

DISTURBANCE AND SITE CHARACTERISTICS RELATE TO CHEATGRASS
(BROMUS TECTORUM) ABUNDANCE ON RANCHES IN MONTANA
FOOTHILLS ECOSYSTEMS

by

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TABLE OF CONTENTS

1. INTRODUCTION AND BACKGROUND.....	1
Fire.....	2
Vegetation.....	3
Livestock and Wildlife.....	7
Human Disturbance.....	10
Abiotic Site Characteristics.....	11
Research from Montana and Other Northern Foothills Grasslands.....	13
Need for Research.....	17
Objectives.....	18
2. METHODS.....	19
Description of Study Locations and Site Selection.....	19
Site Selection 2014.....	20
Site Selection 2015.....	20
2014 Data Collection.....	21
2015 Data Collection.....	23
Data Analysis.....	25
3. RESULTS.....	30
Summary Statistics.....	30
Invaded Plots.....	30
Non-invaded (Zero) Plots.....	32
Regression Model Results.....	35
Red Bluff Models.....	35
Thackeray Models.....	40
4. DISCUSSION.....	44
Red Bluff.....	44
Thackeray.....	51
Ranch Differences.....	56
Limitations of the Study.....	60
Management Implications.....	61
REFERENCES CITED.....	64
APPENDIX A: Supplementary Tables and Figures.....	73

LIST OF TABLES

Table	Page
1. Common perennial vegetation at Red Bluff and Thackeray ranches.....	74
2a. Variables included in Full Red Bluff Model.....	74
2b. Variables included in Full Thackeray Model.....	74
3. Summary Statistics of Invaded Plots.....	31
4. Summary Statistics of Zero Plots.....	33
5a. Estimated Coefficients of Top Red Bluff Models.....	75
5b. Importance of Variables in Full Red Bluff Model.....	75
6a. Importance of Variables in 2014 Red Bluff Models.....	76
6b. Importance of Variables in 2015 Red Bluff Model.....	76
7a. Estimated Coefficients of Top Thackeray Models.....	76
7b. Importance of Variables in Full Thackeray Model.....	77
8a. Importance of Variables in 2014 Thackeray Models.....	77
8b. Importance of Variables in 2015 Thackeray Models.....	77

LIST OF FIGURES

Figure	Page
1. Map of Study Locations.....	78
2. Average Precipitation at the Ranches.....	78
3. Pairwise Scatterplots for Red Bluff Data.....	79
4. Pairwise Scatterplots for Thackeray Data.....	80
5. Residuals vs. Fitted Plots for Initial Models.....	81
6. Cheatgrass Abundance vs. Simpson Diversity at Red Bluff.....	35
7. Cheatgrass Abundance vs. Burrow Cover at Red Bluff.....	37
8a. Cheatgrass Abundance vs. Sin(Aspect) at Red Bluff.....	38
8b. Partial Regression Plot for Sin(Aspect) at Red Bluff in Full Model.....	82
9. Cheatgrass Abundance vs. Perennial Basal Cover at Red Bluff.....	39
10a. Cheatgrass Abundance vs. Simpson Diversity at Red Bluff.....	39
10b. Partial Regression Plot for Simpson Diversity at Red Bluff in Full Model.....	82
11a. Cheatgrass Abundance vs. Litter Cover at Red Bluff.....	83
11b. Partial Regression Plot for Litter Cover at Red Bluff in Full Model.....	83
12a. Cheatgrass Abundance vs. Fecal Count at Red Bluff.....	84
12b. Partial Regression Plot for Fecal Count at Red Bluff in 2014.....	84
12c. Partial Regression Plot for Fecal Count at Red Bluff in 2015.....	85
13. Cheatgrass Abundance vs. Slope at Red Bluff.....	85

LIST OF FIGURES - CONTINUED

Figure	Page
14. Cheatgrass Abundance vs. Cos(Aspect) at Thackeray.....	41
15. Cheatgrass Abundance vs. Sand Content at Thackeray.....	42
16. Cheatgrass Abundance vs. Soil Profile Depth at Thackeray.....	42
16b. Partial Regression Plot for Soil Depth at Thackeray in 2014.....	86
16c. Partial Regression Plot for Soil Depth at Thackeray in 2015.....	86
17a. Cheatgrass Abundance vs. Burrow Cover at Thackeray.....	43
17b. Partial Regression Plot for Burrow Cover at Thackeray in 2014.....	87
17c. Partial Regression Plot for Burrow Cover at Thackeray in 2015.....	87
18a. Cheatgrass Abundance vs. Bare Soil Cover at Thackeray.....	43
18b. Partial Regression Plot for Bare Soil Cover at Thackeray in 2015.....	88
18c. Partial Regression Plot for Bare Soil Cover at Thackeray in 2015.....	88

ABSTRACT

Cheatgrass (*Bromus tectorum* L.), also known as downy brome, is an invasive, exotic annual grass found throughout North America. Cheatgrass has been extensively studied in the Great Basin region of North America, where the majority of precipitation comes in winter and early spring, and the vegetation consists primarily of cool-season species. However, little research has been done in northern foothills grasslands in and near Montana, where most precipitation comes in spring and summer, supporting a mixture of cool- and warm-season plant species. Climate and vegetation differ between the northern foothills grasslands and the Great Basin, so the ecological impacts of cheatgrass in the northern foothills grasslands are unknown. In order to better understand cheatgrass ecology in this region, we assessed cheatgrass abundance in foothills ecosystems in Montana. Fifteen study plots were established at each of two ranches in Montana, both of which are owned and operated by the Montana Agricultural Experiment Station: Thackeray Ranch, southeast of Havre, Montana, and Red Bluff Ranch, east of Norris, Montana. At these plots we examined relationships among cheatgrass abundance, biotic and abiotic site characteristics (e.g. species diversity, soil depth), and disturbance indicators (e.g. livestock fecal counts) in 2014 and 2015. Large generalized linear mixed-effects regression models for each ranch were reduced to simpler models by comparing the Aikake's Information Criterion (AIC) for each fitted model, and selecting for lower AIC to best describe cheatgrass abundance. Multimodel inference based on the best models for each ranch identified important variables to predict cheatgrass abundance. Disturbance and site characteristics such as aspect and soil texture are important predictors that land managers in the northern foothills grasslands could monitor to estimate the risk of cheatgrass invasion or dominance on the landscapes they manage.

INTRODUCTION AND BACKGROUND

Invasive plant populations rapidly spread and grow (Rejmánek and Richardson 1996), usually competing with native or preexisting species for space and/or nutrients, including water (Van Kleunen et al. 2010). Cheatgrass (*Bromus tectorum* L.) is an invasive annual grass in the United States, with impacts in cropland and rangeland ecosystems (Young et al. 1987). It was first documented in Montana in approximately 1900 (Hull and Pechanec 1947) and has since spread to every county in Montana (Menalled et al. 2008). Based on predicted climate change, cheatgrass has the potential to continue invading and expanding its range in Montana (Bradley 2009).

Cheatgrass was initially valued as a winter and early spring forage in the Great Basin (Stewart and Hull 1949; Klemmedson and Smith 1964). Because cheatgrass germinates in the fall, overwinters with a few basal leaves, and then continues to grow when it is exposed to adequate sunlight, temperatures and moisture, it can provide nutritious forage several weeks before other forage plants emerge from dormancy (Stewart and Hull 1949). More recently, however, the negative qualities of cheatgrass have outweighed its benefits. The following review examines relationships among cheatgrass and various disturbances and site characteristics in Western North America with a focus on literature from the Great Basin and Montana. Nomenclature follows the USDA PLANTS database (NRCS 2016).

Fire

Cheatgrass can dominate a site within eight years post-fire (Diamond et al. 2009; Shinneman and Baker 2009), and abundant cheatgrass tends to increase fire frequency and intensity in some areas (Young et al. 1987; Billings 1992). In these areas, fire encourages high cheatgrass abundance, and abundant cheatgrass encourages frequent fire, in a positive feedback loop. Recent research suggests that this positive feedback loop is not present in other parts of the western United States, including some areas of sagebrush steppe, where the summers are relatively cooler and wetter (Bradley 2009; Taylor et al. 2014; Brummer et al. 2016). Where cheatgrass is positively associated to fire, some features of cheatgrass may directly encourage frequent fires. Cheatgrass provides a spatially continuous supply of flammable material, even though the biomass of fine fuels may be lower in cheatgrass patches than in native shrubland or bunchgrass-dominated range, as shrubs and bunchgrasses accumulate litter biomass for relatively long periods of time (Whisenant 1990). Frequent wildfires, often attributed to these continuous fine fuels, present a major change to cheatgrass-invaded landscapes; some regions now experience major fires every five years or less but previously had fire return intervals of up to one hundred years (Whisenant 1990).

Native shrubs and perennial bunchgrasses may be severely reduced by hot, frequent fires, which can damage their growing points (e.g. the crown of a bunchgrass) and limit or eliminate their ability to regrow (Antos et al. 1983). The loss of these species can threaten soil integrity by reducing perennial cover and root stabilization of the soil until subsequent vegetation can establish (Stewart and Hull 1949), and can reduce habitat

suitability for native species such as the greater sage-grouse (*Centrocercus urophasianus*) that rely on shrubs or bunchgrasses for shelter and/or food (Crawford et al. 2004).

Vegetation

The reduction in post-fire competition may be an indirect mechanism by which cheatgrass invades and expands in burned areas. In part, the removal of shrubs can create highly fertile locations for cheatgrass seedlings to establish, and ash can help improve soil-seed contact (Evans and Young 1983). In addition, bunchgrasses can burn relatively hot and for long periods of time because of the accumulation of litter in and around the tussock, and their ability to regrow can be seriously hindered after fire, if they survive the fire at all (Conrad and Poulton 1966). The mortality or reduced vigor of bunchgrasses after fire thus limits competition for resources at and below the soil surface and allows cheatgrass to invade or spread (Davis et al. 2000).

Native vegetation density and cover are inversely related to cheatgrass biomass and density (Beckstead and Ausgpurger 2004). For example, cheatgrass cover and production is lower in communities with closely spaced bunchgrasses than it is in communities with extensive gaps between native plants (Reisner et al. 2013; Rayburn et al. 2014). The combination of large and small-scale aggregation of native plants, which suggests very high native density and cover at both scales, may contribute to community resistance to cheatgrass invasion (Reisner et al. 2013).

Cheatgrass is a common understory species even in undisturbed communities but it does not generally dominate these communities, which suggests that it relies on

disturbances such as fire or heavy grazing to become highly abundant (Stewart and Hull 1949; Hulbert 1955; Brummer et al. 2016). With disturbance, cheatgrass may directly outcompete and replace desirable forage species by growing roots and leaves much more rapidly (Svejcar 1990) and thereby surpassing perennials' ability to compete for resources (Rummell 1946; Harris 1967; Melgoza et al. 1990; Humphrey and Schupp 2004). Once cheatgrass is abundant, many perennial grasses (native and introduced) germinate but fail to establish when seeded into cheatgrass-dominated stands (Stewart and Hull 1949). In addition, mature cheatgrass plants can produce enough seeds to outnumber native perennial seeds by up to three orders of magnitude (Humphrey and Schupp 2001). Thus, if a fire or other disturbance damaged adult perennials, then the superabundant cheatgrass seed would outnumber the few potential perennial recruits and inhibit perennial stand renewal. Occasionally, a second cohort of cheatgrass can establish in late spring and mature within the summer growing season, or existing plants will produce a second crop of seeds (Harris 1967; Mack and Pyke 1983). In these cases, cheatgrass seedlings can take advantage of shallow nutrients between established adults and may crowd out the perennial seedlings (Rummell 1946).

Cheatgrass roots are most abundant in the uppermost 20-30 cm of soil (Hulbert 1955; Cline et al. 1977). As a result, cheatgrass may outcompete natives and deplete shallow soil water available early in the growing season, especially important when deeper soil is relatively dry. Where cheatgrass is present and actively growing, soil water is less available in the top 20 cm and native perennials produce less biomass than the same native species without cheatgrass within a meter radius (Melgoza et al. 1990).

However, cheatgrass root systems often extend as deep as 105 cm, and up to 150 cm deep, much deeper than expected for an annual plant (Hulbert 1955; Harris 1967). These extensive roots could provide a considerable advantage for cheatgrass to compete for water or nutrients at all depths. With incident precipitation, the shallow roots take advantage of shallow moisture; any precipitation that infiltrates beyond the top 30 cm could also carry soluble nutrients away from the soil surface, and the deeper roots of cheatgrass could compete against the perennials' deep roots for these nutrients.

Even compared with other annuals, such as mustards (*Descurainia* and *Sisymbrium* spp.), cheatgrass is very successful at establishing and multiplying in new areas to the exclusion of most other plants (Piemeisel 1951; Young et al. 1987). Water requirements for spring annual forbs to produce seed can be higher than the water needs for cheatgrass to produce seed, so particularly dry regions and/or dry years may favor cheatgrass over invasive annual forbs (Piemeisel 1951).

Occasionally, individual species have positive or negative associations with cheatgrass success. In Idaho, bulbous bluegrass (*Poa bulbosa* L.) was the only broadcast seeded species that successfully established in an established stand of cheatgrass (Stewart and Hull 1949). Crested wheatgrass (*Agropyron cristatum* L. Gaertn.) is rarely successful at establishing in cheatgrass stands, but if it establishes and survives for three years, crested wheatgrass dominates over cheatgrass (Stewart and Hull 1949). Crested wheatgrass is also a strong negative correlate to cheatgrass cover in many sagebrush steppe areas (Brummer et al. 2016). In western Colorado, prairie junegrass (*Koeleria macrantha* [Ledeb.] Schult.) was positively associated with cheatgrass whereas

intermediate wheatgrass (*Thinopyrum intermedium* [Host] Barkworth & D.R. Dewey) and James' galleta (*Pleuraphis jamesii* Torr.) were negatively associated with cheatgrass (Getz and Baker 2008). James' galleta and intermediate wheatgrass are both rhizomatous grasses, but galleta is a warm-season (C4) species and the wheatgrass is a cool-season (C3) species. Prairie junegrass is a cool-season bunchgrass. Because of these differences in structure and phenology, it is unlikely that all of these species interact with cheatgrass in the same way. However, it is unknown whether the species relationships are mutualistic or competitive, or simply correlative (Getz and Baker 2008).

Cheatgrass may take advantage of microclimatic conditions provided by existing vegetation when it first invades a site. Herbaceous litter cover, for example, is directly related to cheatgrass establishment and winter survival (Beckstead and Augspurger 2004). Higher litter cover may increase water retention of the underlying soil and collect wind-dispersed cheatgrass seeds better than bare soil would (Stewart and Hull 1949; Beckstead and Augspurger 2004). Litter cover may also help insulate rosettes of cheatgrass leaves during winter. Based on all of these effects, litter cover could increase the ability of an area to support cheatgrass germination and seedling establishment. However, given that cheatgrass litter biomass is lower than bunchgrass litter biomass (Whisenant 1990), it is unlikely that cheatgrass relies entirely on its own litter for establishment and survival especially when it first invades a community. Instead, cheatgrass seeds may take advantage of litter from preexisting vegetation, which can provide safe sites for cheatgrass establishment.

Shrubs may impact cheatgrass invasion and abundance beyond providing a bed of litter for seed capture and germination. Deep-rooted shrubs such as sagebrush (*Artemisia* spp.) and some deep-rooted perennial grasses may increase local water and nutrient availability by drawing on deep soil resources and relocating them nearer to the surface (e.g. hydraulic lift; Caldwell et al. 1998). Shrubs and large bunchgrasses also provide shade; intercept and channel precipitation (e.g. bluebunch wheatgrass; Ndawula-Senyimba et al. 1971), which can prevent runoff by reducing the force of water reaching the soil surface; and create abundant litter (the “resource island” effect; e.g. Charley and West 1975). Spaces below shrubs may therefore support cheatgrass plants with higher biomass and seed production than cheatgrass plants outside the radius of the shrub’s influence (Meyer et al. 2001; Chambers et al. 2007). If this is the case, shrub abundance may influence the pattern of cheatgrass establishment and expansion, and may explain some of the success that cheatgrass has exhibited when invading sagebrush ecosystems, although variable landscape-scale resource availability contributes substantially to cheatgrass invasion success (Beckstead and Augspurger 2004; Chambers et al. 2007; Brummer et al. 2016).

