of stress, for three potential stress gradients (heat, herbivory, and water) where *Artemisia* and the eight focal species co-occurred (Brooker et al. 2008; Malkinson and Tielbörger 2010), and (2) to capture as many combinations of levels and types of stress as possible. This design allowed us to test the SGH along three continuous and overlapping types of stress gradients.

The design consisted of three strata: (1) soils, (2) landscape, and (3) cattle grazing intensity. ArcGIS 13.0 (ESRI) was used to manipulate all geographic databases and conduct spatial analyses. To reduce potential confounding effects of time since fire, all areas within the study area that had burned since 1930 were excluded using a fire perimeter database (http://sagemap.wr.usgs.gov).

To capture variation in water stress driven by differences in soil properties, Natural Resource Conservation Service (NRCS) digital soil maps were used to stratify the study area into different map units, which consisted of one or more soil map components (http://websoilsurvey.nrcs.usda.gov). Soil map components were matched with corresponding NRCS Ecological Site Descriptions (ESDs). An “ecological site” is “a distinctive type of land with specific physical characteristics that differs from other type of land in its ability to produce distinctive kind and amount of vegetation” (NRCS 2003). If the ESD did not identify *Artemisia* as the dominant shrub species, the component was excluded. Five *Artemisia*-dominated ESDs were identified: (1) Loamy 10-12 Precipitation Zone (PZ) with *P. spicata* and *A. thurberianum* dominating an intact herbaceous understory; (2) Sandy Loam 8-10PZ with *H. comata* and *P. spicata* dominating an intact understory; (3) Clayey 10-12PZ with *A. thurberianum* and *P. secunda* dominating an intact understory; (4) South Slopes 6-10PZ with *A. thurberianum* dominating an intact understory, and (5) North Slopes 6-10PZ with *P. spicata* dominating an intact understory. Water stress was quantified by measuring soil texture (% sand, silt, and clay) at 0-15 cm soil depth using the hydrometer method (Gee and Bauder 1986). Potential effective rooting depth was measured by digging a soil pit until bedrock, a confining layer (clay accumulation layer), or 2m depth was reached (Passey et al. 1982; Jensen 1989; Davies et al. 2007).

To capture variation in heat stress driven by changes in landscape orientation, each of the five ESDs were delineated into three landscape sub-strata using 10 m resolution U.S. Geological Survey Digital Elevation Models: (1) northerly aspects (0-90°, 270-360°), (2) southerly aspects (90-270°), or (3) flat. The aspect and slope of each plot were calculated from DEMs using Arc-GIS 13.0. Heat stress was quantified by calculating potential heat loads for each plot using aspect, slope, and latitude using the method described by McCune (2007). They represent an integrated measure of the influence of aspect and slope on heat stress (McCune and Keon 2002; Davies et al. 2007).

To capture variation in cattle herbivory stress, study sites were located at different distances from the nearest livestock watering location using a BLM database of livestock watering points. Because of the need to stratify the study area by soil and landscape properties, sites were located at variable distances, rather than at fixed intervals, from watering points (Adler and Hall 2005). Potential study sites were selected from random points generated for each of the soil-landscape strata combinations within the study area. Points were selected to ensure that study sites were located: (1) every 200-400 m (starting at 100m and extending to >3200 m) from the nearest watering location; (2) in as many soil-landscape strata combinations as possible; and (3) >200 m from the nearest road to minimize other disturbance-related effects. Cattle herbivory stress was quantified by four indicator measurements: distance from the nearest watering location, cow pie frequency, cow pie density, and bunchgrass basal area. Distance from the nearest watering location for each study site was estimated using Arc-GIS 13.0 and verified in the field using GPS. Distance from water best represents a gradient of cumulative herbivory stress (Adler and Hall 2005; Beever et al. 2006). Repeated defoliations associated with cattle herbivory can reduce the basal area of individual bunchgrasses by fragmenting the largest plants (Butler and Briske 1988). The basal circumference of 30 randomly selected bunchgrasses was measured in each plot and used to calculate the bunchgrass basal area (cm^2) using the following formula: Area = $\pi\ (Cir/2\pi)^2$. Cow pie frequency and density were measured in twelve belt transects (1x50m).

Cumulative stress was quantified by measuring herbaceous biomass in 20 (0.5 x 1.0m) quadrats. Ten located in the interspace and ten located in under-shrub microsites. To quantify potential temporal variation in water stress, the amount and timing of precipitation for each study site was derived from the parameter-elevation regression on individual slopes model (PRISM) at 2 - km^2 cell resolution (Daly et al. 1994; Daly et al. 2008). Sampling-year precipitation for all study plots was estimated for three time periods: (1) 8/1-10/31 (fall), (2) 11/1-3/31 (winter), and (3) 4/1-7/31 (spring-summer). Fall and winter estimates are from the periods preceding the growing season in which the plot was sampled.

Potential study sites were field verified to ensure they satisfied the above criteria. Actual surface ownership patterns, fire perimeters, and soil properties precluded locating two of the sites at the random location. The locations were moved to ensure the sites met all the above criteria, except that they were located <200 m but >100 m from the nearest two-track road.

METHODS

Sampling and measurements

Thirty (30) study sites were sampled in 2008, and 45 sites were sampled in 2009. One randomly located plot was used to sample each study site. The coordinates of each study plot were recorded with a Global Positioning System (GPS). Six 25-m transects were established using a spoke design and used for subsequent sampling (Herrick et al. 2005). All sampling occurred between May 10 and July 15 to capture peak herbaceous biomass. Herbaceous and *Artemisia* foliar cover was measured using line-point intercept at 0.25m increments along the six transects (Herrick et al. 2005).

Statistical analyses

The response variable was species cover; an estimate of abundance (Herrick et al. 2005). For each study plot, three measures of cover were calculated from the line-point intercept data for each of the eight focal species: (1) under-shrub microsite cover, (2) interspace microsite cover, and (3) community level (plot-level) cover.

Under-shrub cover included all pin intercepts of the herbaceous species when the pin intersected *Artemisia* as the “top canopy,” and interspace cover included all other pin intercepts of the species (Herrick et al. 2005). To quantify the spatial patterns of association between *Artemisia* and the eight focal species, the “difference in cover” between the under-shrub and interspace microsites was calculated separately for each focal species using the following equation: difference in cover = (under-shrub cover) – (interspace cover) and combined into a “difference in cover” matrix (8 focal species x 75 study sites). The measures used to quantify the heat, herbivory, water, and cumulative stress levels of each plot were combined into a second matrix (13 stress variables x 75 study sites). Community-level cover, an estimate of community composition, was used to evaluate the status of the eight focal species relative to its “ecological optimum”, defined as the location along the stress gradient where its community composition was greatest (Liancourt et al. 2005; Maestre et al. 2009).

A combination of multivariate and bivariate techniques was used to analyze the resulting dataset. Prior to analyses, the following variables were log-transformed to improve distributional properties, correlations with ordination axes, and the amount of variation explained by the ordinations (McCune and Grace 2002): all measures of cover, distance from nearest water source, cow pie density, bunchgrass basal area, heat loads, soil depth, precipitation, and herbaceous biomass.

Non-metric multidimensional scaling (NMS) ordination was used to ordinate study sites in “spatial patterns of association” space using the “difference in cover” matrix (Kruskal 1964). This approach related spatial patterns association at the community-level (across all eight focal species) to overlapping stress gradients while avoiding assumptions of linearity (Kruskal 1964; McCune and Mefford 1999). NMS ordination was performed using Euclidean distances to accommodate negative values in the “difference in cover” matrix (McCune and Grace 2002). The ordination was run in the “slow and thorough” autopilot mode using a random starting configuration in PC-ORD (McCune and Mefford 2008). The final 3-D configuration was rotated to isolate all the resource-based stress on axis 2 by rotating the ordination to load one of the strongest correlates of non-resource stress, heat load, on axis 1.

Joint plots were used to describe the relationship between stress gradients and the strongest patterns of spatial association at the community-level represented by the NMS ordination axes, (McCune and Mefford 1999). Pierson’s correlation coefficients were used to quantify these relationships. Variables with $r = \pm 0.20$ to 0.29 are described as weakly correlated, those with $r = \pm .30$ to .39 moderately correlated, and those with $r \geq \pm .40$ strongly correlated with the axis. Study sites closer together in ordination space are similar in patterns of spatial association between *Artemisia* and the eight focal species and stress levels.

Non-parametric multiplicative regression (NPMR) in HyperNiche (McCune 2006; McCune and Mefford 2008) was used to more precisely quantify the relationship between spatial patterns of association (interaction outcomes) and the stress gradients for the eight focal species. Because NPMR is not premised on any assumptions concerning the shape of response curves (McCune 2006), this approach provides the flexibility to fit complex, non-linear response curves to describe the relationship. The predictors were the axes 1 and 2 ordination scores. These scores are an integrated measure of the complex stress gradients associated with the dominant patterns of spatial association at the community-level extracted by the ordination. The response variables were the "difference in cover" for each of the eight focal species. The regression used a local mean estimator and Gaussian kernel function. To control for potential interactions between the axes, response curves were generated using partial models and focal variables (McCune 2009; McCune and Mefford 2008). We similarly constructed response curves for the community-level cover data.

Final model fit was assessed with a cross-validated R^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; McCune 2009). Because there are no coefficients or slopes to compare in NPMR, sensitivity analysis was used to evaluate the relative importance of model predictors (McCune 2009). Sensitivities were calculated by measuring the change in the response variable to incremental changes in the values of each predictor for each observed point (McCune 2006; McCune 2009). The sensitivity values across all data points were averaged and standardized as a proportion of the range of the response variable. In ecological terms, a higher sensitivity to one of the predictor axes translated into more pronounced shifts in spatial patterns of association compared to shifts along the stress gradient represented by the other ordination axis.

Hierarchical agglomerative cluster analysis (Euclidean distance and flexible beta linkage, $\beta = -0.25$) of the “differences in cover” matrix was used to identify groups of study sites differing in spatial patterns of association. Multi-variate differences in spatial patterns of association at the community-level and combined levels of heat, herbivory, and water stress between the identified groups were tested using multi-response permutation procedures (MRPP) (Mielke 1984). This procedure generates an A-statistic, the chance-corrected within-group agreement, and a corresponding p-value. When A is close to zero, groups are no more different than expected by chance, while an $A = 1$ means perfect separation of groups (McCune and Grace 2002). A can be interpreted as an effect size with higher values indicating greater differences. Significance was assessed at a p-value $\alpha = 0.05$. Because the stress variables were measured on different scales, they were relativized by standard deviates to put them on equal footing prior to MRPP analyses (McCune and Grace 2002).

The most ecologically meaningful number of groups was pruned from the dendrograms using the A-statistic and associated p-values from the MRPP analyses (McCune and Grace 2002). The identified groups were overlaid onto the ordinations to accentuate the relationships between groups and identified stress gradients. This process identified three easily interpretable groups of plots: low stress, intermediate stress, and high stress. Differences in heat, herbivory, water, and cumulative stress between the groups were assessed using ANOVA ($\alpha = .10$) using S-Plus 8.0. Where significant differences were detected, Bonferroni-adjusted 90% confidence intervals were used to quantify differences between the groups.

Within each of the groups, a t-test ($\alpha = .10$) using a two-sided p-value was used to evaluate whether the difference between the under-shrub and interspace cover was significantly different from zero for each of the focal species. The interaction outcome is indicated by the sign of the difference: a positive difference in cover indicates facilitation (+), a negative difference in cover indicates competition (-), and no difference indicates a neutral outcome (0). The strength of the interaction outcome is represented by the magnitude of the difference. Positive and negative differences greater than three standard deviations (SDs) of the mean difference indicate strong facilitation (+ +) and competition (- -), respectively. The number of focal species for which interaction outcomes were facilitation, competition, or neutral was used to estimate the frequency of interaction outcomes at a given stress level (le Roux and McGeoch 2010).

Differences in focal species' community-level cover among the three stress groups were assessed with ANOVA ($\alpha = .10$) using S-Plus 8.0. Where differences were detected, Bonferroni-adjusted 90% confidence intervals were used to quantify them. For log transformed variables, back-transformed medians and 90% confidence intervals were reported.

RESULTS

NMS ordination and NPMR regression

The final 3-D NMS ordination explained 91% of the variation in the differences in cover between the shrub-canopy and interspace microsites, i.e. variation in the spatial patterns of association between *Artemisia* and the focal species (Fig. 2.1: $p = 0.004$; final stress = 10.6; final instability < 0.00001). Axis 1 and Axis 2 explained 27% and 56% of the variation, respectively. Axis 3 was not analyzed further because of its weak explanation of variation (8%) and lack of correlation with any of the stress indicators.

Stress gradients driving shifts in spatial patterns of association

Axis 1 represented a gradient of increasing non-resource-based stress associated with overlapping gradients of increasing heat and herbivory stress (Fig. 2.1, Table 2.1) (hereafter “heat & herbivory stress gradient”). Heat loads had a moderate positive relationship with the axis. All measures of herbivory stress showed significant relationships with the axis: distance to the nearest water and bunchgrass basal area had strong negative correlations and cow pie frequency and density had positive correlations with the axis. Cumulative stress has a strong negative correlation with the axis.

Axis 2 represented a gradient of increasing resource and non-resource-based stress associated with overlapping gradients of increasing herbivory and water stress (Fig. 2.1, Table 2.1) (hereafter “water & herbivory stress gradient”). Two measures of herbivory stress: distance to the nearest water and bunchgrass basal area had strong negative correlations with the axis. The increasing water stress was driven by an interaction between spatial variation in soil texture and temporal variation in the amount and timing of precipitation between the two sampling years (Table 2.2). There was also spatial variation in the amount and timing of precipitation between study sites sampled in the same year-especially during the 2008/2009 sampling year. Fall and winter precipitation had strong negative correlations with axis, whereas late spring-summer precipitation had a strong positive correlation with the axis. Soil sand content had a moderate positive correlation with the axis, whereas, clay content had a strong negative correlation.

Community composition: focal species location along gradient relative to its ecological optimum

Although the eight focal species co-occurred across study sites, their composition in the herbaceous community differed along the two stress gradients (Fig. 2.2, Table 2.3). Relative cover of *A. thurberianum*, *P. secunda*, and *P. spicata* was greatest at the lowest stress levels, and their relative cover decreased strongly with increasing stress along both gradients. To the contrary, *B. tectorum* and *L. perfoliatum* relative cover was greatest at the highest stress levels, and their relative cover increased strongly with increasing stress. Despite our efforts to include sites where *H. comata* and *A. hymenoides* should have been dominant components of the herbaceous community, relative cover of these two species remained consistently low, less than 2%, which made it impossible to meaningfully infer interaction outcomes from spatial associations.

Spatial patterns of association between *Artemisia* and focal species along the gradients

Spatial patterns of association between *Artemisia* and the eight focal species shifted significantly along the two stress gradients (Fig. 2.3, Table 2.3). At low stress levels along both gradients, focal species showed negative or neutral spatial associations with *Artemisia*, evidenced by greater cover in the interspace compared to under-shrub microsite or no difference in cover, respectively. With the exception of *A. thurberianum* along Axis 1, native focal species showed positive spatial associations with *Artemisia* at high stress levels along both gradients, evidenced by greater cover in the under-shrub compared in interspace microsite. With the exception of *B.* tectorum along Axis 1, non-native focal species showed negative spatial associations with Artemisia at high stress levels.

The strength and shape of the relationship between individual focal species' spatial pattern of association with *Artemisia* and the stress gradients depicted by the response curves varied (Fig. 2.3, Table 2.3). *E. elymoides* and *P. secunda* showed the strongest positive relationship shifting from neutral to strong positive association with *Artemisia* with increasing stress along both gradients. To the contrary, the non-natives *L. perfoliatum* and *B. tectorum* exhibited the only negative relationship shifting from neutral to strong negative association with *Artemisia* with increasing stress along the water & herbivory gradient. Some relationships were linear, but some were non-linear with unimodal and plateau shapes.

Cluster and MRPP analyses

Study sites were separated into three groups (dendrogram pruned with about 50% of the information remaining) characterized by different patterns of spatial association between the eight focal species and *Artemisia* at the community level (MRPP, A = .19, $p < 0.0001$) (Figs. 2.4A-C).

The combined herbivory, heat, and water stress levels of the groups were different (MRPP: A = .19, $p < 0.0001$). The three groups differed in levels of heat, herbivory, water, and cumulative stress (Figs. 2.5A&B). Sites exhibiting low and intermediate stress had similar combined stress levels (MRPP, A = 0.03, p = .33), however, low stress sites were located further from water compared to intermediate stress sites (Figs. 2.5A&B). The high stress group had greater combined stress levels compared to the low stress (MRPP, A = .38, $p < 0.001$) and intermediate stress (A = .12, $p < 0.0001$) groups (Figs. 2.5A&B).

The relative cover of *P. secunda*, *A. thurberianum*, and *P. spicata* was greatest in the low stress groups and lowest in the high stress group (Figs. 2.6A-B). To the contrary, *B. tectorum* and *L. perfoliatum* relative cover was highest in the high stress sites and lowest in the low stress sites (Figs. 2.6A-C).

Positive spatial associations between *Artemisia* and the focal species were strongest and most frequent in the high stress group (Figs. 2.4A-C, 2.6A-C, Table 2.4).

Although negative spatial associations between *Artemisia* and the focal species were most frequent in the low stress group, the strongest negative spatial associations for the native focal species were in the low stress group, but the strongest negative associations for the non-native focal species were in the high stress group.

In the low stress group, *A. thurberianum*, *P. spicata*, *B. tectorum*, and *L. perfoliatum* had negative spatial associations with *Artemisia*. The median interspace cover of *A. thurberianum* was between 9% and 62%, *P. spicata* between 43% and 78%, *B. tectorum* between 14% and 42%, and *L. perfoliatum* between 19% and 66% greater than under-shrub cover (Figs. 2.6A-C). In the intermediate stress group, *P. secunda* and *E. elymoides* had positive spatial associations with *Artemisia*, and the median under-shrub cover of *P. secunda* was between 54% and 126% and *E. elymoides* between 100% and 216% greater than interspace cover (Figs. 2.6A-C). In the high stress group, *E. elymoides*, *P. secunda*, *A. thurberianum*, and *P. spicata* persisted almost exclusively beneath *Artemisia*. The median under-shrub cover of *E. elymoides* was between 435% and 754%, *P. secunda* between 396% and 632%, *A. thurberianum* between 88% and 251% and *P. spicata* between 29% and 123% greater than interspace cover (Figs. 2.6A-C). *B. tectorum* and *L. perfoliatum* had negative associations with *Artemisia*, and the median interspace cover of *B. tectorum* was between 28% and 47% and *L. perfoliatum* between 74% and 81% greater than under-shrub cover (Figs. 2.6A-C).

DISCUSSION

Remarkably, our study is the first to describe shifts in the spatial patterns of association between *Artemisia* and herbaceous species at the landscape level and describe the stress gradients driving such shifts. These findings are important for two reasons. First, they provide new insights into the Stress Gradient Hypothesis (SGH) by evaluating several recent predictions derived from the hypothesis. Second, they provide critical new insights on the foundational role *Artemisia* plays in driving herbaceous species abundances in response to increasing impacts of cattle grazing disturbances and potential changes in community composition following fire.

Our findings are consistent with the only other study examining the spatial relationships between *Artemisia* and mature herbaceous species (Davies et al. 2007). In a study at two locations, a drier-warmer and mesic site, within our study area, Davies et al. (2007) found that *P. secunda* and *E. elymoides* cover was greater in the under-shrub compared to the interspace microsite, but that *P. spicata* and *A. thurberianum* cover did not differ at the drier-warmer site. Our findings at intermediate stress levels are consistent with these findings. At the mesic site, Davies et al. (2007) found no differences in cover between microsites. The neutral outcomes observed for *P. secunda* and *E. elymoides* at low stress levels are consistent with these findings, but the greater interspace cover of *P. spicata* and *A. thurberianum* is not.

By incorporating recommendations from recent synthesis articles regarding the SGH, our study addressed some of the limitations of previous studies and provides new insights into the complexity of the relationship between interaction outcomes and stress gradients. First, this study was conducted at the landscape level across 75 sites and captured the entire range of variation of three overlapping stress gradients (Brooker et al. 2008). Second, the overlapping stress gradients consisted of both non-resource and resource-based stresses (Brooker et al. 2008; Maestre et al. 2009). Third, the study accounted for species-specific effects by examining interaction outcomes between *Artemisia* and eight species with a wide range of competitive response abilities and tolerances to specific types of stress (Brooker et al. 2008; Maestre et al. 2009). Fourth, each stress was quantified (Michalet 2007; Brooker et al. 2008). Finally, the study used nonparametric multivariate statistics capable of describing linear and non-linear relationships between interaction outcomes and overlapping stress gradients (Maestre et al. 2006; Brooker et al. 2008).

Stress gradients driving spatial patterns of association

Two overlapping stress gradients drove the observed shifts in spatial patterns of association between *Artemisia* and the focal species. Cumulative cattle herbivory stress was a predominant component of both gradients. Cattle herbivory is a novel type of stress compared to the stress regimes under which native bunchgrasses recently evolved (10,000-12,000yr) in the Northern Great Basin (Mack and Thompson 1982; Adler et al. 2004). Consequently, many bunchgrasses, including *P. spicata, P.* secunda, A. *thurberianum*, *S. comata*, *A. thurberianum*, are highly sensitive to intense grazing (Blaisdell and Pechanec 1949; Mueggler 1975; Rickard et al. 1975; Mack and Thompson 1982; Ganskopp 1988). Cattle herbivory and associated disturbances are predicted to be important drivers of *Artemisia* community composition and structure (Miller et al. 1994; Briske and Richards 1995). Interactions between herbivory and water stress would not be surprising because defoliation during water stress reduces bunchgrass recovery (Busso et al. 1989; Brown 1995).

Cattle herbivory stress overlapped with heat stress to form the first stress gradient. The increasing heat stress was driven by changes in landscape orientation (aspect and slope). Our findings confirm the prediction of Davies et al. (2007) that heat stress is an important driver of shifts in the spatial patterns of association between *Artemisia* and herbaceous species and others that landscape orientation is an important determinant of *Artemisia* community structure (Passey et al. 1982; Hironaka et al. 1983; Jensen 1990). The only prerequisite to facilitation of this non-resource-based stress gradient is *Artemisia* canopy protection from cattle herbivory and amelioration of heat stress (Callaway 2007; Maestre et al. 2009).

Cattle herbivory stress overlapped with water stress to form the second stress gradient. In *Artemisia* ecosystems, water and nitrogen are both limiting factors to plant growth (Noy-Meir 1973; Fowler 1986), and soil water is an important determinant of plant nitrogen availability (Austin et al. 2004). The amount and timing of precipitation is a pivotal determinant of water availability within the soil profile (Noy-Meir 1973; Comstock and Ehleringer 1992) and interacts with soil properties to create gradients of water stress across landscapes (Passey et al. 1982; Hironaka et al. 1983; Jensen 1990; Davies et al. 2007). Decreasing fall-winter precipitation probably increased water stress at the start of the growing season by preventing recharge of the soil profile (West 1983; Bates et al. 2006). The increasing spring-summer precipitation may not have reduced this water stress later in the growing season because of greater evapotranspiration losses driven by increasing temperatures (Bates et al. 2006). The shift from finer to coarser-textured soils likely increased this water stress by exacerbating evaporative losses, especially in the upper soil layers (Hillel 1998). Because water is a limiting resource for both *Artemisia* and the focal species, facilitation of this water stress would require that *Artemisia* increase water availability (Maestre and Cortina 2004; Maestre et al. 2009).

The stress gradient hypothesis-shifts in interaction outcomes

Consistent with the SGH, facilitation was most frequent and strongest at the highest stress levels and competition most frequent and strongest at the lowest stress levels at the community level (across the focal species) (Bertness and Callaway 1994; Brooker and Callaghan 1998). This pattern was consistent across both overlapping stress gradients and the three groups characterized by different combined levels of heat, water, and herbivory stress. These findings support the general applicability of the SGH across overlapping resource and non-resource-based stress gradients when viewed at the community level (Maestre et al. 2009).

When viewed from the lens of pair-wise interactions between *Artemisia* and the focal species, a more complex picture of the SGH emerged. Our findings support the prediction that the strongest facilitation should occur with competitive species at the limits of their stress tolerance while the strongest competition should occur with stress tolerant species located at their ecological optimum (Bertness and Callaway 1994; Liancourt et al. 2005; Gaucherand et al. 2006; Villarreal-Barajas and Martorell 2009).

The two species with the strongest competitive response abilities, *E. elymoides* and *P. secunda*, showed the strongest facilitation at their upper limits of stress tolerance. Both species have an early phenology (Blaisdell 1958; Hironaka and

Tisdale 1972; Link 1990) and shallow roots (Hironaka et al. 1983) that minimize overlap with *Artemisia*'s most active growth period (Miller et al. 1986; Miller and Shultz 1987) and root system (Sturges 1977). Although both species avoid some water stress by senescing early (Blaisdell 1958; Link 1990), their shallow roots make them vulnerable to water stress (Brown 1995). These species likely benefit from *Artemisia* amelioration of heat stress that increases water availability by reducing evapo-transpiration rates (Davies et al. 2007). These species minimize the costs of competition and maximize the benefits from positive interactions with *Artemisia* (Liancourt et al. 2005; Maestre et al. 2009). The two species with intermediate life history strategies, *P. spicata* and *A. thurberianum*, exhibited the next strongest facilitation at the limits of their tolerance to the overlapping stress gradients. Both species probably benefit from *Artemisia* amelioration of herbivory stress because of their extreme grazing sensitivity (Blaisdell and Pechanec 1949; Ganskopp 1988). However, their weaker competitive response ability probably precludes them from realizing the full benefits of such positive interactions because they incur greater costs competing with *Artemisia* (Maestre et al. 2009). These two water stress tolerant species exhibited the strongest competition at the lowest stress levels that coincided with their ecological optima.

In striking contrast to natives, the non-native focal species, *B. tectorum* and *L. perfoliatum*, exhibited the strongest competition at the highest stress levels, which coincided with their ecological optima (Liancourt et al. 2005). Because of their strong herbivory tolerance and avoidance of water stress, both species may derive few benefits from facilitation but incur the costs of competition (Reichenberger and Pyke 1990).

The strikingly different patterns of interaction outcomes between *Artemisia* and the non-natives, *L. perfoliatum* and *B. tectorum*, compared to the native bunchgrasses strongly suggest 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 negative interactions between *Artemisia* and bunchgrasses for water and nutrients were likely one of the most important selective forces (Caldwell et al. 1987; Caldwell et al. 1991; Miller et al. 1991). Positive interactions were probably limited to *Artemisia* amelioration of heat stress and water stress. Competition and neutral outcomes were probably most frequent, i.e. similar to the interaction outcomes at the lowest levels of stress in this study. The competition between *Artemisia* and the non-natives, *B. tectorum* and *L. perfoliatum*, observed in this study evidences these past interactions and forces.

With the introduction of cattle, *Artemisia* protection from herbivory increased in importance as an underlying positive interaction because of the sensitivity of most bunchgrasses to such grazing (Mack and Thompson 1982). Under this novel selective force, facilitation and neutral outcomes increased in frequency and strength, i.e. similar to the interaction outcomes at the intermediate and high stress levels. The consistent *Artemisia* facilitation of native bunchgrasses provided evidence for the strength of this selective force. We contend that these changes fundamentally altered the structure of interactions between *Artemisia* and many bunchgrass species.

Finally, our findings support for all three proposed general shapes of the relationship between interaction outcomes and stress gradients (Le Roux and McGeoch 2010; Malkinson and Tielbörger 2010). For *P. spicata*, the shape of the relationship changed between the two gradients and for *A. thurberianum*, *L. perfoliatum*, and *B. tectorum*, both the shape and direction of the relationship changed between the two gradients. The response curves for *E. elymoides* along both stress gradients and *A. thurberianum* and *P. secunda* along the water & herbivory stress gradient exhibited a linear-monotonic relationship (Bertness and Callaway 1994; Brooker and Callaghan 1998). The response curves for *P. spicata* and *P. secunda* along the heat & herbivory stress gradient exhibited a plateau relationship with the strength of facilitation increasing until reaching an asymptote (Callaway et al. 2002;

Graff et al. 2007; Kawai and Tokeshi 2007). The response curve for *P. spicata* along the water & herbivory stress gradient exhibited a unimodal relationship with the strongest facilitation at intermediate stress levels (Le Roux and McGeoch 2010). These findings provide convincing evidence that the relationship between interaction outcomes and stress gradients is both species and stress gradient specific and highlight the importance of interpreting such results within such context (Malkinson and Tielbörger 2010).

Management implications

Starting in the 1940s, numerous methods were used to remove sagebrush to maximize herbaceous productivity for livestock grazing (Miller et al. 2010). Recently, there has been renewed interest in selective sagebrush removal to restore herbaceous communities for wildlife habitat and restore ecosystem resilience (McIver and Starr 2001; McIver et al. 2009). While the objective of such removals has changed, the underlying premise remains resolute; *Artemisia* competition with herbaceous species is the dominate driver of community composition, and its removal will result in a competitive release of herbaceous species (McIver et al. 2009).

Valiente-Banuet et al. (2006) found that many species lineages that evolved under more mesic climatic conditions than those of the current Mediterranean are now dependent on positive interactions from nurse plants for their persistence. Similarly, many native bunchgrass species may now be dependent on *Artemisia* facilitation for their continued persistence under otherwise unsuitable levels of herbivory, heat, and water stress (Valiente-Banuet et al. 2006; Callaway 2007; Brooker et al. 2008). In contrast, the highly invasive *B. tectorum* dominates the interspace microsites where its collective avoidance and tolerance mechanisms minimize stress impacts, but is also present under shrubs where *Artemisia* competition limits its dominance.

In *Artemisia* communities characterized by intermediate to high combined levels of heat, water, and cattle herbivory stress levels, sagebrush removal will simultaneously eliminate *Artemisia* competition and facilitation. Released from *Artemisia* competition, *B. tectorum* community composition is likely to increase (Reichenberger and Pyke 1990; Chambers et al. 2007), whereas native bunchgrass cover is likely to decrease without *Artemisia* protection from herbivory and amelioration of heat and water stress. If removal is fire-driven, then the higher fire intensity beneath shrubs may result in bunchgrass mortality (Pyke et al. 2010). The end result is likely to be a near *B. tectorum* monoculture (Knapp 1996; Knick et al. 2010). In these areas, maintaining a minimum level of *Artemisia* cover will likely be required to avoid this type of regime shift unless cumulative stress levels are significantly reduced. Cattle herbivory stress was a predominant component of both stress gradients, but more importantly, it is the only stress subject to management.

Ongoing global climate change may increase heat stress and potentially increase water stress by altering precipitation regimes in these *Artemisia* communities (Neilson et al. 2005; Chambers et al. 2009; Chambers and Wisdom 2009). Reducing cumulative cattle grazing intensities may be the only effective means of reducing cumulative stress levels to avoid these fire-triggered catastrophic regime shifts (Scheffer et al. 2009; Briske et al. 2008).

Our findings suggest two factors that land managers must consider before implementing restoration treatments that manipulate *Artemisia* cover. Foremost, managers must take into account the location of the site along relevant stress gradients. GIS software and readily available geospatial databases combined with field surveys should allow managers to determine the stress levels of a site. Second, the herbaceous community response will be species specific and such responses are likely to have long-term implications for community composition and structure.

The Greater Sage-Grouse was recently listed as a candidate species under the Endangered Species Act. Strategies to retain sufficient sagebrush cover necessary to ensure sage-grouse conservation will require restoration treatments that maintain minimum levels of *Artemisia* cover at the landscape level (Meinke et al. 2008; Pyke 2010). Our findings suggest that *Artemisia* and the refuge native bunchgrass communities in under-shrub microsites can play a pivotal role in passive and active restoration (McIver and Starr 2001; Pyke 2010). Passive restoration involves changing management practices to recover native species, whereas active restoration involves some level of vegetation manipulation (Pyke 2010). In passive restoration, remnant native bunchgrass populations beneath sagebrush canopies in areas where the native understory has been depleted by cattle grazing or other land uses may serve as a vital source of seed availability and accelerate otherwise slow re-colonization rates. In active restoration, *Artemisia* canopies may serve as important locations for planting native seedlings as an intermediate restoration step prior to reducing the shrub component (Huber-Sannwald and Pyke 2005). In communities characterized by intermediate or high combined stress levels, our results suggest that *Artemisia* may increase the restoration success rates by protecting native seedlings from cattle herbivory and ameliorating heat and water stress.

CONCLUSION

The structure of species interactions is a critical determinant of community stability and changes in the structure of species interactions, i.e. a shift from competition to facilitation, can reduce community stability (McCann et al. 1998; Lehman and Tilman 2000; McCann 2000; Fargione and Tilman 2005; Baez and Collins 2008). Our study has described two stress gradients characterized by fundamental shifts in the structure of interactions between *Artemisia* and herbaceous species. More importantly, this study has: (1) revealed strikingly different patterns of shifts in interaction outcomes between native and non-native species-including the highly invasive *B. tectorum*; (2) revealed strong *Artemisia* facilitation of many native bunchgrasses; and (3) identified novel cattle herbivory stress as one of the primary potential drivers of shifts in the structure of species interactions. These findings are likely to have profound implications for the compositional and functional stability of these endangered ecosystems.

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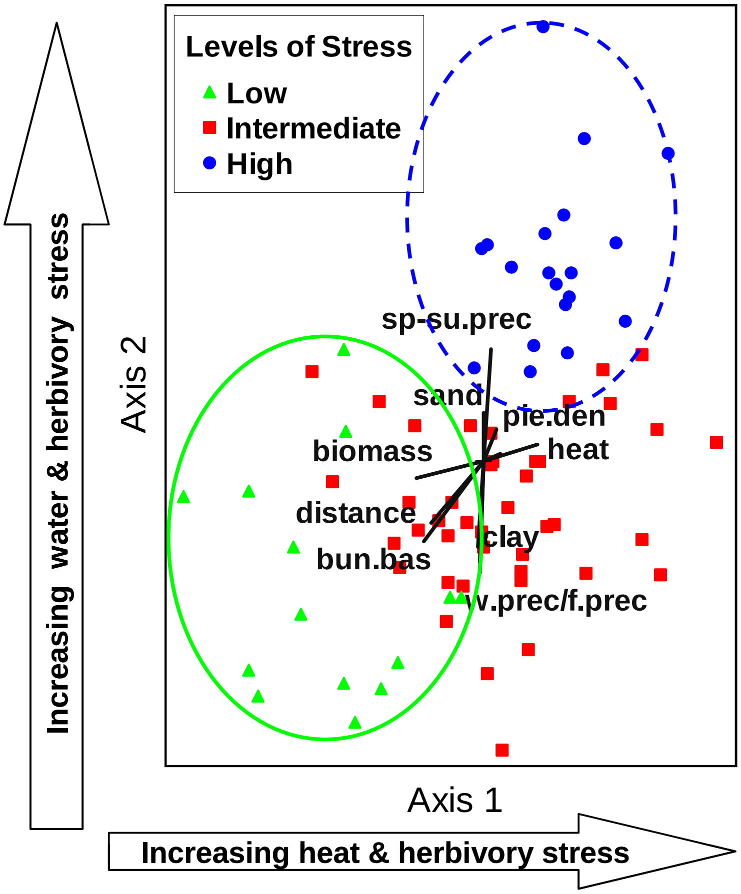

Fig. 2.1 Ordination of plots in patterns of spatial association between *Artemisia* and focal species (difference in under-shrub and interspace cover) space. Axes represent complex gradients in patterns of spatial association at the community level, i.e. across the eight focal species. Vectors show the strength and direction of correlations between the stress indicators and the axes. Only variables with a significant correlation (> 0.20) are shown. Different plot symbols show the three groups derived from the cluster analysis that differ in patterns of spatial association between *Artemisia* and the focal species and stress levels. Descriptions of the vector variables are in Table 1.