Livestock and Wildlife

While most livestock (e.g., horses [*Equus caballus*], cattle [*Bos taurus*], sheep [*Ovis aries*]) and some wild herbivores (e.g., mule deer [*Odocoileus hemionus*], bighorn sheep [*Ovis canadensis*]) will readily consume young cheatgrass, the plant becomes unpalatable and has low forage quality when mature and dry (Hull and Pechanec 1947;

Stewart and Hull 1949; Harris 1967). Livestock that graze mature cheatgrass can be irritated or wounded if its long awns become embedded in wool or hair, nostrils, and gums (Mosley and Roselle 2006). In addition, cheatgrass productivity and nutritive quality vary greatly from year to year (Schmelzer et al. 2014), and producers can struggle to maintain the productivity of their herds if they rely on cheatgrass as a primary forage source (Hull and Pechanec 1947; Klemmedson and Smith 1964).

Intense livestock grazing may encourage cheatgrass establishment (Hull and Pechanec 1947; Reisner et al. 2013). When grazed heavily, areas dominated by perennial bunchgrasses may be more vulnerable to cheatgrass invasion and spread. Intense grazing may reduce bunchgrass productivity and cause populations to decline over time. In bunchgrass communities, native vegetation is generally sparse between bunches, so there is little other competition to cheatgrass invasion (Young et al. 1987; Billings 1992). In a later study, the positive association between cattle and cheatgrass invasion was confounded by high cattle use along roadsides, which are often implicated in cheatgrass invasion and establishment (Getz and Baker 2008). However, insight from other studies may support the idea that heavy grazing encourages cheatgrass. Though it actively grows in fall and winter, cheatgrass may be too short to be eaten by large herbivores during that time. Cheatgrass may only be widely accessible at “grazing height” for cattle (>4 cm) more than two weeks after neighboring perennial grasses due to cheatgrass’s prostrate growth form during the winter (Harris 1967). Adult plants of one variety of bluebunch wheatgrass, “Whitmar”, for instance, begin new leaf growth around the same time as cheatgrass in the fall, and may then have several cm of green leaves early in the

subsequent spring (Harris 1967). As a result, excess early cattle grazing could disproportionately harm the perennials, if they were a more accessible forage option for that time. Even if not excessive, cattle grazing may reduce bunchgrass and biological soil crust cover, and the concurrent increase in bare ground and available soil resources may then encourage cheatgrass invasion (Reisner et al. 2013).

Wild herbivores may also influence cheatgrass abundance. High deer and elk use of burn edges (the boundary between burned and unburned areas) may increase cheatgrass cover along those edges (Getz and Baker 2008). The authors postulate that wildlife could inadvertently bring in cheatgrass seeds from other habitats, and their movement and foraging could disturb the soil. However, high cheatgrass cover and wildlife preference for the edges of burned areas could simply coincide. Cheatgrass may flourish at fire edges due to a combination of outcomes of the fire itself. First, it is likely that fire temperatures are relatively low at edges, such that any cheatgrass seed present at the edges of the fire would be unharmed, and adequate litter to provide a safe site for germination could persist (Young et al. 1976). Secondly, vegetation on the burned side of the edge would no longer be competitive, so any cheatgrass germinating on the edge could have up to 50% less competition than cheatgrass germinating on the unburned side. Essentially, it is unclear whether the deer and elk presence have an additional impact beyond the impact of fire when both disturbances occur.

Rodent activity may cause enough soil disturbance to enable cheatgrass to dominate a community (Hulbert 1955; Young et al. 1987). However, there is little information on which rodent species may be the primary culprits, nor is there information

on how rodent activity appears to facilitate cheatgrass dominance. Rodent burrows may have twice the cheatgrass density and nine times the seed production as non-burrow areas of the same site (Hulbert 1955). Montane voles (*Microtus montanus nanus*) have been present in large numbers where cheatgrass is also abundant, but no causal relationships have been hypothesized (Piemeisel 1951, 1954). In fact, herbivory of cheatgrass along vole “runways” has been documented in eastern Washington beneath snow cover, without soil disturbance in the area (Mack and Pyke 1983). In this case, the voles may have selected for habitats with winter annual plants as food sources, and cheatgrass simply happened to be present.

Insects may also rely on cheatgrass for food. In Utah, two grasshopper species were observed consuming cheatgrass, although the grasshoppers did not reduce cheatgrass abundance (Beckstead and Augspurger 2004). It is also unlikely that grasshoppers or other insects contribute to cheatgrass seed dispersal.

Human Disturbance

Paved and unpaved roads and railroads are often associated with the spread of introduced species. Roads may also function as a measure of disturbance directly from creating and maintaining the road. People remove existing vegetation and relocate soil, often inadvertently translocating exotic seeds (Tyser and Worley 1992; Gelbard and Belnap 2003; Barney 2006). Cheatgrass cover can be much greater near paved roads than near four-wheel-drive vehicle paths at a range of distances from both road types, so it is possible that further invasion of cheatgrass could be limited by avoiding high-impact road

construction (Gelbard and Belnap 2003). In western Colorado, cheatgrass is also more abundant along road edges than in unremediated burned areas (Getz and Baker 2008).

Abiotic Site Characteristics

Slope, elevation, soil texture and depth, aspect, and water availability are among many abiotic characteristics that have been investigated in the context of cheatgrass invasion. Higher elevations, such as those above 1800 m, tend to have lower levels of cheatgrass than areas closer to sea level (Chambers et al. 2007). However, cheatgrass cover does not relate to elevation in western Colorado (Shinneman and Baker 2009), and different relationships between cheatgrass and elevation exist in Nevada (limited cheatgrass establishment at higher elevation) versus in Utah (limited cheatgrass establishment at lower elevation) (Roundy et al. 2005). In Nevada and Utah, even though water-year precipitation increases with increasing elevation, precipitation and soil temperatures may interact to cause the contradictory results of Roundy et al. (2005). Environmental variables may also be influential in other areas (Brummer et al. 2016), such as the timing and amount of precipitation, which can vary within and across elevational gradients.

In Washington, cheatgrass on a north-facing slope can produce nearly one-third greater root biomass and about as many more seeds than on a south-facing slope (Hinds 1975). North-facing slopes may be a more suitable environment for cheatgrass productivity than south-facing slopes with otherwise similar macroclimate characteristics such as precipitation and ambient air temperature. However, in Oregon and Nevada

south-facing slopes more frequently have cheatgrass than north-facing slopes, and often have higher cheatgrass abundance than north-facing slopes (Platt and Jackman 1946; Billings 1992). This apparent conflict may reflect that the Washington experiment included no competing plants; with competition, cheatgrass may be less invasive on north-facing slopes, especially if competitors also grow more vigorously on north aspects than on south aspects. A thriving preexisting community would decrease the niches available for cheatgrass, and thus cheatgrass would not establish as well on north-facing slopes with lush preexisting vegetation. Sun exposure, heat load and moisture are associated with aspect (Buffo et al. 1972; Hanna et al. 1982; McCune and Keon 2002), such that south-facing slopes in the Northern Hemisphere receive higher insolation and have lower effective moisture because of higher evaporation rates. As a result, the harsher microclimate of south-facing slopes may have fewer competitors that compete for more limited resources.

Soil texture may be especially important in saline areas. Cheatgrass is found only on well-drained portions of saline areas in the Snake River Plains in Idaho, where salt-desert shrubs have declined (Stewart and Hull 1949). These areas probably have sandier, coarser soils, which allow salts to dissolve and dilute with precipitation. In Utah, reduced soil compaction has a strong positive effect on cheatgrass biomass and density (Beckstead and Augspurger 2004), which suggests that sandy soils in many systems may support plentiful cheatgrass because they are unlikely to become seriously compacted.

Far-below-average precipitation (82mm) during the cheatgrass growth season (~October-May) in a salt desert shrubland limits cheatgrass establishment, and cheatgrass

fails to reproduce (Meyer et al. 2001). However, experimentally-added water in October and March increases individual cheatgrass plant biomass when growing near shrubs. As a result of this strong response to moisture, Meyer et al. (2001) expresses concern that several consecutive wet years could propagate a gradual expansion of cheatgrass even in a previously intact shrubland in the Great Basin.

In other habitat types, soil moisture directly relates to how early cheatgrass can establish. Moist sites will support cheatgrass germination and seedling emergence in late summer, while dry sites may delay germination until late fall or even winter (Mack and Pyke 1983). Cheatgrass seed production on dry sites also varies more than cheatgrass seed production on mesic or moist sites, probably due to greater fluctuations in resource availability on dry sites from year to year. As a result, dry sites may have unpredictable cheatgrass populations across years, as the seed bank could fluctuate substantially with different environmental conditions.

Research from Montana and Other Northern Foothills Grasslands

Northern foothills grasslands (NFG) encompass certain parts of the region commonly known as the Northern Great Plains (NGP). The NGP encompasses much of central North America, including Montana, Wyoming, the Dakotas, and southern Canada (Coupland 1961; Samson et al. 2004), and is commonly characterized as tallgrass and mixed-grass prairie. In contrast, NFG ecosystems often include mixtures of Great Basin and NGP species (described in the following section), and are located on or near the

central and northern Rocky Mountains foothills. Much of the research from Montana to date has occurred in these NFG and is described here.

Based on climatic envelope models, locations with low summer precipitation are at greater risk of cheatgrass invasion (Bradley 2009). If summer precipitation in southwestern Montana decreases as predicted (Bradley 2009), cheatgrass could expand into currently uninvaded areas. A decline in summer precipitation could also impact wildfire regimes. Contrary to the Great Basin (GB), the Great Plains (GP) and NFG may not support the positive relationship between cheatgrass and fire frequency. Summer precipitation may influence the extent to which fire encourages cheatgrass. Specifically, wetter summers may inhibit the positive feedback loop between cheatgrass and fire that can occur on sites with similar annual precipitation and dry summers (Taylor et al. 2014). For example, summer precipitation the year before a fire was negatively associated with cheatgrass cover after fire (Shinneman and Baker 2009).

Although fine fuels continuity is directly and positively related to cheatgrass cover, litter (i.e. fine fuel) cover in the GP is not directly related to cheatgrass cover (Taylor et al. 2014), similar to findings in the GB. Litter cover is, however, positively related to shrub and bunchgrass cover, which supports the hypothesis that cheatgrass may rely on litter of other species for its seedling establishment. Once established, cheatgrass cover and dominance are inversely related to native species abundance and richness in the NFG/NGP just as in the GB (Shinneman and Baker 2009; Metlen 2010; Taylor et al. 2014).

Voles may be related to cheatgrass abundance in the NGP as they seem to be in the GB. Bird (1930) believes Drummond's vole (*Microtus pennsylvanicus drummondii*, now known as meadow vole) is the most influential animal species in the tall-grass prairie of Manitoba and Saskatchewan. While he does not discuss cheatgrass itself, he reports that these voles actively consume seeds and shoots throughout winter, when cheatgrass might be one of few forage options.

Recent research in Montana has focused on treatment and management of existing cheatgrass stands, rather than understanding – or attempting to prevent – its invasion. Sloane (2011) successfully uses sugar beet pulp to reduce cheatgrass productivity more severely than it reduces productivity of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Á. Löve), a desired native perennial, as a less costly alternative to sucrose application (e.g. Beckstead and Augspurger 2004) for the same purpose. Imazapic herbicide effectively reduces biomass and plant density of cheatgrass after greenhouse and rangeland applications, and application of *Pyrenophora semeniperda*, a fungal pathogen, limits seedling emergence (Ehlert 2013).

In a rangeland setting, elk in western Montana consume cheatgrass and other invasive forage species, especially during fall and winter (Kohl et al. 2012). Metlen (2010) examines cheatgrass in Montana in an invasion context; microsites below Ponderosa pines (*Pinus ponderosa* Lawson & C. Lawson) have more abundant cheatgrass than adjacent open prairie sites. The pines, like shrubs, provide shade which usually increases moisture levels beneath the canopy relative to the surrounding moisture levels (Charley and West 1975). In Metlen's (2010) study, pines are also associated with

relatively high nutrient (nitrogen and phosphorus) content in the surrounding soil, which may further encourage cheatgrass growth once it has invaded. Cheatgrass also competes strongly with Idaho fescue (*Festuca idahoensis* Elmer) both in the nutrient-rich soil from beneath the pines and in less fertile prairie soil, but the fescue is much less competitive in the prairie soil. In general, native cover and cheatgrass cover are inversely related.

Historical research on cheatgrass ecology in Montana is limited. Warg (1938) is among the first in the state to study cheatgrass, its life history, and its response to environmental variables on rangelands and in greenhouses. For example, he records the influence of smut (*Ustilago bromivora*, a fungus) on cheatgrass, and describes low germination rates when seeds are exposed to moisture and freezing temperatures. Under all other tested conditions, cheatgrass has higher germination rates than bluebunch wheatgrass and crested wheatgrass. Further, after only one month of seedling growth in a greenhouse, cheatgrass seedling height and overall vigor are higher than bluebunch wheatgrass seedlings.

Montana crop fields, abandoned for one to ten years, all have cheatgrass as a principal component in the community even as other plants – including bunchgrasses – recolonize the fields (Warg 1938). At the same time, Warg (1938) suggests that cheatgrass dominance in heavily grazed areas may be reversible after only two years of rest from grazing. He makes no indication that cheatgrass would ever be eliminated even after a native bunchgrass (Sandberg's bluegrass, *Poa secunda* J. Presl) rebounds as the dominant species, however.

Need for Research

Cheatgrass is one of the top three undesired weeds encountered in winter wheat plantings and fallowed plots, from a survey of several hundred farms located in central and eastern Montana (Johnson et al. 1997). Although cheatgrass entered the United States over a century ago and it has been studied in the Great Basin since its appearance there, only within the past thirty years has it become a concern in Montana (Menalled et al. 2008). As a result, not much is known about its regional invasion behavior.

The Great Basin (GB) is comprised of most of Nevada, reaching into western Utah, southeastern Oregon, and parts of eastern California and southern Idaho (Comstock and Ehleringer 1992). The NFG These regions have very different climates and associated plant communities.

The GB receives most of its 80-400 mm of annual precipitation in winter (Young and Evans 1973; Comstock and Ehleringer 1992; Knapp 1996), with annual temperatures ranging from an average low of -8°C to an average high of 30°C (Hinds 1975; Comstock and Ehleringer 1992; PRISM Climate Group 2016). In general, the GB is warmer and drier than the NFG, especially in summer. Aside from the Mojave Desert, most of the GB is at elevations above 1200 m (Comstock and Ehleringer 1992; Knapp 1996). Most GB vegetation is comprised of C3 (cool-season) bunchgrasses and shrubs. Lower elevation sites often have saline soils, and are dominated by salt-tolerant plants (Comstock and Ehleringer 1992; Knapp 1996).

In contrast, the NFG, on the edge of the NGP, receives most of its 310-600 mm annual precipitation in spring and early summer (Coupland 1961; Vermeire et al. 2011;

PRISM Climate Group 2016). Annual temperatures range from an average low of -19.5°C to an average high of 28°C (Adams et al. 1986; Mahmood et al. 2004). Elevations range from under 500 m to over 1100 m on peaks near the edges of the NGP, and often somewhat higher in the NFG (Coupland 1961). Common plant communities to the NGP include mixed- and tall-grass prairies and big sagebrush (*Artemisia tridentata* Nutt.) steppe communities with varying combinations of forbs and C3 and C4 grasses, both rhizomatous and caespitose, depending on latitude (Samson et al. 2004; Vermeire et al. 2011).

These fundamental differences in climate and preexisting vegetation between the GB and NFG may cause cheatgrass to invade or dominate Great Basin ecosystems differently than it invades or dominates Montana and other NFG ecosystems. Our objective was to study patterns of cheatgrass invasion and abundance in two foothills regions of Montana and to compare them to patterns in the GB.

Objectives

The specific objectives of this study were: 1) to identify and quantify biotic and abiotic site characteristics including vegetation, disturbance history, and climate that are found in cheatgrass-invaded locations in southwestern and north central Montana; and 2) to identify which of these site characteristics are correlated with cheatgrass presence and abundance in foothills regions in southwestern and north central Montana.

METHODS

Description of Study Locations and Site Selection

Study locations were established at Red Bluff Ranch (45° 35' 14" N, 111° 37' 11" W), east of Norris, MT, and Thackeray Ranch (48° 22' 7" N, 109° 35' 39" W), southeast of Havre, MT (Fig. 1, Appendix). Red Bluff Ranch is in the foothills of the Madison and Gallatin ranges of the Rocky Mountains. The substrate of Red Bluff is characterized by sandy-skeletal to fine-loamy soils, with gravelly to coarse-sandy loam surface horizons derived from gneiss, schist, and granite; some soils are very shallow, and there are occasional rocky outcrops (NRCS 2013b). Parent material beneath Red Bluff Ranch is comprised of the Tertiary Red Bluff formation (siltstone, sandstone, gneiss, and quartz) and Paleoproterozoic and Archean quartzofeldspathic gneiss and quartzite (Vuke et al. 2014). It receives 40.5 cm annual precipitation, mostly as rain in spring and autumn (30-year average; PRISM Climate Group 2016; Fig. 2, Appendix). The 30-year average minimum and maximum temperatures are -9°C and 28°C, respectively, with a range from -17.5°C to 32.8°C (PRISM Climate Group 2016). The dominant perennial vegetation at Red Bluff is summarized in Table 1 (Appendix).

Thackeray Ranch has fine- to coarse-loamy soils developed from igneous alluvial materials and/or glacial till in the foothills of the Bears Paw Mountains (NRCS 2013b). Parent material near the Bears Paw Mountains is almost entirely volcanic in origin, mostly Tertiary mafic and felsic volcanic rocks; some low-elevation draws are overlaid by Quaternary alluvium (Bergantino et al. 2002). Average precipitation at Thackeray is

43.8 cm annually, the majority coming as rain in the late spring and early summer months (PRISM Climate Group 2016; Fig. 2). The 30-year average minimum and maximum temperatures at Thackeray are -10°C and 26°C, respectively, with a range of -18°C to 30°C (PRISM Climate Group 2016). Common perennial plants observed at Thackeray are summarized in Table 1.

Site Selection 2014

In late June and early July, 74 cheatgrass-occupied sites were identified at Red Bluff and 64 sites identified at Thackeray, and their locations recorded by handheld GPS receiver (Garmin eTrex 30) at each ranch. Fifteen sites at each location were randomly selected from all identified cheatgrass-occupied sites. One rectangular 100m² plot (13 m x 7.7 m) was established at each selected site (wooden stakes at the corners of each plot), oriented to best encompass the patch of cheatgrass.

Site Selection 2015

In May and June of 2015, 20 sites not occupied by cheatgrass plants (seeds may have been present in the seed bank) were identified at each ranch and their locations again recorded by handheld GPS receiver. Of these sites, five were randomly selected at each ranch. One 100 m² plot (13 m x 7.7 m) was established at each selected non-invaded site with one corner at the GPS-indicated location, and marked by embedding wooden stakes at the corners. At Red Bluff, two apparently uninvaded plots ultimately contained small amounts of cheatgrass, so two additional uninvaded plots were established at randomly selected sites from the list of remaining identified uninvaded sites. In this way

the desired number of uninvaded plots (five per location) was maintained. The “extra” plots at Red Bluff were retained in the study.

2014 Data Collection

Within each plot, four 13-m transect lines were systematically placed perpendicular to the baseline (one 7.7-m side) of the plot. Plant community and species percent cover were described along these transects using the line-point intercept method (Herrick et al. 2005) every 25cm for a total of 52 points per line and 208 points per plot. Data from each line were aggregated into plot-wide mean values (e.g. mean cover by species or plant type) for analyses. Variables related to vegetative cover, such as bare soil, were also aggregated to the plot level based on line totals. Relative cheatgrass composition (hereafter, “cheatgrass abundance”) was calculated as the proportion of total vegetative cover contributed by cheatgrass. Perennial foliar cover was calculated as the number of perennial foliar hits out of the total possible hits in each plot. Basal perennial cover was calculated as the number of points within each plot that hit the base of a perennial plant at the soil surface divided by the total number of points in the plot (Herrick et al. 2005). Woody, herbaceous, and non-plant (e.g. livestock fecal deposit) litter and rock (e.g. exposed bedrock) at the soil surface were not considered perennial basal cover.

Livestock presence was approximated by counting total livestock fecal deposits (cow pies, clusters of sheep pellets; cattle provided the majority of fecal deposits at both ranches) in each plot. Many plots also had mounds of upturned soil from burrowing

rodents. Burrow mounds were measured by line intercept if the upturned soil appeared “fresh”; that is, the soil was easily moved by hand, with no apparent crust or compaction and no vegetation rooted in the mound. Hardened burrows and mounds were not included, as they were unlikely to be a result of current rodent activity. As a result, the disturbance they represented could have been irrelevant to the contemporaneous plant community, especially to annuals such as cheatgrass.

Soil cores were taken at two locations per transect, for a total of 8 cores per plot. These cores were systematically sampled on each transect; the first at a randomly generated whole number between 1 m and 7 m (inclusive), and the second at the first location plus 6 m. Cores measured approximately 5 cm in diameter and were inserted to a depth of 10 cm or until restrictive rock was encountered. In the event that the soil was not at least 3 cm deep at the sampling location, the core was moved to an immediately adjacent location and re-attempted. Any core shallower than 10 cm but at least 3 cm deep was noted on field data sheets. All cores from a plot were mixed in a single large paper bag in the field and labeled with the date and plot ID. After air drying for at least one month, subsamples of 30-80g were taken from the mixed soil for particle size analysis by the hydrometer method (Gee and Bauder 1986).

Aspect and slope were measured *in situ* with a handheld compass and clinometer, respectively. Elevation was recorded automatically when GPS points were recorded, and retrieved from the handheld GPS unit.

2015 Data Collection

Plots established in 2014 were relocated with the GPS receiver and transects were set up from the same baseline as in 2014. Stakes indicating plot corners had been uprooted and/or chewed by livestock at several plots, and twice, no stakes could be found, so we could not reestablish transects from the exact same baseline in 2015 as was used in 2014 (Plot 2 at Red Bluff, Plot 1 at Thackeray). As a result, some comparisons between years may have been influenced by shifts in plot location, given the limitations of our GPS precision (± 10 m).

Plot data were collected in the exact same manner as in 2014, with transect data aggregated per line and then combined for plot totals as before. In addition to fecal deposits, a common covariate to livestock use of an area, and in particular to cattle use, is the distance to a water source (Roath and Krueger 1982). Perennial and ephemeral streams were identified from a subset of the National Hydrology Dataset (USGS and EPA 2000) in ArcGIS (version 10.3.1) and then overlaid with the GPS locations of each plot. The linear measurement tool was used to estimate the distance of each plot to the nearest accessible water source within the pasture.

Soil core samples for surface soil texture analysis were taken from 2015-established plots and analyzed in the same manner as in 2014, with two differences. First, we could only obtain six of eight soil cores at Plot 20 at Thackeray because bedrock was present at the intended sampling locations on one transect. Second, due to the aggregated nature of the soil in many samples collected in 2015, subsample fine fractions were hand ground with a mortar and pestle to break aggregates into their particulate components

before re-sieving and hydrometer analysis. These samples may have been more aggregated due to the earlier sampling time and higher moisture content, or because many of the samples contained higher clay and silt fractions than most plots established in 2014.

Each plot's ecological site was keyed out using the Revised Montana Rangeland Ecological Site Key (hereafter, Site Key) of the National Range and Pasture Handbook (NRCS 2013a). At each plot, a small pit was dug by hand to 50 cm deep or until further digging was restricted or impractical due to a lithic, paralithic or and/or root-restrictive layer as defined by the Site Key. These pits were dug one pace (approximately 1 m) from the GPS-marked corner of each plot, with care taken to dig where no aboveground rocks obstructed digging. The full area of the plot and adjacent ground (within a buffer zone of 3-4 m) were considered when site features were assessed, such as slope or the predominance of boulders and cobbles on the soil surface. Additional materials were used when relevant to the Site Key, including 1M HCl in a small dropper bottle to determine the presence of carbonates in the soil. Often, hand-textured samples would be described as borderline between two distinct soil textures (e.g., loamy sand versus sandy loam) which could classify the site as a different ecological site type. Hand-textured surface soil was therefore compared to the hydrometer-ascertained surface soil particle size composition, which provides more distinct boundaries between soil textures by providing percentages of clay, silt, and sand. Hydrometer measurements took precedence in the event that a difference in soil texture would result in a different ecological site. Percent

slopes, when relevant to ecological site, were derived mathematically from the measured degree slopes for the plots.

Fire history was obtained from ranch manager records at Thackeray Ranch (Darrin Boss, personal communication) and from GPS-mapped fire perimeter and ranch records at Red Bluff Ranch (Becker et al. 2013; Clayton Marlow, personal communication). Plot locations were compared to locations of known burns, and each plot was recorded as burned or unburned. The most recent burn for all burned plots was the same year, 2012, and no other fires were recorded at our plots in the preceding twenty years. Plot 3 at Red Bluff Ranch was located on a two-track path that functioned as part of the firebreak and was not likely to have burned, so it was not recorded as a burned plot.

Data Analysis

All data were entered into a spreadsheet and identified by sample plot (e.g., “TH1” and “RB1”) for statistical analysis in program R via Rstudio (R version 3.1.1, R Development Core Team July 2014; Rstudio version 0.98.1028, Rstudio, Inc. 2013).

Certain variables were calculated from raw data, such as the Simpson Diversity Index (Simpson 1949). Simpson Diversity values were calculated using the *diversity* function from the *vegan* package in R, and excluded cheatgrass from the calculation to better estimate native diversity. Other variables were calculated by examining raw data and manually calculating relevant values, such as perennial basal cover and species richness. Basic summary statistics (sample means and standard deviations) were

compared between ranches within years, and between years within ranches by two-sample t-tests.

Initial data visualization included pairwise scatterplots for all explanatory variables and cheatgrass (Fig. 3 & 4, Appendix) to examine which relationships might prove useful in assessing cheatgrass invasion. Pairwise scatterplots also allow us to assess collinearity of paired explanatory variables. We reduced the number of variables included in models by eliminating one or more variables that were collinear to a given variable. Fewer variables allowed for relatively simple solutions that still adequately describe the patterns in cheatgrass abundance.

Given the substantial differences between Thackeray and Red Bluff, e.g. common vegetation, parent material, and precipitation, we analyzed each ranch separately. By separating the analyses we also avoided the need to test for interactions or other influences of region on results. However, we therefore sacrificed several degrees of freedom for analysis by splitting the total of 42 plots into groups of 22 plots (Red Bluff) and 20 plots (Thackeray), which limited the total number of variables which we could ultimately include in statistical models for each ranch.

Due to the large number of explanatory variables we measured, and the exploratory nature of this study, we chose stepwise model selection as a useful method to identify relevant explanatory variables. We used the *dredge* function (R package MuMIn, Bartón 2016) to identify the top predictive models for each ranch, based on Akaike's Information Criterion (AIC; Akaike 1987). This function takes a large model with several explanatory variables and fits smaller models using all possible subsets of the original

variables. Each smaller model's AIC is calculated and then compared to the AIC of the other models; models with the lowest AIC values are considered stronger predictive models. Models with AIC values that differ by less than 2 AIC units are generally considered to be equally strong models (Mazerolle 2004). Output models can then be viewed by AIC ranking, e.g. by "best" to "worst" model.

We intended to include as many explanatory variables as possible in initial ranch-specific models given the limited degrees of freedom, without including redundant variables identified in pairwise scatterplots. We did not have enough computational power to allow the *dredge* function to perform every possible model combination from all possible variables. Therefore, redundancy was identified by apparent linearity in the pairwise scatterplots and by high covariances (>0.5) in the covariance output from a large (e.g. twenty variables) fitted model. When no linear relationship was apparent among a group of variables, all of them were included in statistical analyses and the better predictors of the set were retained in final models. When multiple variables correlated to one another, the variable(s) that most clearly correlated to cheatgrass abundance in pairwise comparisons was (were) the variable(s) retained and other correlates were not included in the model. For example, soil sand content and elevation correlated closely; sand content had the stronger correlation to cheatgrass abundance, so it was the variable retained for analysis. Some variables had similar correlations to cheatgrass abundance, and thus both were retained in preliminary models; if one of them was much less important in these models, it was removed from subsequent model analysis, to facilitate simpler computations for model selection.

Binomial regression, in which zeros were incorporated into a continuous cheatgrass abundance variable, was used to describe relationships between cheatgrass abundance and site variables. Cheatgrass abundance was logit-transformed to better fulfill the assumptions of constant variance and linearity, as proportion data tend to violate these assumptions (Warton and Hui 2011). Numerical variables were relativized by dividing the residuals by the standard deviation using the *scale* function in R (base package, version 3.1.1). This process ensured that the variable values were on comparable scales for models to select models with the best predictor variables. For the strongest predictive power we included all data for each ranch in binomial regression models, including plot as a random effect because plots were selected from a larger population of plots, and plots established in 2014 were measured twice. Explanatory variables included in the initial model for each ranch are listed in Tables 2a and 2b (Appendix). Residuals plots were created to assess the assumptions of normality and constant variance in the initial model used for each ranch. The residuals plots indicate that these assumptions were not seriously violated (Fig. 5, Appendix). Top predictive models then included unique subsets of variables from the initial ranch-specific model.

With the limited degrees of freedom within ranches and the relatively large number of variables, we could not include all possible interaction terms in the initial models. For example, we would need 55 additional degrees of freedom to assess all two-way interactions among the eleven variables in the initial Red Bluff model. We would need a minimum of 67 plots to estimate coefficients for the eleven variables, 55 interactions, and intercept value. If we had that many plots, we could have included all

two-way interactions and allowed the AIC ranking to eliminate unnecessary terms. Of course, that many plots at Red Bluff alone was not feasible. Within our limitations, we did not have good reason to include arbitrarily selected interactions; we would need precedent data that suggested which specific interactions might apply in this system. Indeed, our results may provide that precedent for future study of cheatgrass in Montana.

However, we also fit the full models with 2014 and 2015 subsets of our data to try to explain quirks in the overall analysis that could be attributed to a year effect or year interaction. These models contained all the same variables as the original models and the *dredge* function was run on the year-specific models in the same way as for the models that incorporated both years of data. Top models from these single-year sub-models were also compared by AIC.

Variables that are consistently included in strong models are considered “important” variables. Importance values for each variable can be calculated by summing the model weight (calculated by R) for all models which include the variable, and models with low AIC have high weight. Importance scores range from 0.0 to 1.0 for any given variable. The most important variables from our modeling process are then the basis for our assessment of risk factors.

RESULTS

Summary StatisticsInvaded Plots

Table 3 shows a summary of numerical variables in cheatgrass-invaded plots at each ranch. For the purposes of these results and subsequent discussion, p-values ≤ 0.10 are considered evidence for a difference in means or for a linear relationship in t-tests and regression models, respectively. Upon examining the data, the two plots with uncertain plot locations (Red Bluff [RB] 2 and Thackeray [Th.] 1) did not appear to change to a greater extent than other plots between years, so any impact on data from their shift in plot location was probably minimal. Cheatgrass abundance was not statistically different at either ranch between 2014 and 2015 (RB $p=0.73$; Th. $p=0.47$). Red Bluff had more cheatgrass than Thackeray in both years although the difference was not significant in 2015 (2014 $p=0.10$; 2015 $p=0.15$). Plots at Red Bluff were all at higher elevations than plots at Thackeray ($p<0.001$) and plots at Thackeray were steeper (higher slope) than plots at Red Bluff ($p=0.011$). Cattle fecal count at these plots was similar between ranches in 2014 ($p=0.71$) and similar at Thackeray in both years ($p=0.84$); however, fecal count was much lower at Red Bluff in 2015 than 2014 ($p=0.036$).

Burrow cover was higher in 2014 for both ranches (RB $p=0.040$; Th. $p<0.001$); the difference between years was much larger at Thackeray and is likely due to the influence of two highly rodent-impacted plots in 2014. The reduced standard deviation in 2015 suggests that all plots' burrow cover amounts were more similar to one another in

2015 than in 2014. Actual burrow cover was probably larger at both ranches than our measured values, due to the constraint that intercepted burrows were only measured if mounds were “fresh”.

Table 3. Summary statistics for invaded plots at Red Bluff and Thackeray ranches in 2014 and 2015. Data are presented as mean $\pm$ SD. Data from 2015 included two additional invaded plots at Red Bluff. Units are listed in parentheses when applicable. Rel. abund. indicates relative abundance was calculated for that variable; richness is a count of plant species present in a plot. Aspect is not summarizable in the same way as these numerical variables because of its circular nature (i.e., an aspect of 1° [north] is almost the same as an aspect of 359° [north] but they would average out as the opposite aspect of 180° [south]) and therefore aspect was not included in this table.