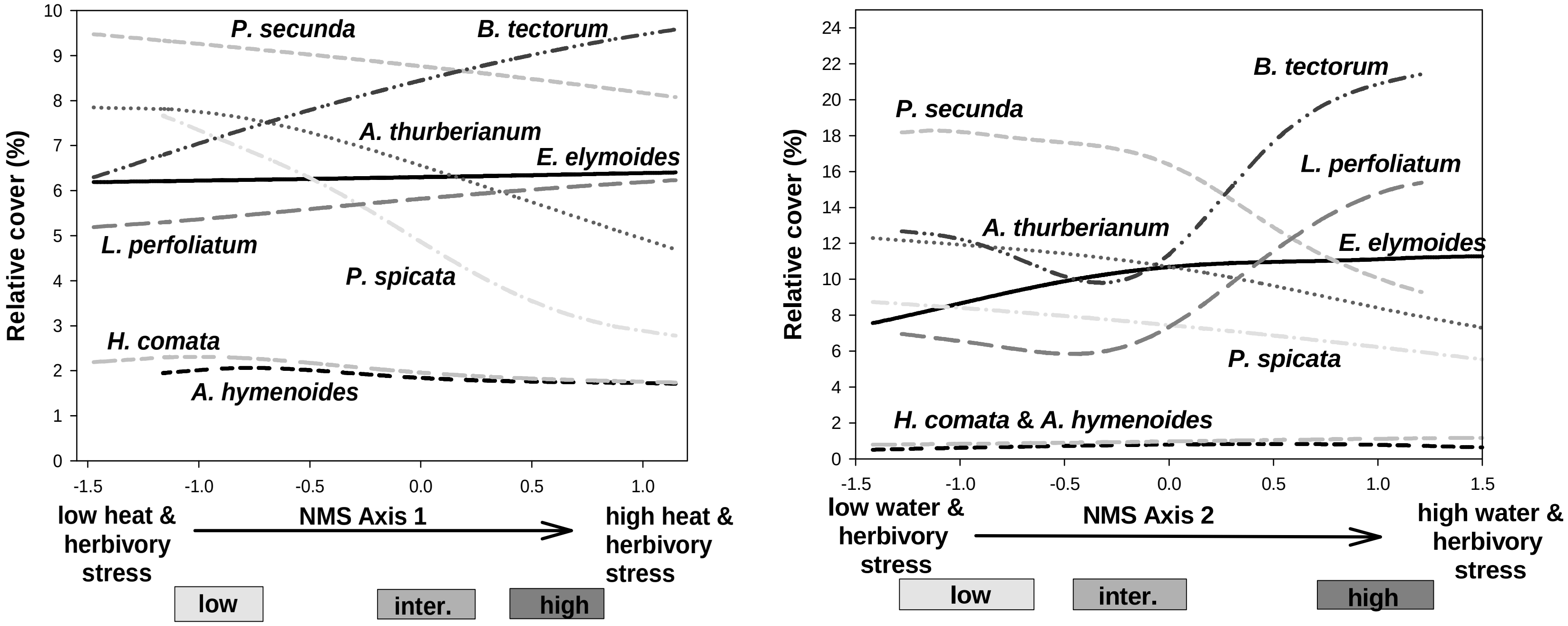

Figure 2.2. NPMR response curves showing the relationship between relative cover of the eight focal species and the stress gradients. Relative cover is a measure of the location of a species relative to its ecological optimum defined as the location of maximum cover along the gradient. Rectangles depict approximate locations of the three groups (90% confidence interval of the group mean ordination score).

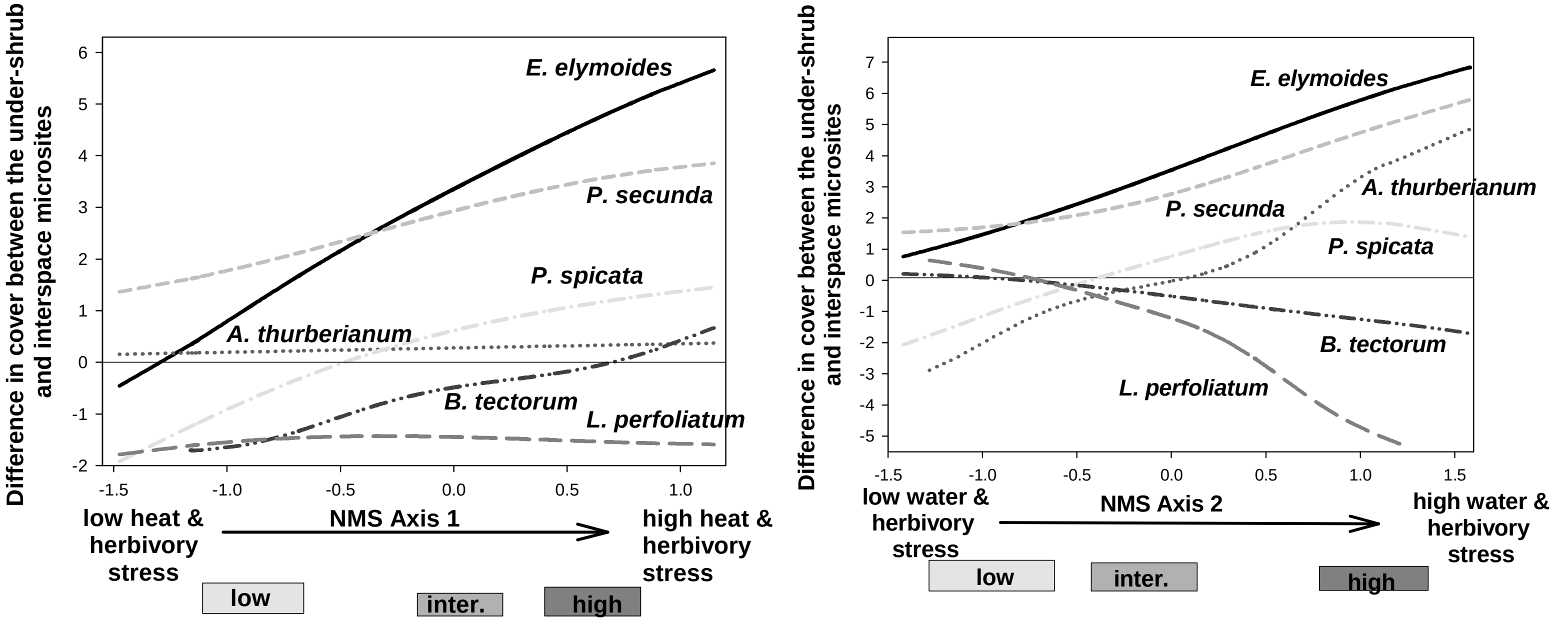

Figure 2.3 NPMR response curves showing the relationships of patterns of spatial association between *Artemisia* and the focal species and the two stress gradients. Values < 0 indicate that focal species cover was greater in the interspace compared to under-shrub microsite (competition), values near 0 indicate no difference in cover (neutral outcome), and values > 0 indicate that focal species cover was greater in the under-shrub compared to interspace microsite (facilitation). Rectangles depict approximate locations of the three groups (90% confidence interval of the group mean ordination score).

Low Stress Group

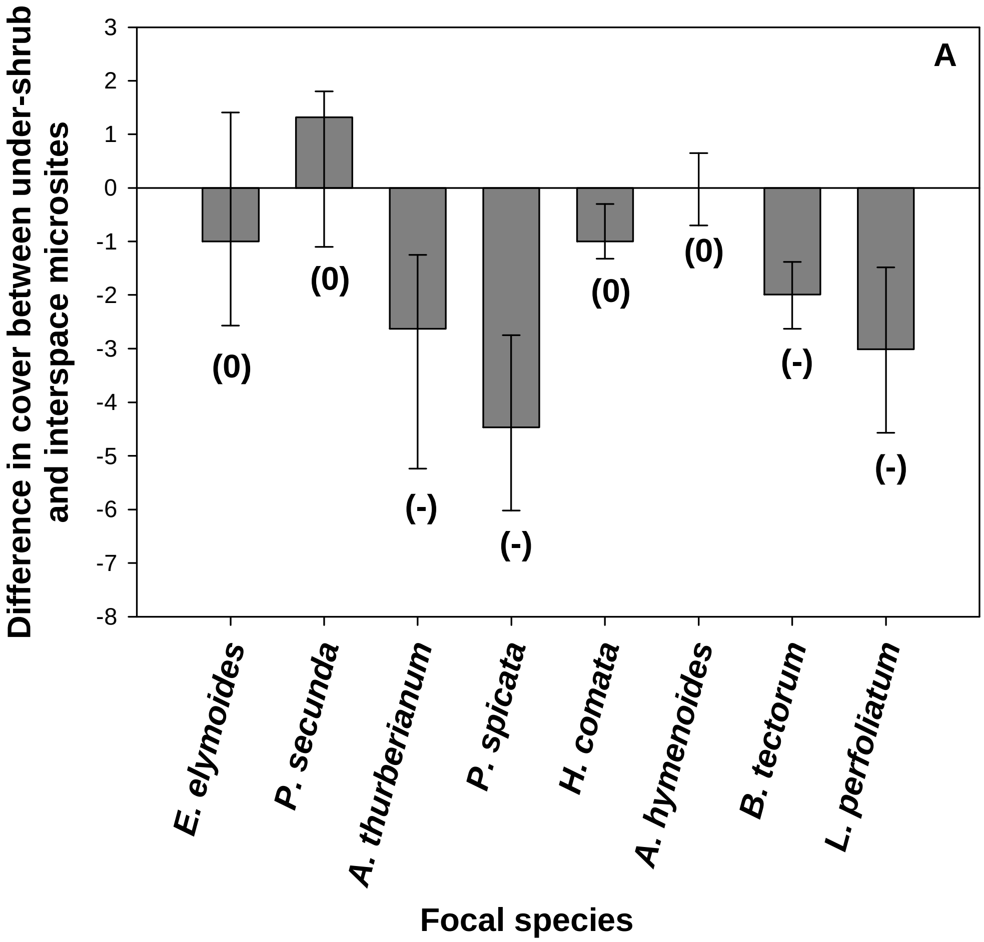

Figure 2.4A Differences in focal species cover between the under-shrub and interspace microsites, a measure of the spatial association between *Artemisia* and the focal species, at the community level (i.e. across all eight focal species) in the low stress group. (--) strong competition (-) competition (0) neutral outcome (+) facilitation (++) strong facilitation.

Intermediate Stress Group

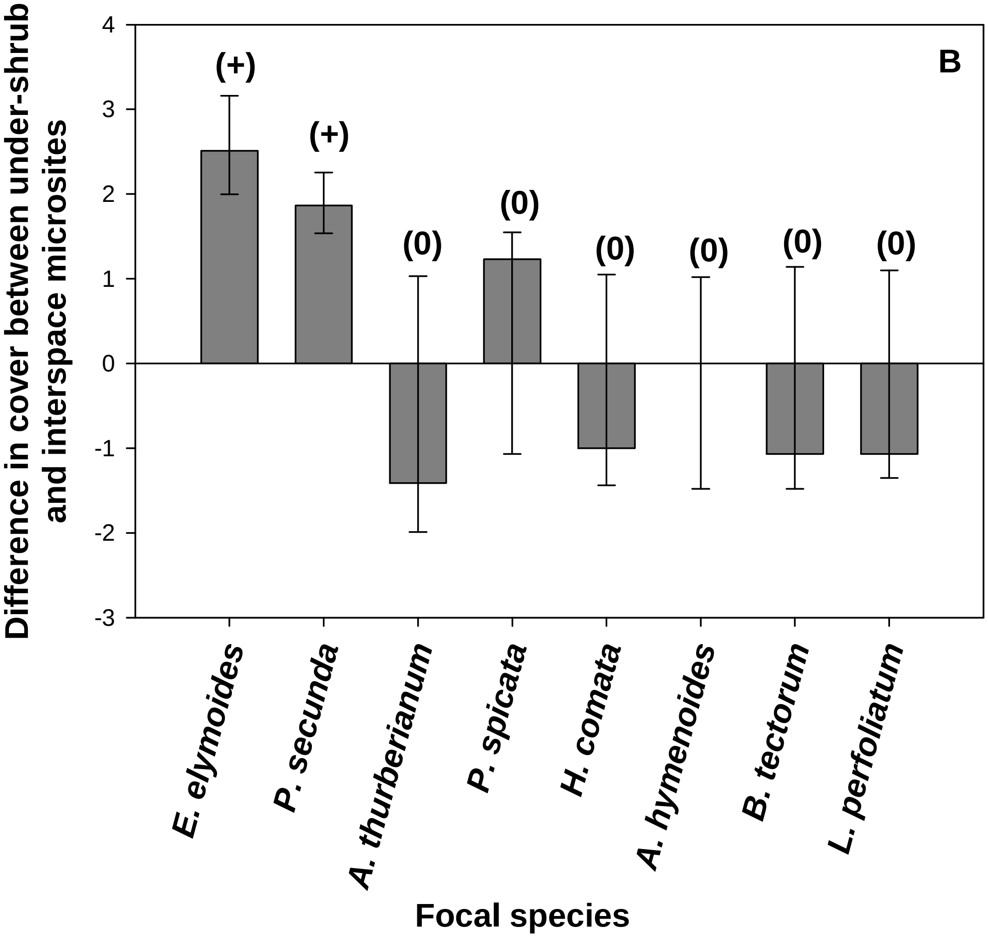

Figure 2.4B Differences in focal species cover between the under-shrub and interspace microsites, a measure of the spatial association between *Artemisia* and the focal species, at the community level (i.e. across all eight focal species) in the intermediate stress group. (--) strong competition (-) competition (0) neutral outcome (+) facilitation (++) strong facilitation.

High Stress Group

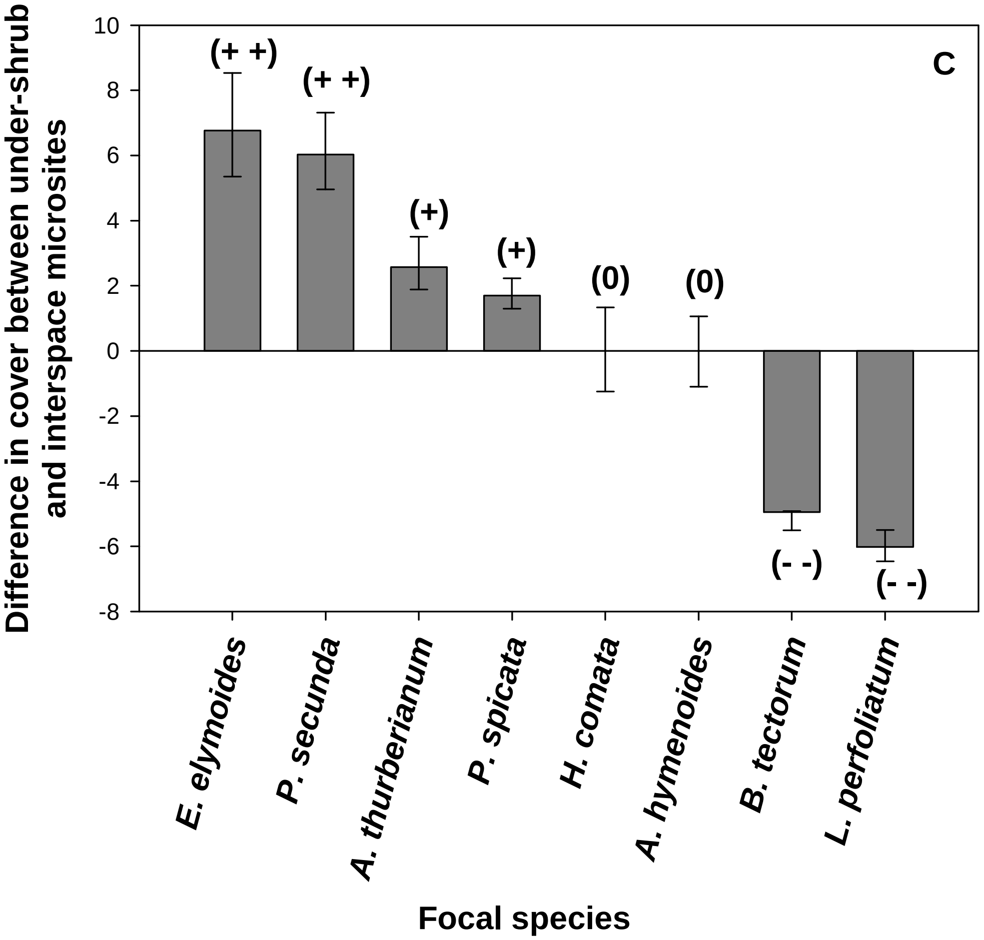

Figure 2.4C Differences in focal species cover between the under-shrub and interspace microsites, a measure of the spatial association between *Artemisia* and the focal species, at the community level (i.e. across all eight focal species) in the high stress group. (--) strong competition (-) competition (0) neutral outcome (+) facilitation (++) strong facilitation.

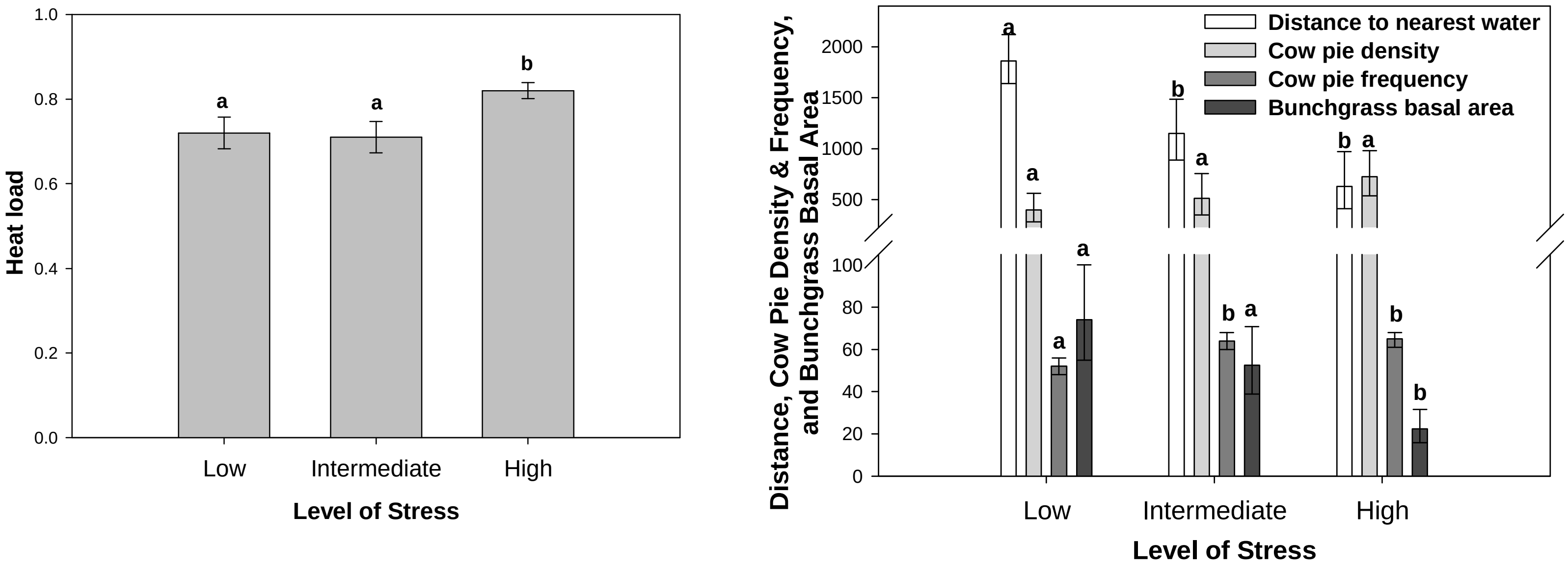

Figure 2.5A Levels of heat and herbivory stress for the low, intermediate, and high stress groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above bars indicate differences between groups (α = 0.10).

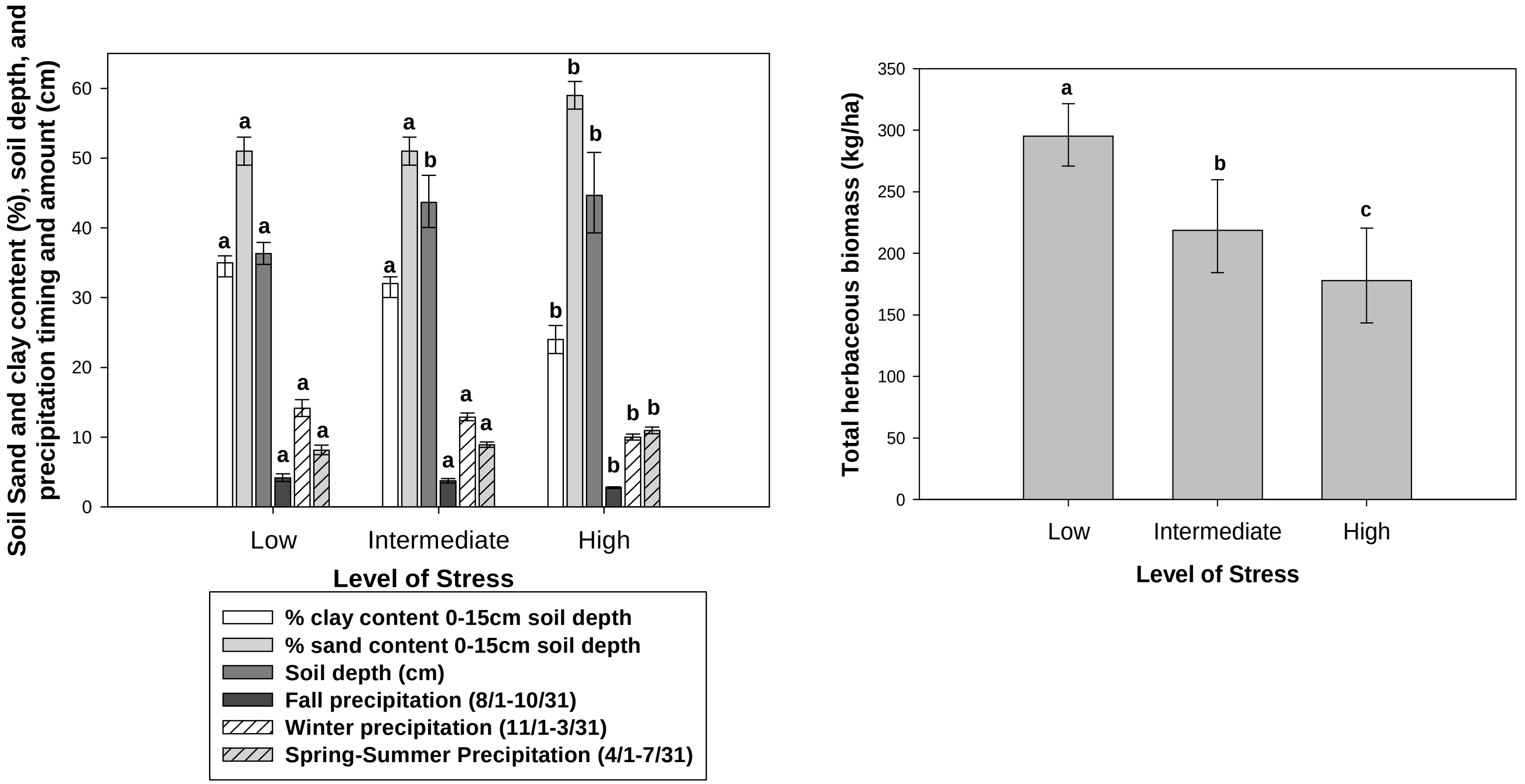

Figure 2.5B Levels of water and cumulative stress for the low, intermediate, and high stress groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above bars indicate differences between groups ($\alpha = 0.10$).

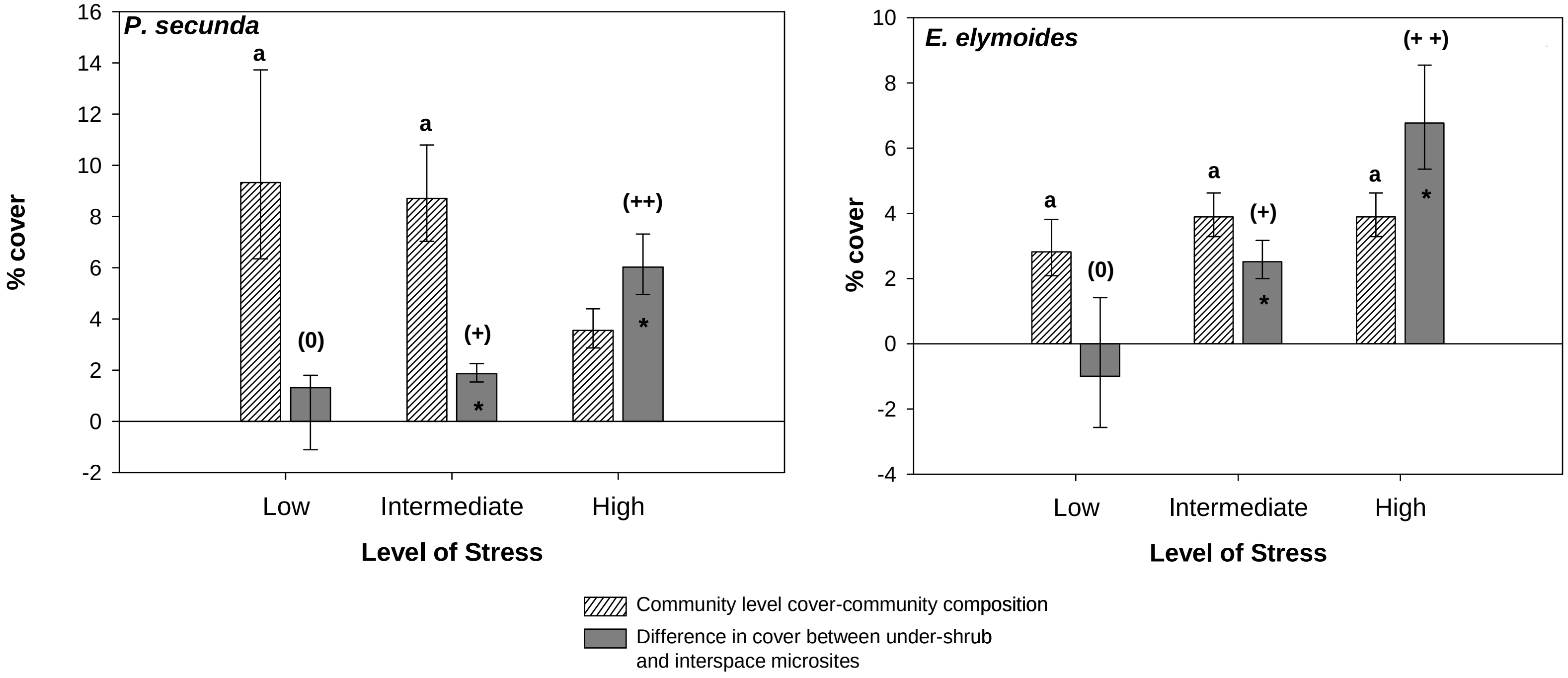

Figure 2.6A Relationship of spatial patterns of association (interactions) between *Artemisia* and focal species; focal species community composition (location relative to its ecological optimum) in three groups. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above the bars indicate differences between the groups (α = 0.10) * indicates that the difference in cover between the under-shrub and interspace microsite was significantly different from zero (α = 0.10). (--) Strong competition (-) Competition (0) Neutral outcome (+) Facilitation (++) Strong facilitation

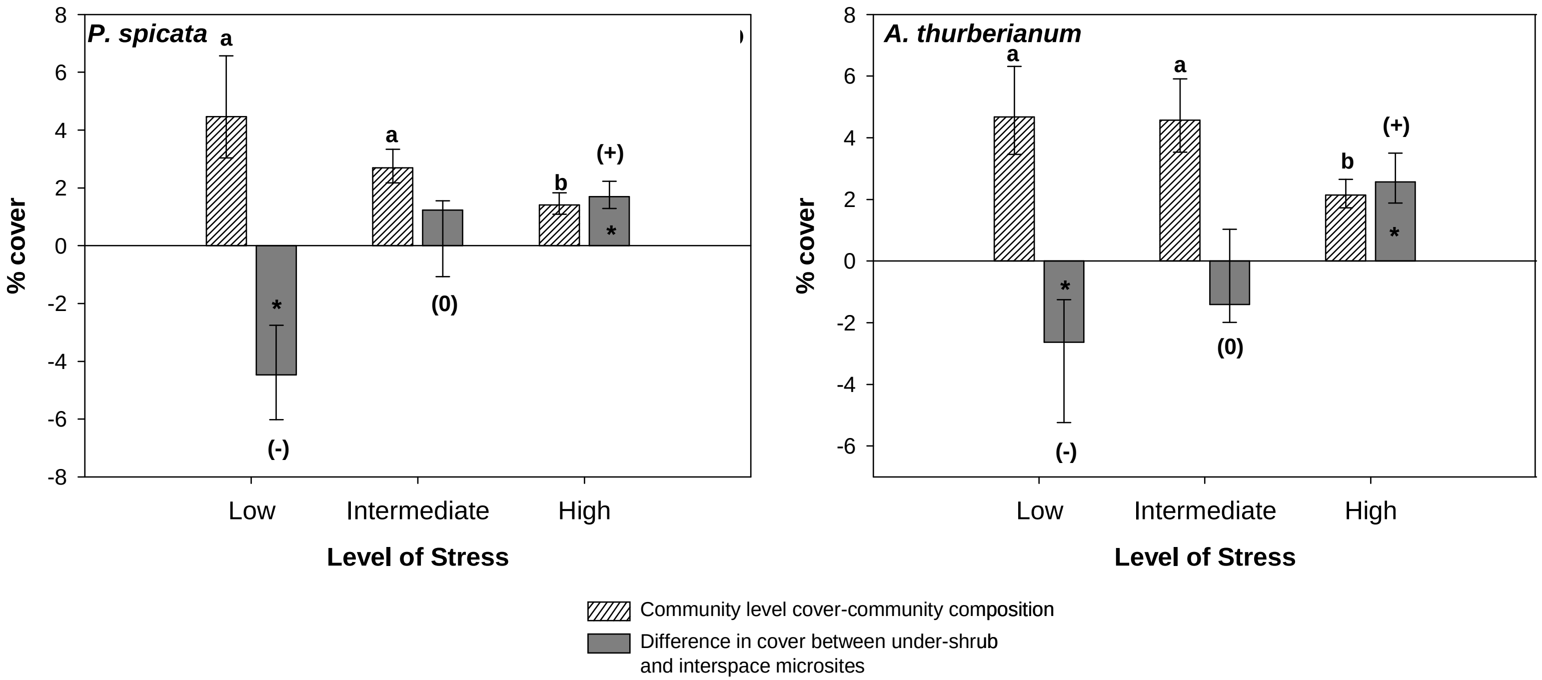

Figure 2.6B Relationship of spatial patterns of association (interactions) between *Artemisia* and focal species; focal species community composition (location relative to its ecological optimum) in three groups. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above the bars indicate differences between the groups (α = 0.10) * indicates that the difference in cover between the under-shrub and interspace microsite was significantly different from zero (α = 0.10). (--) Strong competition (-) Competition (0) Neutral outcome (+) Facilitation (++) Strong facilitation

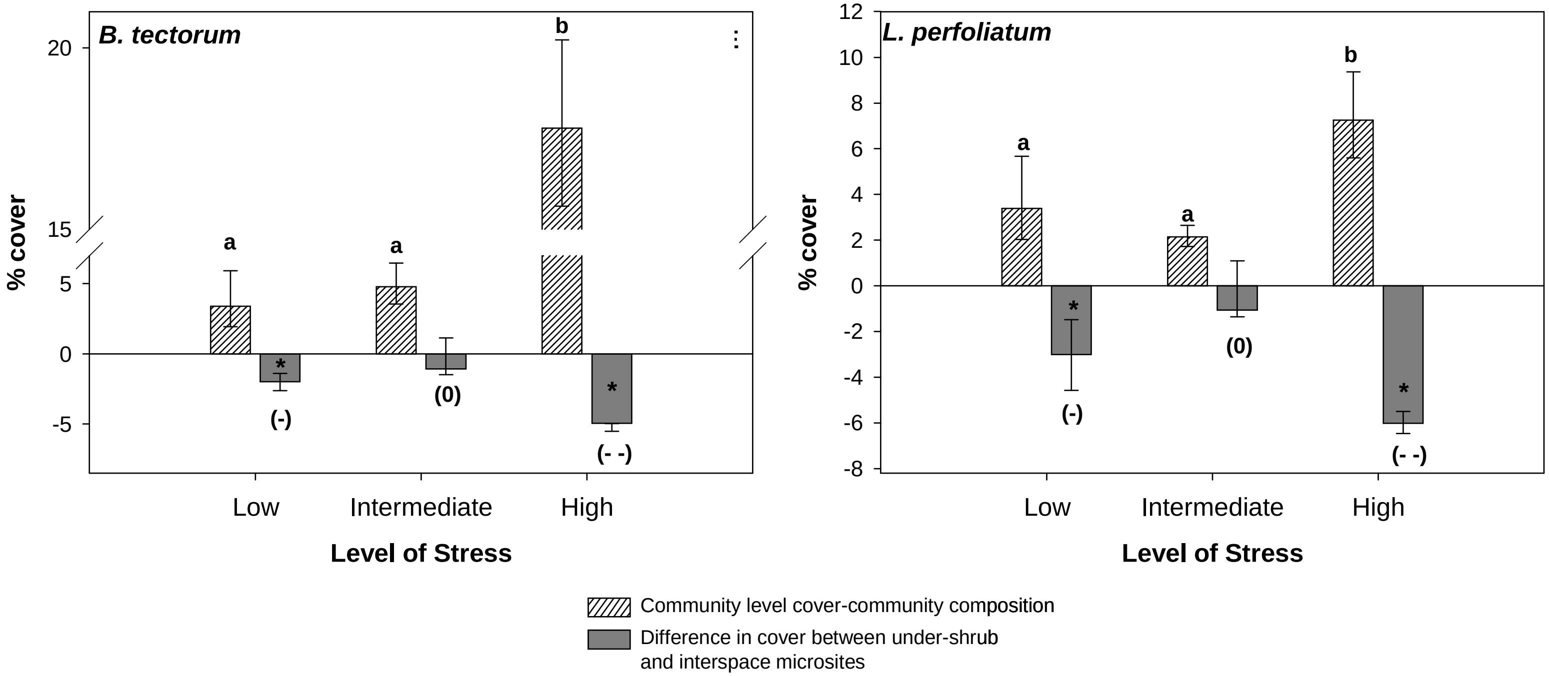

Figure 2.6C Relationship of spatial patterns of association (interactions) between *Artemisia* and focal species; focal species community composition (location relative to its ecological optimum) in three groups. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above the bars indicate differences between the groups (α = 0.10) * indicates that the difference in cover between the under-shrub and interspace microsite was significantly different from zero (α = 0.10). (--) Strong competition (-) Competition (0) Neutral outcome (+) Facilitation (++) Strong facilitation

Table 2.1 Relationship between heat, herbivory, water, and cumulative stress and NMS ordination axes

					Pearson correlations **	
Stress	Abbreviatio	Units	Mininum *	Maximum	Axis 1	Axis 2
Heat						
potential heat loads	heat	n/a	0.32	0.95	**0.38**	0.18
Herbivory						
Distance from nearest water source	distance	m	100	3560	**-0.38**	**-0.41**
Cow pie density	pie.den	cow pies/ha	0	3467	**0.21**	0.14
Cow pie frequency	pie.freq	% of belt transects	0	100	**0.31**	0.18
Deep-rooted bunchgrass basal area	bun.bas	cm2	6	331	**-0.41**	**-0.47**
Water						
Sand content 0-15cm soil depth	sand	%	33	80	0.19	**0.37**
Clay content 0-15cm soil depth	clay	%	14	53	-0.02	**-0.53**
Soil depth	depth	cm	23	120	-0.1	**0.3**
Fall precipitation (8/1-10/31)	f.prec	cm	2.2	5.8	-0.12	**-0.49**
Winter precipitation (11/1-3/31)	w.prec	cm	9	17	-0.11	**-0.56**
Spring-summer precipitation (4/1-7/3	sp-su.prec	cm	6	12	0.13	**0.55**
Cumulative						
Herbaceous biomass	biomass	kg/ha	51	607	**-0.43**	**-0.22**

* Range of values across 75 study sites

****** Variables with a significant correlation with the axis are in bold

Table 2.2 Temporal variation in precipitation amount and timing

		8/1-10/31 (fall)		11/1-3/31(winter)		4/1-7/31(spring-summer)	
Time Period	12-month total (cm)	Amount (cm)	% of total	Amount (cm)	% of total	Amount (cm)	% of total
Time period 1970-2005	24.8	4.4	18	12.2	49	8.3	33
2007-2008 sampling year	29.4	5.5	19	17.1	58	6.8	23
2008-2009 sampling year	23.8	2.6	11	9.9	42	11.3	48

Table 2.3 Relationships between the "difference in focal species cover between the under-shrub and interspace microsites [1] and the NMS ordination axes. Relationship between focal species community level cover and the ordination axes.[2]

	Pearson correlations with NMS ordination		Relative importance of the axis 1 and 2 scores as predictors in an NPMR model			
Focal species	Axis 1	Axis 2	Sensitivity to axis 1	Sensitivity to axis 2	xR2 **	p-value
Difference in cover between under-shrub and interspace microsites						
Elymus elymoides	**0.68**	**0.72**	0.59	0.74	0.56	0.004
Poa secunda	**0.41**	**0.65**	0.44	0.76	0.41	0.004
Achnatherum. thurberianum	0.23	**0.67**	0.1	1.2	0.44	0.004
Pseudoroegneria spicata	**0.58**	**0.4**	0.52	0.94	0.33	0.004
Achnatherum hymenoides	0.07	0.11	-	-	0.02	0.056
Hespirostipa comata	0.19	0.08	-	-	0.04	0.31
Bromus tectorum	**0.38**	**-0.51**	0.63	1.11	0.52	0.004
Lepedium perfoliatum	0.05	**-0.68**	0.25	1.5	0.47	0.004
Community-level cover-community composition						
Elymus elymoides	0.2	0.24	0.07	1.16	0.46	0.004
Poa secunda	**-0.39**	**-0.49**	0.16	1.22	0.29	0.004
Achnatherum. thurberianum	**-0.41**	**-0.33**	0.81	0.64	0.2	0.004
Pseudoroegneria spicata	**-0.58**	**-0.44**	1.15	0.25	0.27	0.004
Achnatherum hymenoides	0.04	0.07	-	-	0.06	0.18
Hespirostipa comata	0.11	0.09	-	-	0.09	0.087
Bromus tectorum	**0.47**	**0.45**	0.3	1.48	0.3	0.004
Lepedium perfoliatum	0.21	**0.43**	0.09	1.59	0.19	0.004

* Variables moderately or strongly correlated with ordination axis are in bold

** Cross-validated coefficient of determination for NPMR model with both axis 1 & 2 ordination scores as predictors

[1] The "difference in cover" was used to quantify the spatial pattern of association between *Artemisia* and the focal species and used to infer interaction outcomes (competition and facilitation) between *Artemisia* and the focal species.