Variable	2014		2015	
	Red Bluff	Thackeray	Red Bluff	Thackeray
Cheatgrass (rel. abund.)	0.2426 $\pm$ 0.1608	0.1580 $\pm$ 0.1031	0.2632 $\pm$ 0.1699	0.1918 $\pm$ 0.1140
Elevation (m)	1686.5 $\pm$ 138.4	1297.1 $\pm$ 40.3	1696.3 $\pm$ 132.4	1297.1 $\pm$ 40.3
Slope (°)	9.2 $\pm$ 4.8	14.4 $\pm$ 5.6	10.2 $\pm$ 5.4	14.4 $\pm$ 5.6
Manure (count)	15.7 $\pm$ 12.4	14.6 $\pm$ 14.7	7.2 $\pm$ 9.0	13.6 $\pm$ 13.9
Burrow cover (%)	3.49 $\pm$ 3.07	8.38 $\pm$ 6.18	1.52 $\pm$ 1.78	1.38 $\pm$ 1.45
Bare soil cover (%)	2.08 $\pm$ 1.94	2.95 $\pm$ 2.80	2.23 $\pm$ 2.12	2.02 $\pm$ 2.18
Sand content (%)	72.82 $\pm$ 14.24	66.13 $\pm$ 7.74	71.73 $\pm$ 14.19	66.13 $\pm$ 7.74
Litter cover (%)	82.46 $\pm$ 14.97	83.18 $\pm$ 6.35	81.48 $\pm$ 9.90	76.67 $\pm$ 9.39
Perennial basal cover (%)	14.49 $\pm$ 23.38	13.87 $\pm$ 8.37	18.89 $\pm$ 25.18	20.29 $\pm$ 14.69
Perennial foliar cover (%)	71.22 $\pm$ 14.37	63.13 $\pm$ 19.15	65.92 $\pm$ 15.29	71.38 $\pm$ 16.96
Richness	17.5 $\pm$ 4.2	23.7 $\pm$ 4.1	22.5 $\pm$ 8.4	28.7 $\pm$ 5.0
Simpson Diversity	0.8057 $\pm$ 0.1055	0.8832 $\pm$ 0.0236	0.7961 $\pm$ 0.1420	0.8948 $\pm$ 0.0311

Soils were sandier on average at Red Bluff than Thackeray, which relates to the younger parent material and less-developed soils at Red Bluff. The low-sand outlier at Red Bluff may contribute to the high p-value ($p=0.17$) by increasing the overlap in soil sand content between ranches. Litter cover was similar between ranches in 2014 ($p=0.75$) and at Red Bluff in both years ($p=0.83$), but it was lower at Thackeray in 2015 than 2014 ($p=0.022$), likely due to earlier sampling dates. Perennial foliar cover was no different at either ranch between years (RB $p=0.32$, Th. $p=0.22$), and did not differ between ranches ($p=0.35$).

Average perennial basal cover was no different in 2015 than in 2014 at Red Bluff ($p=0.61$), but tended to be higher at Thackeray in 2015 than in 2014 ($p=0.15$); similar to foliar cover, basal cover was quite variable, making the comparison between years indistinct. In 2014, Thackeray had more species per plot than Red Bluff (2014 $p<0.001$) and tended to have more in 2015 as well ($p=0.017$); the apparent increase in richness at both ranches in 2015 is likely due to earlier sampling. Simpson Diversity did not change between years (RB $p=0.84$; Th. $p=0.26$), but was higher at Thackeray in both years (2014 $p=0.014$; 2015 $p=0.019$).

Non-invaded (Zero) Plots

Table 4 summarizes numerical variables in cheatgrass-free (“zero”) plots at each ranch. Zero plots at both ranches were at lower elevations than plots with cheatgrass (RB $p=0.099$; Th. $p=0.045$). Slopes at non-invaded plots follow the same pattern as at invaded

plots, in that Thackeray has marginally steeper terrain ($p=0.15$) although the variability in slope steepness makes the comparison inconclusive.

Table 4. Summary statistics for uninvaded plots (established 2015) at Red Bluff and Thackeray ranches. Units are listed in parentheses when applicable. Rel. abund. indicates relative abundance was calculated for that variable; richness is a count of species present in a plot.

Variable	Red Bluff	Thackeray
Cheatgrass (rel. abund.)	0	0
Elevation (m)	1585.6 $\pm$ 110.5	1214.5 $\pm$ 65.7
Slope ($^{\circ}$)	8.8 $\pm$ 2.8	14.2 $\pm$ 6.6
Manure (count)	6.8 $\pm$ 5.0	8.2 $\pm$ 11.9
Burrow cover (%)	0.074 $\pm$ 0.17	0 $\pm$ 0
Bare soil cover (%)	2.60 $\pm$ 2.27	0.38 $\pm$ 0.86
Sand content (%)	64.49 $\pm$ 7.63	43.19 $\pm$ 15.11
Litter cover (%)	59.52 $\pm$ 9.71	86.35 $\pm$ 24.43
Perennial basal cover (%)	63.94 $\pm$ 28.27	25.10 $\pm$ 25.88
Perennial foliar cover (%)	69.90 $\pm$ 12.52	91.15 $\pm$ 16.89
Richness	14.2 $\pm$ 4.0	30.2 $\pm$ 3.8
Simpson Diversity	0.7406 $\pm$ 0.0818	0.8143 $\pm$ 0.0510

Manure counts were similar in non-invaded and invaded plots at Red Bluff ($p=0.91$), and counts on Red Bluff non-invaded plots were similar to the average counts on Thackeray non-invaded plots ($p=0.82$). Because zero plots at Thackeray were extremely variable, ranging from 0 to 27 fecal deposits, there is no meaningful difference

between non-invaded and invaded plot fecal counts at Thackeray ($p=0.42$). Rodent burrows were practically absent on zero plots – only one plot had any burrow cover (0.37% cover). Zero plots and invaded had similar bare soil cover at Red Bluff ($p=0.83$) but zero plots at Red Bluff had more bare soil than at Thackeray ($p=0.096$). Thackeray zero plots also had less bare soil than Thackeray invaded plots ($p=0.028$). Soils in non-invaded plots at both ranches tended to have finer textures (less sand) than the ranches' respective invaded plots, although the difference was more significant at Thackeray (RB $p=0.16$; Th. $p=0.025$) due to the high variability in sand content at Red Bluff's invaded plots. Thackeray zero plots were much less sandy than Red Bluff zero plots ($p=0.031$).

Non-invaded plots at Red Bluff had higher perennial basal cover than invaded plots ($p=0.018$) but basal cover was similar across invaded and non-invaded plots at Thackeray ($p=0.61$). The disparity in perennial basal cover between ranches' zero plots ($p=0.053$) may be because Thackeray zero plots had greater species richness than Red Bluff's zero plots ($p<0.001$). Thackeray zero plots also had higher perennial foliar cover than Red Bluff zero plots ($p=0.054$). Foliar cover was similar at Red Bluff's invaded and zero plots ($p=0.57$) but higher at Thackeray zero plots than invaded plots ($p=0.058$), often due to Kentucky bluegrass dominance and high cover of Thackeray zero plots. Simpson Diversity was higher at Thackeray than Red Bluff in zero plots ($p=0.084$), comparable to the difference between ranches at invaded plots. Diversity was also slightly higher in invaded plots than non-invaded plots at Thackeray but diversity at Red Bluff invaded and zero plots did not differ (RB $p=0.32$; Th. $p=0.10$; Fig. 6).

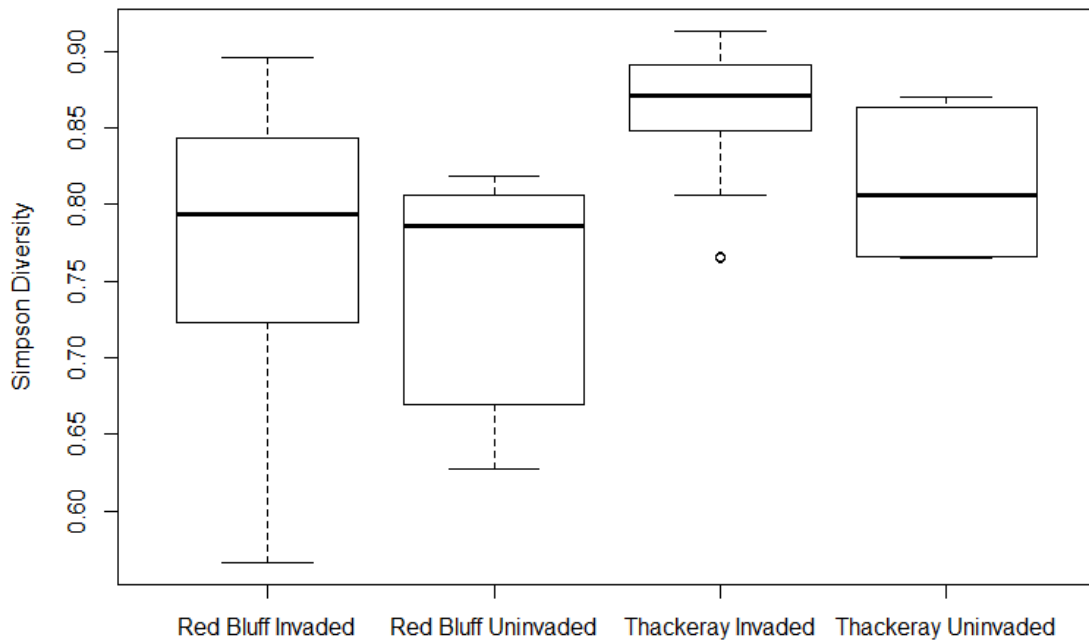


Figure 6. Simpson Diversity at cheatgrass-invaded and uninvaded plots at Red Bluff and Thackeray ranches in 2015.

Regression Model Results

Soil depth, soil sand content, slope, and aspect were selected to best represent differences in ecological site, given that there were 13 unique sites keyed out at Thackeray alone, and no good way to assign numerical values to ecological sites relative to one another. Scatterplots (Figs. 7-15) show the p-value for the linear correlation between cheatgrass abundance and each given variable in each year. These relationships are not directly related to the AIC-ranked model relationships but may reflect the strength of the relationship between cheatgrass abundance and the variable. A variable that has a comparable relationship both in the linear form and in the binomial regression model has a strong relationship to cheatgrass abundance regardless of the influence of other variables.

Red Bluff Models

The Red Bluff initial model variables are listed in Table 2a (Appendix). In exploratory models, $\cos(\text{aspect})$ was not strongly related to cheatgrass abundance, so only $\sin(\text{aspect})$ was included. Plot was included as a random variable.

From the included variables, the best predictors were year, burrow cover and $\sin(\text{aspect})$ (Table 5a,5b, Appendix). Importance values included in Table 5b are derived by adding all model weights for models that include the variable of interest, with a maximum importance of 1.00 because all model weights sum to 1 (Mazerolle 2004; Bartón 2016). The positive year effect could be attributed to variable precipitation before we sampled vegetation each year, earlier sampling in 2015, or many other variables which we did not measure in this study. Burrow cover was positively associated with cheatgrass abundance (Fig. 7). The positive relationship between $\sin(\text{aspect})$ and cheatgrass abundance indicated that cheatgrass had higher abundance on east-facing slopes than west-facing slopes (Fig. 8a). Although the pattern of higher cheatgrass abundance on east-facing slopes appeared in raw data for both years, once other variables were included there was no strong relationship within either year (Fig. 8b, Appendix). Raw data in the pairwise scatterplots also suggest there may be a slight positive correlation between $\sin(\text{aspect})$ and litter cover, and a slight negative correlation of $\sin(\text{aspect})$ to perennial basal cover (Fig. 3, Appendix).

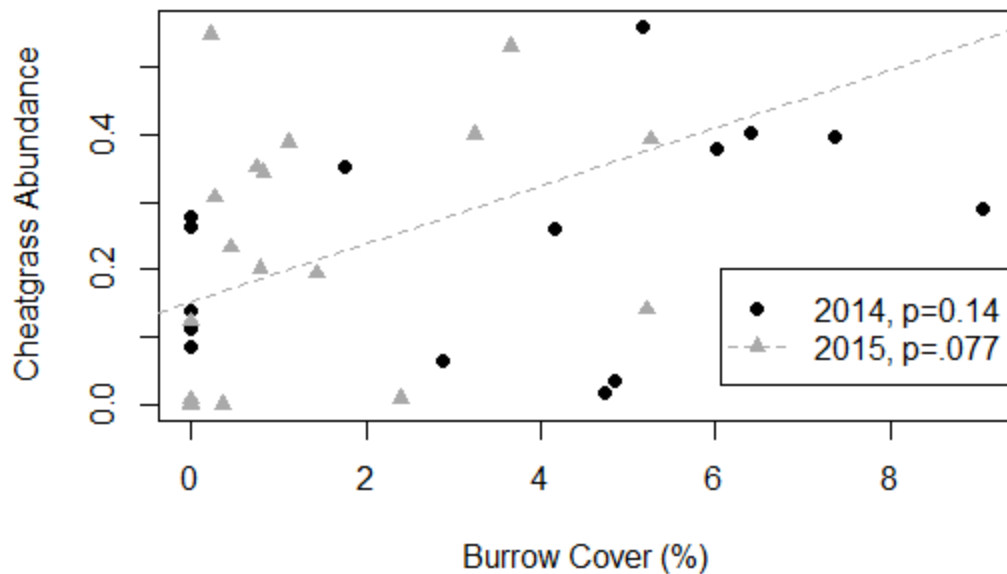


Figure 7. Cheatgrass abundance versus burrow cover at Red Bluff in 2014 (circles) and 2015 (triangles).

When the full Red Bluff model was subdivided into 2014 and 2015 models, new variables were important, and some variables deemed important in the full model were not as important in the year-specific models (Table 6a,6b). In the year-specific models, $\sin(\text{aspect})$ was not important in either year, and burrows were not important in 2014. Perennial basal cover was important and negatively related to cheatgrass abundance in both years, but the relationship was not important in the full model. This may be a result of two non-zero plots having fairly low cheatgrass abundance and high perennial basal cover, in combination with all zero plots having high perennial basal cover (Fig. 9); excluding zero plots leaves behind a trendless scatterplot. Simpson diversity and burn history were important only in 2014. The estimated coefficients for burn indicate a negative relationship between cheatgrass abundance and having burned. Diversity was likely not important in 2015 because most of the zero plots had relatively low diversity

(Fig. 10a). Their low values neutralize the otherwise strongly negative correlation between cheatgrass abundance and diversity, and probably drive the relative unimportance of diversity in the full model (Fig. 10b, Appendix). Litter cover (Fig. 11a,b, Appendix), manure (Fig. 12a,b,c, Appendix), and burrow cover were only important in 2015, and all three variables were positively related to cheatgrass abundance. The positive estimated coefficient for manure is not reflected in the scatterplot of cheatgrass regressed against fecal count in 2015 (Fig. 12a, Appendix). This relationship only arises when the other variables, e.g. litter or burrow cover, are accounted for (Fig. 12c, Appendix), and even then the trend appears highly impacted by a single plot's data. Although slope was not important in the modeling process, cheatgrass was slightly more abundant on flatter slopes, especially once zero plots were included (Fig. 13, Appendix).

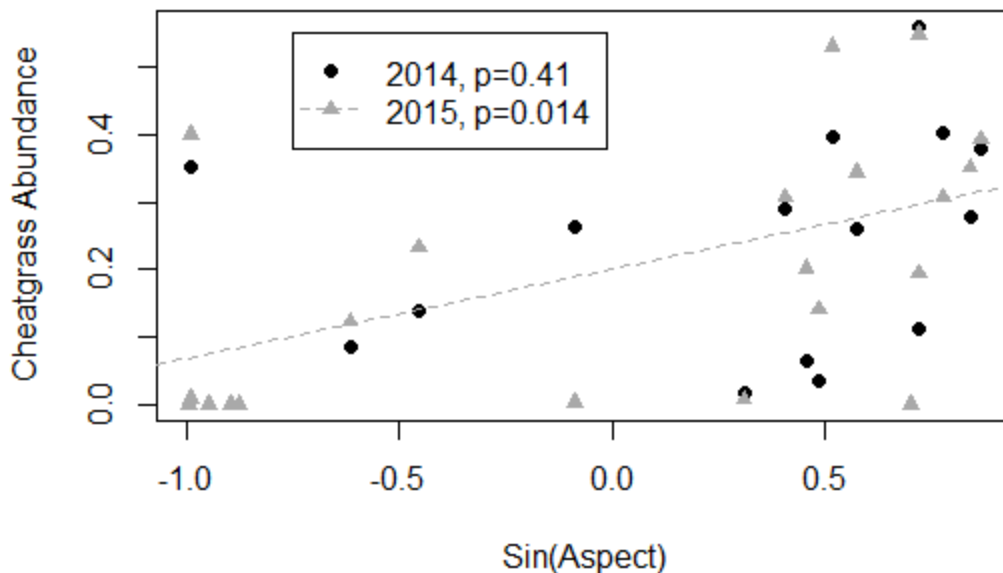


Figure 8. (a) Cheatgrass abundance versus sin(aspect): scatterplot of raw data showing the positive relationship between sine of aspect and cheatgrass abundance at Red Bluff, where sin(aspect) of +1 indicates a due east aspect and -1 is due west.

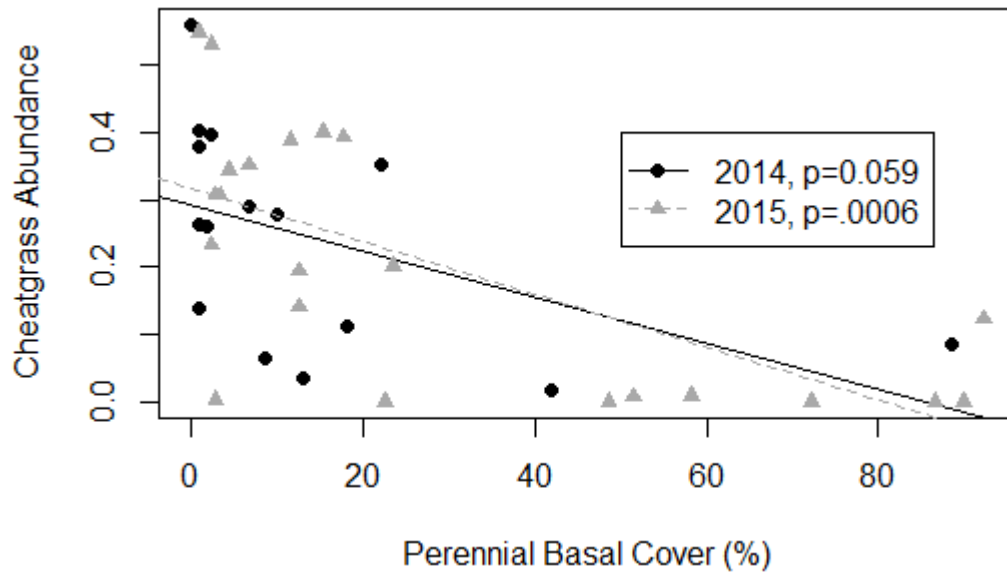


Figure 9. Cheatgrass abundance versus perennial basal cover at Red Bluff. Note only two plots in 2014 had perennial basal cover above 40%, and all zero plots from 2015 had relatively high perennial basal cover.

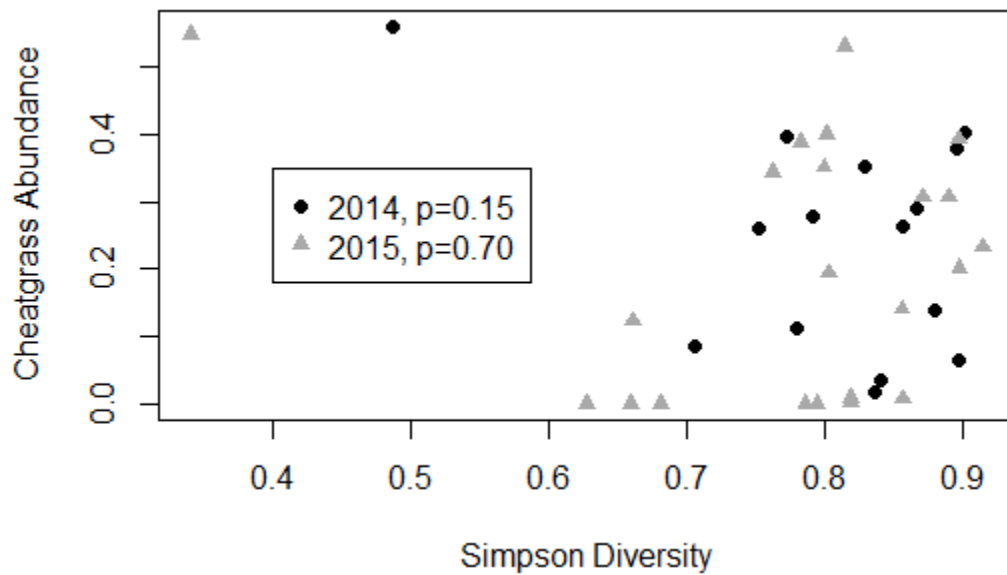


Figure 10. (a) Cheatgrass abundance versus Simpson Diversity at Red Bluff in 2014 (circles) and 2015 (triangles).

Thackeray Models

Thackeray initial model variables are listed in Table 2b (Appendix). High-ranked models from this large model indicated that $\cos(\text{aspect})$, sand, soil depth, and burrows were the most important variables for predicting cheatgrass abundance at Thackeray (Table 7a,7b, Appendix).

The negative association to $\cos(\text{aspect})$ indicates that there is likely to be more cheatgrass on south-facing slopes (Fig. 14). High sand content was also associated with high cheatgrass abundance (Fig. 15). Shallow soil profiles (<51 cm, or $<20''$) were associated with lower cheatgrass abundances (Fig. 16a). In 2014, there appears to be no relationship, if outliers are excluded (Fig. 16b, Appendix); in 2015, there appears to be curvature, or a more binary division between zero plots and invaded plots (Fig. 16c, Appendix), which is reflected by the distribution of depths in the original boxplot (Fig. 16a). Unlike at Red Bluff, burrows were negatively associated to cheatgrass abundance at Thackeray (Fig. 17a). The emergent negative association may be a result of a few outlying plots with extreme values (e.g. 21-22% burrow cover at plots 1 and 2) in 2014 but much less extreme values (2-3%) in 2015.

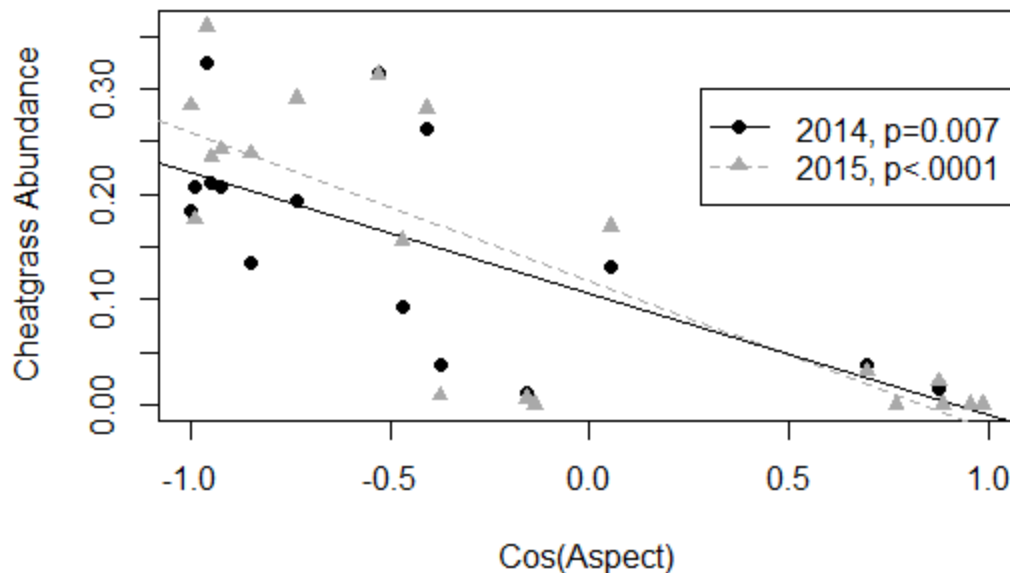


Figure 14. Cheatgrass abundance versus $\cos(\text{aspect})$ at Thackeray in 2014 (circles) and 2015 (triangles). A $\cos(\text{aspect})$ value of +1 indicates a plot faces due north, while a value of -1 indicates due south.

When we re-fit the initial Thackeray model as separate 2014 and 2015 models, $\cos(\text{aspect})$, bare soil cover, and sand content were the most important variables in both sub-models (Table 8a,8b, Appendix). Cosine of aspect related high cheatgrass abundance to south-facing slopes (Fig. 14); high bare soil cover related to low cheatgrass abundance (Fig. 18a); and high sand content related to high cheatgrass abundance (Fig. 15), in both models. The conflict between model and scatterplot relationships for bare soil suggests that bare soil had a negative relationship to cheatgrass abundance in 2015 only when the other included variables are considered (Fig. 18b,c, Appendix). The absence of burrows from both separate models suggests that burrows may only be important in the full Thackeray model because of differences in the relationship of cheatgrass abundance to burrow cover between years (e.g. a year x burrows interaction; Fig. 17b,c, Appendix).

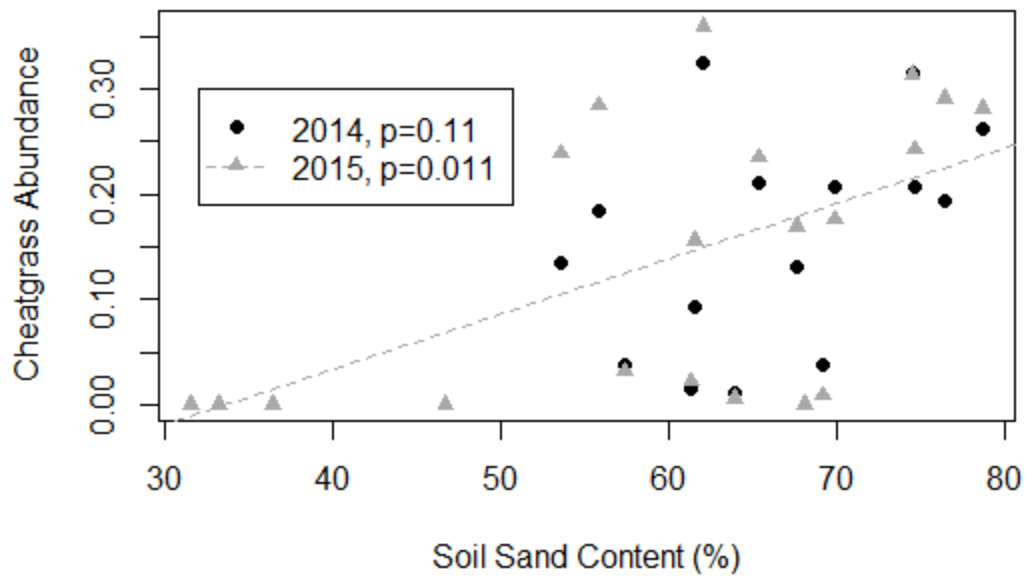


Figure 15. Cheatgrass abundance versus soil sand content at Thackeray in 2014 (circles) and 2015 (triangles).

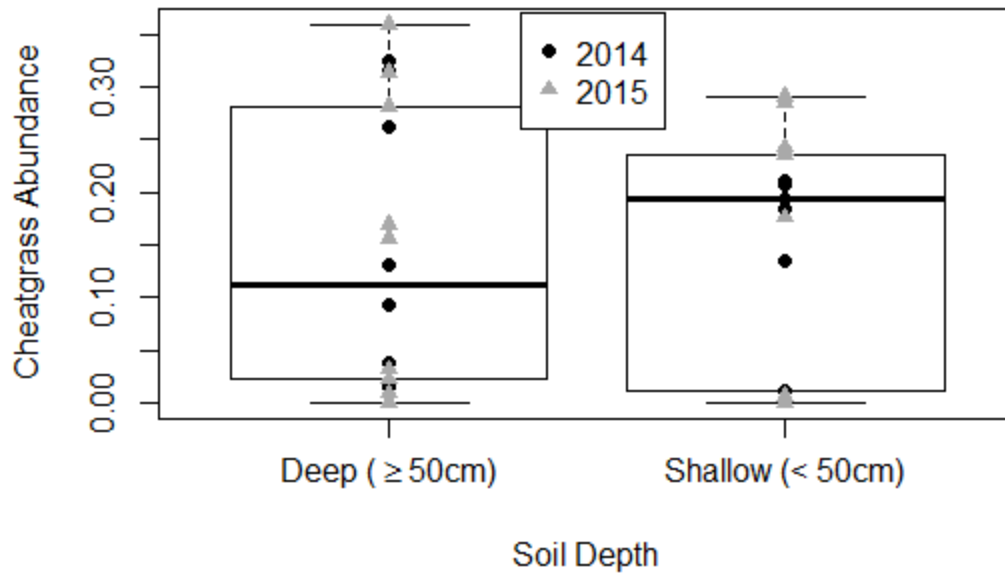


Figure 16. (a) Cheatgrass abundance versus soil depth at Thackeray in 2014 (circles) and 2015 (triangles).

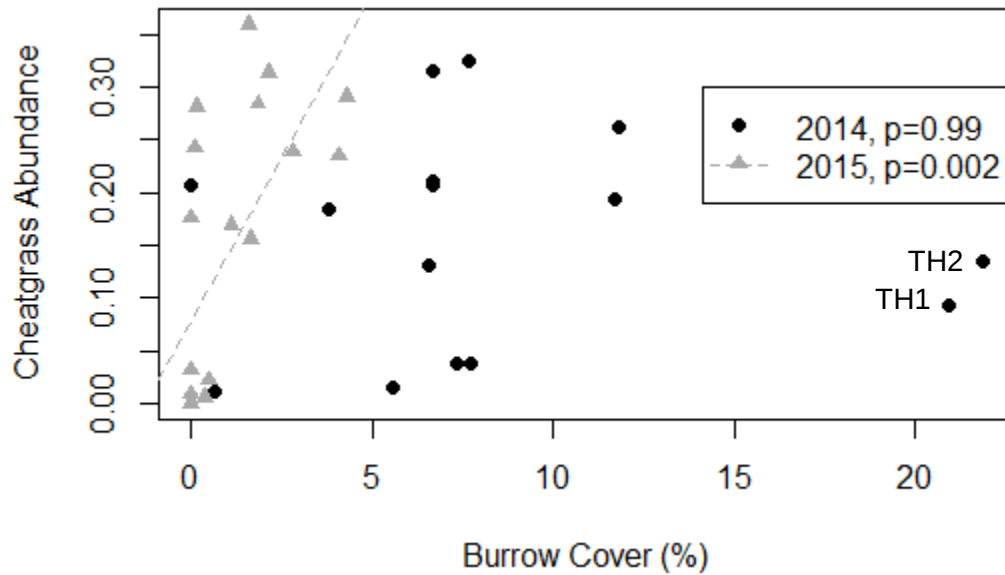


Figure 17. (a) Cheatgrass abundance versus burrow cover at Thackeray in 2014 (circles) and 2015 (triangles).

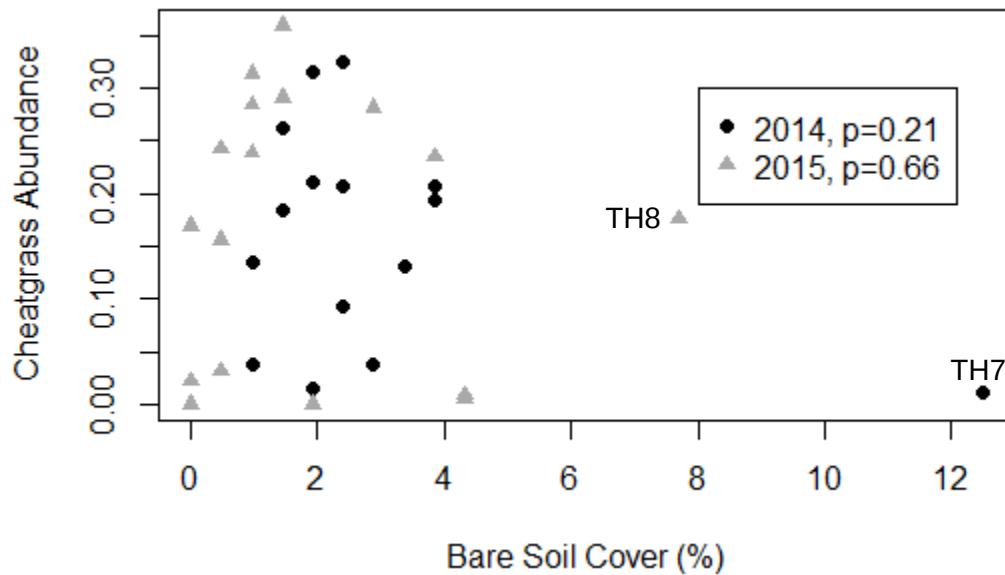


Figure 18. (a) Cheatgrass abundance versus bare soil cover at Thackeray in 2014 (circles) and 2015 (triangles).

DISCUSSION

Red Bluff

At Red Bluff, three variables were the most important from our full model: year, burrow cover, and sine of aspect. The positive association between year and cheatgrass abundance is likely a coincidence of higher cheatgrass in 2015 than 2014, and could be associated with higher spring precipitation received in 2015 (19.1 cm, March to May) than in 2014 (17.6 cm, March to May; PRISM Climate Group 2016). Preceding fall precipitation followed the opposite trend (14.2 cm and 10.2 cm, September to November of 2013 and 2014, respectively; PRISM Climate Group 2016), which may contrast the assumption that fall precipitation is not strongly related to cheatgrass abundance while spring/summer precipitation is directly related (Bradley 2009; Taylor et al. 2014). Additional years of data would be beneficial to explore this relationship further at Red Bluff as cheatgrass cover may also fluctuate based on other factors such as grazing patterns and seed predation.