[2] Community level cover was used to measure focal species species community composition and estimate the location of a focal species relative to its ecological optimum, defined as the location of maximum composition in the community, along the gradients.

Table 2.4 Frequency and strength of interaction outcomes between the low, intermediate, and high stress groups of study sites

	Interaction Outcomes *				
Group	Strong competition	Competition	Neutral Outcome	Facilitation	Strong facilitation
Low stress	0	4	2	0	0
Intermediate stress	0	2	2	2	0
High stress	1	1	0	2	2

* Excluding *H. comata* and *A. hymenoides* , there are a total of six pair-wise interaction outcomes between *Artemisia* and the six remaining focal herbaceous species in each of the three groups

CHAPTER 3

Facilitation by the foundational shrub, *Artemisia tridentata* ssp. *wyomingensis* increases and decreases community stability

Michael D. Reisner, Paul S. Doescher, David A. Pyke, and Bruce McCune

ABSTRACT

Shifts in the structure of species interactions, i.e. shifts from competitive to facilitative outcomes, can reduce community stability. Facilitation is predicted to increase community stability at intermediate levels of stress but decrease stability at high stress levels and is predicted to decrease community invasibility when one native increases the abundance and/or diversity of other species, which in turn reduces the magnitude of the invasion. We tested these predictions in three groups of communities characterized by different combined levels of heat, water, and herbivory stress and differences in interaction outcomes between the foundational shrub *Artemisia tridentata* ssp. *wyomingensis* (*Artemisia*) and six native and two non-native herbaceous species.

This study reports the first evidence of native species facilitation decreasing community invasibility. *Artemisia* facilitation increased native bunchgrass composition, which reduced the magnitude of *Bromus tectorum* invasion in under-shrub compared to interspace communities. Unfortunately, this decreased invasibility did not translate into lower invasibility at the community level because of the limited spatial scale over which such facilitation occurs. Also, we report that *Artemisia* facilitation increased community compositional and functional stability at intermediate

stress levels but decreased community stability at high stress levels. Facilitation became a destabilizing force when native bunchgrass species became “obligate” beneficiaries, i.e. strongly dependent on *Artemisia* facilitation for their continued persistence in the community.

Finally, shifts in the structure of interaction outcomes between *Artemisia* and native bunchgrasses, from competitive/neutral at low stress to facilitative/strongly facilitative at high stress, were associated with a decrease in community compositional and functional stability. A perfect storm of factors likely explain the especially pronounced destabilizing effects we observed. *Artemisia* is a dominant foundational species that exerts strong control over negative and positive interactions in the community, increasing cattle grazing was a predominant driver of shifts in the structure of interactions between *Artemisia* and bunchgrasses, and the structure of interactions between *Artemisia* and the invasive *B. tectorum* was fundamentally different than those with native bunchgrasses. Conserving and restoring the stability of these communities will require significantly reducing cumulative stress levels, and reducing cumulative cattle grazing levels by adjusting utilization rates and/or seasons of use.

INTRODUCTION

Plant interactions are fundamental drivers of community composition and structure (Clements 1916; Gleason 1926; Grime 1976; Connell 1983; Tillman 1988; Bruno et al. 2003). Interactions are mechanistically comprised of simultaneously occurring positive and negative interactions (Hunter and Aarssen 1988; Holmgren et al. 1997; Holzapfel and Mahall 1999). The balance of the strength of these underlying processes determines whether the interaction outcome is competition, neutral, or facilitation (Malkinson and Tielbörger 2010).

Stress, defined as any external constraint that limits the rate of photosynthesis of a plant and reduces its ability to convert energy to biomass (Grime 1976), plays a pivotal role in determining interaction outcomes because it drives the strength of underlying positive and negative interactions. 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 (Bertness and Callaway 1994; Brooker and Callaghan 1998; Callaway 2007). Although shifts in interaction outcomes predicted by the SGH and the effects of facilitation have been well documented at the individual and species level, the consequences of such shifts and facilitation at the community-level remain poorly understood (Tewksbury and Lloyd 2001; Brooker et al. 2008; Cavieres and Badano 2009).

Shifts in the structure of interaction outcomes along stress gradients are likely to have profound implications for community stability (Tilman 1996; Callaway 2007; Ives and Carpenter 2007; Butterfield 2009). The structure of interactions is a critical determinant of community compositional stability (McCann et al. 1998; Lehman and Tilman 2000; McCann 2000; Fargione and Tilman 2005). Community compositional stability can be defined as changes in species abundances that do not drive directional changes in community composition (Collins 2000; Baez and Collins 2008). There is growing evidence that changes in interaction structure can reduce such stability (McCann 2000; Baez and Collins 2008; Villarreal-Barajas and Martorell 2009). These destabilizing effects are predicted to be especially pronounced in communities where a single species has strong effects on interaction structure or where a disturbance or invasion fundamentally alters the structure of those interactions (De Ruiter et al. 1995; Tielborger and Kadmon 1997; Holzapfel and Mahall 1999; McCann 2000; Tielborger and Kadmon 2000; Baez and Collins 2008). Compositional stability is likely one of the mechanisms by which community functional stability (i.e. nutrient cycling, decomposition, invasibility), is maintained (McNaughton 1977; Tilman 1996; Hooper et al. 2005; Krushelnycky and Gillespie 2008).

Facilitation may increase or decrease community stability (Bruno et al. 2003; Brooker et al. 2008; Butterfield 2009). Recent conceptual models predict that facilitation will increase stability at intermediate levels of stress but decrease stability at high stress levels (Michalet et al. 2006; Butterfield 2009). A shift to obligate facilitation where many species only persist next to a benefactor is predicted to be the tipping point between facilitation stabilizing versus destabilizing a community (Butterfield 2009).

One measure of community functional stability is its invasibility, its susceptibility to invasion by non-native species, with greater functional stability associated with lower invasibility. Biotic resistance, the reduction in invasion success caused by competition with resident species, is an important determinant of community invasibility because it reduces resources available to potential invaders (Daehler 2003; Levine et al. 2004; Mitchell et al. 2006). Facilitation is predicted to increase functional stability, i.e. decrease community invasibility, by increasing resistance when one resident native species increases the abundance and/or diversity of other species, which in turn reduces the magnitude of the invasion (Zavaleta and Hulvey 2004; Fargione and Tilman 2005; Brooker et al. 2008).

Wyoming big sagebrush, *Artemisia tridentata ssp. wyomingensis* (hereafter *Artemisia*) communities are one of the most widespread but endangered ecosystems in North America (Noss et al. 1995). Livestock grazing and other disturbances are believed by many to have significantly compromised the ecosystem’s resistance to

Bromus tectorum (cheatgrass) invasion (Knapp 1996; Miller and Eddleman 2001; Chambers et al. 2007). *B. tectorum* currently dominates 7% of the Northern Great Basin (Bradley and Mustard 2006), and Suring et al. (2005) estimated that about 50% of the Great Basin has a moderate or high probability of *B. tectorum* dominance of the herbaceous understory. In *B. tectorum*-invaded communities, fire, the dominant historical disturbance, is increasingly triggering a “catastrophic regime shift,”(Scheffer et al. 2001; Scheffer et al. 2009) whereby native shrub-steppe communities co-dominated by *Artemisia* and a diverse assemblage of native bunchgrasses are transformed into annual grasslands dominated by *B. tectorum* and other non-native species (Billings 1990; D'Antonio and Vitousek 1992; Knapp 1996; Pyke and Brooks 2001; Knick et al. 2010). These regime shifts indicate that a combination of disturbances and stressors has compromised the functional stability of these communities (McNaughton 1977; Foster et al. 2002; Scheffer et al. 2009).

Not only are these communities characterized by strong overlapping gradients of heat and water stress (Passey et al. 1982; Hironaka et al. 1983; West 1983; Bates et al. 2006; Davies et al. 2007), but the arrival of cattle grazing in the late 1800s introduced a novel disturbance regime in a region where most native bunchgrasses are highly sensitive to herbivory (Mack and Thompson 1982). Livestock grazing remains the most pervasive land use across this region (Knick et al. 2010).

In a previous paper (Chapter 2), we described strong shifts in the interaction structure between the foundational shrub *Artemisia* and six native and two non-native herbaceous species driven by overlapping gradients of heat, herbivory, and water stress. The primary goal of this paper is to determine whether findings observed at the species-level translate into ecologically meaningful effects at the community level, and more specifically, on community compositional and functional stability. Generally, we predicted that the pronounced shift in interaction structure between *Artemisia* and bunchgrasses, a shift from competitive/neutral to facilitative/strongly facilitative outcomes, would reduce community compositional and functional stability. The following specific hypotheses are tested:

1. *Artemisia* facilitation of native bunchgrasses would increase functional stability, i.e. decrease invasibility, by maintaining greater bunchgrass composition in under-shrub compared to interspace communities, which in turn would reduce non-native composition of under-shrub compared to interspace communities. We had no *a priori* prediction regarding how such facilitation effects might translate to the community level.

2. *Artemisia* facilitation of native bunchgrasses would both increase and decrease community compositional and functional stability. Facilitation would increase stability at intermediate stress levels, but decrease stability at high stress levels if obligate facilitation resulted in many bunchgrass species persisting only beneath *Artemisia* canopies.

METHODS

The study consisted of 75 sites located in the Northern Great Basin floristic province of central Oregon (Anderson et al. 1998). The study area consisted of three Bureau of Land Management (BLM) grazing allotments in the Burns District, Three Rivers Resource Area. We employed a stratified random sampling design with two objectives. The first was to capture a complete severity gradient for three potential stress gradients (heat, herbivory, and water) where *Artemisia* and the eight focal species co-occurred (Brooker et al. 2008; Malkinson and Tielbörger 2010). The second was to capture as many combinations of levels and types of stress as possible (see Chapter 2 for more detail).

Selected sites consisted of combinations of *Artemisia* and eight focal herbaceous species – six native bunchgrasses and two non-native annual species. The eight species represent a wide range of relative competitive response abilities and tolerances to water, heat, and herbivory stress. *Poa secunda* (Sandberg bluegrass) and *Elymus elymoides* (bottlebrush squirreltail) are short-lived, shallow-rooted bunchgrasses, have high competitive response abilities (Hironaka and Tisdale 1963; Booth et al. 2003; Humphrey and Schupp 2004), are sensitive to heat and water stress (Link 1990; Johnson and Aguirre 1991; Donovan and Ehleringer 1994; Jones 1998), but tolerant to herbivory stress (Trilica and Cook 1971; Jones 1998). *Hespirostipa* *comata* (needle-and-thread grass) and *Achnatherum hymenoides* (Indian ricegrass) are long-lived, deep-rooted bunchgrasses, highly tolerant of heat and water stress (Ellison and Woolfolk 1937; Platou et al. 1986), but highly sensitive to herbivory stress (Rickard et al. 1975; Jones 1990). *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Achnatherum thurberianum* (Thurber's needlegrass) have intermediate life history strategies. Both are relatively tolerant of heat and water stress (Passey et al. 1982), but are sensitive to herbivory stress (Blaisdell and Pechanec 1949; Mueggler 1975; Ganskopp 1988). The two non-natives, *Bromus tectorum* (cheatgrass), a highly invasive annual grass, and *Lepidium perfoliatum* (clasping pepperweed), an annual forb, are ruderal species that avoid water and heat stress by senescing. Both species exhibit grazing avoidance and tolerance mechanisms that make them extremely tolerant of herbivory stress (Pyke 1986; Archer and Pyke 1991; Hempy-Mayer and Pyke 2009).

Study approach

Previous hierarchical agglomerative cluster analysis and Multi-Response Permutation Procedures (MRPP) separated the study sites into three groups representing a gradient of increasing stress (see Chapter 2). Groups differed in combined cattle herbivory, water, and heat stress and interaction outcomes between *Artemisia* and native focal species. Low stress was characterized by neutral and competitive outcomes between *Artemisia* and bunchgrasses (hereinafter "low stress group or communities"). Intermediate stress was characterized by neutral or facilitative outcomes between *Artemisia* and bunchgrasses (hereinafter "intermediate stress group or communities"). High stress was characterized by facilitative and strongly facilitative outcomes between *Artemisia* and bunchgrasses (hereinafter "high stress group or communities").

To test our first hypothesis, the composition of herbaceous communities beneath *Artemisia* canopies (hereinafter "under-shrub") and in adjacent interspaces between *Artemisia* canopies (hereinafter "interspace") were compared. At a given stress level (low, intermediate, high stress groups), greater bunchgrass and lower invasive species composition in the under-shrub compared to interspace communities was interpreted as evidence in support of the hypothesis.

The second hypothesis was tested with the following approach. First, we used blocked Indicator Species Analysis (ISA) and MRPP to evaluate spatial changes in composition among the under-shrub, interspace, and site-level (community-level) communities within each of the three groups (low, intermediate, and high stress levels). Second, we used Mantel tests to evaluate whether observed spatial changes in community composition in the under-shrub, interspace, and site-level communities impacted patterns of community similarities, i.e. community compositional stability, among these three groups of communities. Third, we looked for any directional change in community compositional stability across the three groups of communities associated with increasing stress and increasing *Artemisia* facilitation of and shifts in interaction structure with bunchgrasses. Finally, we evaluated whether observed changes in community compositional stability were associated with changes in functional stability by comparing differences in invasibility, cover of *B. tectorum* at the community level among the three groups.

Sampling and measurements

Thirty (30) and 45 study sites were sampled in 2008 and 2009. One randomly located plot (0.39 ha) was used to sample each study site. The coordinates of each study plot were recorded with a Global Positioning System (GPS) unit. Six 25-m transects were established for sampling using a spoke design (Herrick et al. 2005). All sampling occurred between May 10 and July 15 to capture peak herbaceous biomass. Herbaceous and *Artemisia* foliar cover was measured using line-point intercept at 0.25m increments along the six transects (Herrick et al. 2005). For each study site, three measures of cover were calculated from the line-point intercept data for each of eight focal species: (1) under-shrub, (2) interspace, and (3) community level (plot-level) cover. Under-shrub cover included all pin intercepts of the herbaceous species when the pin intersected *Artemisia* as the “top canopy,” and interspace cover included all other pin intercepts of the species (Herrick et al. 2005). The resulting dataset consisted of three cover types (under-shrub, interspace, and community level), 8 species x 75 sites matrices.

Overall community stability was measured using a “composite index” comprised of five indicators of soil and site stability (Herrick et al. 2005; Herrick et al. 2006; Bestelmeyer et al. 2009; Herrick et al. 2010). Bare soil cover was calculated using line-point intercept data and defined as all the ground surface contacts not covered by vegetation, visible biological crusts, dead vegetation, litter, or rocks (Herrick et al. 2005). Soil surface aggregate stability was measured using a soil stability kit (Herrick 2001) in interspace microsites, where cattle trampling was most likely to occur, at 18 random sampling points along the six transects using soil from the upper 0-4 mm of the soil (Herrick 2001; Herrick et al. 2005). Two indicators of soil resistance to erosion were calculated from the soil stability test: mean soil stability and the proportion of surface soil samples that were rated as extremely stable (Herrick 2001; Beever et al. 2006; Bestelmeyer et al. 2009). Basal gap intercept was used to quantify the size and distribution of gaps between bases of perennial plants (Herrick et al. 2005). Mean basal gap length and proportion of transects covered by large gaps (> 200 cm in length) were calculated. Smaller basal gaps and lower proportions of the transect covered by large gaps indicate higher resistance to soil erosion, disturbance, and invasion (Herrick et al. 2005).

Statistical Analyses

Prior to analyses, all cover data were log transformed to improve distributional properties (normality and equal variance) for subsequent multivariate and bi-variate analyses (McCune and Grace 2002). Blocked Multi-Response Permutation Procedures (MRPP) in PC-ORD could not be used to test for differences in composition between the under-shrub and interspace communities using groups as a blocking factor because of an unbalanced design (different number of study plots in the three groups) (McCune and Mefford 2008). Instead, the three matrices were sorted into low, intermediate, or high stress groups. The resulting dataset consisted of 3 sets of 3 (8x75) matrices (under-shrub, interspace, and plot-level cover matrix) for each of the three stress groups.

For each group, we ran MRPP using Sǿrenson distance to quantify differences in composition between the herbaceous communities of the under-shrub, interspace, and at the site level. This approach emphasized differences within the three groups of communities. MRPP generates an A-statistic, the chance-corrected within-group agreement, and a corresponding p-value. When *A* is close to zero, groups are no more different than expected by chance, while an *A* of 1 means perfect separation of groups

(McCune and Grace 2002). *A* can be interpreted as an effect size with higher *A* values indicating greater differences among groups. Significance was assessed at a $\alpha = 0.05$. The three pair-wise comparisons within each group were not corrected for multiple comparisons.

Blocked Indicator Species Analysis (ISA) in PC-ORD was used to elucidate whether any of the eight focal species were uniquely associated with the under-shrub or interspace microsite communities. This approach differs from traditional ISA (Dufrene and Legendre 1997) because species abundances are relativized within blocks (three groups). The relativization changes the relative abundance portion of the Indicator Value (IV) Index to focus on within block (group) differences (Root et al. 2010).

A Mantel test using Sorenson’s distance was used to evaluate patterns of similarities between communities of the under-shrub, interspace and at the site-level, or alternatively whether they occupied the same location in species ordination space, i.e. communities were compositionally stable in space. Three Mantel tests were performed within each group for a total of nine regression tests: (1) the under-shrub and interspace matrices, (2) under-shrub and site-level matrices, and (3) interspace and site-level matrices. Large, significant positive Mantel statistics (r) indicate that communities are compositionally similar or stable, and small, non-significant statistics indicate communities are compositionally unrelated or unstable.

Traditional ISA was used to quantify composition at the community level to measure invasibility across the three groups and determine whether any of the eight focal species were uniquely associated with one of the groups. Differences in each focal species' community-level cover between the three groups were assessed with ANOVA ($\alpha = .10$) using S-Plus 8.0. Bonferroni-adjusted 90% confidence intervals were used to quantify differences.

Multivariate differences in the five indicators of community stability (bare soil cover, soil aggregate stability, proportion of highly stable aggregates, basal gap size, and proportion of large basal gaps) among the groups were tested using traditional MRPP using Euclidean distances (Mielke 1984). Significance was assessed at a $\alpha = 0.05$. Because variables were measured on different scales, they were relativized by standard deviates to put them on equal footing prior to MRPP analyses (McCune and Grace 2002). Differences in indicators among groups were assessed with ANOVA ($\alpha = .10$) using S-Plus 8.0. Bonferroni-adjusted 90% confidence intervals were used to quantify differences among groups.

RESULTS

Similarities among the under-shrub, interspace, and site-level communities

In low stress communities characterized by neutral and competitive outcomes between *Artemisia* and bunchgrasses, the composition of the herbaceous communities of the under-shrub, interspace, and at the site-level were similar (Blocked MRPP, Table 3.1). There was a moderate to strong positive relationship between the under-shrub and interspace communities and those at the site-level (Mantel Test, Table 3.1). None of the focal species were uniquely associated with either the under-shrub or interspace communities (Table 3.2).

In intermediate stress communities characterized by facilitative and neutral outcomes between *Artemisia* and native bunchgrasses, composition of the communities of the under-shrub compared with interspace and under-shrub compared with the site-level differed (Blocked MRPP, Table 3.1). However, differences in community composition were relatively weak, and only one species, *E. elymoides* was uniquely associated with under-shrub communities (Table 3.2). Similar to low stress communities, a moderate positive relationship between communities in the under-shrub and interspace was maintained (Mantel Test, Table 3.1). Importantly, the positive relationship between the under-shrub and site-level communities increased in strength between the low and intermediate stress communities (from r = 0.51 to r = 0.71).

In high stress communities characterized by facilitative and strongly facilitative outcomes between *Artemisia* and bunchgrasses, composition of herbaceous communities of under-shrub, interspace, and at the site-level were different (Blocked MRPP, Table 3.1). Differences in composition were most pronounced between under-shrub and interspace and between site-level and under-shrub communities (Table 3.1). These differences in composition were more pronounced than differences observed in the intermediate stress communities, and six of the eight focal species were uniquely associated with either the under-shrub or interspace communities (Table 3.2). Native bunchgrasses *P. secunda, E. elymoides, P. spicata,* and *A. thurberianum* were uniquely associated with and dominated under-shrub communities; whereas non-natives, *B. tectorum* and *L. perfoliatum*, dominated interspace communities (Table 3.2). In contrast to the same two community comparisons at low and intermediate stress, high stress communities compared between the under-shrub and interspace communities and between under-shrub and site-level communities were unrelated (Mantel Test, Table 3.1). Even the positive relationship between interspace and site-level communities was weaker (Mantel Test, Table 3.1).

Community-level cover

Community-level cover of *P. secunda*, *A. thurberianum*, and *P. spicata* differed among low, intermediate, and high stress groups of communities (Figs. 3.1A-C). The difference of the high stress group is most apparent (ANOVA: $p < 0.008$; $p = 0.008$; $p < 0.001$, respectively). *B. tectorum* and *L. perfoliatum* cover increased with increasing stress (ANOVA: both $p < 0.001$).

Community-level composition of herbaceous understory communities found in low, intermediate, and high stress groups differed (MRPP: $p < 0.001$; $A = 0.12$). Differences in composition were especially pronounced between low and high stress groups (MRPP: $p < 0.001$; $A = 0.21$) and intermediate and high stress groups (MRPP: $p < 0.001$; $A = 0.11$) compared to the low and intermediate stress groups (MRPP: $p = 0.040$; $A = .02$). *P. spicata*, *A. thurberianum*, and *P. secunda* were uniquely associated with and dominated both the low and intermediate stress communities, and *B. tectorum* and *L. perfoliatum* community composition was low (Table 3.3, Figs. 3.1A-C). In contrast, *B. tectorum* and to a lesser degree, *L. perfoliatum* were uniquely associated with and dominated high stress communities, where *P. spicata*, *A. thurberianum*, and *P. secunda* community composition was low (Table 3.3, Fig. 3.1A-C).

Community stability

The low, intermediate, and high stress groups of communities differed in the combined indicators of overall community stability (MRPP: $p < 0.001$; $A = 0.07$). Bare soil cover (ANOVA: $p = 0.005$), basal gap size (ANOVA: $p < 0.001$), and the proportion of large gaps (ANOVA: $p < 0.001$) differed significantly among the three groups (Fig. 3.2). Soil aggregate stability and proportion of highly stable aggregates did not differ among groups (ANOVA: $p = 0.74$, $p = 0.69$, respectively). Although the overall community stability of the low and intermediate stress groups was similar, the stability of the high stress group was lower compared to the intermediate and low stress groups (Fig. 3.2).

DISCUSSION

Our study reports the first evidence of native species facilitation increasing community functional stability by increasing the community composition of other natives, which decrease invasibility by reducing the magnitude of non-native invasions (Bruno et al. 2003; Brooker et al. 2008). In high stress communities, there was *Artemisia* facilitation of four native bunchgrass species (Chapter 2). These species were uniquely associated with and dominated the composition of the under-shrub compared to interspace communities. In contrast, *B. tectorum* and *L. perfoliatum* were uniquely associated with and dominated interspace communities. Although not an absolute barrier to invasion, the *Artemisia*-facilitated refuge for bunchgrasses (Brooker et al. 2008) limited the magnitude of the invasion in the under-shrub community (Mitchell et al. 2006).

Unfortunately, this facilitation-mediated decrease in invasibility at the under-shrub-interspace community scale did not translate into lower invasibility at the site-level. The simplest reason for this finding is the limited spatial scale over which *Artemisia* facilitation occurs. *Artemisia* cover ranged between 9 and 30% across our study sites (Chapter 3), and after fire, *Artemisia* cover would be near zero. Consequently, between 70-94% of these communities are beyond the influence of *Artemisia* facilitation increased biotic resistance to *B. tectorum* invasion.

Consistent with our second hypothesis, this study reports the first evidence of facilitation increasing community stability at intermediate stress levels, but decreasing stability at high stress levels (Brooker and Callaway 2009; Butterfield 2009). The low stress communities were analogous to “low severity” environments described by Butterfield (2009). Low stress communities had high community compositional stability. Not only was composition of the under-shrub, interspace, and site-level communities similar, but these three communities had moderate to strong positive relationships to one another. This high compositional stability was associated with high functional stability to the extent measured by low invasibility to *B. tectorum* and *L. perfoliatum* invasion (Tilman 1996; Krushelnycky and Gillespie 2008).

Despite differences in composition between under-shrub, interspace, and site-level communities in intermediate stress environments, the strength of the positive relationship among the three communities either stayed the same or increased (under-shrub vs. interspace and under-shrub vs. site-level) compared to the low stress group. Only *E. elymoides* was uniquely associated with the under-shrub community, but it was still a significant component of the interspace communities. Although the importance of positive interactions between *Artemisia* and bunchgrasses may have increased, these findings suggest that most species were not 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 of bunchgrasses. This high compositional stability was again associated with high functional stability at the community level where *B. tectorum* and *L. perfoliatum* composition remained low.

Butterfield, p. 1197, (2009) predicted that facilitation would destabilize communities if species shifted from “facultative” to “obligate” beneficiaries of facilitation, “such that a greater 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. The four native bunchgrass species were uniquely associated with under-shrub communities, and the frequencies and community composition of these species are strikingly lower in the interspace. In contrast to the same two community comparisons at low and intermediate stress, high stress communities compared between the under-shrub and interspace communities and between under-shrub and site-level communities were unrelated. This low compositional stability was associated with a decrease in functional stability at the community level where *B. tectorum* and *L. perfoliatum* dominated. As bunchgrasses became increasingly dependent on *Artemisia*-facilitation, the decrease in the interspace bunchgrass community increased resource availability and substantially increased the magnitude of *B. tectorum* invasion (Beckstead and Augspurger 2004; Chambers et al. 2007; James et al. 2008)

High stress communities were characterized by lower overall community stability. The increased size of and connectivity between basal gaps in these communities indicate that native bunchgrass communities were becoming increasingly aggregated beneath *Artemisia*. Increasing spatial aggregation of vegetation in semi-arid systems is an early warning indicator that ecosystem resilience has been compromised and that disturbance, like fire, is likely to trigger a “catastrophic regime shift” (Scheffer et al. 2009).

Our findings add to growing evidence that changes in the structure of species interactions, i.e. shifts from competitive to facilitative outcomes between *Artemisia* and bunchgrasses, may reduce community compositional and functional stability (McCann 2000; Baez and Collins 2008; Villarreal-Barajas and Martorell 2009). The destabilizing effects associated with these shifts in the structure of *Artemisia*-bunchgrass interactions were similar to those associated with the replacement of a competitive with a facilitative dominant species during *Larrea tridentata* (creosote bush) invasion of *Bouteloua eriopoda* (black grama) grasslands (Baez and Collins 2008).

A perfect storm of factors likely explain the especially pronounced destabilizing effects associated with shifts in the structure of *Artemisia*-bunchgrass interactions: a single dominant foundational species that exerts strong control over interactions and a disturbance and invasion that alters the structure of such interactions (De Ruiter et al. 1995; Holzapfel and Mahall 1999; McCann 2000; Baez and Collins 2008). The foundational shrub *Artemisia* (Davies et al. 2007) strongly controls the structure of interactions (Chapter 2) because it simultaneously competes with herbaceous species for resources (Caldwell et al. 1987; Reichenberger and Pyke 1990; Miller et al. 1991) and facilitates them by protecting them from herbivory (France et al. 2009), ameliorating heat stress (Davies et al. 2007), and enhancing nutrient and water availability (Charley and West 1975; Doescher et al. 1984; Chambers 2001; Chambers et al. 2007; Davies et al. 2007).

Second, increasing cattle grazing disturbance was a predominant component of the stress gradients driving shifts in the structure of *Artemisia*-bunchgrass interactions (Chapter 2). Cattle grazing is a relatively novel type of disturbance in the Intermountain West, and most native bunchgrasses are highly sensitive to such herbivory (Mack and Thompson 1982). Cattle preferentially graze interspace bunchgrasses until utilization levels reach 40% when they begin to graze bunchgrasses located under shrubs; however, cattle continue to preferentially graze interspace bunchgrasses up to utilization levels exceeding 90% (France et al. 2009). These two factors likely make bunchgrasses especially vulnerable to destabilizing "obligate" *Artemisia* facilitation.

Third, the structure of *Artemisia* interactions with the invasive *B. tectorum* was fundamentally different than those with native bunchgrasses. In striking contrast to the shifts from competitive to facilitative outcomes between *Artemisia* and native bunchgrasses, *Artemisia* had competitive outcomes with *B. tectorum* along the entire stress gradient (Chapter 2). Because of *B. tectorum's* high tolerance to cattle grazing and its water and heat stress avoidance strategies, *B. tectorum* is not dependent on *Artemisia*-facilitation. *B. tectorum*'s rapid growth, nutrient uptake, reproductive rates allow it to exploit increased resource availability in the interspaces left void of bunchgrasses (Chambers et al. 2007).

Management Implications

Conserving and restoring the stability of these communities will require significantly reducing cumulative stress levels. Cattle grazing in combination with heat and water stress has fundamentally altered the role of *Artemisia* as a driver of community stability. Ongoing climate change will likely increase heat stress and potentially water stress within this region by altering precipitation regimes (Neilson et al. 2005; Chambers et al. 2009). Cattle grazing is the predominate land use of these landscapes (Knick et al. 2010) and ongoing dispersal of watering locations to optimize cattle utilization of forage (Holechek 1988; Holechek et al. 2003) may inadvertently increase cumulative herbivory stress levels across *Artemisia* landscapes. These stress increases may drive communities currently characterized by intermediate stress levels where “facultative” *Artemisia* facilitation of bunchgrasses increases community stability to high stress levels where “obligate” *Artemisia* facilitation decreases community stability (Bradley 2009). Of the three stresses, management can only adjust cattle grazing. Consequently, reducing cumulative cattle grazing levels by adjusting utilization rates and/or seasons of use may be the only effective means of reducing cumulative stress levels.

This need is especially urgent in communities similar to the high stress communities of this study. Without simultaneous reductions in stress levels and active restoration to restore native bunchgrass communities (Pyke 2010), increasingly frequent fires (Neilson et al. 2005; Baker 2010) will likely transform these communities into *B. tectorum*-dominated annual grasslands (Knick et al. 2010). In communities characterized by stress levels similar to the intermediate levels in this study, *Artemisia* facilitation plays a determinative stabilizing role by maintaining community compositional and functional stability. Our findings suggest that management actions or natural disturbances (fire) that reduce *Artemisia* cover may decrease community stability unless cumulative stress levels are simultaneously reduced.

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Low Stress Group

Competitive-neutral interactions between *Artemisia* and bunchgrasses

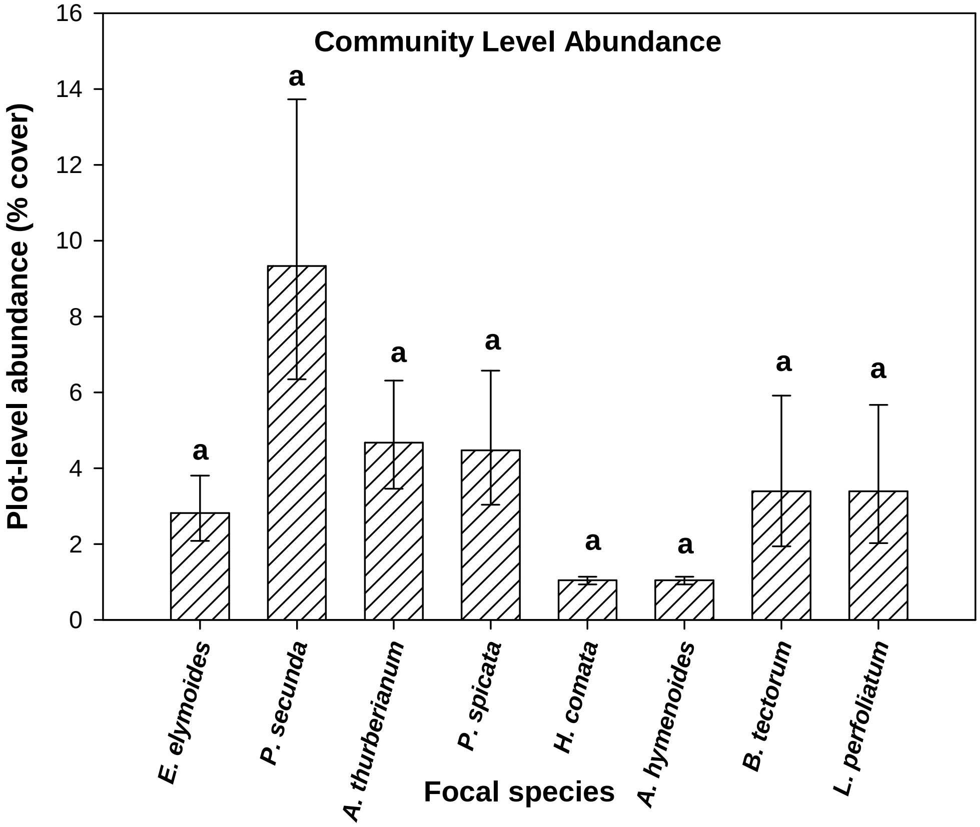

Figure 3.1A Herbaceous understory community composition at the community level (plot-level) in the low stress group. Different letters above bars indicate a significant difference in the community level cover of that species between low, intermediate, and high stress groups of communities (α = 0.10). Error bars represent Bonferroni-adjusted 90% confidence intervals.

Intermediate Stress Group

Facilitative and neutral interactions between *Artemisia* and bunchgrasses

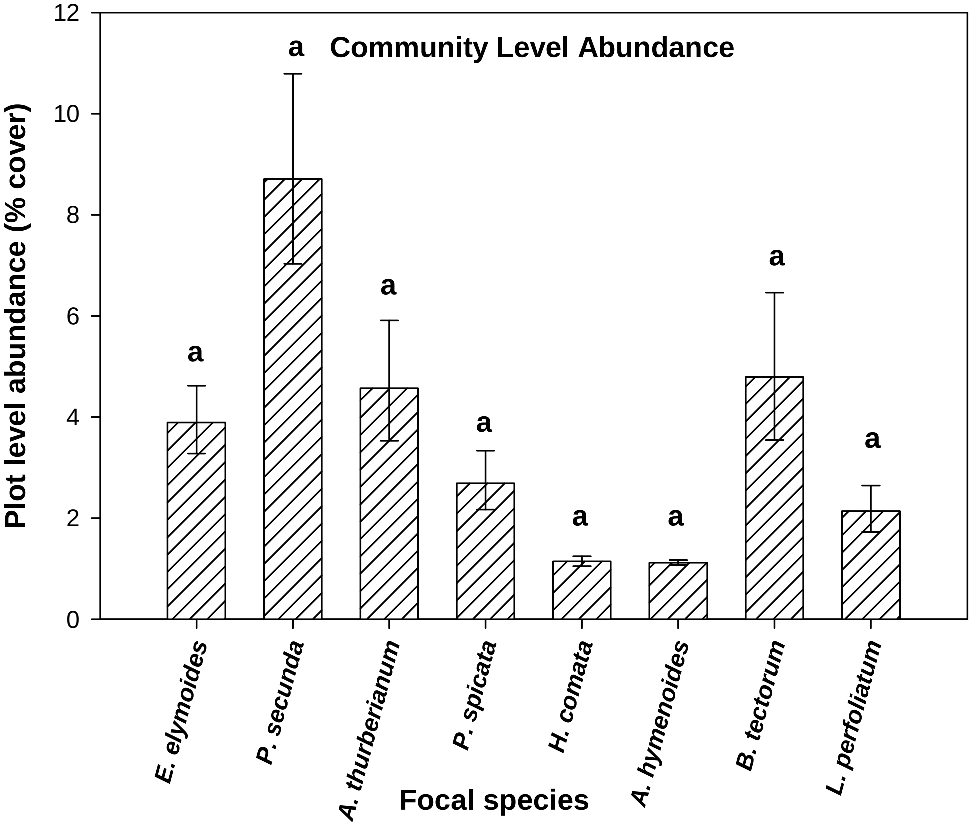

Figure 3.1B Herbaceous understory community composition at the community level (plot-level) in the intermediate stress group. Different letters above bars indicate a significant difference in the community level cover of that species between low, intermediate, and high stress groups of communities ($\alpha = 0.10$). Error bars represent Bonferroni-adjusted 90% confidence intervals.