The positive association we found at Red Bluff between rodent burrows and cheatgrass abundance could be explained by a number of factors. We cannot be certain whether cheatgrass attracts rodents, or rodent burrows encourage cheatgrass to proliferate on a site, or whether both organisms simply prefer similar habitats, but any of these relationships is possible. The most common rodents at Red Bluff during this study were Richardson's ground squirrels (*Spermophilus richardsonii* Sabine), a diurnal species of ground squirrel which creates extensive burrows in easily dug (i.e., sandy) soil on flat to

gently sloped sites (Bailey 1893; Quanstrom 1971). Cheatgrass was somewhat more abundant on flatter slopes at Red Bluff, so rodents and cheatgrass may be positively related because both species occupy gentle over steep slopes. The large particle size of soils preferred by ground squirrels may also support a greater amount of cheatgrass relative to perennials, because water can drain rapidly out of the profile of relatively coarse soils (Hillel 1998). The rapid draining and lower water-holding capacity of sandy soils makes these soils effectively drier than finer-textured soils with the same precipitation inputs. Cheatgrass may be more tolerant than natives such as bluebunch wheatgrass of these harsh soil conditions (Warg 1938; Harris and Wilson 1970).

Regardless of soil texture, Richardson's ground squirrels seem to select habitats with relatively short, uniform vegetation, such as pastures and hay fields, presumably to keep a wide visual range to watch for predators (Bailey 1893; Gilmer and Stewart 1983). Areas dominated by cheatgrass are likely to fulfill these habitat qualifications. Cheatgrass grows to heights below 60 cm (Warg 1938; Stubbendieck et al. 2011) and it senesces early in the season, so any visual obstruction from cheatgrass could be short-lived. In contrast, big sagebrush can be 50-200 cm tall or higher depending on climate and browsing pressure (Wamboldt and Frisina 2002; Stubbendieck et al. 2011), and it is generally broader than it is tall, creating large visual obstructions year-round. At the Red Bluff plots, all big sagebrush (mostly *A. tridentata* subsp. *vaseyana* [Rydb.]) we observed were below 150 cm tall and most individuals were broader than they were tall. Because of the physical structure, a mosaic of sagebrush and bunchgrasses could easily obscure aerial predators from a ground squirrel perspective. Further, Richardson's ground

squirrels rely on graminoids (rangeland grasses, rushes, grain crop stems) for nesting material (Quanstrom 1971). As a result, a near-monoculture of an annual grass such as cheatgrass could be preferable habitat over a sagebrush community for ground squirrels, and this may explain the relationship between burrows and cheatgrass abundance.

In the Great Basin, the relationship between rodents and cheatgrass has also been studied, but the primary rodents of concern seem to be voles, and no strong relationships to cheatgrass have been described. Voles were abundant on some sites dominated by cheatgrass in the GB (Piemeisel 1951,1954) and in one case voles appeared to consume cheatgrass along their winter “runways” (Mack and Pyke 1983). At Red Bluff, voles were occasionally seen on and around our study plots, but their burrow entrances were narrow and never had large mounds of disturbed soil. Rodent burrowing in general is perceived to be sufficient disturbance to facilitate cheatgrass dominance (Young et al. 1987). However, Richardson’s ground squirrels and other large burrowing rodents are more likely to encourage cheatgrass than voles are, based on the greater aboveground disturbance associated with the ground squirrels’ burrow entrances in comparison to those of voles (Quanstrom 1971; Mack and Pyke 1983). Because cheatgrass seeds have poor soil contact on flat surfaces (Kelrick 1991; Beckstead and Augspurger 2004), freshly disturbed soil, such as a new burrow mound, provides ideal sites for cheatgrass establishment.

From the top models, sine of aspect indicates that east-facing slopes had higher cheatgrass abundance than west-facing slopes. Moreover, when we first located study plots, the majority of sites on which we found cheatgrass tended not to face west. The

relative lack of west slopes within our observed plots suggests that cheatgrass may be more likely to invade east-facing slopes than west-facing slopes. East-facing slopes had less available water than south-facing slopes in one Nebraska study (Hanna et al. 1982) but this is an uncommon result. More often, south- and southwest-facing slopes are considered the driest in the Northern Hemisphere because they receive the highest heat load in the form of afternoon sunlight (Buffo et al. 1972; Hanna et al. 1982; McCune and Keon 2002).

Indeed, aspect was not important in either of the year sub-models. Thus there may be other factors influencing the relationship between east-facing slopes and cheatgrass abundance, such as propagule dispersal or interactions with other site characteristics, which we did not examine. The positive correlation between $\sin(\text{aspect})$ and litter cover and the negative correlation between $\sin(\text{aspect})$ and perennial basal cover may both contribute to higher cheatgrass abundance on east-facing plots. Because west-facing plots were uncommon in our sample of plots, additional data from more west-facing plots could more thoroughly describe the relationship of cheatgrass abundance to aspect at Red Bluff.

While not important in our full Red Bluff model, diversity was important in both sub-models, and cheatgrass abundance negatively relates to species diversity in the GB. The negative relationship between cheatgrass abundance and species diversity at Red Bluff corroborates many findings from the Great Basin and parts of Montana (Shinneman and Baker 2009; Metlen 2010), although some studies described inconsistent relationships between diversity and cheatgrass cover (Gelbard and Belnap 2003).

Cheatgrass can establish monocultures, which are, by default, communities with very low diversity. Thus, diversity has a logical inverse relationship to cheatgrass abundance and dominance. It is unclear whether cheatgrass displaces diverse native communities or simply enters existing niches on the landscape where nothing previously grew. However, greater diversity in time as well as in space, e.g., having vegetation that occupies many ecological niches throughout the year, could hinder cheatgrass invasion and abundance by precluding it from most sites with adequate resources.

Perennial basal cover was also important in both year sub-models. Perennial basal cover was similar at all plots in both years, averaging 14-19%, although perennial foliar cover was often near 70% (Table 3). In comparison, total perennial cover in the Great Basin averages around 25%, and perennial basal cover is therefore an even smaller percentage of the landscape (Comstock and Ehleringer 1992). The disparity in perennial cover between ecoregions (GB and GP) may partly explain why cheatgrass has been more of a concern in the GB than in the GP. Climate also likely explains a significant portion of cheatgrass success in the GB relative to the GP (e.g., precipitation regime differences), and climate constrains the dominant vegetation. Perennials provide competition for space, sunlight, and soil resources year-round. In the GB, lower cheatgrass cover and biomass are associated with closely spaced perennials, e.g. with high perennial density and cover (Reisner et al. 2013; Rayburn et al. 2014). Furthermore, in arid and semiarid ecosystems such as the GB and the GP, competition is greater for belowground resources than for sunlight (Reichenberger and Pyke 1990), and aboveground biomass often represents less than half of a plant's total biomass (Caldwell

et al. 1981). Because of this biomass distribution which is common to bunchgrasses, regions with higher perennial grass cover are also likely to have more extensive root systems, and thus may better exclude cheatgrass from below- and aboveground spatial niches in all seasons.

However, in the full model, perennial basal cover may not have been important due to the skewed distribution of basal cover values across plots (few plots with >40% perennial basal cover). Across the range of observed basal cover values (0%-92%, highest cover values reflect high cover of spikemoss at some plots), cheatgrass abundance varied greatly, which resulted in no strong relationship. Any relationship between basal cover and cheatgrass abundance might be better defined if we had additional plots with the intermediate basal cover values between the extremes and had more years of data from the same plots.

Although litter cover positively correlates to cheatgrass abundance in previous research, it did not have a strong relationship to cheatgrass abundance at Red Bluff. Litter cover was only important in the 2015 model, which may reflect the influence of zero plots similar to their influence on diversity. Zero plots had fairly low litter cover, skewing the already positive relationship between litter and cheatgrass abundance to a steeper and stronger relationship. The absence of litter as a variable in most top models from the full model suggests that once other variables are included, litter is not a particularly strong associate to cheatgrass abundance at these plots. Litter cover was quite high at all invaded plots in both years, while cheatgrass abundance had a wide range. The narrow range of litter cover across most levels of cheatgrass abundance at our plots reduces the likelihood

of a strong relationship to cheatgrass. When it was included in models, litter was positively associated to cheatgrass abundance. As a result, the absence of litter importance at our plots does not necessarily disagree with studies from the GB which found strong relationships between cheatgrass presence and litter (Evans and Young 1970; Kelrick 1991; Bates et al. 2004; Beckstead and Augspurger 2004). Additionally, most of these studies recorded litter presence or absence which does not correlate directly to litter cover. Therefore, our results are not directly comparable to those of studies with different litter quantification techniques.

Livestock fecal count, our proxy variable for livestock presence and abundance, did not strongly relate to cheatgrass abundance. Fecal count was important only in the 2015 sub-model. Even so, a positive relationship to fecal count would indicate a positive relationship between livestock presence and cheatgrass abundance, which is suggested by many GB studies (Harris 1967; Young et al. 1987; Billings 1992; Reisner et al. 2013). More years of data at our plots could further clarify whether this relationship holds true at Red Bluff as livestock presence and cheatgrass abundance fluctuate over time. Additional years would also allow experiments directly manipulating livestock presence.

Fire history was not a strong predictor at Red Bluff in the full model, and when it was included in the sub-models, the estimated coefficient suggested a negative relationship between burning and cheatgrass abundance. This lack of a strong relationship to cheatgrass abundance corroborates previous findings at the same ranches, in which cheatgrass levels did not differ on burned and unburned sides of a fireline (Tulganyam 2015). Taylor et al. (2014) also described how regions with summer precipitation did not

tend to have a positive relationship between cheatgrass and fire. Red Bluff receives most precipitation in the late spring/early summer, and our results and those of Tulganyam (2015) suggest that there is not a strong cheatgrass-fire relationship at the ranch. Further years of study could better establish whether this is the case, since so few plots burned and the fire history at our plots only spans twenty years.

Thackeray

At Thackeray, a different set of variables were important: burrow cover, soil sand content, and aspect. Unlike at Red Bluff, burrow cover was negatively related to cheatgrass abundance at Thackeray. This relationship may reflect the combination of a slight increase in average cheatgrass abundance and a decrease in burrow cover between years. Plot 1 was one of the plots impacted by livestock moving or destroying plot stakes, so 2015 transects may have overlaid different parts of the plot than the 2014 transects overlaid; if this is the case, transects in 2015 may have bypassed the burrows measured in 2014. Slight changes in transect location should not contribute drastically to differences in coverage, however, since burrows were only measured if they were “fresh”. If rodents abandoned the burrows on these plots, then there would be far less recent activity for us to measure and could cause changes as large as those we observed.

Nevertheless, when 2014 and 2015 subsets of the data were fit to the same initial model and then dredged in the same way as the full model, burrows were not important in either year sub-model. Figures 13b and 13c show how burrow cover relates to cheatgrass abundance when all other variables in the yearly models are accounted for. The

difference between years is a more reasonable explanation than burrowing actually being negatively associated with cheatgrass abundance, given previous discussion about rodent burrows and cheatgrass at Red Bluff (Piemeisel 1951,1954; Quanstrom 1971; Mack and Pyke 1983; Young et al. 1987) and given that there appears to be a positive relationship to burrows in 2015, and the apparent negative relationship in 2014 is a result of the outliers TH1 and TH2. While it is possible that large rodent populations consumed cheatgrass and drove the negative association, there is no literature to support that ground squirrels consume significant amounts of cheatgrass foliage or seeds specifically. The positive relationship in 2015 may be a result of the zero plots having negligible burrow cover. As such, the invaded plots' lack of relationship between cheatgrass and burrows outweighs the difference between invaded and non-invaded plots. With more plots a stronger relationship to cheatgrass presence or abundance and burrow cover could arise at Thackeray, but it is not an important variable within our limitations.

As with burrow coverage, the negative relationship of cheatgrass abundance to bare soil may have emerged from the influence of outlying plots. Plot 7 in particular had very little soil cover in 2014 and very low cheatgrass cover and abundance. Because the abundance at this plot (and all other plots) was slightly higher and bare soil was lower in 2015 than in 2014, there is an apparent negative association between cheatgrass abundance and bare soil. Nonetheless, cheatgrass abundance and bare soil cover may be confounded. Bare soil was important in both sub-models, and negatively associated to cheatgrass abundance. Research from the GB has described similar relationships between cheatgrass and bare ground. Undisturbed bare ground may not be an ideal site for

cheatgrass establishment (Evans and Young 1970; Bates et al. 2004) and this may be caused by low seed-soil contact between cheatgrass seeds and a relatively flat soil surface (Kelrick 1991; Beckstead and Augspurger 2004). Litter increases moisture retention in the surface soil and moderates soil temperature (Evans and Young 1970), creating a more suitable microenvironment for cheatgrass germination and establishment (Beckstead and Augspurger 2004).

Cheatgrass abundance was negatively associated to shallow soils at Thackeray, although a more complicated relationship seems likely. Shallow soils may restrict cheatgrass abundance. In the GB, cheatgrass grew taller and more densely on deep soils than on shallow soils in rocky areas, where perennial vegetation was also limited (Hulbert 1955). Cheatgrass and perennials thus appear to respond similarly in the two soils. However, most of the root mass of cheatgrass is located in the top 20-30 cm of the soil profile (Hulbert 1955). Thus, in deep soils, cheatgrass is probably more competitive for surface water than deep water because of its shallow rooting profile. Cheatgrass may outcompete perennials for surface moisture which would be available early in the spring and immediately after precipitation events during the growing season (Melgoza et al. 1990). By depleting surface water, cheatgrass competition could slow perennial growth unless the perennials had active roots below the zone of cheatgrass root domination and the lower soil profile had adequate water. Over several years of outcompeting perennials early in the season, particularly in dry years, cheatgrass could occupy a greater proportion of the community composition of deeper sites.

Nevertheless, the simple linear relationship described in our models may not appropriately describe the relationship between soil depth and cheatgrass at Thackeray. Although deep sites supported the highest cheatgrass abundance, shallow sites more commonly had moderately high cheatgrass abundance, and zero plots were usually on deeper sites. While previous discussion of cheatgrass competition on sites with deep soils is still relevant, the overall pattern seems to describe that cheatgrass frequently becomes abundant on shallow soils and infrequently does so on deep soils. Cheatgrass abundance may depend on other site characteristics to be so successful on the deeper, richer sites. Of the deep sites with high cheatgrass abundance, most sites also had high manure counts and/or relatively high burrow coverage. Both of these metrics relate to disturbance of the soil and/or existing vegetation and it may be that the disturbance is necessary to open a niche for cheatgrass on deeper sites. Once cheatgrass is established, then it can successfully compete for resources as described above.

Soil texture was only important in the sub-models for Thackeray, although raw data suggest soil sand content related positively to cheatgrass abundance when the years were combined as well. Research in other parts of the western US have mixed results about the relationship between cheatgrass and sandy soils. One study found that cheatgrass establishment and growth rates on sandy versus loamy soils depend on the season (Miller et al. 2006); another found that sandy sites generally had no cheatgrass (Brummer et al. 2016). Sandy soil does not get as compacted as clay-rich soils do, and compaction resulted in lower cheatgrass density and biomass production in the GB by reducing the number of emergent seedlings or slowing seedling emergence (Beckstead

and Augspurger 2004). In addition, water retention is relatively low on sandy sites (Hillel 1998). Rapidly draining, sandy soil may be a greater stressor on native perennial growth than on cheatgrass growth. Cheatgrass needs less moisture to create seeds for the next generation before senescing than perennials need to accumulate enough energy stores for the following winter dormancy. Under experimentally-imposed dry conditions, native bluebunch wheatgrass seedlings senesced one to two weeks earlier than cheatgrass seedlings did, although seedlings of the introduced perennial desert wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.) persisted even after cheatgrass senesced (Harris and Wilson 1970). If cheatgrass seedlings consistently outlast native perennials under drought conditions, cheatgrass could become abundant on sandy sites with native perennial grasses that then fail to recruit new plants. This phenomenon may also explain why crested wheatgrass, a close relative of desert wheatgrass, is one of few perennials that can establish when planted in cheatgrass stands (Stewart and Hull 1949; Jessop and Anderson 2007).

Great Basin and other research has repeatedly described abundant cheatgrass on south-facing slopes (Platt and Jackman 1946; Billings 1992; Metlen 2010), and our results suggest the same relationship to aspect. The full model and both sub-models indicate a negative relationship between cheatgrass abundance and cosine of aspect, which means there is evidence for a positive relationship between cheatgrass and south aspects. Because south aspects in the Northern Hemisphere receive more incident solar radiation year-round, they tend to be warmer and drier than north aspects under otherwise equal climatic conditions (McCune and Keon 2002). Cheatgrass may be more

competitive than native perennials on these dry slopes due to its winter annual life history. Cheatgrass grows its roots during autumn and winter, and as soon as environmental conditions are amenable to aboveground growth it can access moisture from snowmelt and precipitation before natives are fully out of their winter dormancy (Stewart and Hull 1949; Melgoza 1990). In addition, because cheatgrass is capable of setting seed on even very short tillers (e.g. 10-12 cm), it can take advantage of early season moisture and nutrient availability and then go to seed before conditions are excessively warm or dry (Warg 1938; Hulbert 1955), and this could also explain the abundance of cheatgrass on sandy sites.

Ranch Differences

Given that cheatgrass is frequently associated with disturbance (Hulbert 1955; Young et al. 1987; Gelbard and Belnap 2003; Reisner et al. 2013), it may have invaded Red Bluff earlier than Thackeray and thus have had more time to expand on the ranch to its present levels. Red Bluff was a mining hub and a stagecoach stop in the late 1860s to early 1900s (Flaherty 2006) and was probably subject to a wider variety and more intense disturbances than Thackeray Ranch, which was not a focus of mining activity. Furthermore, the much higher flux of human activity likely provided more introduction opportunities for cheatgrass at Red Bluff.

Regardless of human use history, Red Bluff and Thackeray ranches' modern differences influence what factors associate to cheatgrass abundance. Red Bluff's relatively uniform, coarse substrate and shallow soils reduces the likelihood that soil

characteristics are directly related to whether cheatgrass is abundant on a site or not when comparing sites within Red Bluff. Red Bluff plots encompassed only seven unique ecological sites, whereas Thackeray plots comprised thirteen unique ecological sites. Thus, vegetation and disturbance variables are much more important than abiotic characteristics for predicting cheatgrass abundance at Red Bluff given our models. Disturbance at Red Bluff currently comes in the form of rodent burrowing, livestock grazing, and the occasional wildfire. Wildfire data on these plots are minimal, and livestock presence as quantified by fecal counts was not a strong predictor in our models. The lack of livestock influence on cheatgrass may reflect that grazing management at the ranch tends not to leave widespread disturbed soil even though it likely impacts plant community composition. Even the sheep bedding grounds, which created large bare soil patches, mainly disturbed the vegetation. On these sites, soil surfaces – whose roughness influences cheatgrass establishment – were not visibly roughened in a way that would encourage cheatgrass. Bedding ground soils were probably more susceptible to erosion given the absence of protective vegetation, but burrowing seems to have the strongest relationship to cheatgrass abundance at this time. Because burrowing was frequently observed and resulted in obvious soil and vegetation disturbance, it may continue to have the strongest relationship to cheatgrass abundance.

Disturbance at Thackeray often came from cattle rather than from rodents; several plots at Thackeray had high fecal counts (>25 fecal deposits) which were rarer at Red Bluff plots, but burrowing was comparable between years, excluding the outliers at Thackeray. Cattle use, although not an important variable itself at Thackeray, may have

contributed to the unusually high cheatgrass abundance on a few of the deep plots at Thackeray. Plots 11, 12 and 15, all with deep soils, had high fecal counts and among the highest cheatgrass abundance (18-36%, the maximum relative cheatgrass abundance at Thackeray). In comparison, most of the uninvaded plots at Thackeray had low fecal counts. Although only two of the zero plots were deep, four of the five also had fine-textured soils. Essentially, the impact of disturbance on cheatgrass abundance appears to depend on soil characteristics such as depth and surface texture, which varied substantially at Thackeray. At Red Bluff, soil characteristics were very similar across plots and had little influence on the impact of disturbance.

Diversity at Red Bluff is not a particularly important risk factor of high cheatgrass abundance. Cheatgrass-invaded plots tended to have several species with comparable cover values (e.g., 20 species with less than 30% cover each) but non-invaded plots tended to have dominant species (e.g., 19 species, where Idaho fescue and bluebunch wheatgrass each have over 50% foliar cover and all other species have less than 15% foliar cover each). Because Simpson Diversity considers both number of species and “evenness” of species abundance (Simpson 1949), zero plots generally had lower Simpson Diversity values than invaded plots. However, based on the high cover values of the dominant native plants, it is likely that even though the diversity values were considered low, the zero plots at Red Bluff were fully occupied sites in terms of resource availability.

The negative relationship to perennial basal cover in year-specific Red Bluff models is strongly influenced by the presence of spikemoss (*Selaginella* spp.) on large

areas of the ranch. For example, spikemoss is the dominant source of basal cover and on some plots provided up to 90% basal cover. In the same plots, cheatgrass abundance was low or zero. Though we did not test this relationship statistically, spikemoss may be a valuable ground cover in cheatgrass-prone areas until or unless other vegetation is present and able to compete with cheatgrass. Few plots had very high basal cover, so the regressed relationship between cheatgrass abundance and basal cover is weak. Higher cheatgrass plots had low perennial cover, however, and the binary comparisons (t-tests) in the summary statistics show a significant difference in basal cover between invaded and non-invaded plots at Red Bluff.

Spikemoss was rare at Thackeray, and provided little cover even when present. Although still fairly rare, there were more warm-season grasses (e.g. little bluestem [*Schizachyrium scoparium* (Michx.) Nash], red threeawn [*Aristida purpurea* Nutt.], and blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths]) at Thackeray than at Red Bluff (blue grama), which may make communities at Thackeray less open to invasion by having vegetation that occupies more temporal niches. In addition, Kentucky bluegrass provided dense vegetation on several plots with low cheatgrass at Thackeray, and it may be a valuable competitor with cheatgrass in areas where the bluegrass is well established. Areas with abundant Kentucky bluegrass also tended to be relatively moist sites. As such, vegetation itself may not drive relationships at Thackeray. Abiotic site characteristics which encourage certain vegetation types, e.g. native or naturalized perennials, may be particularly important in limiting cheatgrass abundance, and merit further study.

On an even broader scale, climate likely drives some differences between ranches' cheatgrass relationships. Thackeray ranch has cooler temperatures year-round by 1-2°C (PRISM Climate Group 2016) which could limit the success of overwintering cheatgrass through higher winter mortality of seeds or poorly-insulated seedlings (Warg 1938; Beckstead and Augspurger 2004). Thackeray has higher annual precipitation, which peaks later in the spring and is lower in the fall than it is at Red Bluff. This slight difference in the timing of precipitation may decrease cheatgrass success by simultaneously reducing its fall germination and establishment and delaying spring moisture until more perennials are out of dormancy (Cline et al. 1977; Melgoza et al. 1990). Despite the differences between ranches, the predominant risk factors of abundant cheatgrass as described in the Great Basin and in previous Montana research do not differ greatly from what we observed on these ranches.

Limitations of the Study

All of these findings must be considered within the limitations of the study. Most importantly, we only collected data from two years, and ecological processes work on much longer time scales. Plant populations often fluctuate annually for a number of reasons including competition and poor recruitment (Crawley and Ross 1990), so it is impossible to know whether the change in cheatgrass abundance that we observed will continue to be the dominant pattern of cheatgrass abundance at our plots. It is possible that we have data from two years in which abundances differed, but in the following year cheatgrass abundance could return to 2014 levels or could exponentially increase. A

much longer study, on the scale of a decade or more, would provide a better idea of the overall trend in cheatgrass populations at these sites.

Additional data would also prove useful, such as GPS perimeters of cheatgrass patches and cheatgrass density within these patches over time in these plots. Data from further years of study could target specific variables, and future studies could examine interactions which were suggested by our results but not fully tested.

Finally, we have a maximum of 22 plots at each ranch. Though our findings apply to all possible plots from which our study plots were selected, there are many other sites which we did not identify at these ranches, let alone sites in many other ecosystems in Montana. As such, extrapolation to other systems is limited.

Management Implications

The apparent phenotypic plasticity of cheatgrass (Harris 1967) may present great challenges to reduction or elimination of the species once it is present on a site. Young et al. (1987) described a vast range of cheatgrass populations, from single, heavily seed-bearing individuals, to extremely dense stands of plants bearing far fewer seeds. Mack and Pyke (1983) observed populations in a single location where three different phenologies – fall emergence, late winter emergence, and summer emergence – were exhibited. With cheatgrass so adaptable, it is likely to successfully reestablish even after major restoration inputs have been made to invaded ecosystems. As such, it seems imperative to identify risks of cheatgrass invasion and monitor sites with the highest risks.

Due to the limitations of this study, we recommend that these results are considered within land managers' existing procedure for invasive plants. In foothills grasslands dominated by Idaho fescue and bluebunch wheatgrass on poorly-developed soils, soil and vegetation disturbance appears to be one of the primary factors encouraging abundant cheatgrass. If managers can reduce the intensity or frequency of disturbances such as grazing or road construction, thereby reducing negative impacts on desired forage species, cheatgrass may be less able to dominate those sites. Grazing management appropriate for the existing desired vegetation is therefore a key tool in managing or preventing abundant cheatgrass. Other disturbances may be less preventable. Rodents such as Richardson's ground squirrels seem to indicate sites ideal for cheatgrass invasion and proliferation, and may contribute to cheatgrass abundance by creating mounds of fresh soil for it to colonize. Managers may want to control rodent populations and assess rodent-infested sites for other characteristics that may encourage cheatgrass to become abundant, such as sandy soils or vegetation monocultures. Although soil texture cannot be altered on any useful time scale, managers can encourage perennial vegetation diversity through grazing management or other tools to prevent cheatgrass from finding establishment niches.

On rough fescue-dominated grasslands, south-facing slopes are key locations to monitor cheatgrass invasion. These slopes are more likely to have cheatgrass, and to support higher amounts of cheatgrass than north-facing slopes will. South-facing slopes could function as early warning locations for risks of cheatgrass invading or dominating the larger area. Regardless of aspect, sites typified by coarse soils are also likely to have

cheatgrass, but are less likely to support the highest cheatgrass levels. Sites with wetter, deeper, or well-developed soils are less likely to have cheatgrass in the absence of vegetation or soil disturbance. With grazing or rodent activity, however, cheatgrass may be able to dominate existing vegetation and capitalize on the resources available on these richer sites. Managers may want to monitor these areas carefully to ensure that existing management practices, e.g. grazing, are maintaining robust desired vegetation and soil integrity.

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APPENDIX A

SUPPLEMENTARY TABLES AND FIGURES

Table 1. Common perennial vegetation at Red Bluff and Thackeray ranches.

Plant Type	Red Bluff	Thackeray
Graminoids	Idaho fescue (<i>Festuca idahoensis</i> Elmer)	rough fescue (<i>Festuca campestris</i> Rydb.)
	bluebunch wheatgrass (<i>Pseudoroegneria spicata</i> [Pursh] Á. Löve)	bluebunch wheatgrass
	Sandberg bluegrass (<i>Poa secunda</i> J. Presl)	Kentucky bluegrass (<i>Poa pratensis</i> L.)
		sedge (<i>Carex</i> spp.)
Forbs	spikemoss (<i>Selaginella</i> spp.)	yarrow (<i>Achillea millefolium</i> L.)
		<i>Thermopsis</i> spp.
Woody Species	big sagebrush (<i>Artemisia tridentata</i> Nutt.)	snowberry (<i>Symphoricarpos occidentalis</i> Hook.)
	fringed sage (<i>Artemisia frigida</i> Willd.)	Lupine (<i>Lupinus</i> spp.)

Table 2. (a) Explanatory variables included in the initial Red Bluff model, aside from the random effect of plot. (b) Explanatory variables included in the initial Thackeray model, aside from the random effect of plot.

(a)

Year (binary)	Sin(aspect)	Burn (binary)	Litter cover
Fecal count	Burrow cover	Perennial basal cover	Ecological site (binary)
	Simpson Diversity	Soil sand content	

(b)

Year (binary)	Cos(aspect)	Burn (binary)	Litter cover
Fecal count	Burrow cover	Bare soil cover	Perennial basal cover
Ecological site (binary)	Soil sand content	Slope	Simpson Diversity

Table 5. (a) Estimated coefficients from the top ten models derived from the Red Bluff initial model. Zeros in a column indicate that the variable was not included in the model identified at the beginning of the row. Burr indicates burrows; Sin.A, sin(aspect); Sa., soil sand content; Litt., litter cover; FC, fecal count; Peren Basal, perennial basal cover; Sim Div, Simpson Diversity; and Shal. ES, shallow ecological site. (b) Importance values for variables in the Red Bluff initial model. Importance is the sum of model weights for all models that include the variable; models with low AIC have high weight. The highest possible value for importance is 1.

(a)

Model; AIC	Year	Burr	Sin.A	Burn	Slope	Sa.	Litt	FC	Peren Basal	Sim Div	Shal. ES
1; 369.3	.475	.173	1.594	0	0	0	0	0	0	0	0
2; 370	.474	.171	1.548	0	0	.587	0	0	0	0	0
3; 370	.439	.162	1.603	0	0	0	0	0	0	-.140	0
4; 370	.482	.163	1.527	0	0	0	.114	0	0	0	0
5; 370.6	.475	.173	1.485	0	-.428	0	0	0	0	0	0
6; 370.7	.475	.172	1.479	0	0	0	0	0	0	0	-.881
7; 370.9	.475	.172	1.604	1.163	0	0	0	0	0	0	0
8; 371.2	.468	.171	1.647	0	0	0	0	0	.0665	0	0
9; 371.3	.485	.169	1.594	0	0	0	0	.0143	0	0	0
10; 370.3	.474	.171	1.369	0	-.648	.750	0	0	0	0	0

(b)

Year	Burr	Sin.A	Burn	Slope	Sand	Litt.	FC	Peren Basal	Simp Div	Shal. ES
1.00	1.00	0.93	0.20	0.26	0.31	0.29	0.18	0.18	0.29	0.22

Table 6. (a) Importance of variables included in the 2014-only Red Bluff model and direction of estimated relationship. (b) Importance of variables included in the 2015-only Red Bluff model and direction of estimated relationship. For both tables, Burr indicates burrows; Sin.A, sin(aspect); Sa., soil sand content; Litt., litter cover; FC, fecal count; Peren Basal, perennial basal cover; Sim Div, Simpson Diversity; and Shal. ES, shallow ecological site. Symbols indicate a positive (+) or negative (-) estimated coefficient for the relationship between cheatgrass abundance and the explanatory variable in the top ten models. A zero (0) indicates the variable was not included in any of the top ten models.

(a)

Simp Div	Peren Basal	Burr	Sin.A	Shal. ES	Litt.	Slope	Sand	FC	Burr
0.81	0.74	0.52	0.30	0.29	0.23	0.22	0.13	0.10	0.09
-	-	-	-	-	-	-	+	+	-

(b)

Litt.	FC	Burr	Peren Basal	Sand	Slope	Sin.A	Burr	Simp Div	Shal. ES
0.74	0.61	0.56	0.55	0.28	0.23	0.22	0.18	0.17	0.16
+	+	+	-	+	-	+		0	0

Table 7. (a) Estimated coefficients from the top ten models from the Thackeray initial model. Zeros in a column indicate that the variable was not included in the model identified at the beginning of the row. Cos.A indicates cos(aspect), and Shal ES, shallow ecological site.

Model; AIC	Cos.A	Sand	Shal ES	Burrow cover	Bare Soil	Burr	Litter	Slope
1 ; 275.9	-1.744	.942	-1.214	-.135	-.160	-1.006	0	0
2 ; 277.4	-1.794	.849	-1.286	-.135	-.169	0	0	0
3 ; 277.9	-1.769	.924	-1.324	-.159	0	-1.137	0	0
4 ; 277.1	-1.812	.868	-1.459	-.123	0	-1.185	-.151	0
5 ; 279.8	-1.829	.817	-1.418	-.160	0	0	0	0
6 ; 279.1	-1.872	.754	-1.555	-.124	0	0	-.151	0
7 ; 276.2	-1.855	.866	-1.362	-.135	-.168	-1.245	0	.296
8 ; 280.5	-1.460	1.103	0	-.134	-.174	0	0	0
9 ; 278	-1.828	.798	-1.402	-.112	-.147	0	-.111	0
10 ; 276.4	-1.778	.896	-1.328	-.111	-.137	-1.059	-.114	0

Table 7. (b) Importance values for variables in the Thackeray initial model. The highest possible value for importance is 1. Sim Div indicates Simpson Diversity; Peren Basal, perennial basal cover; and Man, manure (fecal) count.