High Stress Group

Facilitative interactions between *Artemisia* and bunchgrasses

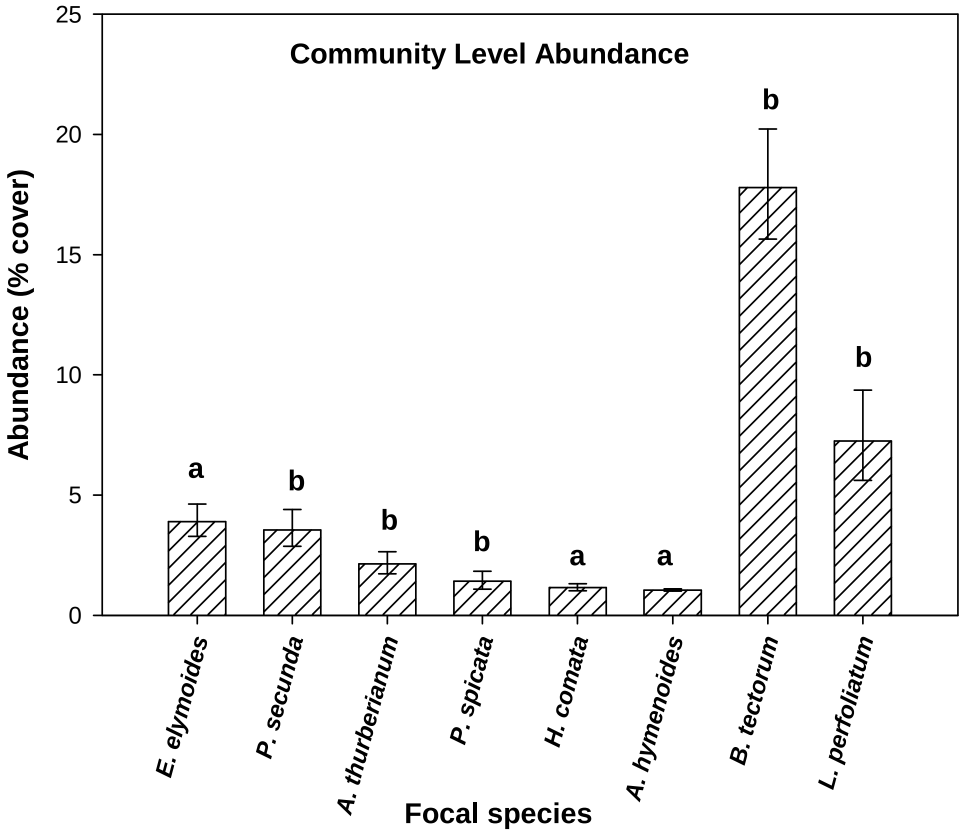

Figure 3.1C Herbaceous understory community composition at the community level (plot-level) in the high stress group. Different letters above bars indicate a significant difference in the community level cover of that species between low, intermediate, and high stress groups of communities ($\alpha = 0.10$). Error bars represent Bonferroni-adjusted 90% confidence intervals.

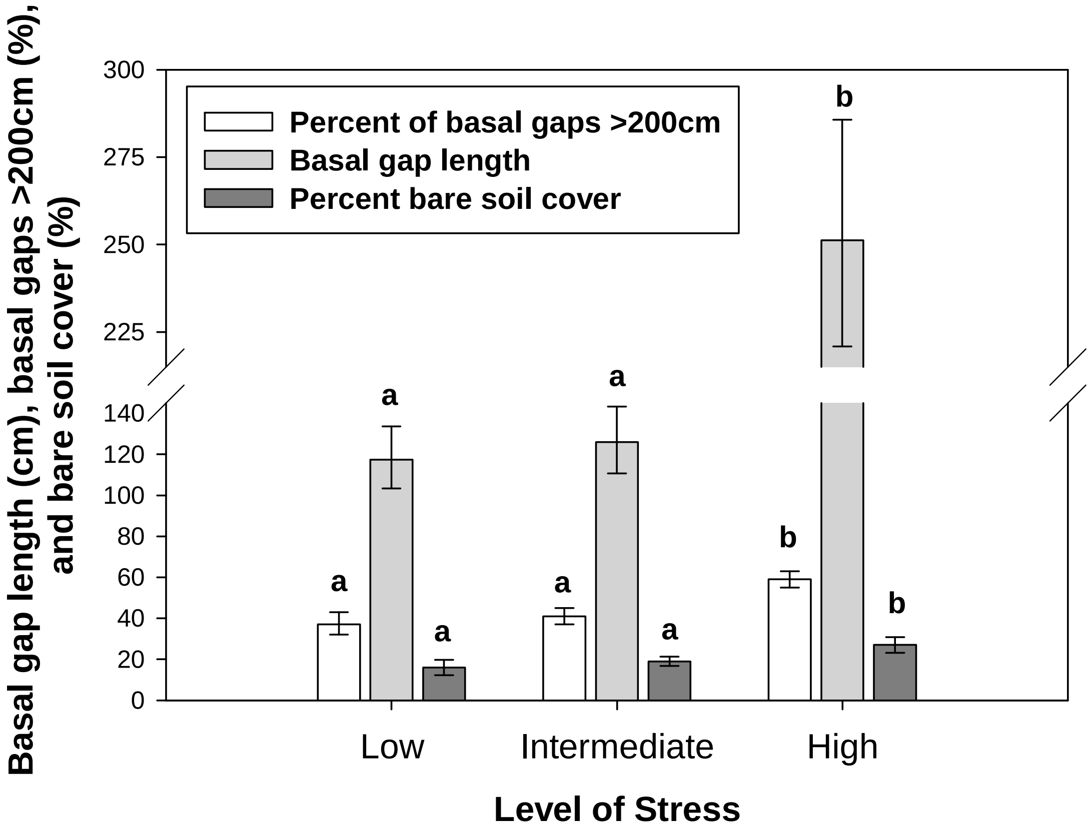

Figure 3.2 Indicators of overall community stability. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different letters above the bars indicate significant differences in the between the groups (α = 0.10).

Table 3.1 Comparison of community composition of the under-shrub, interspace, and site-level herbaceous understory communities

	Blocked MRPP: chance-corrected A and associated p-value			Mantel test results: standardized mantel statistic and associated p-value		
Stress Level of Group	Canopy v. interspace	Canopy v. plot-level	Interspace v. plot-level	Canopy v. interspace	Canopy v. plot-level	Interspace v. Plot-level
Low	A = 0.01; p = 0.349	A = -0.01; p = 0.537	A = -0.03;p = 0.968	R = 0.42; p = 0.003	R = 0.51; p < 0.001	R = 0.93; p < 0.001
Intermediate	A = 0.03; p < 0.001	A = 0.02;p = 0.013	A = -0.01; p = 0.786	R = 0.50; p < 0.001	R = 0.71; p < 0.001	R = 0.91; p < 0.001
High	A = 0.28; p < 0.001	A = 0.17;p < 0.001	A = 0.07; p < 0.001	R = 0.24; p = 0.328	R = .06; p = 0.592	R = 0.74; p = 0.004

Table 3.2 Blocked indicator species analysis comparing the composition of the herbaceous communities of under-shrub and interspace microsites within the low, intermediate, and high stress groups. Significant indicators are in bold type.

Group Stress Level	Canopy microsite			Interspace microsite			
Low	RF	RA	IV	RF	RA	IV	P-value
E. elymoides	50	31	29	86	34	15	0.4689
A. thuberianum	57	25	35	93	38	14	0.3349
P. spicata	29	15	37	86	44	4	0.0964
H. comata	7	53	1	7	18	4	1
A. hymenoides	0	0	4	7	53	0	1
P. secunda	93	36	32	100	32	33	0.9808
B. tectorum	43	27	29	79	37	11	0.5659
L. perfoliatum	29	20	26	64	41	6	0.4571
	Canopy microsite			Interspace microsite			
Intermediate	RF	RA	IV	RF	RA	IV	P-value
E. elymoides	**83**	**45**	**37**	**83**	**23**	**19**	**0.0188**
A. thuberianum	67	31	21	83	34	29	0.6655
P. spicata	64	38	24	62	29	18	0.8144
H. comata	0	0	0	21	52	11	0.1648
A. hymenoides	2	7	0	14	48	7	0.4259
P. secunda	95	38	37	95	29	28	0.0528
B. tectorum	69	33	23	83	33	28	0.8096
L. perfoliatum	43	33	14	57	33	19	0.6663
	Canopy microsite			Interspace microsite			
High	RF	RA	IV	RF	RA	IV	P-value
E. elymoides	**100**	**56**	**56**	**63**	**13**	**8**	**0.0002**
A. thuberianum	**84**	**53**	**45**	**58**	**17**	**10**	**0.01**
P. spicata	**42**	**57**	**24**	**16**	**16**	**2**	**0.0173**
H. comata	5	46	2	5	25	1	1
A. hymenoides	16	45	7	11	25	3	0.854
P. secunda	**100**	**56**	**56**	**63**	**13**	**8**	**0.0002**
B. tectorum	**100**	**16**	**12**	**100**	**42**	**42**	**0.0012**
L. perfoliatum	**100**	**17**	**37**	**100**	**33**	**33**	**0.0496**

Table 3.3 Indicator species analysis comparing the composition of the herbaceous understory communities at the community level among the low, intermediate, and high stress groups. Significant indicators are in bold type.

	Low Stress			**Intermediate Stress**			**High Stress**			
Species	**RF**	**RA**	**IV**	**RF**	**RA**	**IV**	**RF**	**RA**	**IV**	**P-value**
E. elymoides	93	28	26	90	36	33	100	36	36	0.2691
A. thuberianum	**93**	**40**	**37**	**83**	**40**	**33**	**89**	**20**	**18**	**0.047**
P. spicata	**86**	**52**	**45**	**74**	**35**	**26**	**42**	**12**	**5**	**0.005**
H. comata	7	18	1	24	61	14	5	21	1	0.2314
A. hymenoides	7	12	1	14	45	6	21	43	9	0.6197
P. secunda	**100**	**39**	**39**	**100**	**38**	**38**	**100**	**22**	**22**	**0.0214**
B. tectorum	**79**	**22**	**17**	**83**	**28**	**23**	**100**	**51**	**51**	**0.0002**
L. perfoliatum	**64**	**31**	**20**	**62**	**19**	**12**	**100**	**50**	**50**	**0.0004**

CHAPTER 4

Multi-process control over the resilience of North America's endangered Wyoming big sagebrush ecosystems

Michael D. Reisner, James B. Grace, David A. Pyke, Paul S. Doescher, and Bruce McCune

ABSTRACT

Ecosystem resilience to disturbance and resistance to invasion are controlled by a causal network of factors and processes including: the disturbance regime, the vulnerability of natives and non-native species to the disturbance regime; biotic resistance; and community structure. We conducted a study in *Artemisia tridentata* ssp. *wyomingensis* communities highly susceptible to *Bromus tectorum* invasion. We sampled 75 sites spanning a wide range of conditions predicted to be important determinants of community resilience. We used structural equation modeling (SEM) to assess the relationship between and relative importance of the simultaneously operating factors and processes driving resilience to disturbance and *B. tectorum* invasion. The linchpin of ecosystem resilience was the size of and connectivity between basal gaps in perennial vegetation, driven by shifts in the structure of the native community, especially the spatial aggregation of the perennial bunchgrasses. Two environmental factors, landscape orientation and soil physical properties, determined the inherent resilience of these communities to disturbance and invasion. Resident bunchgrasses provided biotic resistance to invasion by reducing the size of and connectivity between basal gaps and thereby limiting available resources. Biological soil crust (BSC) communities provided resistance by reducing safe sites for *B. tectorum* establishment.

Consistent with the invasional meltdown hypothesis, increasing levels of cattle grazing facilitated *B. tectorum* invasions by reducing native bunchgrass abundance, shifting bunchgrass community composition, and reducing BSC abundance, which in turn reduced community resilience. This invasional meltdown was likely the result of differences in grazing avoidance and tolerance attributes between native and non-native species. Most native bunchgrass species lack strong grazing resistance and tolerance strategies compared to *B. tectorum*. We found no evidence that cattle increased *B. tectorum* propagule pressure, or that cattle grazing increased resilience by directly reducing *B. tectorum* abundance. These findings provided important insight into the role of cattle grazing as potential determinant of community resilience and place it in the context of the resilience causal network.

INTRODUCTION

Functional stability of a community is the system's ability to resist changes in aggregate properties or processes such as invasibility (McNaughton 1977; Lehman and Tilman 2000; Foster et al. 2002). Community invasibility consists of two related concepts. Resistance is the system's ability to prevent or minimize establishment and dominance of non-native species (Sax et al. 2007). Resilience is a system's ability to recover from disturbance (Holling 1973) or withstand disturbance before transitioning to another successional state (Gunderson 2000). Invasibility is an emergent property of an ecosystem and thus under the control of multiple operating factors connected simultaneously by a causal network of underlying mechanisms (Lonsdale 1999).

Successful invasion depends on: (1) characteristics of invading species or species invasiveness (Daehler 2003) and (2) community invasibility. Community invasibility is determined by: (a) the type and amount of disturbances and the relative resilience of natives and non-native species to such disturbance regimes, (b) biotic resistance to invasion that is determined by the competitive abilities of resident native species, (c) community structure and (d) propagule pressure (Hobbs and Huenneke 1992; Williamson and Fitter 1996; Lonsdale 1999; Richardson and Pysek 2006; Rilov et al. 2009). All of these factors determine resource availability and the timing of this availability relative to the interacting organisms.

Mechanistically, invasibility may be linked to increases in resource availability (Davis et al. 2000). Communities are predicted to be more vulnerable to invasion when there is an increase in the amount of unused resources because resident species are satiated, resource supplies increase faster than they can be utilized, or both (Stohlgren et al. 1999; Davis et al. 2000). Any factor that increases resource availability will increase invasibility and communities are predicted to be most susceptible to invasion when new, intense disturbances increase resource availability (Davis et al. 2000).

Recent studies, including two meta-analyses, predict that grazing and associated disturbances caused by non-native herbivores will exacerbate the magnitude of non-native invasions by decreasing the abundance of native species compared to non-native species (Parker et al. 2006; Simberloff 2006; Nunez et al. 2008; Nuñez et al. 2010). These shifts in relative abundance can drive changes in community composition and alter ecosystem processes (Nuñez et al. 2010). The predicted “invasional meltdowns” are most common and severe when there is no evolutionary history between the native plants and non-native herbivores. It may lead to plants with a lack of grazing resistance and tolerance traits in the community (Nuñez et al. 2010).

Community succession is driven by a combination of equilibrium and non-equilibrium processes (Holling 1973; Bestelmeyer et al. 2009; Briske et al. 2009).

Non-equilibrium processes are characterized by thresholds where disturbances may lead to non-linear shifts from one stable community to another (Scheffer et al. 2001; Scheffer et al. 2009). Once crossed, these thresholds are nearly irreversible from a management perspective and will require investments in active restoration to potentially return to the original community (Bestelmeyer et al. 2009; Miller et al. 2010; Pyke 2010). Equilibrium processes describe linear shifts between different community phases within a given state (Briske et al. 2006; Briske et al. 2009; Peterson 2009) that are reversible by reducing stressors through passive restoration (Bestelmeyer et al. 2009; Pyke 2010). A phase-at-risk community is the least resilient community within an ecological state, where continued action of stressors may force the community across a threshold to an alternative state (Bestelmeyer et al. 2009; Briske et al. 2009). State-and-transition succession and degradation models incorporate both these dynamics.

In semi-arid ecosystems, shifts in community structure characterized by increasing spatial aggregation of native perennial vegetation is predicted to be an early warning indicator that ecosystem resilience has been compromised and a threshold shift between alternatives states is imminent (Scheffer et al. 2001; Okin et al. 2009; Scheffer et al. 2009; Herrick et al. 2010). These structural changes are probably sensitive indicators of reduced ecosystem resilience because increasing spatial aggregation of vegetation is associated with detrimental changes in the fundamental biotic, hydrologic and soil stability attributes necessary for ecosystem resilience (Pyke et al. 2001; Herrick et al. 2005; Herrick et al. 2006; Bird et al. 2007; Miller 2008; Bestelmeyer et al. 2009; Scheffer et al. 2009; Herrick et al. 2010).

Given the complex context-dependent nature of ecosystem invasibility, accurately characterizing effects of one factor or mechanism requires taking into account potential effects of others. Gaining a predictive understanding of the complexity driving an ecosystem's susceptibility to invasion requires placing the effect of one factor or mechanism in context relative to the importance of others operating simultaneously. Not surprisingly, untangling and understanding such complexity has proven elusive to ecologists.

In this study, we describe patterns of resistance and resilience a semi-arid landscape using the sagebrush steppe as a model system and using conventional multivariate methods (McCune and Grace 2002). Second, we evaluate a complex, multivariate hypothesis of a causal network of factors and processes that operate simultaneously and may control observed patterns of resilience and invasibility. We will use structural equation modeling (SEM) to predict the strength and directionality of these control factors and processes (Grace 2006; Grace and Bollen 2008; Grace et al. 2010).

A PRIORI MODEL OF COMMUNITY INVASIBILITY

The *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) (henceforth "*Artemisia*") ecosystems of North America are one of North America's most widespread and endangered semi-arid ecosystems (Noss et al. 1995; Miller et al. 2010). The invasive annual grass *Bromus tectorum* currently dominates 7% of the Northern Great Basin (Bradley and Mustard 2005; Bradley and Mustard 2006), and Suring et al. (2005) recently estimated that 50% of the Great Basin Ecoregion has a moderate or high probability of *B. tectorum* dominance of the herbaceous understory. In *Artemisia* communities, fire is the dominant historical disturbance driving community phase transitions in the reference state of this ecosystem. However, *B. tectorum* is increasingly triggering a "catastrophic regime shift,"(Scheffer et al. 2001; Scheffer et al. 2009) whereby native shrub-steppe communities co-dominated by *Artemisia* and a diverse assemblage of native bunchgrasses are transformed into annual grasslands dominated by *B. tectorum* and other non-native species (Billings 1990; D'Antonio and Vitousek 1992; Knapp 1996; Pyke and Brooks 2001; Knick et al. 2009; Knick et al. 2010; Miller et al. 2010). These regime shifts indicate that a combination of disturbances and stressors has compromised the functional stability of these communities (McNaughton 1977; Tilman 1996; Foster et al. 2002; Scheffer et al. 2009). Many communities have *B. tectorum* within the community, yet predicting when a community will experience a state change has eluded scientists and managers alike.

We used a SEM analysis to address three objectives. First, we evaluated the numerous causal mechanisms by which cattle grazing influence the susceptibility of these communities to *B. tectorum* invasion. Second, we placed the role of cattle grazing in context by controlling and accounting for the influences of other factors known to be important determinants of the composition, structure, and invasibility of these communities (i.e. to partition relationships). Third, we assessed the relative importance of these inter-correlated factors and processes (Grace 2006).

Using *a priori* knowledge from a panel of ecologists with expertise in *Artemisia* ecosystems, previous work in these ecosystems, and ecological theories, we developed a multivariate hypothesis of the causal network for a regime shift to occur. The causal network incorporates the predicted relationships between and among all controlling factors based on processes thought to operate in regime shifts within this ecosystem (Fig. 4.1, Table 4.1). The conceptual model was based on an *a priori* assumption that cattle grazing influences ecosystem invasibility through four primary processes: (1) Cattle grazing directly decreases invasibility by reducing *B. tectorum* abundance; (2) Cattle directly increases invasibility by serving as a dispersal vector and increasing propagule pressure; (3) Cattle grazing indirectly increases invasibility by decreasing biotic resistance because grazing reduces bunchgrass abundance and/or shifts bunchgrass community composition, which in turn increase resource availability; and (4) Cattle trampling indirectly increases invasibility by decreasing biotic resistance because trampling reduces biological soil crust (BSC) abundance and thereby creates safe sites for *B. tectorum* establishment.

The conceptual model represents a collective multivariate hypothesis of the causal network of factors and processes driving the invasibility of *Artemisia* ecosystems based on the best available scientific and theoretical information available (Grace 2006; Riginos and Grace 2008). The essence of the SEM approach involves evaluating how well the structure of our data matches the structure predicted by the conceptual model, and more importantly, why or why not? The conceptual model served as a roadmap to guide analyses and interpretations.

METHODS

Study area and sampling design

The study consisted of 75 sites located in the Northern Great Basin floristic province of central Oregon (Anderson et al. 1998). The study area consisted of three Bureau of Land Management (BLM) federal grazing allotments in the Burns District, Three Rivers Resource Area-the West Warm Springs (122, 884 ha), East Wagontire (38, 000 ha), and Capehart (24,500 ha) allotments. The elevation of the sites varied between 1265 and 1580 m. We employed a stratified random sampling design to capture within the study area as much variation as possible. The design consisted of three strata: (1) soils; (2) landscape; and (3) cattle grazing intensity. ArcGIS 13.0 (ESRI, Redlands, CA) was used to manipulate geographic databases and conduct spatial analyses. To reduce potential confounding effects of time since fire, all areas within the study area that had burned since 1930 were excluded using a fire perimeter database (http://sagemap.wr.usgs.gov last accessed 03/17/2008).

Natural Resource Conservation Service (NRCS) digital soil maps were used to stratify the study area into different map units, consisting of one or more soil components, to provide spatial variation in water stress driven by differences in soil properties. (http://websoilsurvey.nrcs.usda.gov). Soil map components were matched with corresponding NRCS Ecological Site Descriptions (ESDs). If the ESD did not identify *Artemisia* as the dominant shrub species, the component was excluded from study. Five *Artemisia*-dominated ecological sites that varied in co-dominant grasses in the herbaceous understory were identified: (1) Loamy 10-12PZ (10-12PZ = 10 to 12 inch Precipitation Zone or 254 to 305 mm) with perennial bunchgrasses *P. spicata* and *A. thurberianum*; (2) Sandy Loam 8-10PZ (203 to 254 mm) with perennial bunchgrasses *H. comata* and *P. spicata*; (3) Clayey 10-12PZ with perennial bunchgrasses *A. thurberianum* and *P. secunda*; and (4&5) North slopes 6-10PZ (152 to 254 mm) and South slopes 6-10PZ with *P. spicata* and *A. thurberianum* co-dominating north and south slopes, respectively.

Each of the five ESDs were delineated into three landscape sub-strata using 10-m resolution U.S. Geological Survey Digital Elevation Models (DEMs) to capture variation in heat loads driven by changes in landscape orientation: (1) northerly aspects (0-90°, 270-360°), (2) southerly aspects (90-270°), or (3) flat. Study sites were located at different distances from the nearest livestock watering location using a BLM database of livestock watering points to capture variation in cattle grazing intensity disturbances. Sites were located at variable distances, rather than at fixed intervals, from watering points because of the need to stratify the study area by soil and landscape properties (Adler and Hall 2005). Potential study sites were selected from random points generated for each of the soil-landscape strata combination within the study area. Random points were selected using the following rules to ensure that study sites were located: (1) every 200-400 m (starting at 100 m and extending to >3200 m) from the nearest water location; (2) in as many soil-landscape strata combinations as possible; and (3) > 200 m from the nearest road to minimize potential road-related effects. Potential study sites were field verified to ensure they satisfied above criteria.

Sampling

Thirty 0.39-ha study plots were sampled in 2008 and 45 in 2009. Six, 25-m transects were established using a spoke design, and herbaceous, shrub, and BSC cover was measured using line-point intercept (Herrick et al. 2005). All sampling occurred between May 10 and July 15 each year to capture peak herbaceous biomass. Aspect and slope of each plot were calculated from DEMs using Arc-GIS 13.0, and with latitude, were used to calculate potential heat loads for each plot (McCune 2007).

Potential variation in water stress was quantified by measuring soil texture (% sand, silt, and clay) at 0-15 cm soil depth using the hydrometer method (Gee and Bauder 1986). Potential effective rooting depth was measured by digging a soil pit until bedrock, a restrictive confining layer (clay accumulation layer), or 2m depth was reached (Passey et al. 1982; Jensen 1989; Davies et al. 2007). To quantify potential temporal variation in water stress, the amount and timing of precipitation for each study site was derived from PRISM at 2 - km^2 cell resolution (Daly et al. 1994; Daly et al. 2008). Sampling-year precipitation for all study plots was estimated for three seasons: 8/1-10/31 (fall), 11/1-3/31 (winter), and 4/1-7/31 (spring-summer).

Cattle grazing disturbance intensity was quantified by four measurements: distance from the nearest watering location field verified; cow pie frequency and cow pie density from twelve 1 x 25 m belt transects; and bunchgrass basal area (Pond 1960; Hickey 1961; Butler and Briske 1988; Briske and Richards 1995). 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 = $\pi\ (C/2\pi)^2$.

We measured two indicators of soil resilience. Bare soil cover was calculated using the line-point intercept data and represents the exposed soil surface not covered by vegetation, visible biological crusts, dead vegetation, litter, or rocks (Herrick et al. 2005). Soil surface aggregate stability was assessed in interspace microsites at 18 random sampling points along the transects using soil from the upper 0-4 mm (Herrick et al. 2001; Herrick et al. 2005). Two indicators of soil resistance to erosion were calculated from the soil stability data: mean soil stability and proportion of surface soil samples that were rated as extremely stable (Herrick et al. 2001; Beever et al. 2006; Bestelmeyer et al. 2009).

Community structure, the spatial aggregation of native perennial vegetation, was measured using the basal gap intercept method (Herrick et al. 2005). Basal gap intercept quantifies the size and connectivity of basal gaps between perennial vegetation (Herrick et al. 2005). We calculated mean basal gap length and the proportion of transects covered by large gaps (>200 cm in length). Herbaceous biomass was measured in twenty 0.5 x 1.0 m-quadrats. Ten located in the interspace and ten located in under-shrub microsites.

Conventional multivariate analysis

Prior to analyses, species cover, distance from nearest water source, cow pie density, bunchgrass basal area, heat loads, soil depth, precipitation, basal gap size, and herbaceous biomass data were log-transformed to improve distributional properties, correlations with ordination axes, and the amount of variation explained by ordinations (McCune and Grace 2002).

Non-metric multidimensional scaling (NMS) ordination using Sorenson distances (McCune and Grace 2002) was used to relate patterns in community composition to potential complex environmental gradients (Kruskal 1964; McCune and Mefford 1999). NMS ordination was performed. The ordination was run in the “slow and thorough” autopilot mode using a random starting configuration in PC-ORD (McCune and Mefford 2008).

Joint plots and Pierson’s correlations were used to describe the relationship between environmental gradients and the strongest patterns of herbaceous community composition represented by the NMS ordination (McCune and Mefford 1999). We used non-parametric multiplicative regression (NPMR) in HyperNiche to more precisely quantify the relationship between species’ cover and the environmental gradients (McCune 2006; McCune and Mefford 2008). Predictors were the three axes ordination scores. These scores represented an integrated measure of complex environmental gradients associated with dominant patterns of herbaceous community composition extracted by the ordination. Response variables were the cover of each species using a local mean estimator and Gaussian kernel function. Several species exhibited moderate or strong relationships with both ordination axes. To control for potential interactions between axes, response curves were generated using partial models and focal variables (McCune 2009). A total of 30 response curves were generated, one for each of the seven bunchgrass species, a functional group comprised of native perennial and annual forbs, and two non-native species along each of the three ordination axes.

A final NPMR model was run using the three axes scores as predictors. Final model fit was assessed with a cross-validated R^2 (XR^2) (McCune 2006; McCune 2009). The sensitivity values across all the data points are averaged and standardized as a proportion of the range of the response variable. A higher sensitivity to one of the predictor axes translates into more pronounced shifts in cover compared to shifts along the environmental gradient represented by the other ordination axes.

Hierarchical agglomerative cluster analysis (Sorenson's distance and flexible beta linkage ($\beta = -0.25$)) was used to identify groups of sites differing in community composition. The resulting dendrogram was pruned at the grouping level with the highest number of significant indicator species and second lowest average p-value from ISA and with about 40% of the information remaining (McCune and Grace 2002). Multi-variate differences in community composition between identified groups were tested using multi-response permutation procedures (MRPP) ($\alpha = 0.05$) (Mielke 1984). When A is close to zero, groups are no more different than expected by chance, while an A = 1 means perfect separation of groups (McCune and Grace 2002). Identified groups were overlaid onto ordinations to accentuate relationships between groups and identified environmental gradients. Multivariate differences in relativized environmental variables between groups were tested with MRPP ($\alpha = 0.05$) using Euclidean distances (Mielke 1984). Differences in individual environmental variables between groups were assessed with ANOVA ($\alpha = .10$) using S-Plus 8.0. Where significant differences were detected, Bonferroni-adjusted 90% confidence intervals were used to quantify differences between groups.

Structural equation modeling

We used a “nested-models approach” under which the range of possible models was constrained by assumptions of the above-described conceptual model of community invasibility (Grace 2006; Riginos and Grace 2008). Using this approach, our analysis consisted of three steps: (1) model specification and indicator selection, (2) evaluation of alternative models, and (3) comparison of the final inferential models each alternative model.

Model specification and indicator selection is the process by which conceptual ideas are translated into a statistical form (Grace 2006; Grace et al. 2010). This process focused on using the available data to identify “indicator variables”- the observed variables that serve as measures for the conceptual variables in the meta-SEM (Travis and Grace 2010). We used bivariate scatter-plots, Pearson’s correlations, and linear regression to evaluate relationships between indicator variables. This process was also used to evaluate whether the relationships between the selected indicator variables met the necessary normality and linearity assumptions for SEM. *B. tectorum* cover was log-transformed to satisfy distributional and linearity assumptions. All other relationships were approximately linear. In this analysis, we also tested for “grazing allotment” and “ecological site” interaction effects on key relationships in the model. With the exception of a potential weak allotment effect, we found no interaction effects. The results from these exploratory analyses are presented in the Appendix.

Except for “safe sites,” we identified single indicators for all model construct variables. *Bromus tectorum* cover was selected as the indicator to measure “ecosystem invasibility.” Bunchgrass and sagebrush cover were selected to measure their abundance. NMS ordination of the cover data for *only* the bunchgrass species was used to develop an indicator of “bunchgrass community composition” with three resulting ordination axes that explained 51%, 22%, and 19% of the variation in bunchgrass composition. The three axes were used as indices of “bunchgrass community composition.” Distance from the nearest water source was selected as the indicator to measure “cattle grazing disturbance” and is best interpreted as a measure of cumulative cattle grazing disturbance (Adler and Hall 2005). Heat load was selected to measure “landscape orientation”, and % 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 indicator to measure perennial vegetation spatial distribution, i.e. “community composition.” Two indicators were selected to measure “safe sites”- BSC cover and percent bare soil cover.

Within the confines of the conceptual model, we evaluated two main alternative models. Model A did not include the conceptual variable “herbaceous community composition” and thus, did not evaluate the influence of cattle grazing on community composition (Fig. 1, path #4) or effects of such shifts in composition (Fig.1, paths #7 and #8). Model B was identical to Model A except it evaluated whether cattle grazing increased invasibility indirectly by shifting the composition of the native herbaceous community (path #4), which in turn directly influenced invasibility (path #9), or indirectly influenced invasibility by altering community structure (paths #8 & #14).

All SEM analyses were conducted using Amos 18.0 SEM software (SPSS 2010). Maximum likelihood procedures were used for model evaluation and parameter estimation. We examined Bayesian estimates for comparison to maximum likelihood parameter estimates (Lee 2007). Model fit was evaluated by sequentially using the single-degree-of-freedom χ^2 goodness-of-fit statistic and associated p-value. In the SEM context, larger p-values indicate a good fit between the model and the data (Grace 2006; Anderson et al. 2007). Software provided modification indices were used to evaluate the need to include paths or correlations not in the original conceptual model. The significance of individual pathway coefficients was assessed using path p-values ($\alpha = 0.05$) and the effect of path removal on overall model fit (using χ^2 and associated p-values) and thus, *a priori* hypotheses concerning the causal network of factors and processes driving invasibility (Grace 2006; Grace et al. 2010). Non-significant pathways were removed and new significant pathways were added unless the difference in the statistic did not satisfy the critical minimum difference ($\chi^2 = 3.84$).

This model evaluation process produced two final inferential models: Models A and B. We again tested for "allotment" and "ecological site" interaction effects by including them as categorical variables in the final inferential models. Neither variable improved model fit nor the amount of variation in ecosystem invasibility explained, which suggests there are no significant interactions. Similarly, other available indicators for model construct variables were sequentially included in the final inferential model to determine whether they represented independently operating processes. None of the alternative indicators improved model fit or amount of variation in ecosystem invasibility explained, which suggests that selected indicators adequately represent construct variables for this dataset.

Finally, we evaluated the parsimony of the two final alternative models using model chi-square and associated p-value, percent of variation in ecosystem invasibility explained by the model, study objectives, and four objective indicators of model fit generated by the Amos software: Akaike information criterion (AIC) and Bayesian information criteria (BIC) from the maximum likelihood procedures and deviance information criteria (DIC) and posterior predictive p-value values from the Bayesian procedures. Generally, smaller values for AIC, BIC, and DIC indicate better model fit (Gelman et al. 2004; Lee 2007). Posterior predictive p-values nearer to 0.50 are indicative of better model fit.

Standardized (by standard deviations) and un-standardized path coefficients are reported for the final inferential model. These coefficients estimate the influence of one variable on another and the amount that the influenced variable should respond if the other variable is manipulated and all other variables in the model are held constant. We reported total effects for selected variables. A variable's total effects include its influence on another variable through both direct and indirect paths and represent the amount that the influenced variable should respond if a variable was manipulated and all the variables it influences in the model are allowed to simultaneously vary (Grace 2006; Grace and Keeley 2006). R^2 values for response variables show the proportion of variation explained by relationships in the model.

RESULTS

Patterns of invasibility-conventional multivariate results

Nearly 92% of the total variation in community composition was explained by the final 3-dimensional ordination (Fig. 4.2). Axis 1 was the dominant axis explaining

60.9% of the variation in the composition data. Axes 2 and 3 represented weaker relationships explaining 19.3% and 11.6% of the variation, respectively. Axis 1 was strong gradient of decreasing cattle grazing disturbance and heat stress. All of the indicators of cattle grazing had moderate or strong relationships with the axis: cow pie density (r = -0.35) and cow pie frequency (r = -0.36) had strong negative relationships and distance from water (r = 0.41) and deep-rooted bunchgrass basal area (r = 0.71) had strong positive relationships with the axis (Fig. 4.2; Table 4.2). Heat loads had a strong negative relationship with the axis (r = -0.44).

In addition, biological soil crust cover, soil aggregate stability, and the proportion of soil aggregate stability values rated as highly stable increased; whereas bare soil cover decreased along Axis 1 (Fig. 4.2). Spatial aggregation of native perennial vegetation, i.e. size of and connectivity between basal gaps, decreased strongly along Axes 1 and 2 (Fig. 4.2; Table 4.2).

Axis 2 represented a strong gradient of decreasing soil sand and increasing clay content and increasing fall and winter precipitation (Fig. 4.2; Table 4.2). Axis 3 represented a weaker gradient of decreasing cattle grazing associated with decreasing cow pie density and frequency and increasing deep-rooted bunchgrass basal area (Table 4.2).

NPMR model sensitivities indicate that Axis 1 was a greater predictor of both non-native species compared to the other axes (Table 4.3). The strength of the relationship between cover of individual native species and these three axes varied considerably (Figs.4.3A-C; Table 4.3). *P. spicata*, *A. thurberianum*, *Poa secunda*, and forbs had strong positive relationships with Axis 1, *P. secunda* and forbs had strong positive relationships with Axis 2, and *E. elymoides* had a strong positive relationship with Axis 3 (Figs. 4.3A-C; Table 4.3).

Cluster analysis identified five distinct groups of communities. There was a complete division of study plots with 0% of the information remaining (Fig. 4.4A). These results were used to develop a conceptual degradation model of *Artemisia* ecosystem invasibility that incorporates key concepts of state-and-transition models of succession (Fig. 4.4B). The five groups of communities were divided into three distinct community states. State 1 consisted of two groups of communities with intact herbaceous understory communities dominated by native bunchgrasses and forbs (State 1A and 1B, Figs. 4.4A&B & 4.5A-E) and a phase-at-risk community with an understory co-dominated by native species and *B. tectorum* (Figs. 4.4A&B & 4.5A-E). States 2 and 3 consisted of communities with understories dominated by *B. tectorum* and the non-native annual forb, *Lepidium perfoliatum* (pepperweed).

The community composition of these groups differed (MRPP using species data: A = 0.33, $p < 0.01$; Figs. 4.5A-E). Several species were uniquely associated with one or more groups (Table 4.4). The combined cattle grazing levels, heat stress, water stress, soil resilience, and size of and connectivity of basal gaps differed significantly among groups (MRPP using environmental data: A = 0.59, p < 0.0001) (Table 4.5).

The intact communities comprising groups 1A and 1B had the lowest levels of cattle grazing and smallest and least connected basal gaps between perennial vegetation, and included none of the Sandy Loam 10-12PZ ecological sites (Figs. 4.6A-E, Table 4.6). Group 1B communities had higher heat loads and finer-textured soils compared to those of group 1A (Figs. 4.6A-E). Group 1A communities were dominated by *P. spicata*, *A. thurberianum*, and *P. secunda*, while Group 1B communities were dominated by *P. secunda*, *E. elymoides*, and native forbs (Figs. 4.5A&B; Table 4.4). *B. tectorum* cover was <2% in both groups. Communities comprising the phase-at-risk communities of State 1 were characterized by intermediate levels of cattle grazing, heat loads, water stress, and size of and connectivity between basal gaps (Figs. 4.6A-E, Table 4.6). Native species *A. thurberianum*, *P. spicata*, *H. comata* and the non-native *B. tectorum* co-dominated these communities (Figs. 4.5C; Table 4.4).

State 2 communities were characterized by intermediate to high levels of cattle grazing and intermediate levels of heat loads and water stress (Figs. 4.6A-E). *B. tectorum* and *L. perfoliatum* dominated State 2 communities along with the native *P. secunda* (Fig. 4.5D; Table 4.4). State 3 communities had the highest levels of cattle grazing, highest bare soil cover, largest and most connected basal gaps, lowest levels of fall and winter precipitation, and lowest soil aggregate stability (Figs. 4.6A-E). *B. tectorum* and *L. perfoliatum* dominated these communities along with the native *E. elymoides* (Fig.4.5E; Table 4.4).

Causal networks-SEM results

In both Models A and B, the inclusion of a new (unpredicted) path from "community structure" to bare soil cover, one of the indicator variables for the construct variable "safe sites," significantly improved overall model fit and the amount of variation in ecosystem invasibility explained by the model (Figs. 4.7 & 4.8).

The final Model A of *Artemisia* ecosystem invasibility had a χ^2 value of 11.73 with a P value of 0.590 with 16 degrees of freedom. The final Model B had a χ^2 value of 18.88 with a P value of 0.539 with 20 degrees of freedom. Both final models were demonstrated good fits with the data ($p > 0.05$) (Grace 2006; Anderson et al. 2007). Maximum likelihood and Bayesian estimates confirmed that unstandardized coefficients of all paths retained in final inferential models were different from zero (Table 4.7). The average difference between maximum likelihood and Bayesian estimates for the path coefficients was < 0.5% (Table 4.7). Models A and B each explained 72% of the variation in *B. tectorum* cover (Figs. 4.7 & 4.8). The four objective measures of model fit suggest that Model A was slightly more parsimonious than Model B (Table 4.8).

However, Model B explained significantly more of the variation in community structure compared to Model A, 72% versus 53% respectively. Model A showed positive direct effects of landscape properties and soil physical properties on community structure, i.e. increases in soil sand and heat loads are associated with increases in the size of and connectivity between basal gaps. Model B showed no such direct effects, rather landscape properties and soil properties exert indirect effects on community structure through their direct effects on community composition. Given the importance of community structure in explaining *B. tectorum* cover for this dataset, we selected Model B for making inferences.

Changes in community structure, i.e. increases in the spatial aggregation of bunchgrasses and increases in the size of and connectivity between basal gaps in perennial vegetation, exerted a strong positive total effect on *B. tectorum* cover (0.678). This total effect included both a strong direct effect (0.83) and, contrary to the *a priori* model, a strong indirect effect through a positive direct effect on safe sites as measured by bare soil cover (0.40).

Cattle grazing had a positive association with *B. tectorum* cover through three independent processes. 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. Thus, cattle grazing had three indirect effects on *B. tectorum* cover through its direct negative effects on bunchgrass abundance

(0.34), BSC abundance (0.29), and bunchgrass community composition (Axis 2) (0.22). There was no evidence that cattle grazing directly decreased or increased *B. tectorum* cover.

Landscape orientation exerted a strong positive total effect on *B. tectorum* cover (0.372) that consisted entirely of indirect effects through its negative direct effects on bunchgrass community composition (Axis 2), bunchgrass abundance, and BSC abundance. Soil physical properties exerted a strong positive total effect on *B. tectorum* cover (0.416) through a direct positive effect and an indirect effect through its direct effects on safe sites as measured by bare soil cover and bunchgrass community composition (Axes 2 and 3).

DISCUSSION

Patterns of Invasibility

Artemisia ecosystems within this portion of Oregon are characterized by pronounced gradients in ecosystem invasibility as measured by *B. tectorum* cover. These gradients likely exist across much of the *Artemisia* biome of the northern Great Basin because climate, soils, plant communities and livestock grazing management is similar throughout. These gradients demonstrate shifts in the resilience of sagebrush steppe communities to cattle grazing and resistance to *B. tectorum* invasions. Along these invasibility gradients, we identified three distinct community states separated by threshold shifts in community composition and structure, and to a lesser degree, abiotic factors consistent with state-and-transition succession (Bestelmeyer et al. 2009; Briske et al. 2009) and degradation models (Whisenant 1999) (Fig. 4.4B)

Conventional multivariate approaches provide support that these gradients were associated with increasing levels of cattle grazing, heat loads, and water stress.

The causal network of factors driving patterns of ecosystem invasibility

Our *a priori* multivariate model provides convincing evidence that a complex causal network of simultaneously operating factors and processes are driving resilience to cattle grazing and resistance to *B. tectorum* invasion in *Artemisia* ecosystems. Standardized total effects show the relative importance of different controlling factors and provide important insight for an early warning system of ecosystem resilience and resistance (Grace 2006; Grace and Keeley 2006). Total effects of variables driving *Artemisia* ecosystem invasibility in order of importance were: community structure, soil physical properties, safe sites (bare soil cover), landscape orientation, bunchgrass community composition, safe sites (BSC abundance), cattle grazing levels, and bunchgrass abundance.

Shifts in community structure characterized by increases in the spatial aggregation of perennial herbaceous vegetation and size of and connectivity of basal gaps between vegetation were the linchpin of ecosystem invasibility. This finding is consistent with the growing body of evidence in semi-arid and arid ecosystems around the world where increases in spatial aggregation of vegetation (Scheffer et al. 2001;

Scheffer and Carpenter 2003; Scheffer et al. 2009) and increases in the connectivity between gaps in native vegetation (Busso and Bonvissuto 2009; Okin et al. 2009) are associated with a loss of ecosystem resilience. This loss of resilience sets the stage for threshold, nearly irreversible shifts between community states (Briske et al. 2006; Bestelmeyer et al. 2009; Briske et al. 2009) and in the worst case scenario, catastrophic regime shifts (Scheffer and Carpenter 2003; Scheffer et al. 2009; Herrick et al. 2010). We provide evidence that increases in the size of and connectivity between basal gaps in perennial vegetation increases the susceptibility of *Artemisia* ecosystems to *B. tectorum* invasions (Herrick et al. 2005; Okin et al. 2009). Our findings also support the prediction by James et al. (2008 at p. 646) that “although the particular resource or combination of resources facilitating annual grass invasion may change depending on the timing and amount of water input and soil chemistry, *the main mechanism of invasion resistance likely depends on how species abundance is distributed in the plant community*.”

Artemisia ecosystems of the Great Basin are characterized by wide temporal variability in soil water and nutrients that peak in early spring and thereafter peak after pulse precipitation events during the spring and early summer (Miller et al. 1991; Huxman et al. 2004; Schwinning et al. 2004). *B. tectorum* is predominantly a winter annual but can germinate anytime between fall and spring (Mack and Pyke 1983). It has an early phenology characterized by rapid root and shoot growth in winter and early spring before native bunchgrasses commence their period of active growth (Harris and Wilson 1970), and high nutrient acquisition rates (MacKown et al. 2009; Vasquez et al. 2009; Blank 2010). These collective attributes probably allow *B. tectorum* to preempt and exploit pulses of resource availability in gaps between perennial vegetation.

The two environmental factors, landscape orientation and soil physical properties set the invasibility stage by determining the inherent resilience of *Artemisia* ecosystems to cattle grazing disturbance and resistance to *B. tectorum* invasion (Lonsdale 1999). The combined total effects of these two factors in our model were 0.79. All other things being equal and consistent with other studies, communities located on coarser-textured soils (Doescher et al. 1986; Link et al. 1994; Beatley 1996) or characterized by higher potential heat loads (Stewart and Hull 1949; Hulbert 1955; Klemmedson and Smith 1964; Hinds 1975) were inherently least resilient to cattle grazing and least resistant to *B. tectorum* invasion. These communities are characterized by higher levels of heat and water stress and lower productivity (Chapter 2; Passey et al. 1982; Davies et al. 2007). The inherent structure of these communities that consists of larger and more connected basal gaps and higher amounts of bare soil makes them especially vulnerable to cattle grazing and *B. tectorum* invasion.

Consistent with the findings of other studies, biotic resistance from resident bunchgrass and BSC communities played pivotal roles in limiting the magnitude of *B.*

tectorum invasion (Levine et al. 2004; Mitchell et al. 2006; Richardson and Pysek 2006; D'Antonio et al. 2009). Several studies have found a strong negative association between BSC community integrity and *B. tectorum* abundance (Kaltenecker 1997; Kaltenecker et al. 1999; Ponzetti et al. 2007; Ponzetti and McCune 2008) and showed that BSC communities reduce *B. tectorum* germination and establishment rates by impeding root penetration and growth (Kaltenecker et al. 1999; Serpe et al. 2006; Deines et al. 2007; Serpe et al. 2008). BSC communities likely reduced the availability of safe sites for *B. tectorum* establishment (Harper 1977; Fowler 1988). Water availability is the primary controlling factor of seedling establishment in these ecosystems (Schupp 1995; Chambers and Linnerooth 2001; Humphrey and Schupp 2004), and *B. tectorum* seedlings are vulnerable to desiccation (Mack and Pyke 1983; Mack and Pyke 1984).

Consistent with the theory of fluctuating resource availability (Davis et al. 2000), we found that bunchgrasses reduced the magnitude of *B. tectorum* invasions (Booth et al. 2003; Beckstead and Augspurger 2004; Humphrey and Schupp 2004; Chambers et al. 2007; Prevéy et al. 2010). Native bunchgrasses reduce water and nutrient availability and thus reduce invasibility (Booth et al. 2003; Beckstead and Augspurger 2004; Chambers et al. 2007; James et al. 2008). Our findings provide important insight into this mechanism. Nearly all of the biotic resistance effect was indirect through the strong direct effect of bunchgrass abundance and composition on community structure. Further, three species, *P. spicata*, *A. thurberianum,* and *P. secunda*, were 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 reflect their differing abilities to acquire resources at different soil depths (James et al. 2008) and seasons and thereby provide continuous interaction with *B. tectorum.*

By using SEM to statistically control for several potentially confounding factors (differences in soil properties, landscape orientation, biotic resistance, and community structure etc.), we were able to gain important new insights into the role of cattle grazing as a determinant of ecosystem resilience and resistance to *B. tectorum* invasion (Miller et al. 1994; Knick et al. 2010). We found no evidence that cattle grazing, even at the highest intensities near livestock watering developments, reduced *B. tectorum* abundance (non-significant pathway #1).

To the contrary, increasing intensity of cattle grazing and associated disturbances was associated with a decrease in ecosystem resilience and increase in the magnitude of *B. tectorum* invasions. Increasing intensity of cattle grazing decreased ecosystem resilience by reducing native bunchgrass abundance, shifting the composition of the bunchgrass community, and increasing the aggregation of bunchgrasses beneath *Artemisia* canopies. 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. *P. spicata* and *A. thurberianum* are highly sensitive to grazing (Blaisdell and Pechanec 1949; Ganskopp 1988). Although *P. secunda's* small stature allows it to avoid some grazing, it is highly sensitive if grazed (Mack and Thompson 1982). *E. elymoides* is the most grazing tolerant bunchgrass (Wright 1967; Jones 1998). In contrast, *B. tectorum* exhibits a collection of grazing avoidance and tolerance mechanisms that makes it extremely tolerant of even intensive grazing (Hempy-Mayer and Pyke 2009).

But more importantly, increasing intensity of cattle grazing was associated with a fundamental shift in the structure of the bunchgrass community and the structure of *Artemisia's* interactions with bunchgrasses (Chapter 1 & 2). At low levels of cattle grazing, *Artemisia* interactions with bunchgrasses were neutral or competitive (Chapter 1), bunchgrasses were spatially dispersed across the landscape, and the composition of the under-shrub, interspace, and site-level communities were similar (Chapter 2). *B. tectorum* cover in these resilient communities was low (Chapter 2). As cattle grazing levels increased, *Artemisia* interactions with bunchgrasses shifted to facilitative or neutral (Chapter 1); however, bunchgrasses remained spatially dispersed and the under-shrub, interspace, and site-level communities remained positively related to one another (Chapter 2). *Artemisia* “facultative” facilitation of bunchgrasses maintained community resilience: although bunchgrasses likely benefited from facilitation, they were not entirely dependent upon it for their continued persistence. *B. tectorum* cover in these resilient communities remained low (Chapter 2). At the highest cattle grazing levels, *Artemisia* interactions with bunchgrasses shifted to facilitative (Chapter 1), bunchgrasses became aggregated beneath *Artemisia* canopies, and the most grazing sensitive bunchgrasses, *P. spicata* and *A. thurberianum* became entirely dependent on facilitation for their continued persistence (Chapter 2). This "obligate" facilitation increased the size of and connectivity between basal gaps in perennial vegetation and resource availability within those gaps. These gaps created the window of opportunity for *B. tectorum* invasion (Davis et al. 2000).

Furthermore, increasing cattle grazing intensity was associated with a decrease in BSC community abundance, an increase in bare soil cover, and decrease in soil aggregate stability. The trends for these indicators strongly suggest that cattle grazing and related disturbances may be altering soil resilience to erosion and the hydrological cycle in *Artemisia* ecosystems (Clausnitzer et al. 2003; Herrick et al. 2005).

Management Implications

These collective findings raise serious red flags regarding proposals to use cattle grazing to control *B. tectorum* in *Artemisia* ecosystems where remnant bunchgrass communities persist (Miller et al. 1994; Mosely 1996; Olson 1999). In contrast, numerous studies have recommended reducing cumulative livestock grazing levels as one of the most effective means of passively restoring *Artemisia* ecosystem resilience (McIver and Starr 2001; Suring et al. 2005; Wisdom and Chambers 2009; Pyke 2010). Our findings suggest that shifts in the size of and connectivity between basal gaps in perennial vegetation may serve as an important early warning indicator of when cattle grazing or other stressors are compromising *Artemisia* ecosystem resilience and resistance. Future research should focus on gathering information concerning the distribution of basal gaps for reference sites of different ecological sites.

Inherent differences in invasibility driven predominately by environmental factors mean that *Artemisia* ecosystems consist of a mosaic of communities that differ substantially in their resilience to cattle grazing levels they can withstand before crossing a threshold to an alternative state (Bestelmeyer et al. 2009; Briske et al. 2009). If the management goal is sustaining and restoring ecosystem resilience, our findings suggest that cumulative cattle grazing levels must match levels that maintain resilience and resistance and prevent the most susceptible communities within a grazing management unit from crossing these thresholds (Bestelmeyer et al. 2009). Otherwise, the resilience of more vulnerable communities will likely be compromised and *B. tectorum* will dominate them. Once *B. tectorum* begins to expand in gaps between perennial bunchgrasses, these communities will become at risk for fires

(Knick et al. 2010) and may serve as foci for subsequent spread to surrounding communities.

Unfortunately, our findings suggest that passive restoration efforts are unlikely to restore ecosystem resilience in many invaded communities. Consistent with recent predictions (Suring et al. 2005), 45% of our study plots had crossed degradation thresholds and had understory communities dominated by *B. tectorum* with remnant native bunchgrasses persisting beneath *Artemisia* canopies. The next fire will likely eliminate these remnant native bunchgrasses. Once these thresholds are crossed, restoring ecosystem resilience requires both active restoration, i.e. vegetation manipulation, and reducing stressors driving degradation (Whisenant 1999; Pyke 2010).

If the management goal is to restore ecosystem resilience, our findings suggest that such efforts should focus on restoring biotic resistance and preemption of resources provided by the native BSC and bunchgrasses within the interspaces between *Artemisia* individuals. To maximize this preemption of resources, managers should focus on three priorities. First, maintain high overall bunchgrass abundance/dominance and community structure characterized by spatially dispersed bunchgrasses in interspaces and small basal gaps between such individuals to capture large amounts of otherwise available resources in space (Grime 1987; Grime 1987; Hooper and Vitousek 1997; Crawley et al. 1999; James et al. 2008). Second, maintain a diverse assemblage of bunchgrass species with different spatial and temporal patterns of resource use to capture available resources at different soil depths and times (Tillman et al. 1997; Naeem et al. 2000; Fargione and Tilman 2005; James et al. 2008). Third, maintain a BSC community to limit safe sites for *B. tectorum* establishment in gaps between perennial native vegetation.

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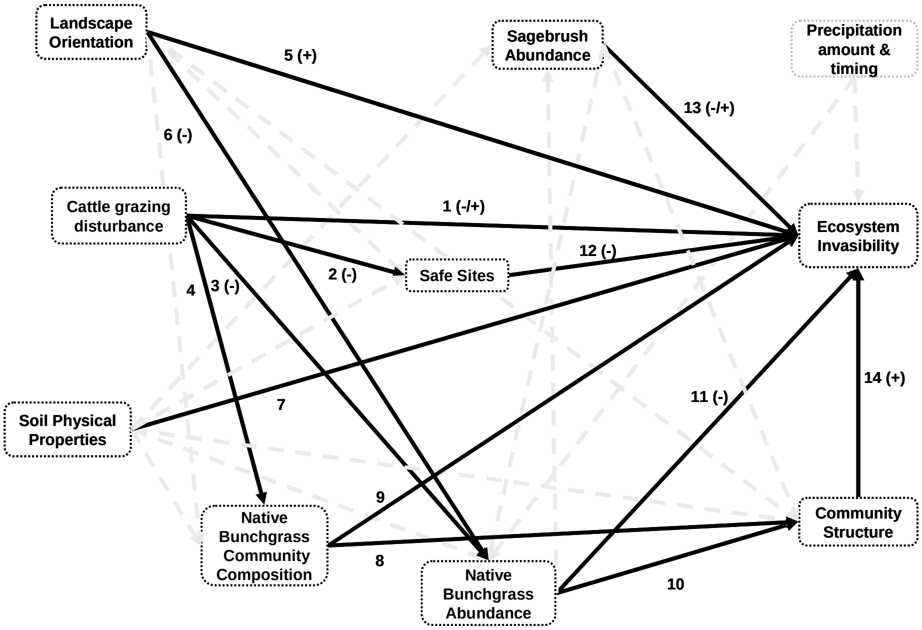

Figure 4.1 Conceptual model depicting the *a priori* multivariate model of *Artemisia* ecosystem invasibility. Dotted-line boxes represent conceptual variables predicted to influence the susceptibility of these communities to invasion. Black solid arrows depict predicted underlying causal mechanisms or processes operating between two variables that we were specifically interested in examining (paths of interest). Gray dotted arrows depict potential processes we wanted to control for during the modeling process because such variables and processes may influence community composition and structure (control paths). Effects of a variable can be direct or indirect. For example, cattle grazing effects on invasibility can be direct (path #1) or indirect because of grazing induced changes in “safe sites” for plant establishment (2 → 12), native community composition (4 → 9, 8 → 14) or bunchgrass abundance (3 → 11, 10 → 14). Table 1 provides a description of the hypothesized causal process depicted by each path of interest.

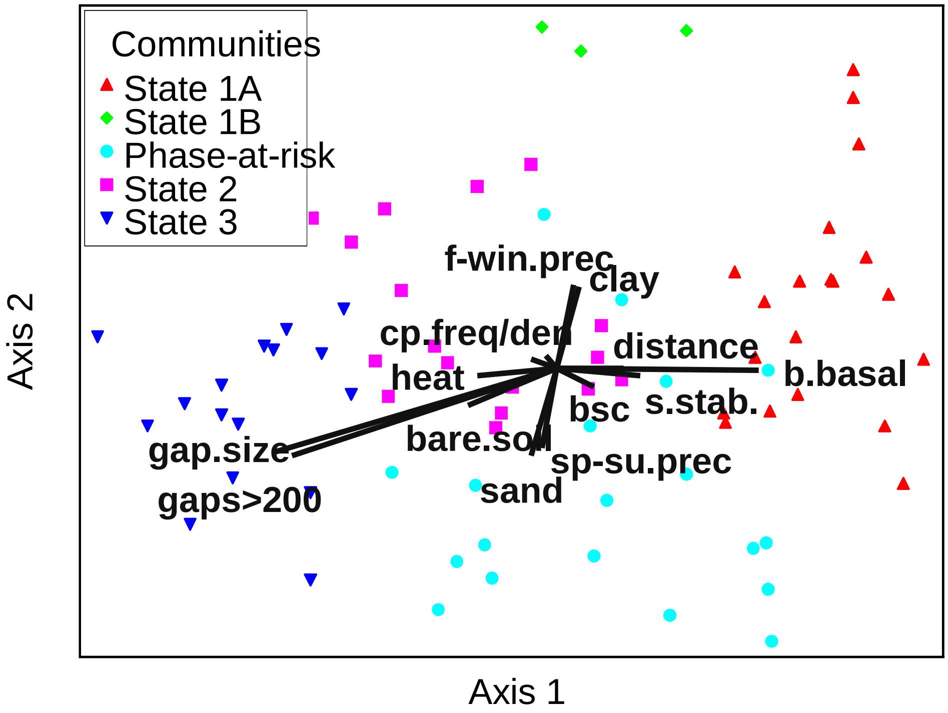

Figure 4.2 Ordination of plots in community composition space. NMS ordination with final stress of 9.92; final instability of < 0.01; Monte Carlo test p-value < 0.05. The two axes represent complex gradients in herbaceous community composition. Vectors show the strength and direction of correlations between the environmental variables and the axes. Only variables with a significant correlation (> 0.20) are shown. Different plot symbols show the groups derived from the cluster analysis that differ in composition and environmental factors. State 1A and 1B communities have understories dominated by native bunchgrasses; phase-at-risk communities are co-dominated by bunchgrasses and non-natives, and State 2 and 3 communities are dominated by non-native species. Descriptions of the vector variables are in Table 2.

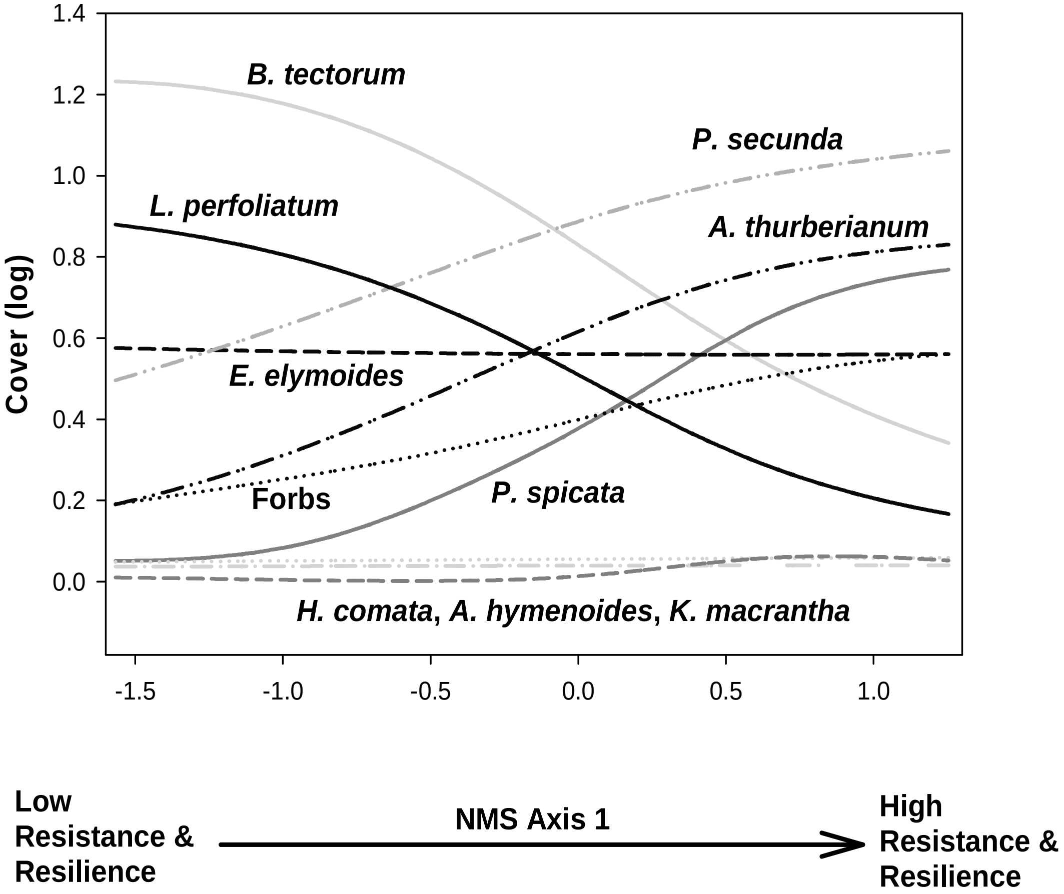

Figure 4.3A NPMR response curves showing the relationship between species cover and the gradient of increasing resistance and resilience represented by NMS ordination axis 1. Axis 1 is a gradient of decreasing cattle grazing disturbance and heat stress.

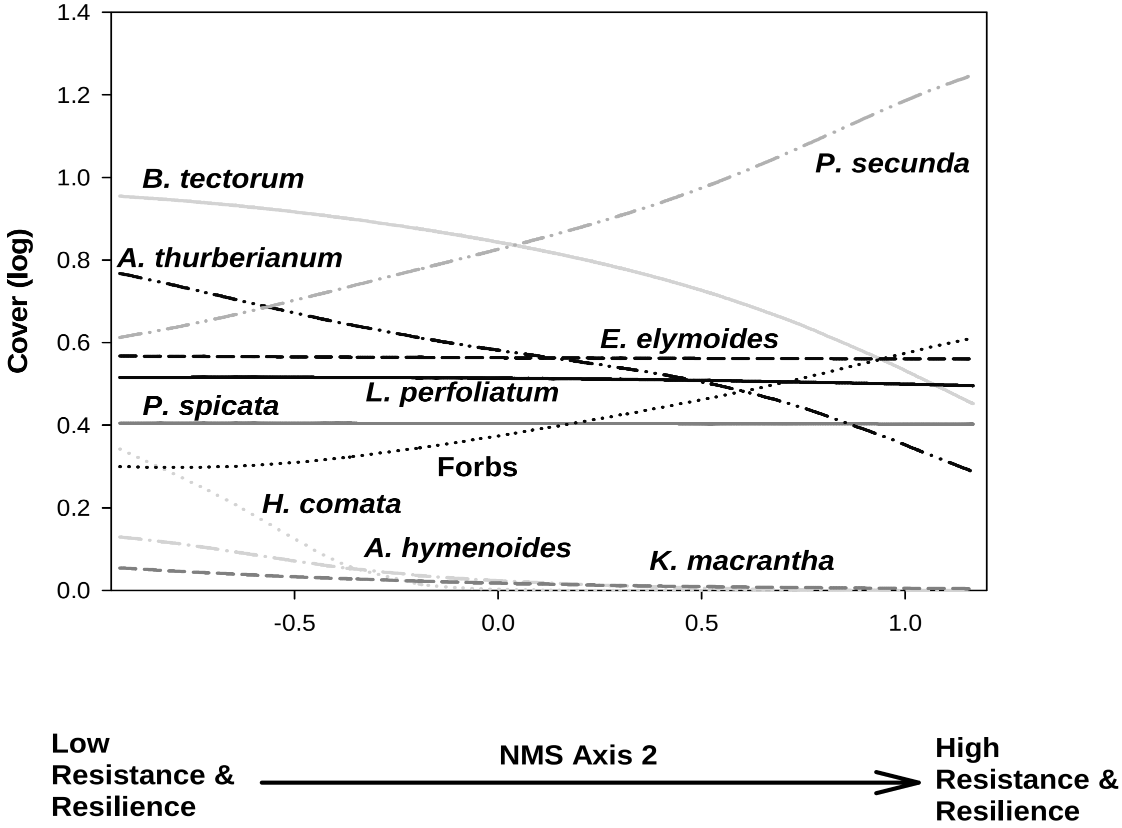

Figure 4.3B NPMR response curves showing the relationship between species cover and the gradient of increasing resistance and resilience represented by NMS ordination axis 2. Axis 2 is a gradient of decreasing water stress.
]

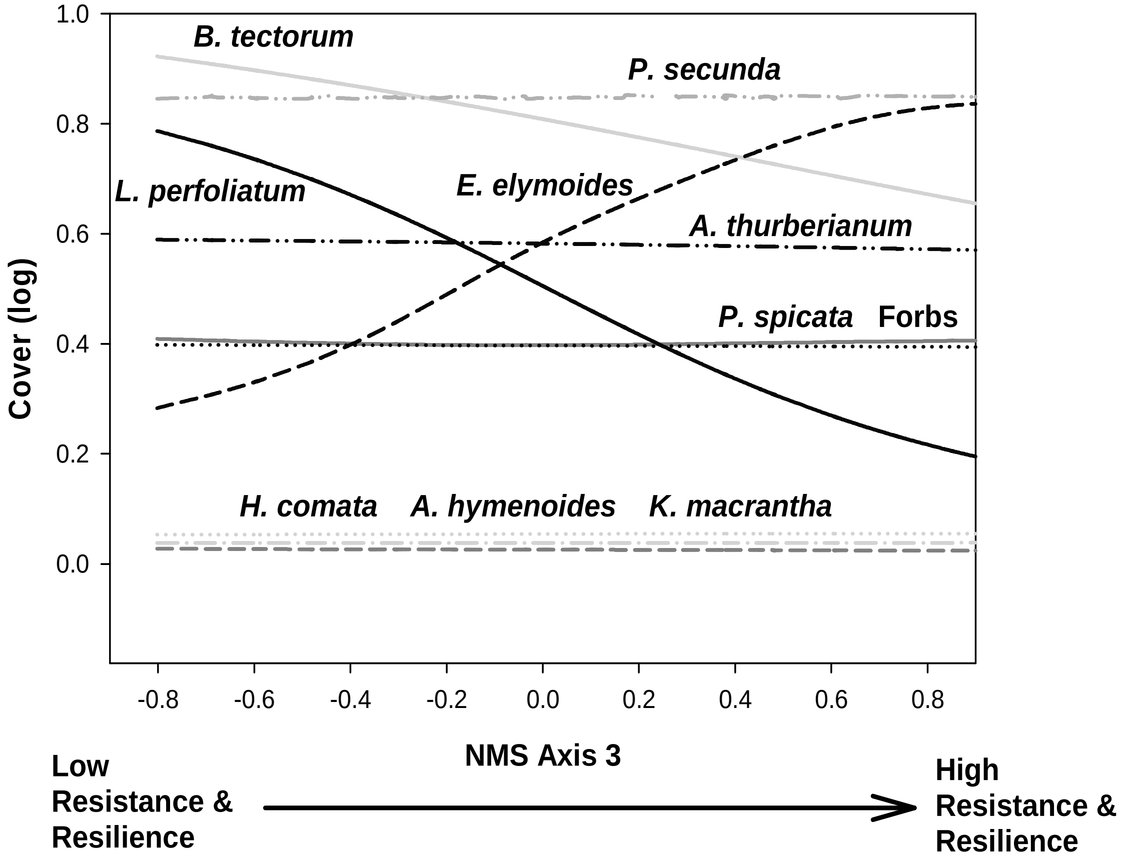

Figure 4.3C NPMR response curves showing the relationship between species cover and the gradient of increasing resistance and resilience represented by NMS ordination axis 3. Axis 3 is a gradient of decreasing cattle grazing disturbance.

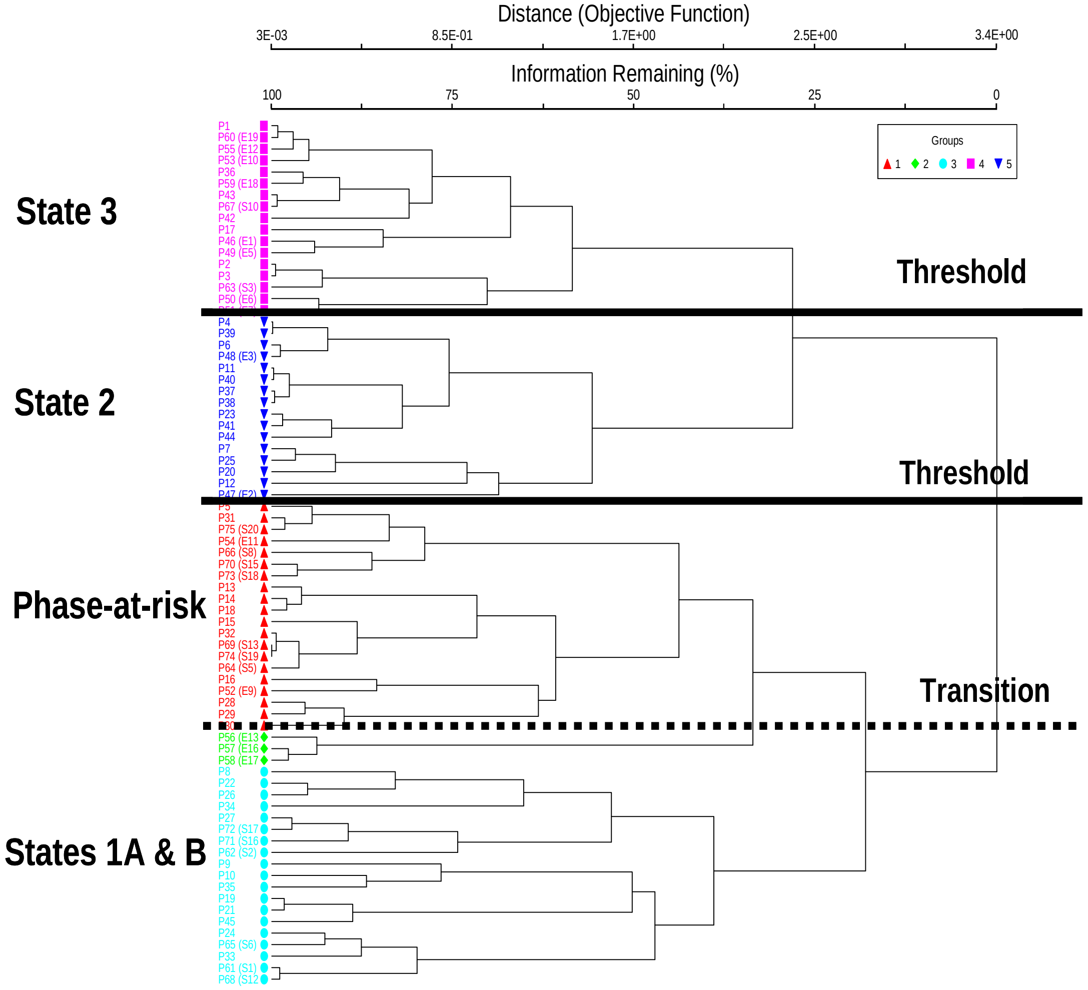

Figure 4.4A Hierarchical cluster analysis dendrogram. State 1A and 1B communities have understories dominated by native bunchgrasses; phase-at-risk communities are co-dominated by bunchgrasses and non-natives, and State 2 and 3 communities are dominated by non-native species.

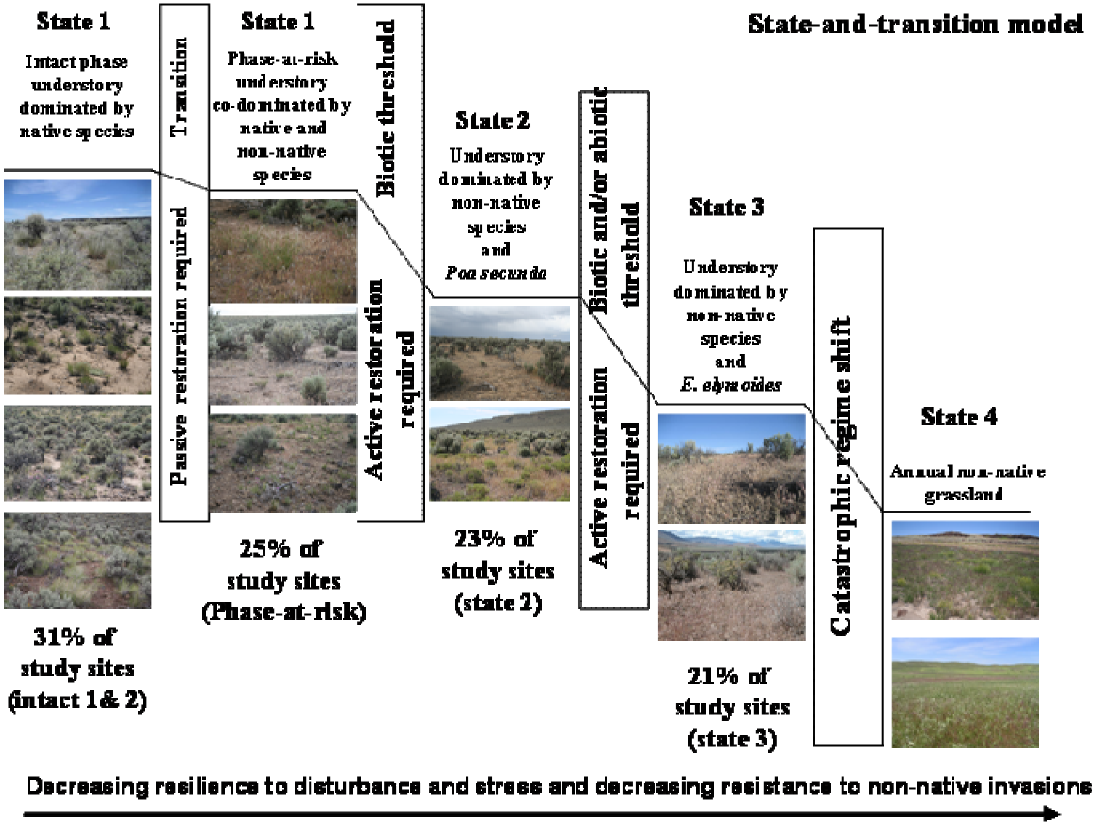

Figure 4.4B Model of *Artemisia* ecosystem invasibility to *B. tectorum* invasion incorporating state-and-transition models of succession (Briske et al. 2009), degradation (Whisenant 1999), restoration (Pyke 2010), and resilience (Holling 1973; Gunderson 2000; Folke et al. 2004).

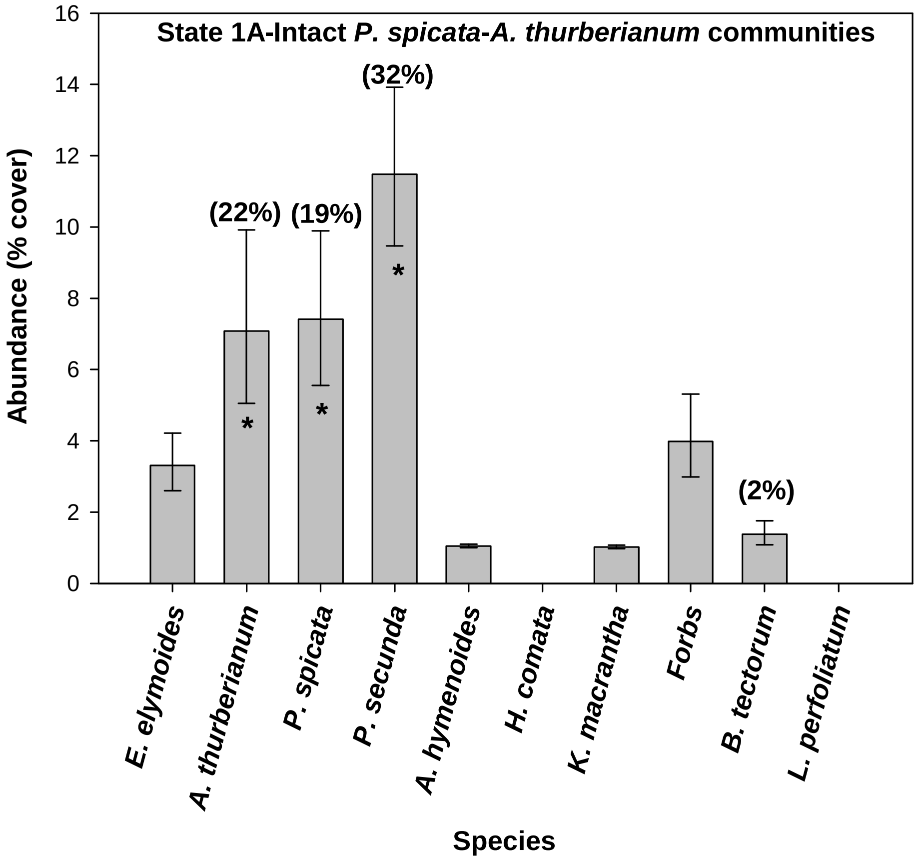

Figure 4.5A Community composition of the five groups derived from cluster analysis: State 1A communities. * denotes the species with highest three Indicator Values for the group from ISA. Reported values are back-transformed means and error bars are 90% Bonferroni-adjusted confidence intervals. (%) is the relative abundance of the species calculated as the proportion of the total herbaceous cover of the group.

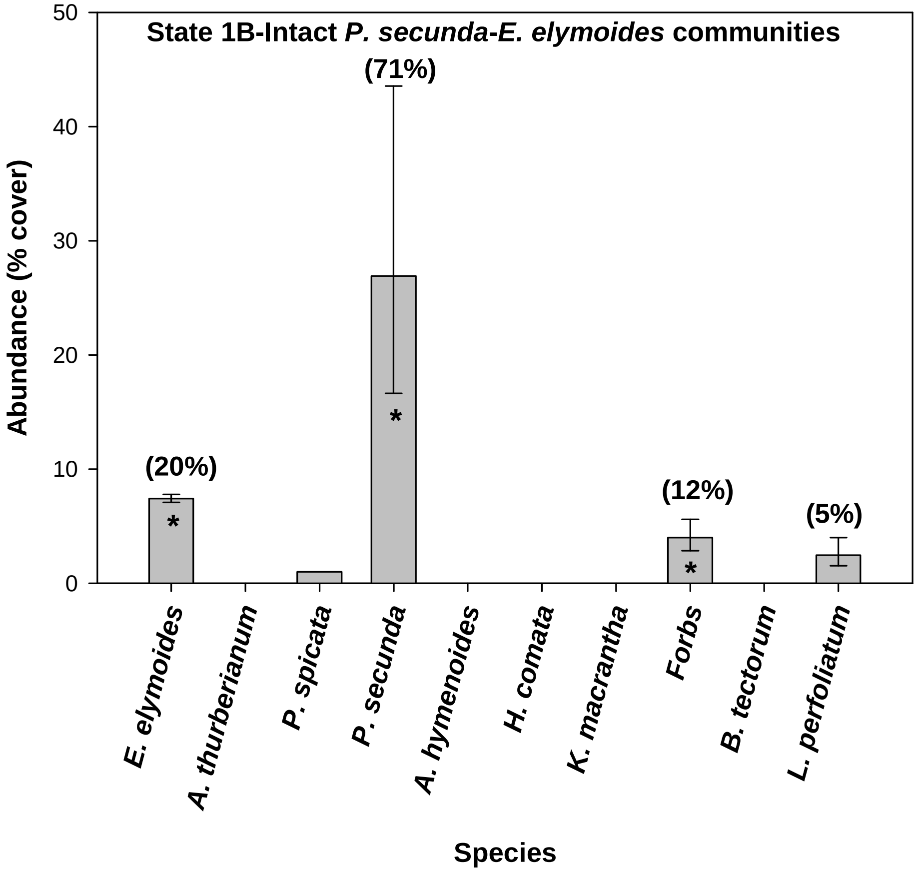

Figure 4.5B Community composition of the five groups derived from cluster analysis: State 1B communities. * denotes the species with highest three Indicator Values for the group from ISA. Reported values are back-transformed means and error bars are 90% Bonferroni-adjusted confidence intervals. (%) is the relative abundance of the species calculated as the proportion of the total herbaceous cover of the group.

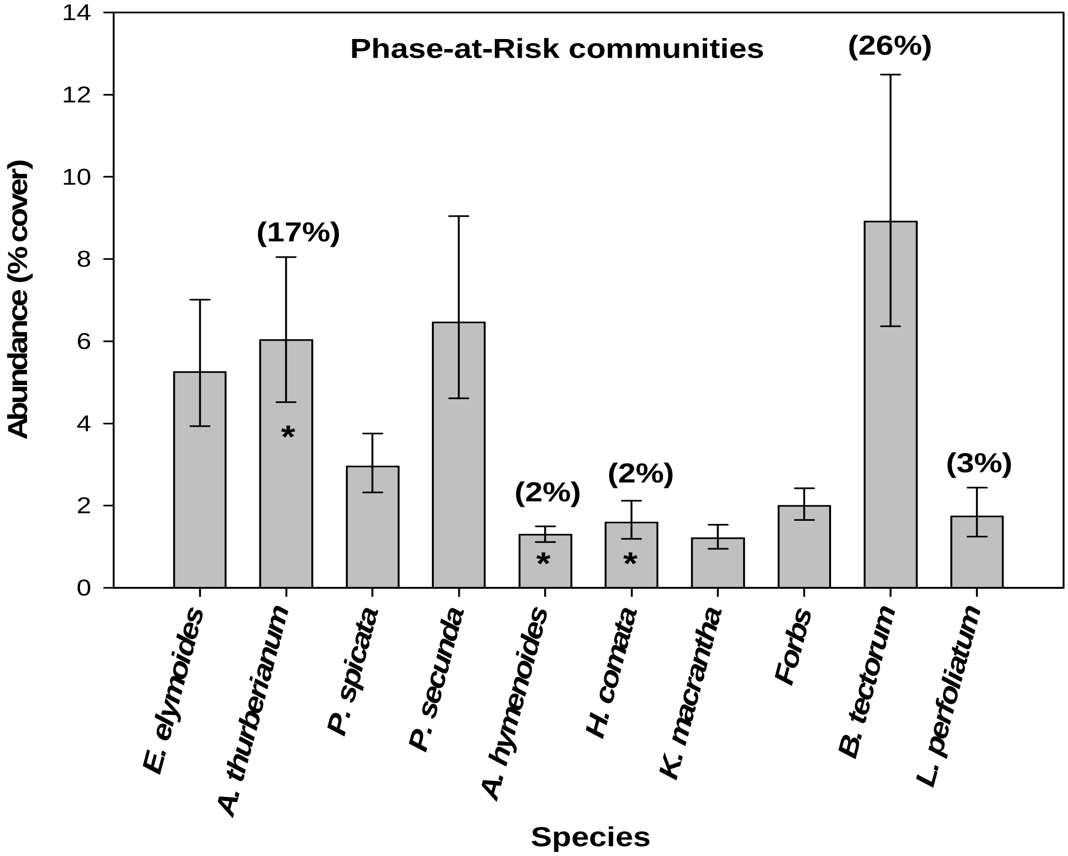

Figure 4.5C Community composition of the five groups derived from cluster analysis: Phase-at-Risk communities. * denotes the species with highest three Indicator Values for the group from ISA. Reported values are back-transformed means and error bars are 90% Bonferroni-adjusted confidence intervals. (%) is the relative abundance of the species calculated as the proportion of the total herbaceous cover of the group.

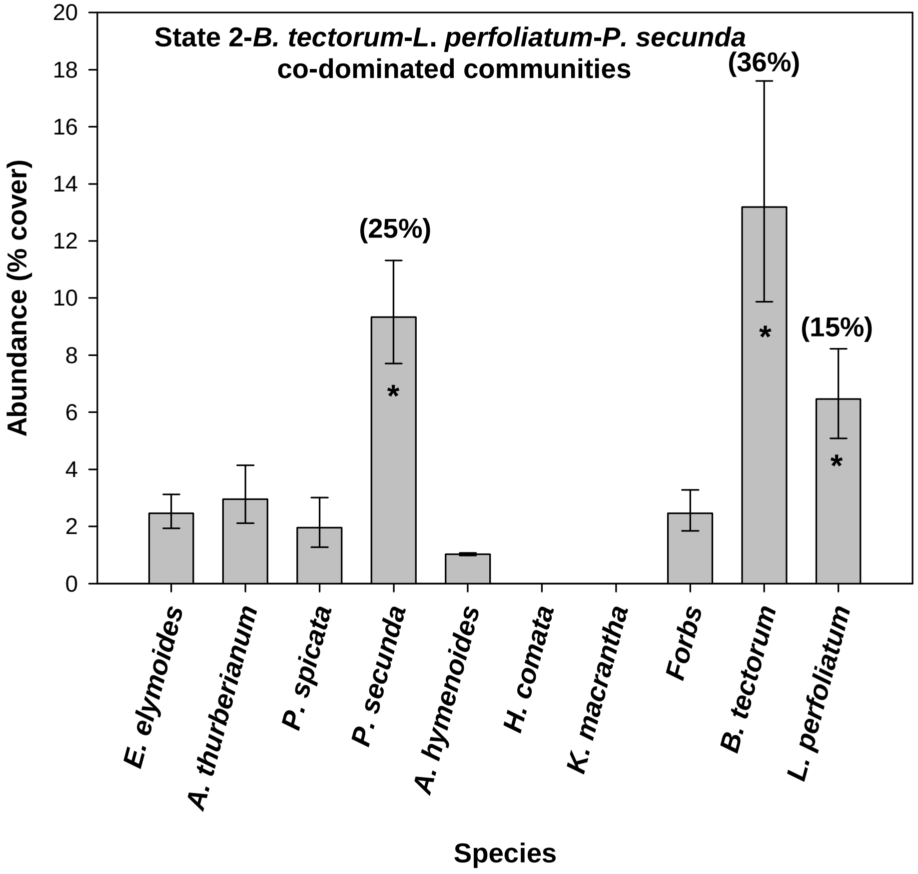

Figure 4.5D Community composition of the five groups derived from cluster analysis: State 2 communities. * denotes the species with highest three Indicator Values for the group from ISA. Reported values are back-transformed means and error bars are 90% Bonferroni-adjusted confidence intervals. (%) is the relative abundance of the species calculated as the proportion of the total herbaceous cover of the group.

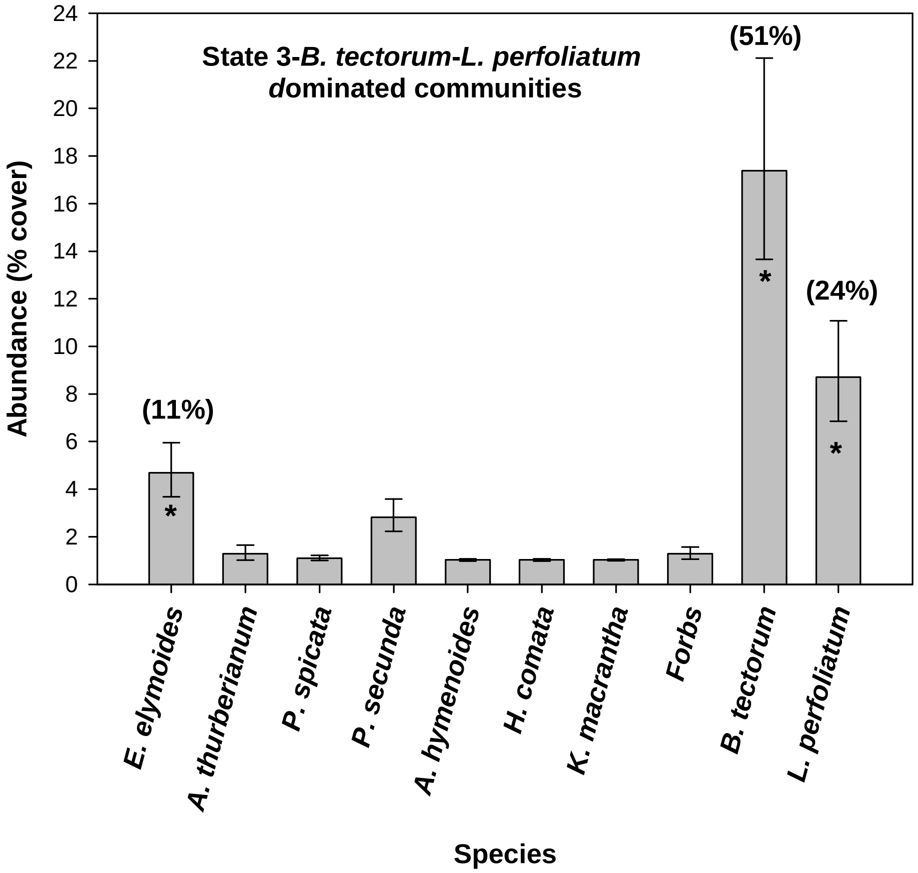

Figure 4.5E Community composition of the five groups derived from cluster analysis: State 3 communities. * denotes the species with highest three Indicator Values for the group from ISA. Reported values are back-transformed means and error bars are 90% Bonferroni-adjusted confidence intervals. (%) is the relative abundance of the species calculated as the proportion of the total herbaceous cover of the group.

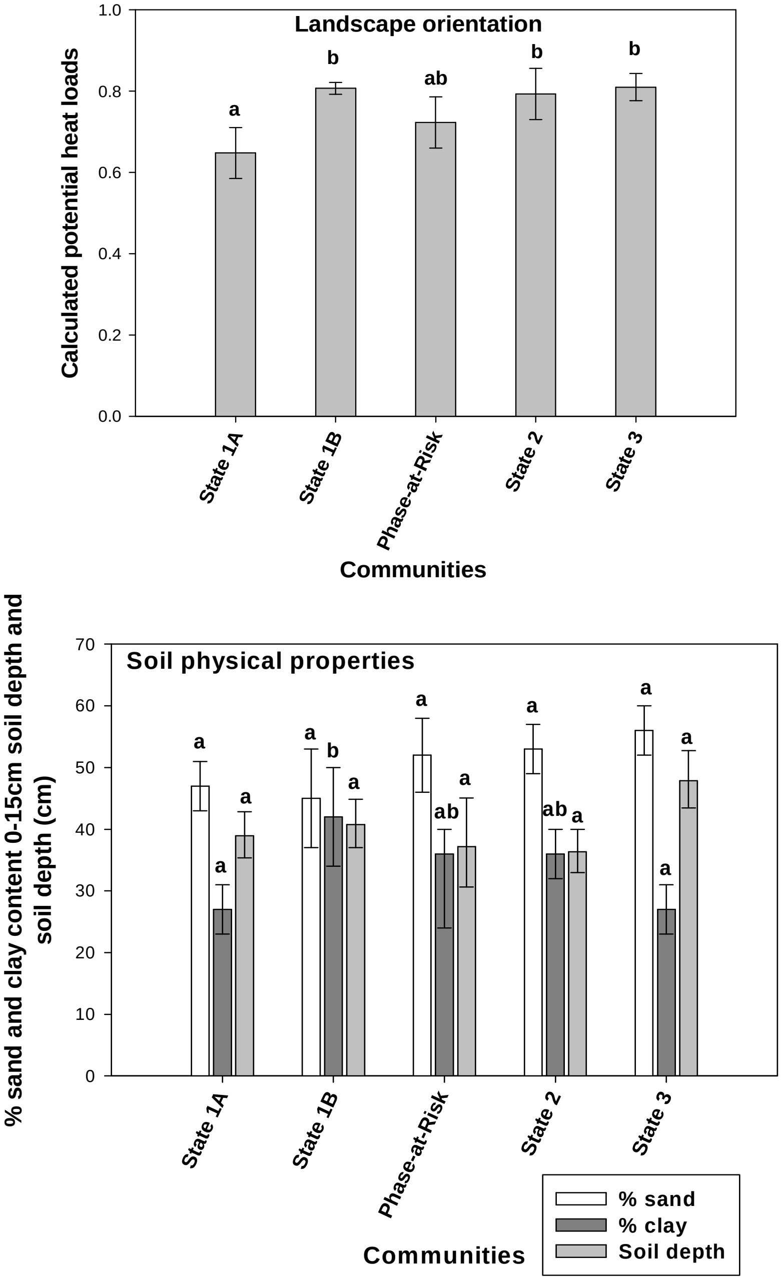

Figure 4.6A Differences in heat stress and soil properties between the five groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different lower case letters above the bars indicate significant differences between the groups ($\alpha = 0.10$).

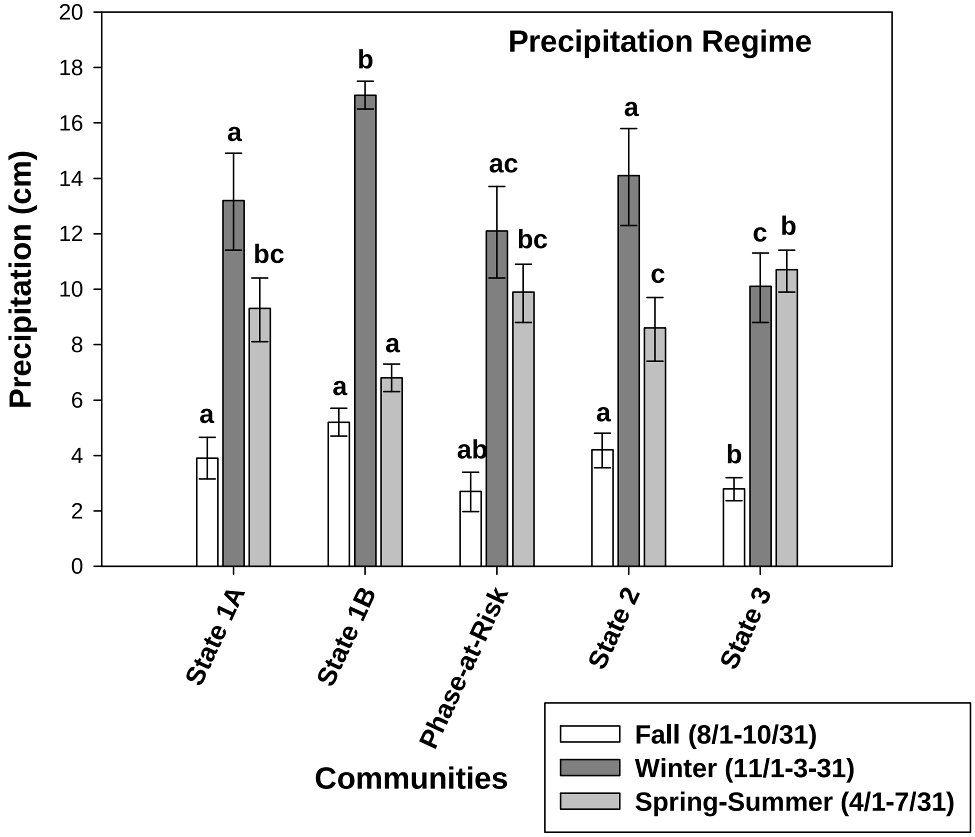

Figure 4.6B Differences in the amount and timing of precipitation between the five groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different lower case letters above the bars indicate significant differences between the groups (α = 0.10).

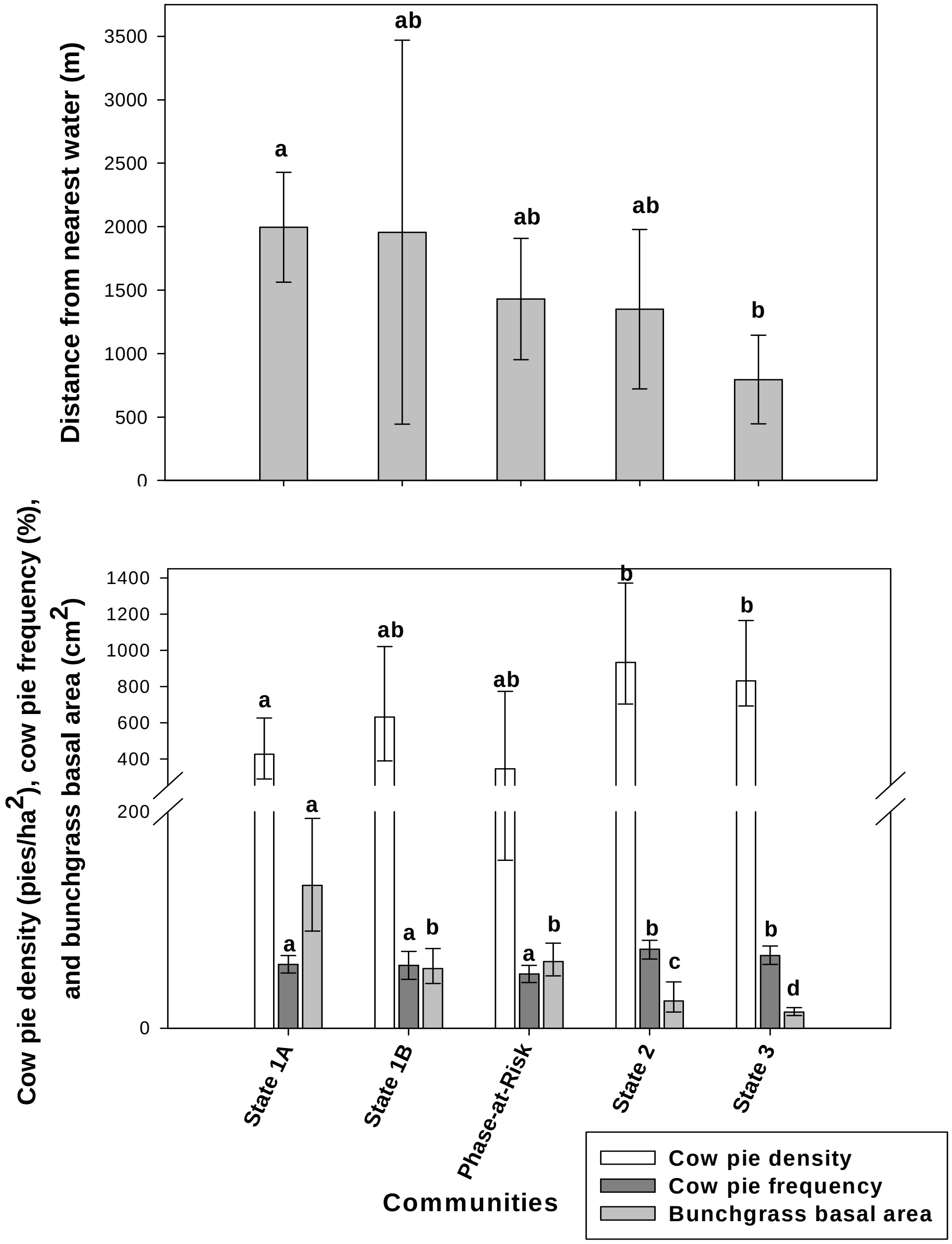

Figure 4.6C Differences in cattle grazing disturbance levels between the five groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different lower case letters above the bars indicate significant differences between the groups (α = 0.10).

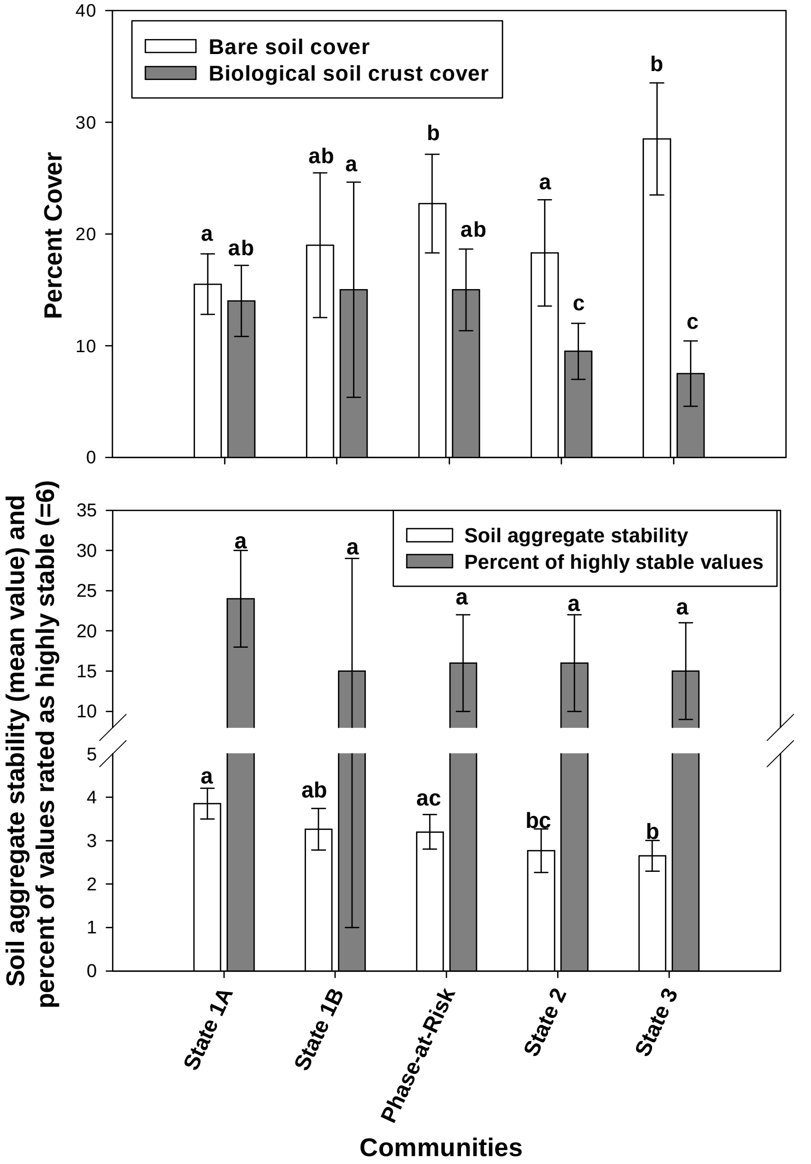

Figure 4.6D Differences in soil resilience between the five groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different lower case letters above the bars indicate significant differences between the groups (α = 0.10).

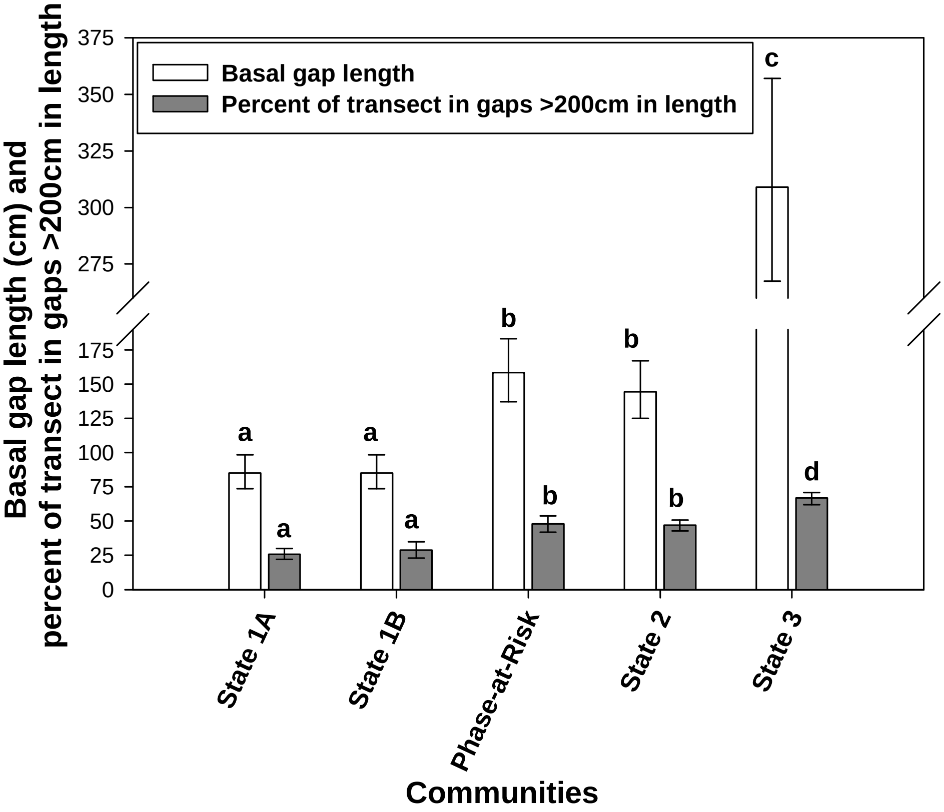

Figure 4.6E Differences in the size of and connectivity between basal gaps in perennial vegetation between the five groups identified by cluster analysis. Error bars represent Bonferroni-adjusted 90% confidence intervals. Different lower case letters above the bars indicate significant differences between the groups (α = 0.10).

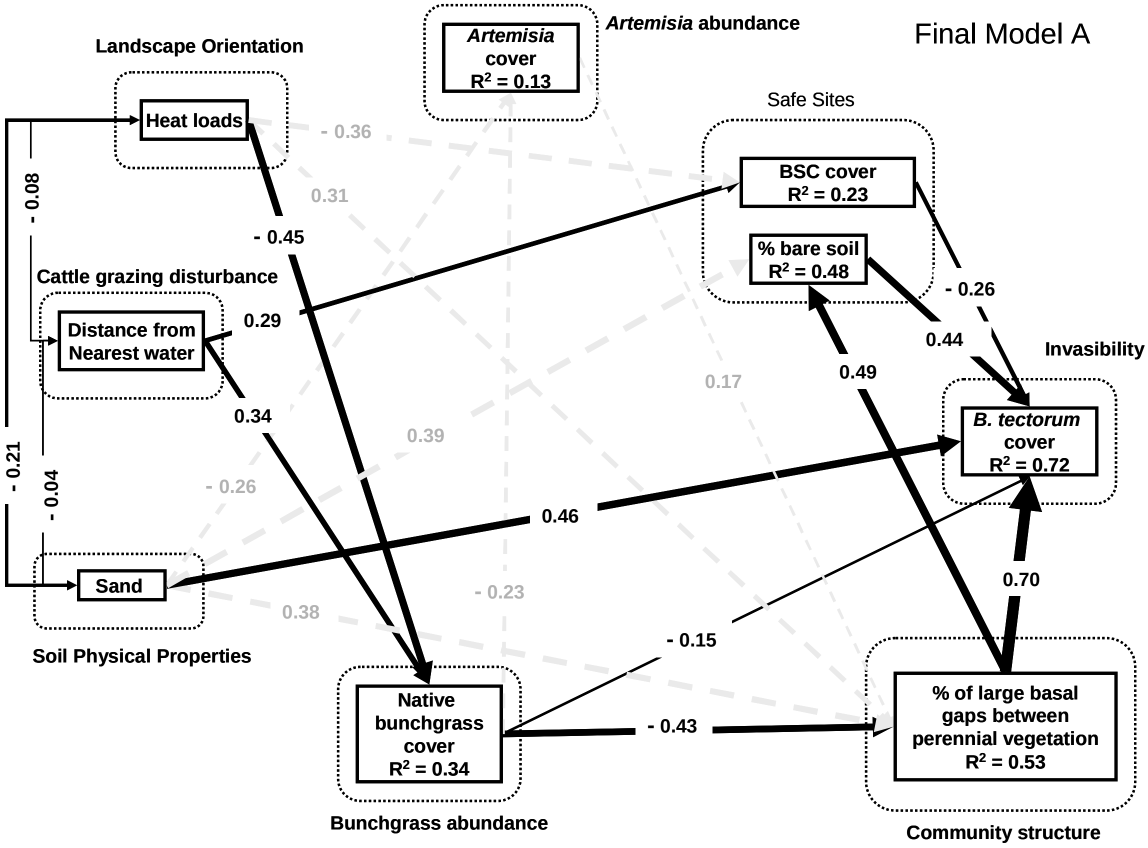

Figure 4.7 Model A Final Inferential Model of the susceptibility of *Artemisia* ecosystems to *B. tectorum* invasion. Single-headed arrows indicate significant causal effects of one variable on another (α= 0.05). Double-headed arrows indicate significant correlations between variables. The relative importance or strength of a given causal effect is indicated by the thickness of the arrow and the standardized path coefficient. Because distance from water is inversely related to cattle grazing intensity (i.e. cattle grazing intensity increases with decreasing distance to water), positive path coefficients indicate an inverse relationship between cattle grazing intensity and the other variable (i.e. increasing cattle grazing intensity decreases bunchgrass abundance). R2 depict the proportion of variation of each endogenous (response) variable explained by the model. The dotted boxes depict the conceptual variables of the meta-SEM (Fig. 1).

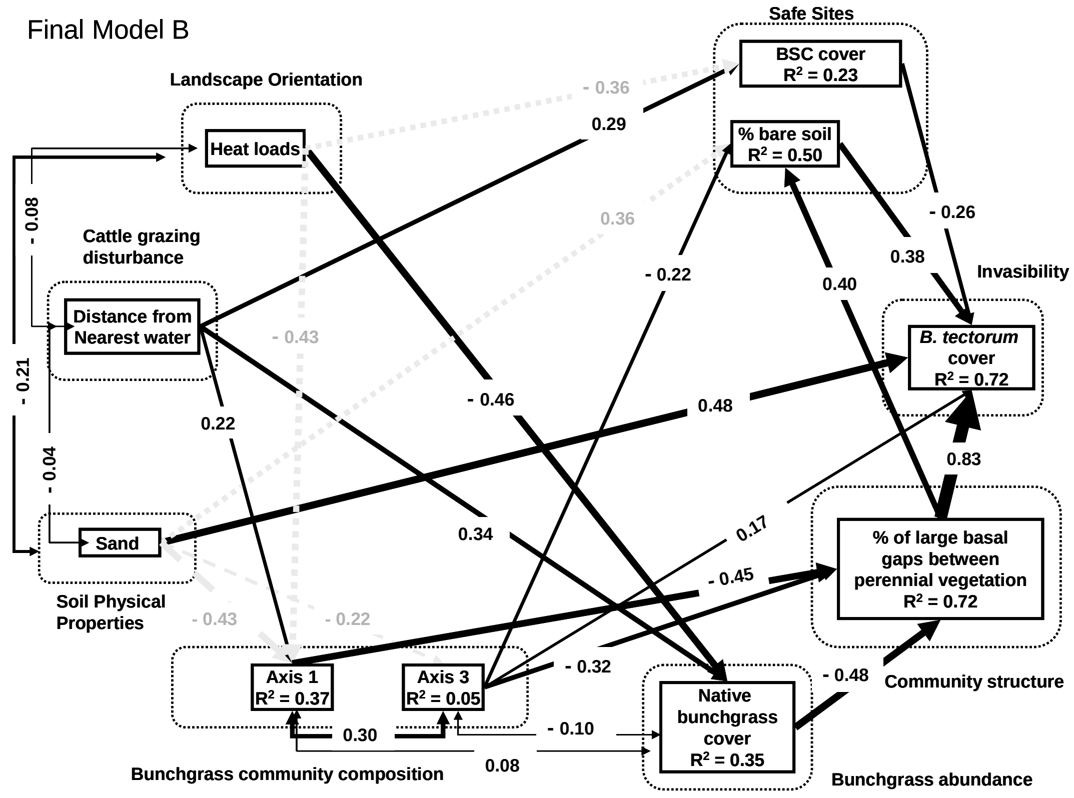

Figure 4.8 Model B Final Inferential Model of the susceptibility of *Artemisia* ecosystems to *B. tectorum* invasion. Single-headed arrows indicate significant causal effects of one variable on another (α= 0.05). Double-headed arrows indicate significant correlations between variables. The relative importance or strength of a given causal effect is indicated by the thickness of the arrow and the standardized path coefficient. Because distance from water is inversely related to cattle grazing intensity (i.e. cattle grazing intensity increases with decreasing distance to water), positive path coefficients and correlations indicate an inverse relationship between cattle grazing intensity and the variable (i.e. increasing cattle grazing intensity decreases bunchgrass abundance). R2 depict the proportion of variation of each endogenous (response) variable explained by the model. The dotted boxes depict the conceptual variables of the meta-SEM (Fig. 1)

Table 4.1 Descriptions of processes and associated causal mechanisms predicted to control ecosystem invasibility. The numbers in the “Path” column are the same as those next to the arrows in Figure 1, the model of community invasibility.

Path	Description	Potential causal mechanism or process
1	Cattle grazing direct effects on invasibility	Cattle grazing may directly decrease invasibility by reducing *B. tectorum* abundance (Daubenmire 1940; Klemmedson and Smith 1964; Mack and Pyke 1984; Pyke 1986; Pyke 1987; Tausch et al. 1994; Mosely 1996). Alternatively, cattle may directly increase invasibility by dispersing seeds and increasing propagule pressure (De Clerck-Floate 1997; Schiffman 1997; Brown and Carter 1998; Hempy-Mayer and Pyke 2009).
2	Cattle trampling effects on biological soil crust (BSC) abundance	Cattle trampling decreases BSC abundance, and thereby decreases biotic resistance to invasion (Anderson et al. 1982; Anderson et al. 1982; Brotherson et al. 1983; Eckert et al. 1986; Johansen 1986; Beymer and Klopatek 1992; Belnap et al. 2001; Ponzetti et al. 2007).
3	Cattle grazing effects on native bunchgrass abundance	Cattle grazing decreases resident bunchgrass abundance and the competitive ability of individual bunchgrasses (Miller et al. 1994; Briske and Richards 1995).

Table 4.1 (Cont.) Descriptions of processes and associated causal mechanisms predicted to control ecosystem invasibility

Path	Description	Potential causal mechanism or process
4	Cattle grazing effects on native bunchgrass community composition	Cattle grazing alters composition of native bunchgrass communities by favoring species with more grazing resistance or avoidance life history strategies (Archer and Pyke 1991; Pyke and Archer 1991; Miller et al. 1994; Briske and Richards 1995).
5	Landscape orientation direct effects on invasibility	Higher heat loads and spring insolation of south-facing slopes (Hinds 1975) and flat terrain (Monsen 1994) increase invasibility (Stewart and Hull 1949; Hulbert 1955; Klemmedson and Smith 1964; Chambers et al. 2007).
6	Landscape orientation effects on bunchgrass abundance	Lower heat loads and evapo-transpiration rates of north-facing slopes increase bunchgrass productivity (Passey et al. 1982; Jensen 1990; Davies et al. 2007).
7	Soil physical properties direct effects on invasibility	Deeper, coarser-textured soils increase invasibility (Doescher et al. 1986; Link et al. 1994; Beatley 1996).

Table 4.1 (Cont.) Descriptions of processes and associated causal mechanisms predicted to control ecosystem invasibility

Path	Description	Potential causal mechanism or process
8	Bunchgrass community composition effects on community structure	Changes in composition of bunchgrass communities influence community structure because species have different life forms, life history strategies, and patterns of resource use (Grime 1977; Passey et al. 1982; James et al. 2008).
9	Bunchgrass community composition direct effects on invasibility	Changes in bunchgrass community composition influence invasibility because species have different competitive abilities (Goldberg and Barton 1992) and patterns of resource use (James et al. 2008).
10	Bunchgrass abundance effects on community structure	Bunchgrass abundance is inversely related to the size of and connectivity between gaps in perennial vegetation and aggregation of vegetation into patches and thereby alters the spatial arrangement or structure of communities (Herrick et al. 2005; Okin et al. 2009)
11	Bunchgrass abundance effects on invasibility	Native bunchgrass abundance is inversely related to invasibility because greater abundance increases biotic resistance, which decreases resource (water and nutrients) availability and decreases invasibility (Davis et al. 2000; Beckstead and Augspurger 2004; Humphrey and Schupp 2004; Chambers et al. 2007; Prevéy et al. 2010).

Table 4.1 (Cont.) Descriptions of processes and associated causal mechanisms predicted to control ecosystem invasibility

Path	Description	Potential causal mechanism or process
12	Safe site effects on invasibility	Safe sites are positively related to invasibility because increases in safe sites for *B. tectorum* establishment increase invasibility (Harper 1977; Fowler 1988).
13	Sagebrush abundance direct effects on invasibility	Sagebrush abundance may increase invasibility if facilitation increases *B. tectorum* abundance (Griffith 2010) but may decrease invasibility if competition decreases its abundance (Reichenberger and Pyke 1990).
14	Community structure effects on invasibility	Shifts in community structure associated with increases in the size of and connectivity between gaps in perennial vegetation (aggregation of native herbaceous vegetation) are positively related to invasibility because such shifts decrease resilience (Scheffer et al. 2001; Okin et al. 2009; Scheffer et al. 2009) and increase resource availability (Herrick et al. 2005) (Lonsdale 1999; Davis et al. 2000; James et al. 2008; Okin et al. 2009).

Table 4.2 Relationships between environmental variables and NMS ordination axes

Environmental Variables	Pearson correlations with NMS ordination			Abbreviation	Units	Min. *	Max.
	Axis 1	Axis 2	Axis 3				
Landscape orientation							
potential heat loads ***	**-0.44**	-0.13	-0.12	heat	n/a	0.32	0.95
Cattle grazing disturbance							
Distance from nearest water source	**0.41**	0	0.13	distance	m	100	3560
Cow pie density	**-0.35**	0.14	**-0.3**	cp.den	cow pies/ha	0	3467
Cow pie frequency	**-0.36**	0.18	**-0.27**	cp.freq	% of transects	0	100
Deep-rooted bunchgrass basal area	**0.71**	-0.08	**0.31**	b.basal	cm2	6	331
Soil physical properties							
Sand content 0-15cm soil depth	-0.25	**-0.46**	**-0.25**	sand	%	33	80
Clay content 0-15cm soil depth	0.23	**0.44**	0.19	clay	%	14	53
Soil depth	-0.19	-0.11	0.13	depth	cm	23	120
Precipitation timing and amount							
Fall precipitation (8/1-10/31)	0.19	**0.41**	0.13	f.prec	cm	2.2	5.8
Winter precipitation (11/1-3/31)	0.19	**0.45**	0.13	win.prec	cm	9	17
Spring-summer precipitation (4/1-7/31)	-0.19	**-0.44**	-0.1	sp-su.prec	cm	6	12
Soil Resilience-Resistance							
Mean surface aggregate stability	**0.45**	-0.13	0.15	s.stab	values b/t 1-6	1.5	5.2
% of aggregate stability values rated as highly stable	**0.3**	-0.19	0.04	h.stab	%	0	57
bare soil cover	**-0.47**	**-0.3**	0.18	bare.soil	%	3	53
biological soil crust cover	**0.35**	-0.05	**0.3**	bsc	%	0	39
Community Structure							
Mean basal gap length between perennial veg.	**-0.83**	**-0.45**	-0.1	gap.size	cm	55	473
% of transects covered by basal gaps >200cm	**-0.81**	**-0.46**	-0.09	gaps>200	%	0	83

* Range of values across 75 study sites

** Moderate or strong corrlelations with the axes are in bold

*** Final indicator variables in SEM are in bold

Table 4.3 Relationships between herbaceous species community composition (cover) and NMS ordination axes

	Pearson correlations with NMS ordination axes *			Relative importance of the axes scores as predictors in NPMR model with all three as predictors					
Species	Axis 1	Axis 2	Axis 3	Sensitivity to axis 1	Sensitivity to axis 2	Sensitivity to axis 3	xR2 **	Neighborhood Size	p-value
E. elymoides	-0.04	-0.04	**0.79**	0.53	0.9	1.3	0.71	16.3	0.004
P. secunda	**0.64**	**0.66**	0.05	0.63	0.66	0.22	0.61	17.1	0.004
A. thurberianum	**0.67**	**-0.44**	-0.1	0.87	0.54	0.18	0.68	17.1	0.004
P. spicata	**0.73**	-0.02	-0.02	1.02	0.2	0.12	0.54	15.5	0.004
A. hymenoides	0.09	**-0.43**	0.02	0.04	1.12	0.03	0.15	28.4	0.008
H. comata	0.09	**-0.5**	0.03	0.02	1.05	0.02	0.34	20.22	0.004
B. tectorum	**-0.78**	**-0.46**	**-0.51**	0.92	0.27	0.14	0.76	15.5	0.003
L. perfoliatum	**-0.72**	-0.07	**-0.67**	1.06	0.01	0.65	0.47	23.7	0.004
K. macrantha	0.16	-0.27	-0.07	0.45	0.45	0.47	0.07	15.5	0.007
Forbs	**0.57**	**0.43**	-0.03	0.69	0.4	0.2	0.35	19.8	0.004

* Variables moderately or strongly correlated with ordination axes are in bold

** Cross-validated coefficient of determination for NPMR model with all three axes as predictors

Table 4.4 Indicator Species Analysis comparing the composition of the herbaceous understory communities between the five groups. Relative frequency (RF) is the proportion of plots in the group with the species present in the plot. Relative abundance (RA) is the species' proportion of the total abundance in the plots relative to its abundance in other groups (measure of exclusiveness, concentration of abundance into a particular group). Indicator values (IV) are the maximum of 100*RF*RA for the relevant group

	State 1 A			**State 1B**			**Phase-at-risk**			**State 2**			**State 3**			
																P-value
Species	**RF**	**RA**	**IV**	**RF**	**RA**	**IV**	**RF**	**RA**	**IV**	**RF**	**RA**	**IV**	**RF**	**RA**	**IV**	**0.013**
E. elymoides *	100	18	18	**100**	**28**	**28**	89	21	19	82	13	10	**100**	**20**	**20**	0.005
A. thuberianum	**95**	**36**	**34**	33	2	1	**100**	**33**	**33**	94	22	20	63	7	4	<0.001
P. spicata	**100**	**49**	**49**	33	4	1	**95**	**26**	**25**	47	18	9	25	3	1	0.013
H. comata	0	0	1	0	0	0	**47**	**93**	**44**	0	0	0	13	7	1	0.048
A. hymenoides	10	11	0	0	0	0	42	73	22	6	7	0	6	9	1	0.348
K. macrantha	5	11	1	0	0	0	111	82	9	0	0	0	6	7	0	0.003
P. secunda	**100**	**28**	**28**	**100**	**29**	**29**	100	16	16	**100**	**22**	**22**	100	9	9	0.002
Forbs	100	24	24	**100**	**29**	**29**	89	15	13	88	18	16	81	10	8	0.057
B. tectorum	65	6	4	0	0	0	**100**	**25**	**25**	**100**	**33**	**33**	**100**	**36**	**36**	<0.001
L. perfoliatum	35	7	3	100	15	15	58	10	6	**100**	**31**	**31**	**100**	**37**	**37**	<0.001

**** Top three significant indicator species of each group based on Indicator Values are in bold***

Table 4.5 Pairwise MRPP comparisons of groups derived from cluster analysis using both species cover (community composition) and environmental data (heat loads, cattle grazing disturbance, etc.)

Groups compared	MRPP using species cover (community composition) data	MRPP using environmental data
State 3 and 1A	0.42	0.32
State 3 and 1B	0.32	0.78
State 3 and phase-at-risk	0.23	0.41
State 2 and 1A	0.25	0.32
State 2 and 1B	0.23	0.74
State 2 and phase-at-risk	0.12	0.46
State 2 and 3	0.15	0.21
Phase-at-risk and 1A	0.13	0.2
Phase-at-risk and 1B	0.18	0.65

* Not adjusted for multiple group comparisons; all associated p-values < 0.001

Table 4.6 Other characteristics of groups derived from cluster analysis

Community state	1	1	1	2	3
Name	Intact 1A	Intact 1B	Phase-at-risk	State 2	State 3
Number of study plots (% of total study plots)	20 (27%)	3 (4%)	19 (25%)	17 (23%)	16 (21%)
ESD *****					
Clayey 10-12PZ	1 (10%)	0	2 (18%)	3 (27%)	5 (45%)
Loamy 10-12PZ	13 (31%)	3 (8%)	9 (21%)	11 (26%)	6 (14%)
South Slopes 10-14PZ	3 (38%)	0	1 (13%)	3 (37%)	1 (13%)
North Slopes 10-14PZ	3 (75%)	0	1 (25%)	0	0
Sandy Loam 10-12PZ	0	0	6 (60%)	0	4 (40%)
Sagebrush % cover	19	20	18	18	21

***** Number of plots (% of total plots in relevant ESD)

Table 4.7 Bayesian and maximum likelihood estimates of unstandardized regression coefficients for both models

	Model A			Model B		
Path (relationship)	Maximum likelihood	Bayesian	% difference	Maximum likelihood	Bayesian	difference
B. tectorum < sand	0.034	0.034	0.00	0.031	0.031	0.00
B. tectorum < gaps>200	0.034	0.034	0.00	0.041	0.041	0.00
B. tectorum < bare.soil	0.052	0.051	1.96	0.045	0.045	0.00
B. tectorum < bsc	-0.042	-0.042	0.00	-0.042	-0.042	0.00
B. tectorum < bunchgrass abundance	-0.022	-0.022	0.00	n/a	n/a	n/a
B. tectorum < Axis 3	n/a	n/a	n/a	0.338	0.328	3.05
gaps>200 < bunchgrass abundance	-1.267	-1.278	-0.86	-1.369	-1.362	
gaps> 200 < sand	0.561	0.566	-0.88	n/a	n/a	n/a
gaps>200 < heat	47.815	47.921	-0.22	n/a	n/a	n/a
gaps>200 < Axis 2	n/a	n/a	n/a	-22.178	-22.118	0.27
gaps>200 < Axis 3	n/a	n/a	n/a	-12.794	-12.72	0.58
gaps>200 < *Artemisia* abundance	0.75	0.743	0.94	n/a	n/a	n/a
bunchgrass abundance < distance	0.003	0.003	0.00	0.003	0.003	0.00
bunchgrass abundance < heat	-23.363	-23.547	-0.78	-23.801	-23.714	0.37
Artemisia abundance < bunchgrass abundance	-0.159	-0.157	1.27	n/a	n/a	n/a
Artemisia abundance < sand	-0.088	-0.089	-1.12	n/a	n/a	n/a
bsc < distance	0.002	0.002	0.00	0.002	0.002	0.00
bsc< heat	-16.744	-16.777	-0.20	-16.744	-16.82	-0.45
bare.soil < sand	0.243	0.245	-0.82	0.22	0.221	-0.45
bare.soil < gaps>200	0.207	0.205	0.98	0.169	0.17	-0.59
bare.soil < Axis 3	n/a	n/a	n/a	-3.687	-3.618	1.91
Axis 2 < sand	n/a	n/a	n/a	-0.013	-0.013	0.00
Axis 2 < distance	n/a	n/a	n/a	0.001	0.001	0.00
Axis 2 < heat	n/a	n/a	n/a	-1.329	-1.329	0.00
Axis 3 < sand	n/a	n/a	n/a	-0.008	-0.008	0.00

Table 4.8 Comparison of alternative models A and B using indicators of model fit

			Objective measures of model parsimony				
Model	Chi-Square (P-value)	d.f	AIC	BCC	Posterior p	DIC	Variation in invasibility (*B. tectorum* cover)
Model A	15.026 (.594)	16	88	99.6	0.54	89.71	72%
Model B	18.884 (0.529)	20	109	125	0.5	111.11	72%

CHAPTER 5

General Conclusions

Nearly two decades have passed since sage steppe ecosystems were identified as one of North America's most endangered (Noss et al. 1995). During this time, degradation and *B. tectorum* invasions of these ecosystems has continued (Knick et al. 2010). The conservation and restoration of these widespread ecosystems will require a timely and concerted effort across these landscapes (Suring et al. 2005; Meinke et al. 2008; Connelly et al. 2010).

The first objective of these studies was to gain a better understanding of the role of *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush) as a driver of herbaceous species abundances, community composition, and community stability by: (1) using spatial patterns of association between *Artemisia* and native and non-native species to infer interaction outcomes, i.e. competition and facilitation; (2) characterizing shifts in such interaction outcomes along overlapping gradients of cattle grazing, water, and heat stress; and determining whether shifts in the structure of *Artemisia* interactions with herbaceous species and *Artemisia* facilitation altered community stability. The second objective was to gain a better understanding of the susceptibility of these ecosystems to *B. tectorum* invasion by: (1) describing patterns of resistance and resilience of a semi-arid landscape using the sagebrush steppe as a model system; and (2) evaluating a multivariate hypothesis of the causal network of factors and processes driving observed patterns of resilience and assessing the relative importance of those factors and processes.

Role of the foundational shrub Artemisia as a driver of community dynamics

Findings from Chapters 2 and 3 provide new insights concerning the role of *Artemisia* as a driver of community organization. Contrary to the dominant paradigm and conventional wisdom that *Artemisia* competition suppresses the native herbaceous community and that its removal will release the understory community (Holechek et al. 2003), the structure of *Artemisia* interactions with herbaceous species is not the same with all species and across all locations.

Across 75 sites representative of the northern Great Basin, cumulative cattle herbivory was a predominant stress component that overlapped with heat and water stress gradients to drive the structure of *Artemisia* interactions with herbaceous species. Consistent with the stress gradient hypothesis (SGH), *Artemisia* facilitation of herbaceous species was most frequent and strongest at the highest stresses, and competition was most frequent and strongest at the lowest stresses. Two herbaceous species with the highest competitive abilities, *Elymus elymoides* and *Poa secunda*, showed the strongest facilitation at the limits of their stress tolerances. The structure of *Artemisia* interactions with the invasive *B. tectorum* was strikingly different than those with native bunchgrasses. *Artemisia* interactions with native bunchgrasses shifted from competition to facilitation with increasing stress, but its interactions remained competitive with *Bromus tectorum* along the entire stress gradient. Response curves showed linear-monotonic, hump-shaped, and plateau relationships between interaction outcomes and stress gradients, which suggests both species and stress gradient specific-relationships.

These shifts in the structure of interactions between *Artemisia* and native bunchgrasses were associated with both an increase and decrease in community compositional and functional stability. *Artemisia* facilitation decreased invasibility by increasing native bunchgrass composition, which reduced the magnitude of *B. tectorum* invasion in under-shrub compared to interspace communities. This decreased invasibility did not translate into lower invasibility at the community level because of the limited spatial scale over which such facilitation occurs. *Artemisia* facilitation increased community compositional and functional stability at intermediate stress levels, but decreased community stability at high stress levels. Facilitation became a destabilizing force when native bunchgrass species became “obligate” beneficiaries, i.e. strongly dependent on *Artemisia* facilitation for their continued persistence in the community.

These findings suggest several broad conclusions and recommendations:

1. The “stress gradient hypothesis” could provide a practical and accurate framework for predicting responses of native and non-native species in *Artemisia* communities to disturbances (fire, livestock grazing, off-road-vehicle use, etc.) and for predicting responses to management actions that remove or reduce *Artemisia* cover.

2. The highly stress tolerant foundational shrub *Artemisia* could play a pivotal role in increasing the success rate of efforts to restore native understory herbaceous communities. At locations characterized by intermediate to high combined herbivory and water stress, land managers could use autogenic

processes associated with *Artemisia* facilitation to increase restoration success rates and reduce costs. Remnant native bunchgrass populations beneath *Artemisia* canopies could serve as vital sources of seed and could accelerate otherwise slow re-colonization rates. In addition, *Artemisia* canopies could serve as important locations for planting native seedlings as an intermediate restoration step prior to reducing the shrub component. However, seedlings should be planted far enough from the shrub to prevent mortality in the event of a fire. At locations characterized by low combined stress levels, land managers might attempt to reduce *Artemisia* competition by thinning sagebrush stands and releasing native herbaceous species, especially more stress tolerant natives like *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Achnatherum thurberianum* (Thurber's needlegrass).

3. *Artemisia* competition likely reduces the magnitude of *B. tectorum* invasions across many parts of the landscape. Prescribed burns, wildfires, or other activities that completely eliminate *Artemisia* removal are likely to release *B. tectorum* and increase its cover if the bunchgrass community has been depleted. This release is likely to be especially problematic at sites characterized by high combined stress levels where many bunchgrass species are dependent on obligate *Artemisia* facilitation for their continued persistence in the community. Complete *Artemisia* removal may reduce bunchgrass abundance.

4. As heat and water stress increase with global climate change, *Artemisia* may increase community stability to a point. When combined stress levels are sufficiently high that many native species persist only beneath *Artemisia* canopies, *Artemisia* facilitation will decrease community stability. This reduced stability could set the stage for a regime shift to an annual exotic grassland triggered by the next fire.

The findings from Chapters 2 and 3 are observational and based on spatial patterns of association. This approach precludes making definitive inferences regarding causal mechanisms driving shifts in the structure of *Artemisia* interactions with herbaceous species and the implications of such shifts for community stability.

However, this approach has identified several factors and processes ripe for manipulation in future studies:

1. A mechanistic understanding will require teasing apart underlying positive and negative interactions in multi-factorial field experiments. These experiments need to encompass the entire range of the overlapping stress gradients and use a combination of shrub removal and mimic treatments to manipulate underlying positive and negative interactions. These studies should quantify shifts in the strength of underlying positive and negative interactions and examine how such shifts drive interaction outcomes. They should quantify how treatments influence levels of each type of stress, incorporate focal herbaceous species with diverse life history strategies, and measure several response variables at the individual level (growth, survival, fitness), species level (abundance), and community level (diversity, stability).

2. Future research should also consist of observational studies using spatial patterns to infer interaction outcomes between *Artemisia* and herbaceous species across complete heat, water, and herbivory severity gradients over which *Artemisia* occurs. *Artemisia* communities of North America are characterized by significantly different evolutionary histories with generalist herbivores like cattle and future studies should account for these differences. A better understanding of these causal networks is vital to improving our ability to accurately predict herbaceous responses at the species-level, such as forbs critical for maintaining Greater Sage Grouse populations and invasive non-native species, and at the community-level to climate change, wildfire, anthropomorphic disturbances, and management actions that alter *Artemisia* cover.

Causal network driving Artemisia ecosystem resilience

In Chapter 4, we demonstrated that ecosystem resilience to disturbance and resistance to invasion is an emergent property of *Artemisia* ecosystems and thus under multivariate control. Structural equation modeling assessed a multivariate hypothesis of the causal network of factors and processes driving community resilience to disturbance and *B. tectorum* invasion. The linchpin of ecosystem invasibility was the size of and connectivity between basal gaps in perennial vegetation, driven by shifts in the structure and spatial aggregation of the native bunchgrass community. Landscape orientation and soil physical properties determined inherent risk to invasion. The resident bunchgrass community provided biotic resistance to invasion by reducing the size of and connectivity between basal gaps and thereby limiting available resources. Biological soil crust communities (BSC) provided biotic resistance by reducing safe sites for B. tectorum establishment. Cattle grazing facilitated *B. tectorum* by reducing native bunchgrass and BSC abundance and altering bunchgrass community composition. If the management goal is to conserve and restore resilience of these imperiled ecosystems, these findings suggest several broad conclusions and recommendations:

1. Resource managers should take into account the fact that ecological thresholds are context dependent because they are under multi-process control. Inherent differences in resilience driven by landscape orientation and soil properties create a mosaic of communities that differ substantially in the cattle grazing disturbance levels they can withstand before crossing a threshold to an alternative state. Communities located on coarser-textured soils, flat terrain or south-facing slopes are the least resilient to disturbance because of their lower productivity. Cumulative cattle grazing levels must be reduced to levels that prevent the most susceptible communities within a grazing management unit from crossing these thresholds. Otherwise, the resilience of more vulnerable communities is likely to be compromised and they are likely to be invaded by *B. tectorum*. Once invaded, these communities will increase the risk of fires and may serve as foci for subsequent invasions of surrounding communities.

2. Reduce cumulative stress levels at landscape levels. Global climate change is likely to increase heat and water stress. Reducing cumulative cattle grazing intensities by altering utilization rates and/or seasons of use and

other management strategies may be the only effective means of accomplishing these goals.

3. Restore biotic resistance provided by the native BSC and bunchgrasses communities by maintaining or restoring: (a) high overall bunchgrass abundance/dominance and community structure characterized by spatially dispersed bunchgrasses in interspaces and small basal gaps between such individuals to capture large amounts of otherwise available resources in space; (b) a diverse assemblage of bunchgrass species with different spatial and temporal patterns of resource use to capture available resources at different soil depths and times; (c) a BSC community to limit safe sites for *B. tectorum* establishment in gaps between perennial native vegetation.

Understanding the relative importance of these controlling factors, instead of factoring some out, is vital to understanding and predicting ecosystem responses (Grace 2006). Future research should focus on using knowledge of this causal network to develop better predictive models (Marcot 2006). Models capable of accurately predicting ecosystem responses to different management scenarios or changes in circumstances are urgently needed to conserve and restore resilience of these highly endangered ecosystems (Suring et al. 2005; Meinke et al. 2008; Connelly et al. 2010). Future research should also focus on expanding this study across the entire distribution of *Artemisia* in North America. These studies should focus on gaining a better understanding of how the relative importance of the different factors and processes vary across ecoregions characterized by different climates, soil properties, disturbance regimes, and evolutionary histories with large-bodied herbivores.

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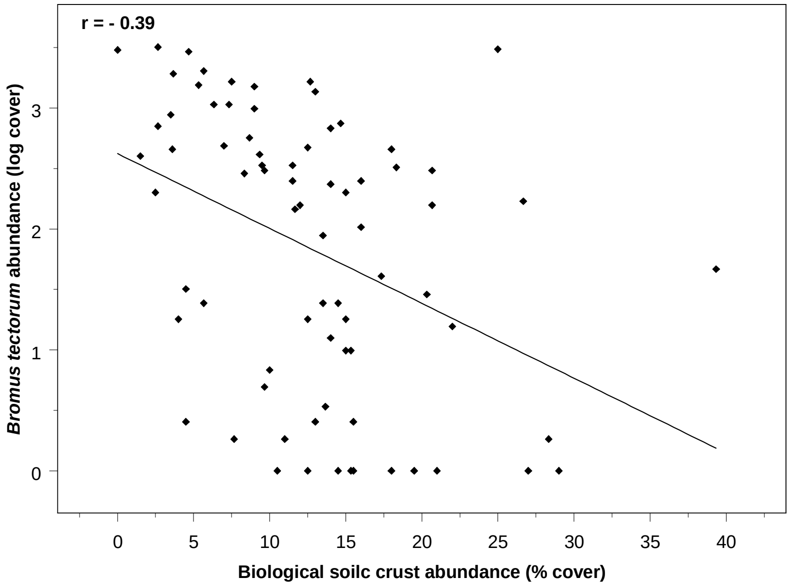
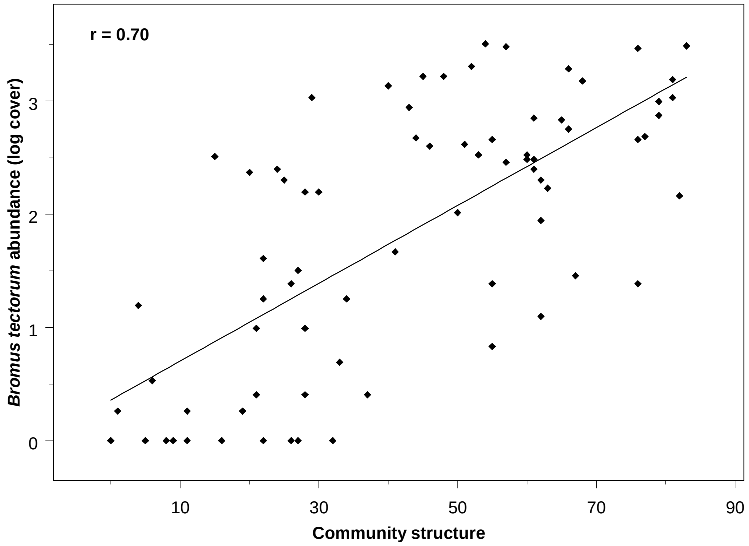
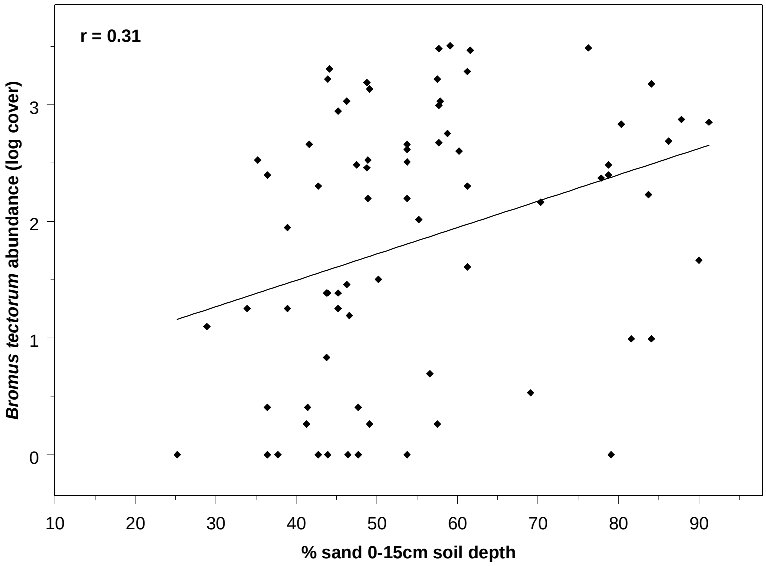
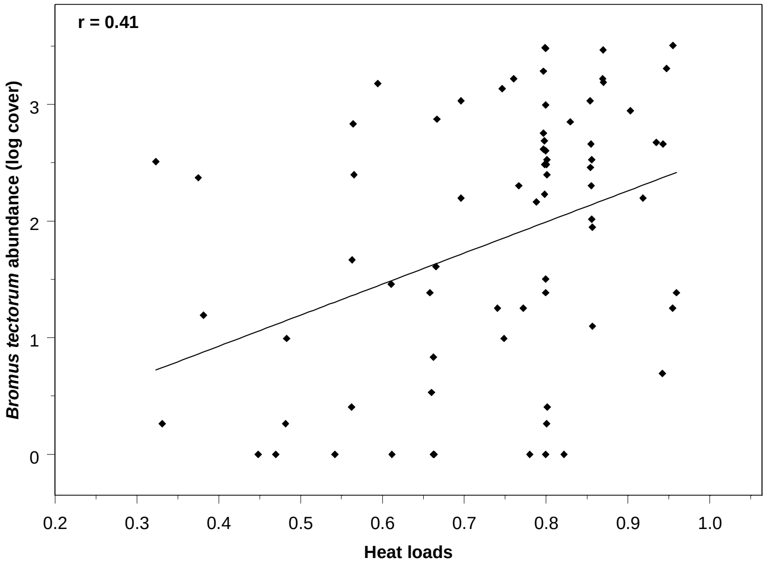
APPENDICES



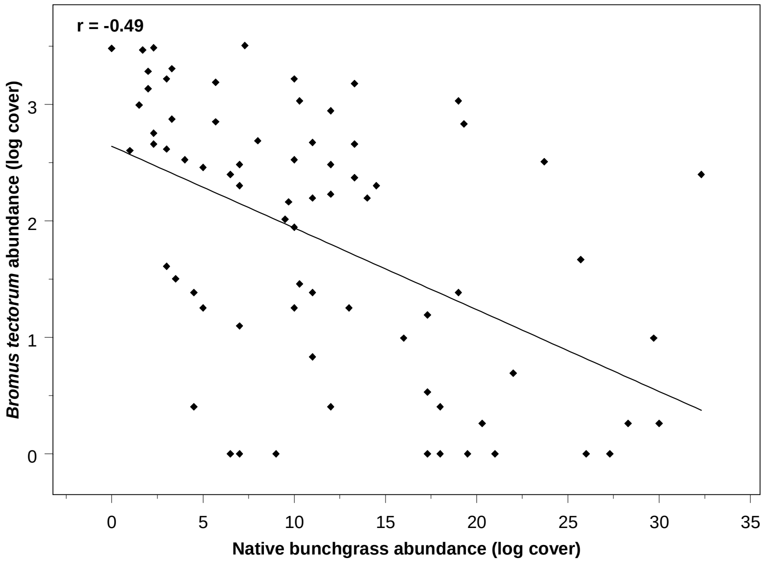


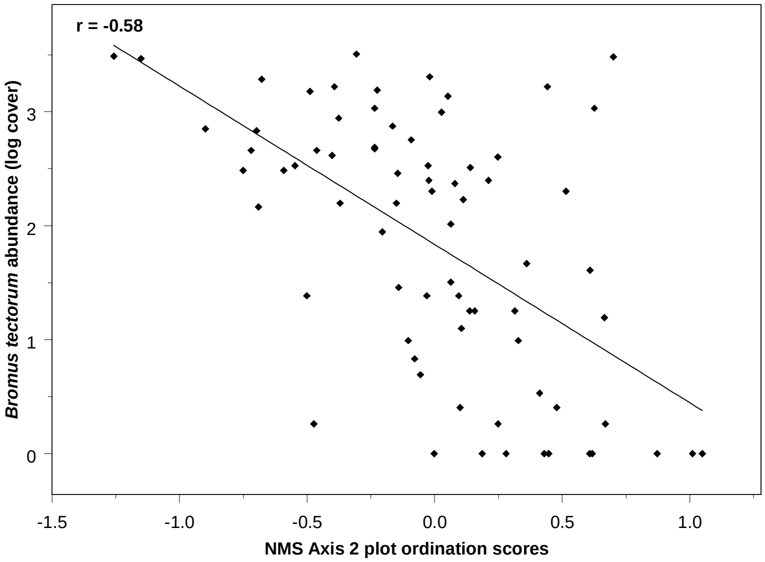
Appendix A1 Bivariate relationships between *B. tectorum* cover and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).



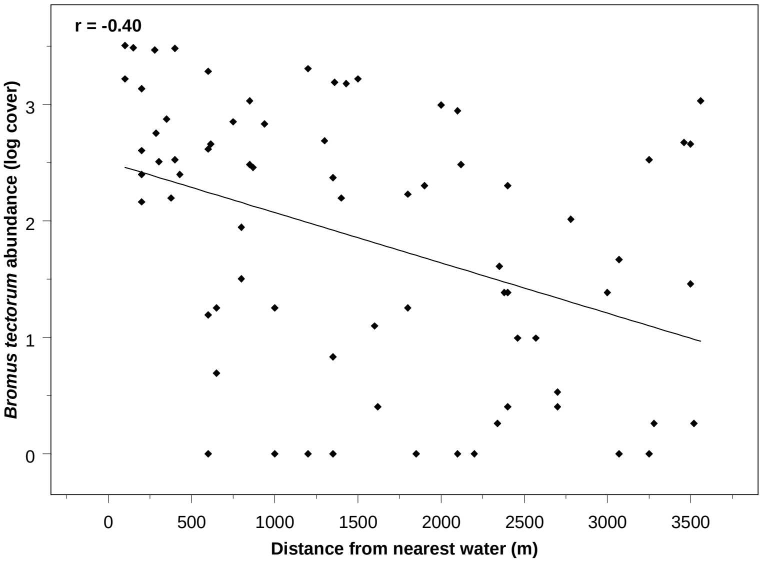


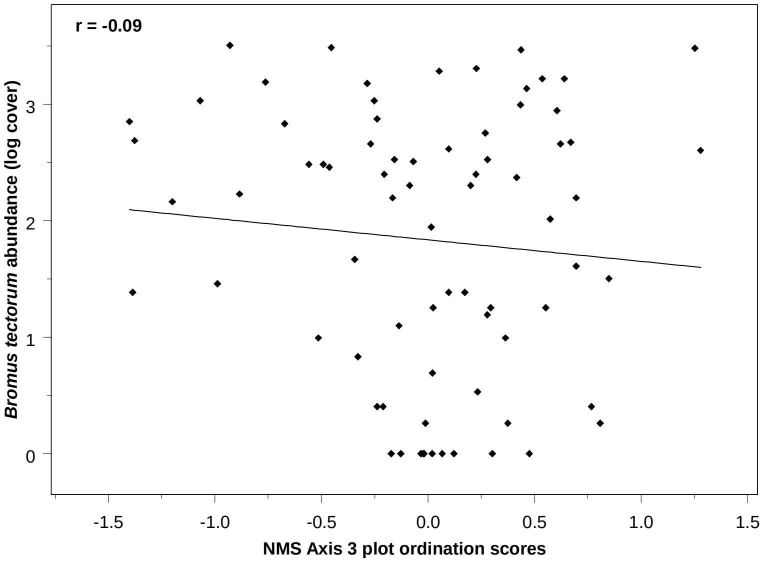
Appendix A1 (continued) Bivariate relationships between B. *tectorum* cover and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).



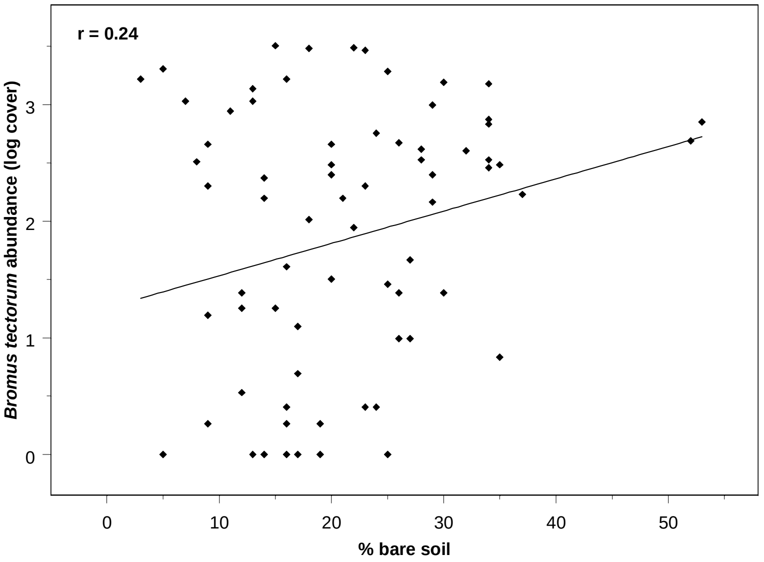


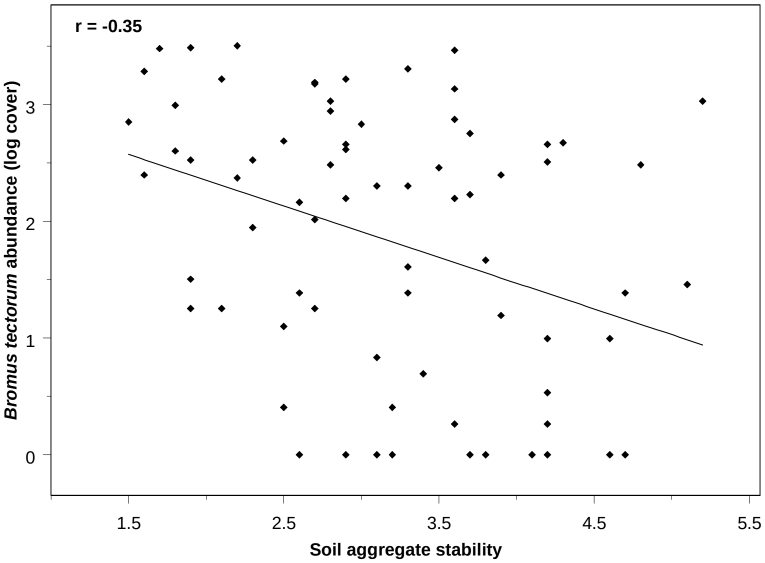
Appendix A1 (continued) Bivariate relationships between B. *tectorum* cover and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).



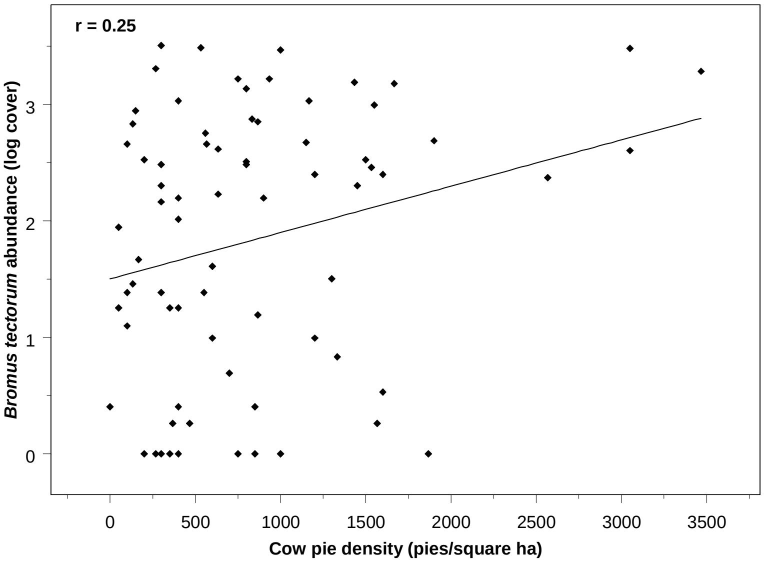


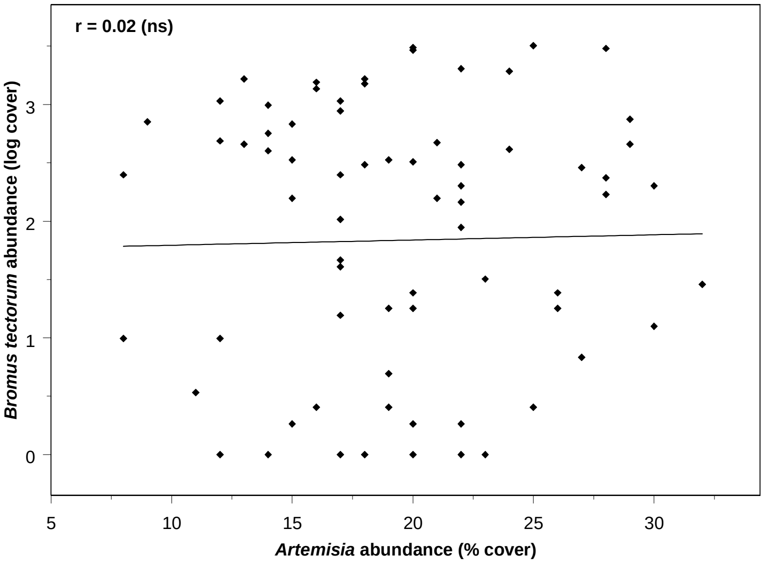
Appendix A1 (continued) Bivariate relationships between B. *tectorum* cover and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).



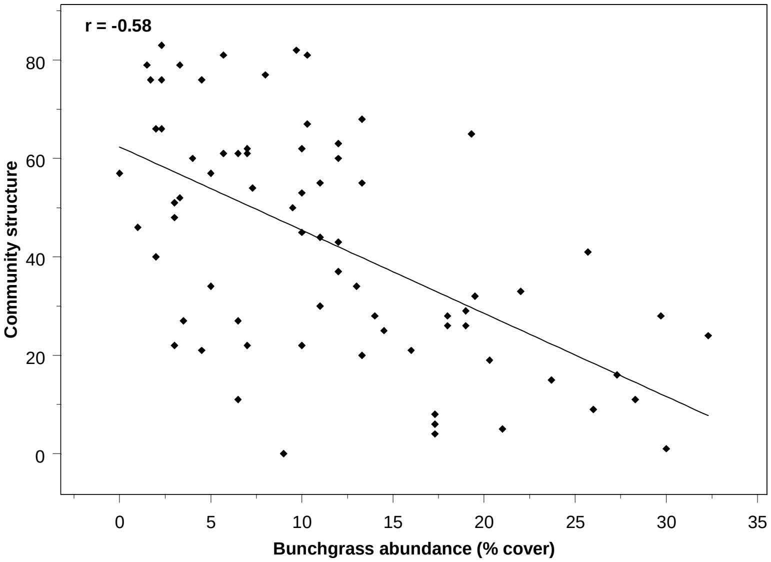


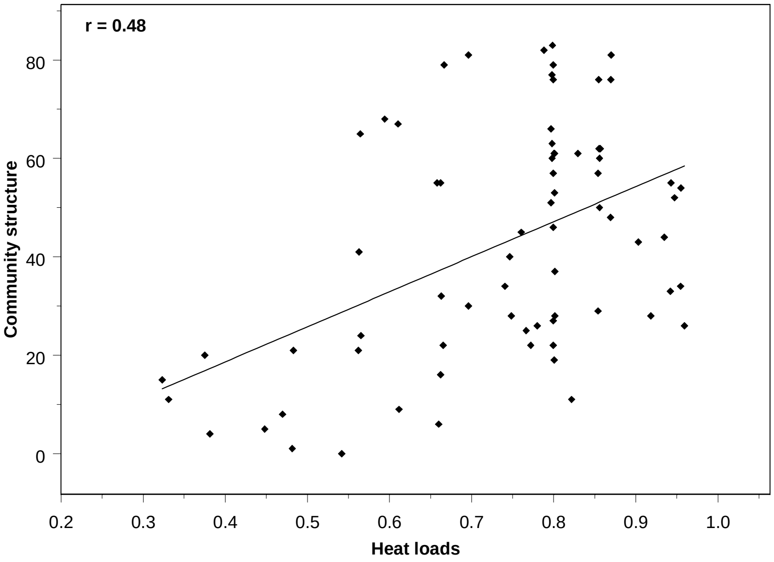
Appendix A1 (continued) Bivariate relationships between B. *tectorum* cover and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).



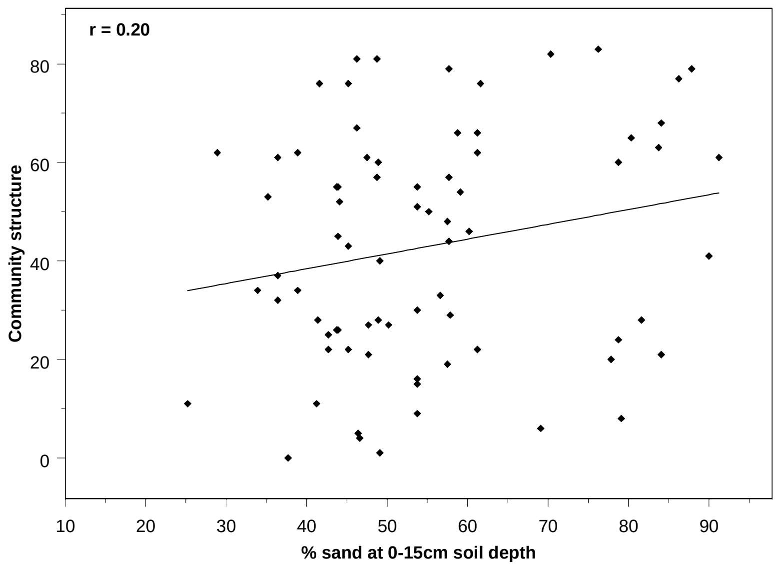


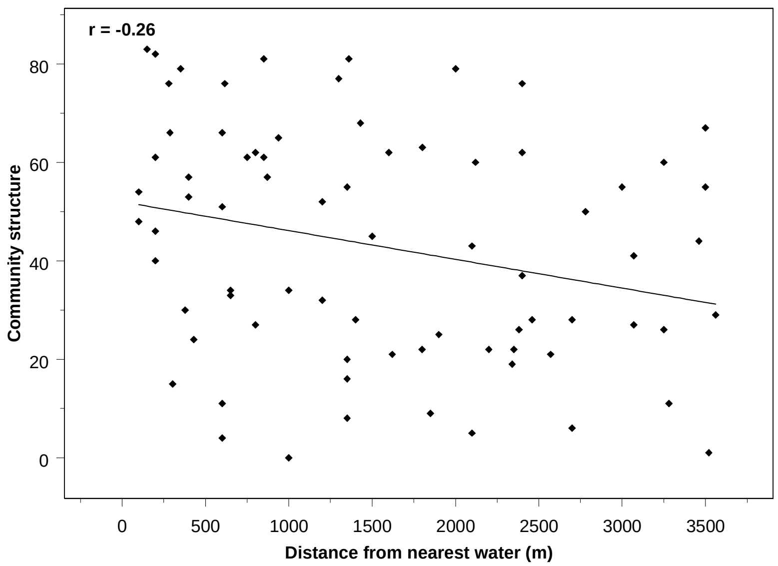
Appendix A1 (continued) Bivariate relationships between B. *tectorum* cover and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).



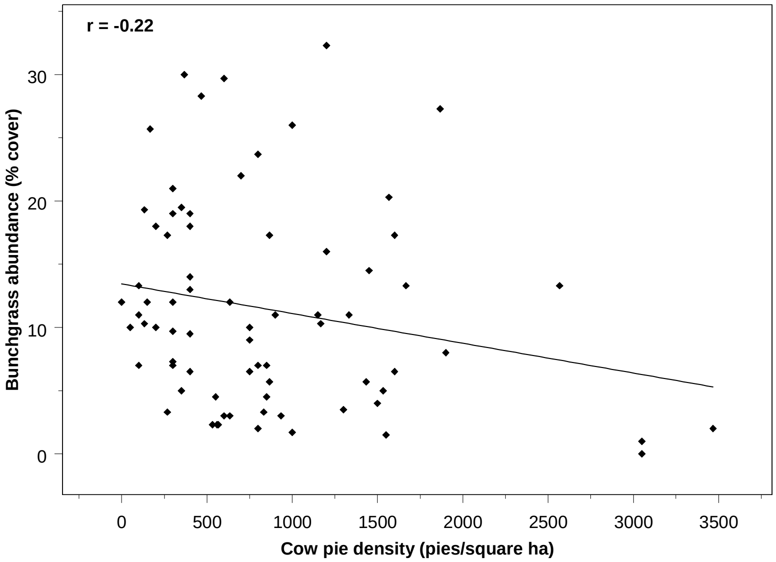


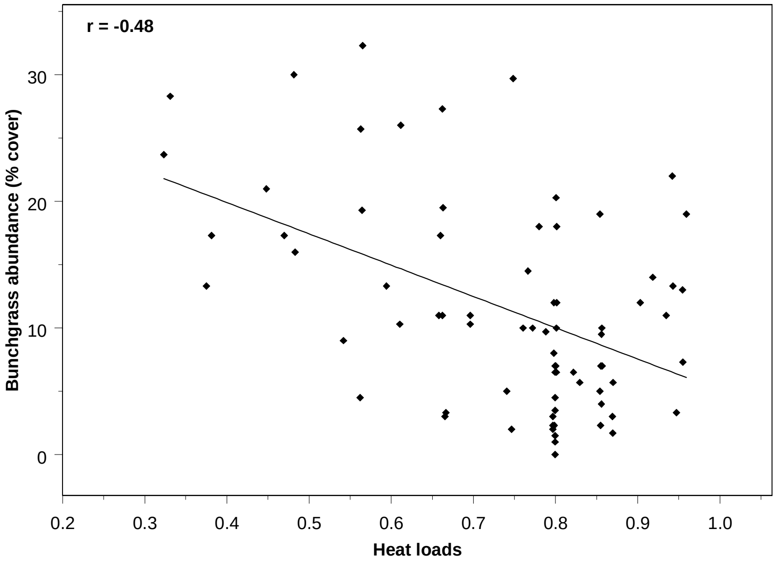
Appendix A2 Bivariate relationships between community structure and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).



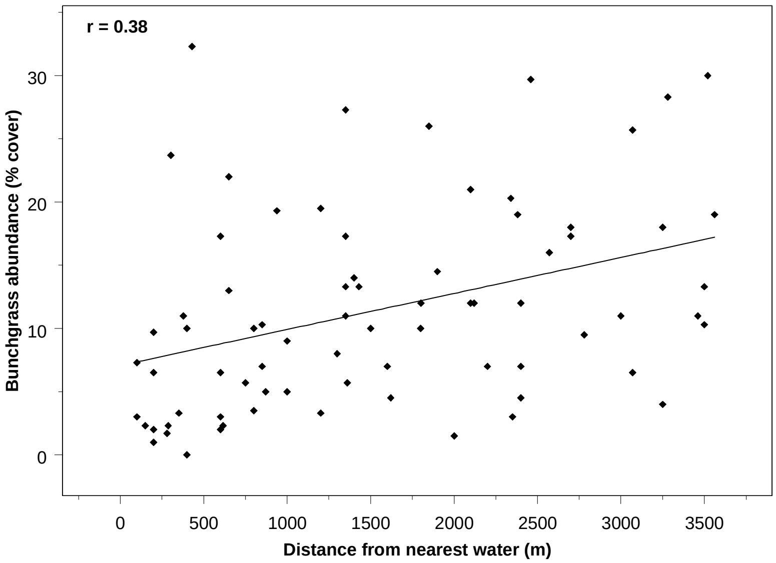


Appendix A2 (continued) Bivariate relationships between community structure and selected model variables. Community structure is the percent of transects covered by basal gaps between perennial native vegetation > 200cm (gaps>200cm).

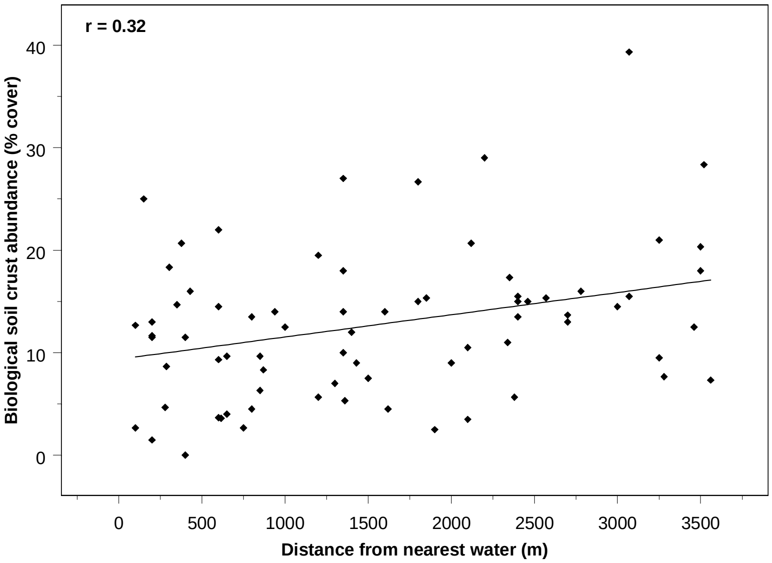


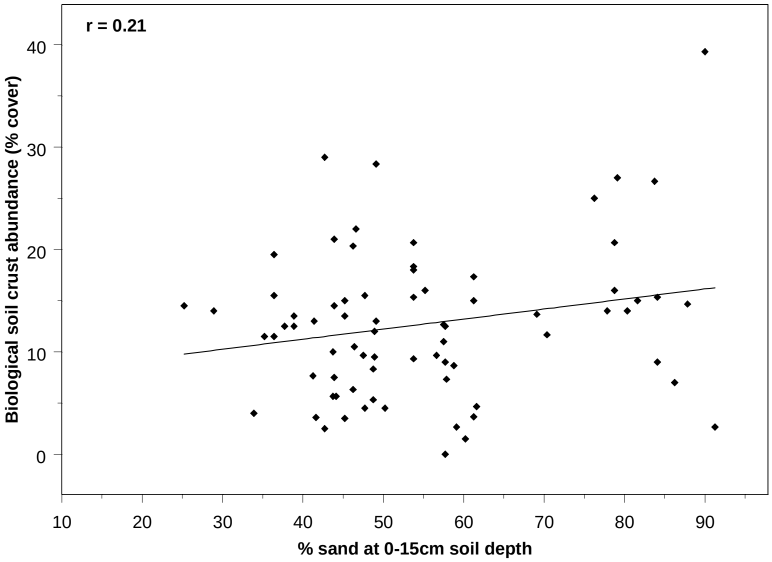


Appendix A3 Bivariate relationships between native bunchgrass cover and selected model variables.

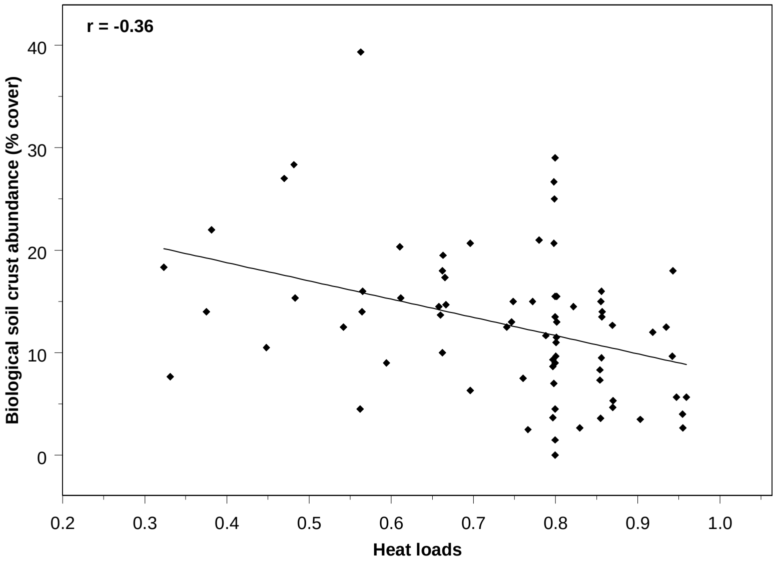


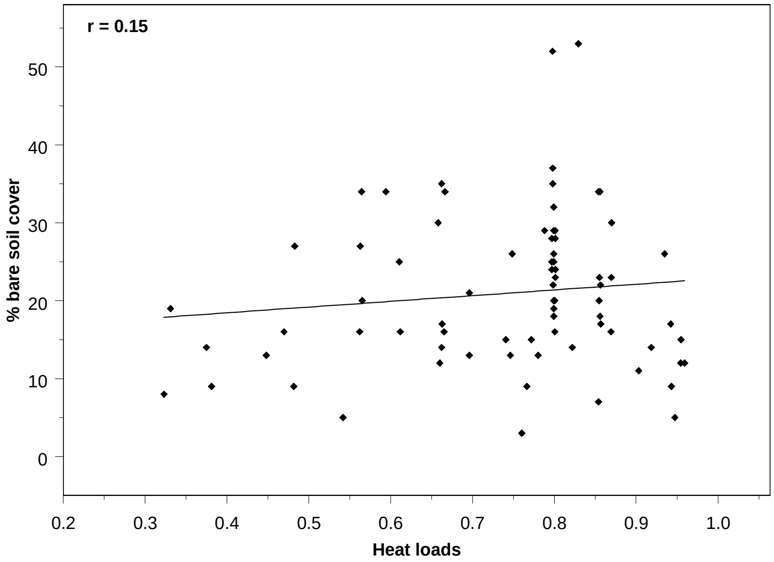
Appendix A3 (continued) Bivariate relationships between native bunchgrass cover and selected model variables.



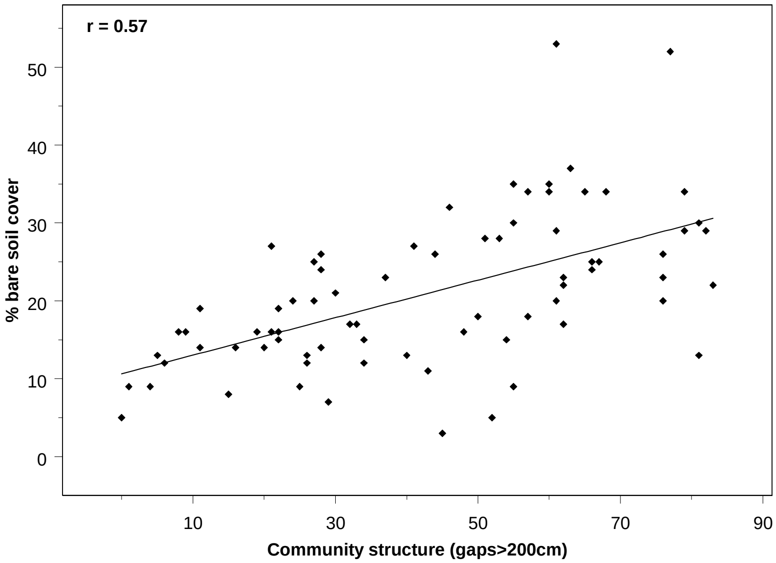


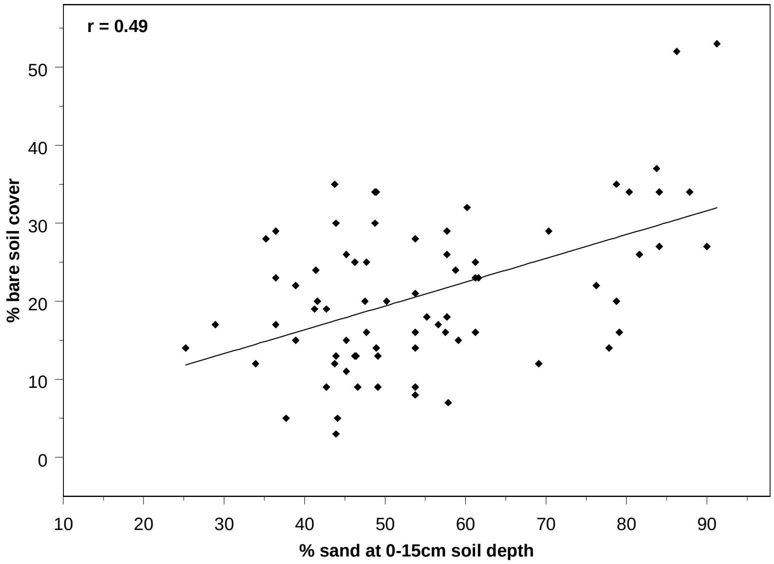
Appendix A4 Bivariate relationships between soil biological crust and bare soil cover and selected model variables.



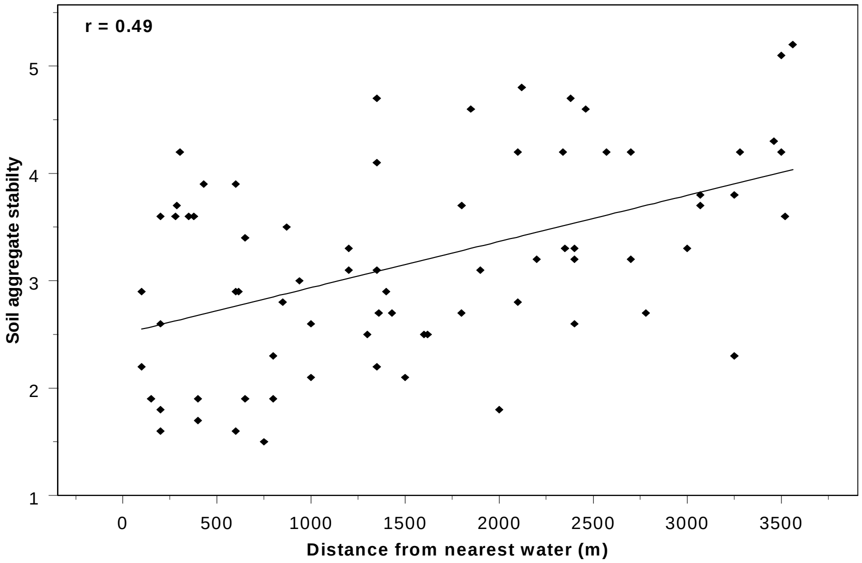


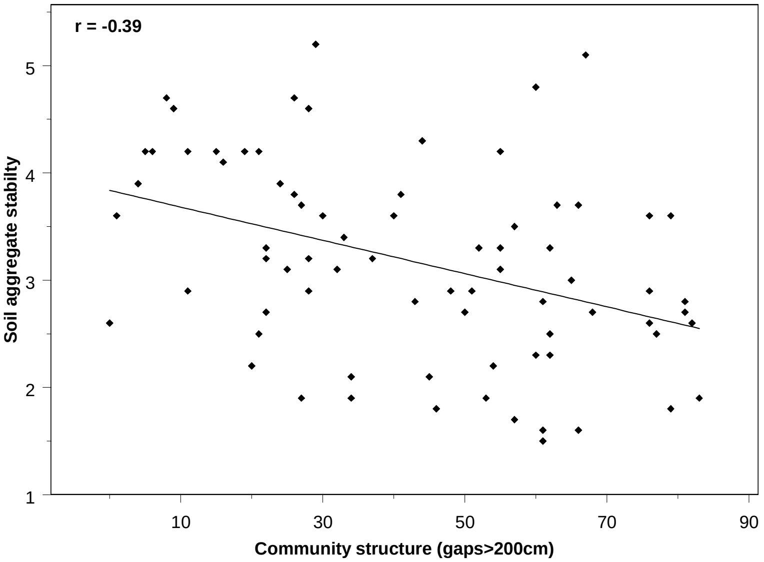
Appendix A4 (continued) Bivariate relationships between soil biological crust and bare soil cover and selected model variables.



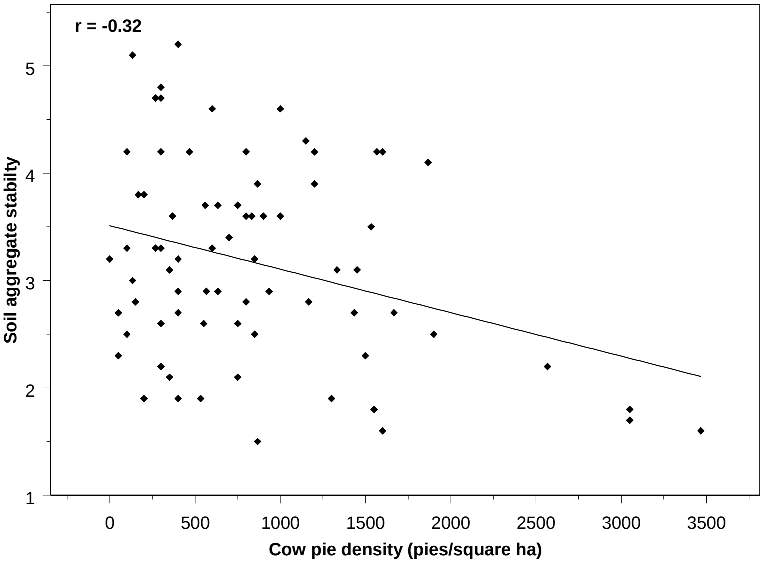


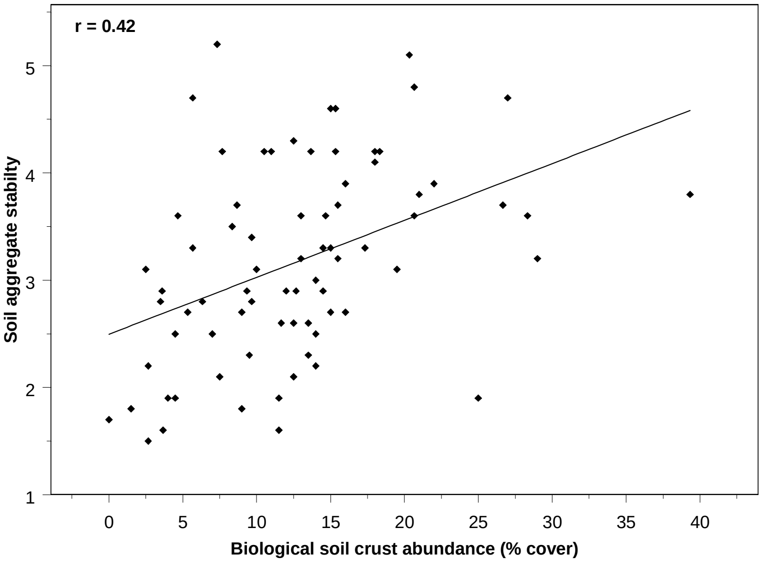
Appendix A4 (continued) Bivariate relationships between soil biological crust and bare soil cover and selected model variables.



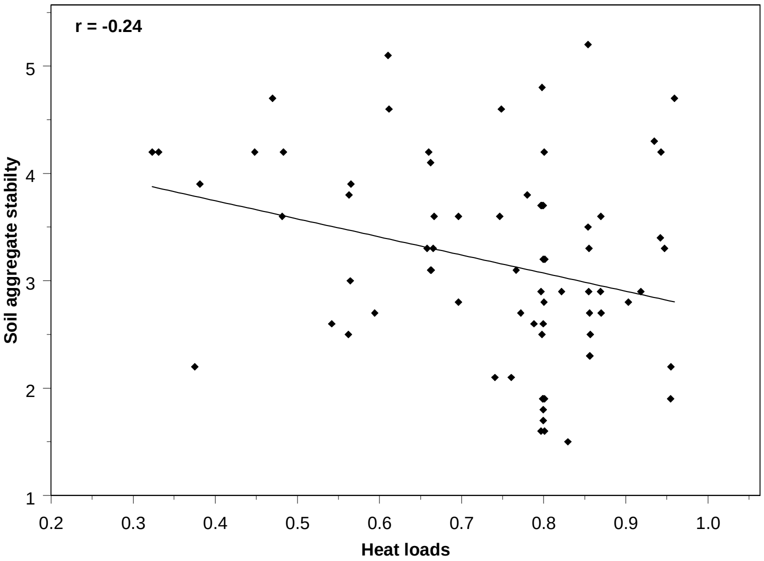


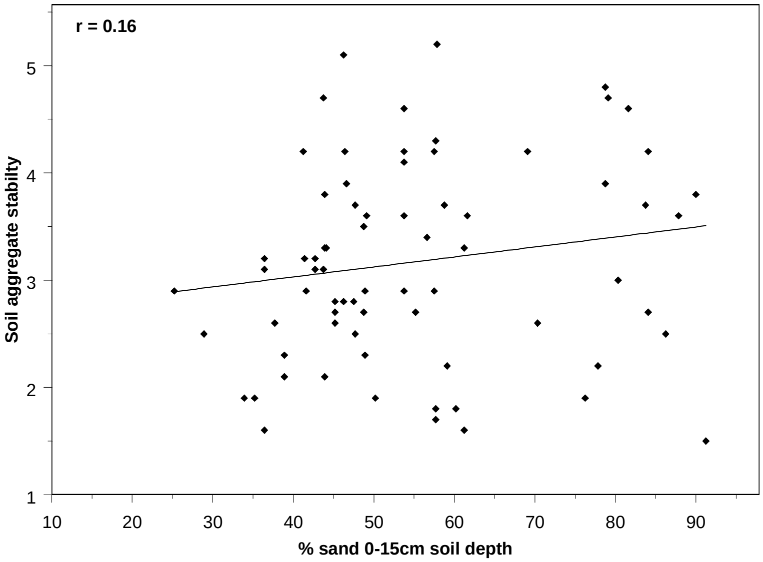
Appendix A5 Bivariate relationships between soil aggregate stability and selected model variables.





Appendix A5 (continued) Bivariate relationships between soil aggregate stability and selected model variables.





Appendix A5 (continued) Bivariate relationships between soil aggregate stability and selected model variables.