Cos. A	Sand	Shal ES	Burrow	Bare Soil	Burn	Sim Div	Litt.	Year	Slope	Peren Basal	Man
1.00	0.89	0.76	0.74	0.53	0.48	0.34	0.34	0.34	0.20	0.18	0.29

Table 8. (a) Importance of variables included in the 2014-only Thackeray model and direction of estimated relationship. (b) Importance of variables included in the 2015-only Thackeray model and direction of estimated relationship. Cos.A, indicates cos(aspect); Simp Div, Simpson Diversity; FC, fecal count; Shal. ES, shallow ecological site; Litt., litter cover; Peren Basal, perennial basal cover; and Burr, burrow cover. Symbols indicate a positive (+) or negative (-) estimated coefficient for the relationship between cheatgrass abundance and the explanatory variable in the top ten models. A zero (0) indicates the variable was not included in any of the top ten models.

(a)

Cos.A	Sand	Bare Soil	Simp Div	FC	Shal. ES	Litt.	Burn	Slope	Peren Basal	Burr
1.00	0.72	0.64	0.33	0.19	0.16	0.15	0.13	0.10	0.10	0.09
-	+	-	-	+	+	-	-	-	+	0

(b)

Cos.A	Sand	Bare Soil	Shal. ES	Simp Div	Burn	Peren Basal	Burr	Litt	Slope	FC
0.99	0.74	0.50	0.45	0.43	0.36	0.29	0.25	0.22	0.20	0.16
-	+	-	-	+	-	-	+	0	+	0

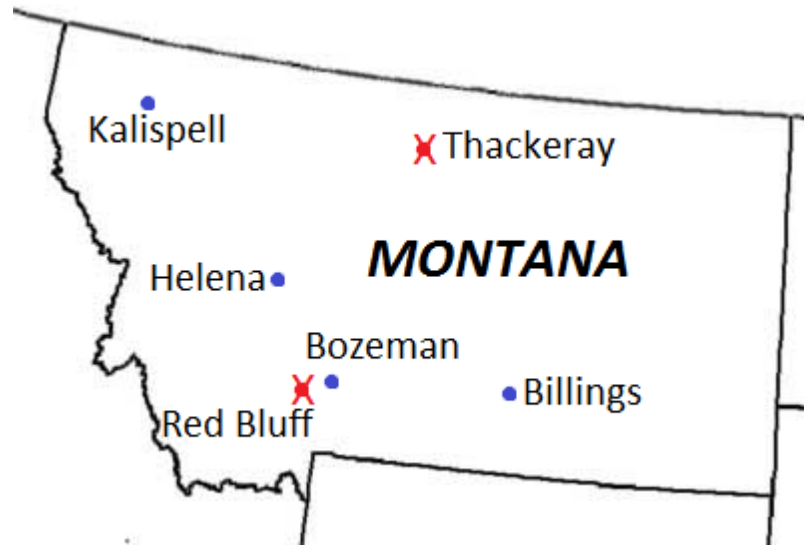


Figure 1. Map of Montana showing the locations of Red Bluff (near Norris, Mont.) and Thackeray (near Havre, Mont.) ranches. Cities are indicated for reference.

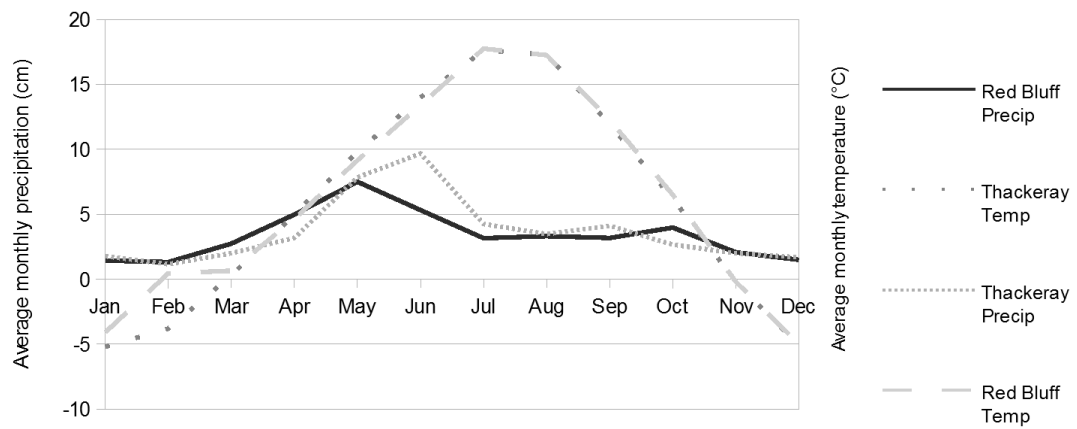


Figure 2. Average precipitation (cm) and average monthly temperatures (30-year averages, °C) at Red Bluff and Thackeray ranches. Average annual precipitation: Red Bluff, 40.5 cm; Thackeray, 43.8 cm.



Figure 3. Pairwise scatterplots of selected variables at Red Bluff.

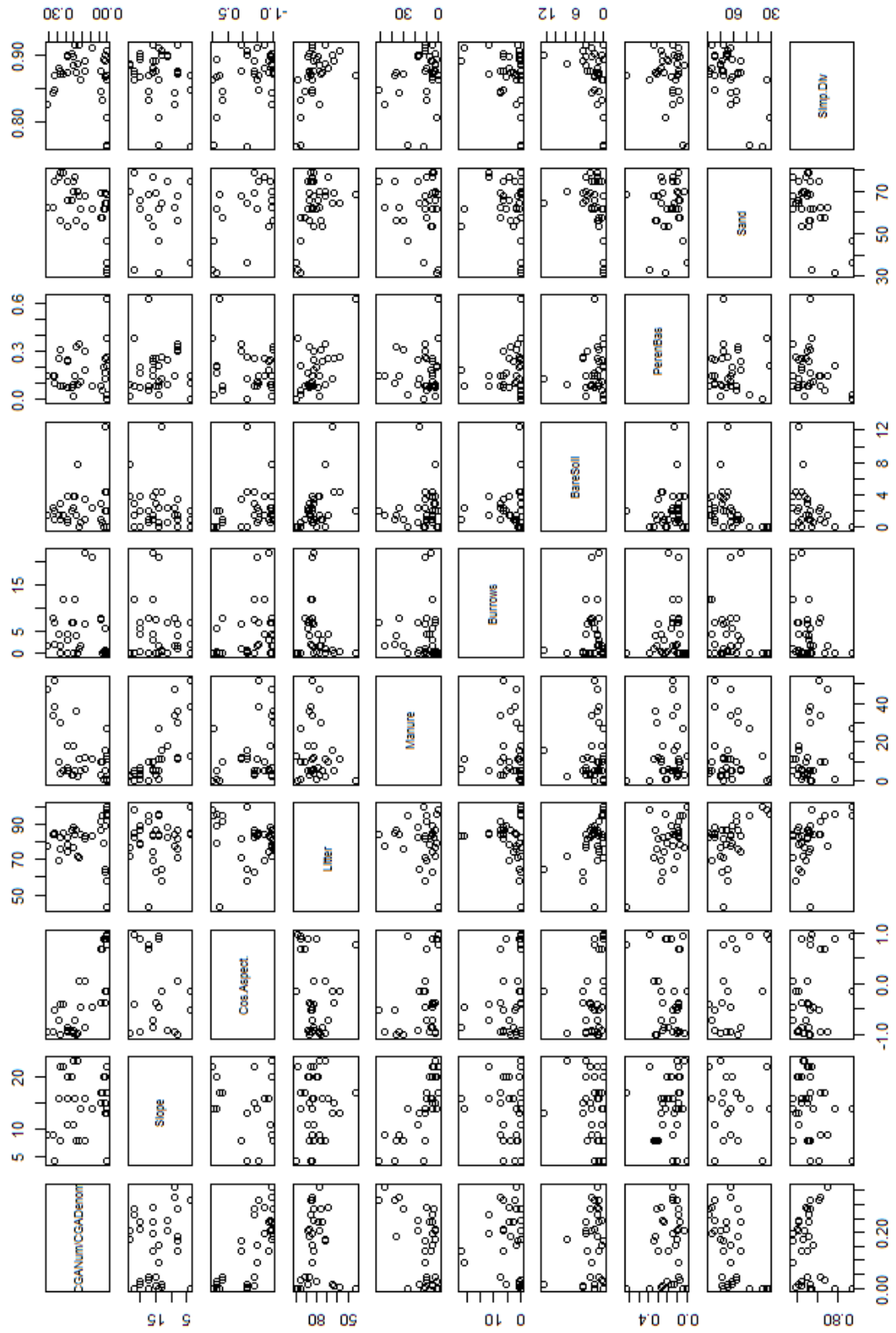


Figure 4. Pairwise scatterplots of selected variables at Thackeray.

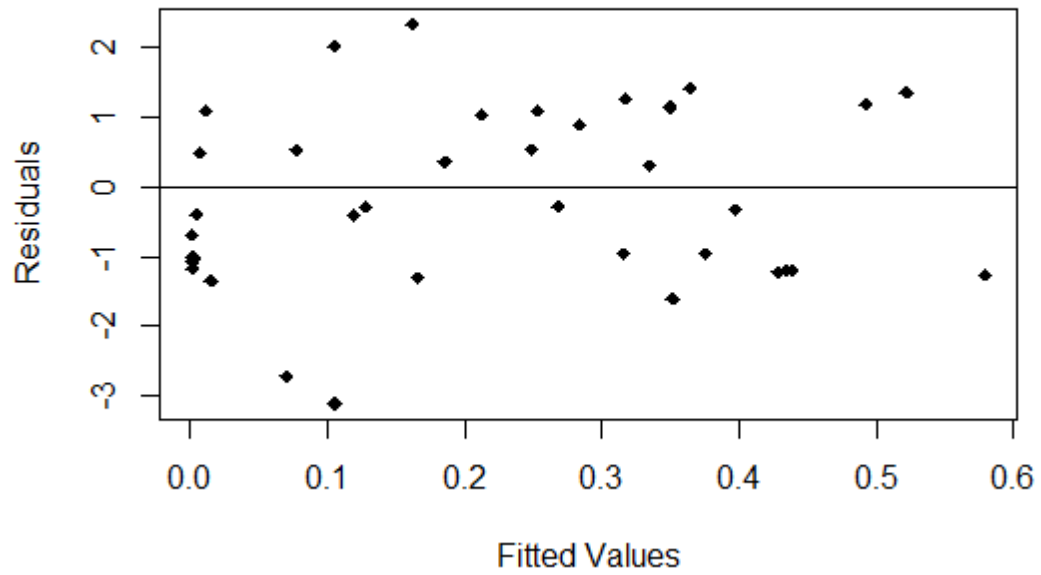
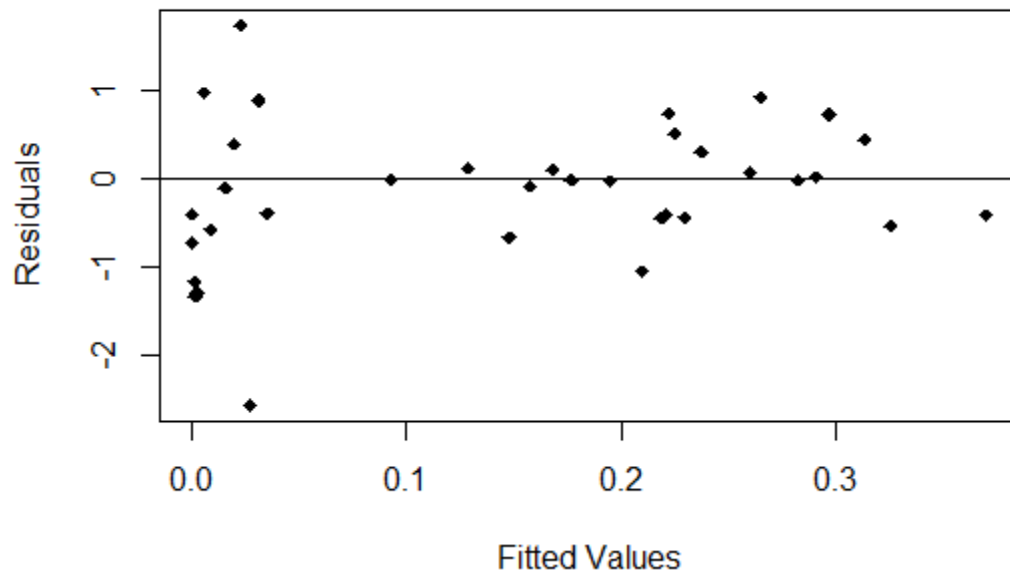
Residuals vs. Fitted Values for Full Red Bluff Model**Residuals vs. Fitted Values for Full Thackeray Model**

Figure 5. Residuals vs. fitted values for Red Bluff and Thackeray initial models.

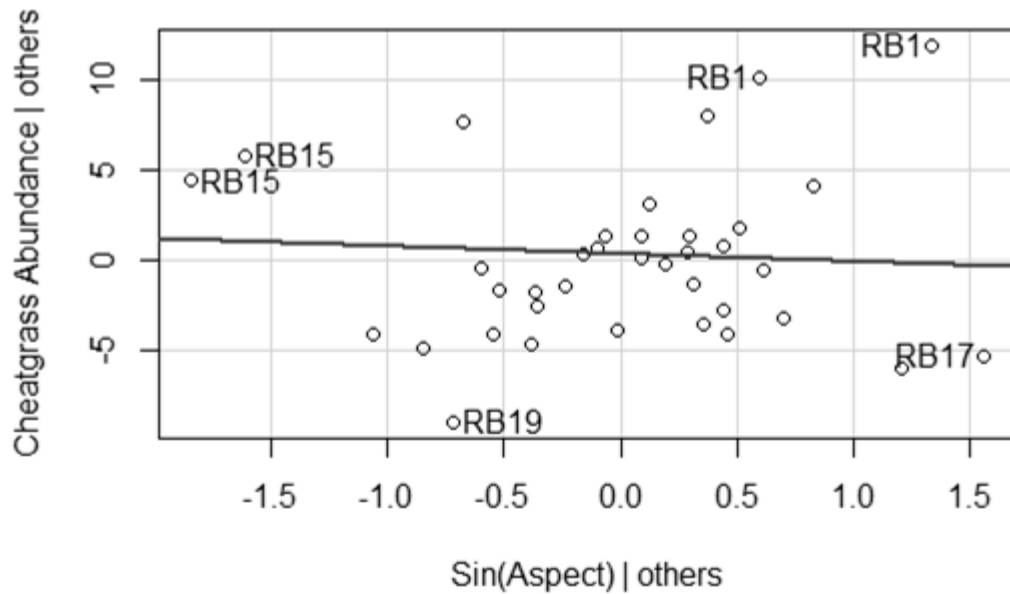


Figure 8. (b) Partial regression plot showing the relationship between cheatgrass abundance and sin(aspect) at Red Bluff once all other variables from the full model are included. Note the influence of outliers RB15 and RB17 on the fitted trend line.

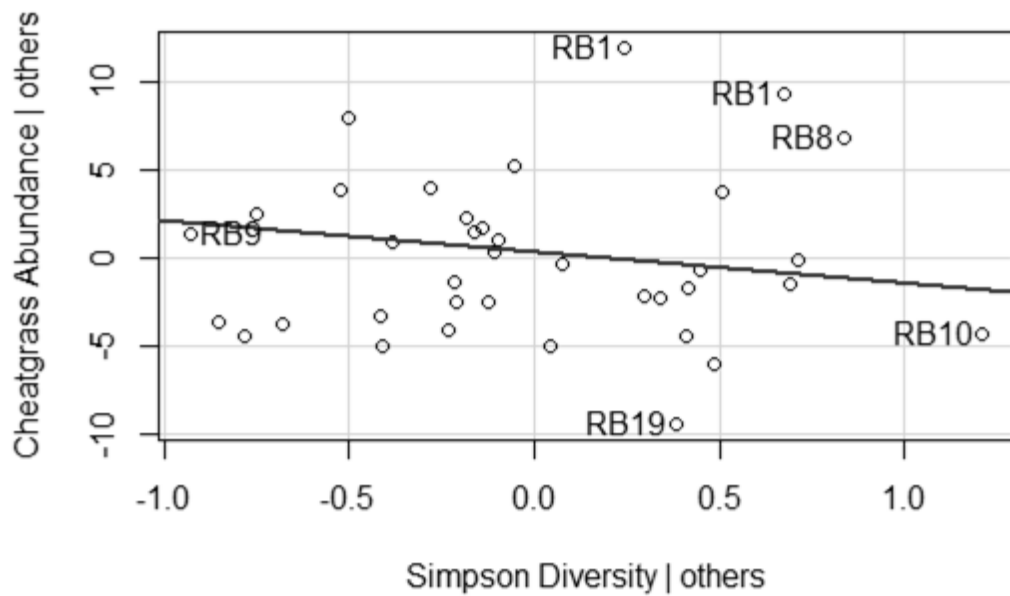


Figure 10. (b) Partial regression plot showing the relationship between Simpson Diversity and cheatgrass abundance at Red Bluff in once all other variables in the full model are accounted for.

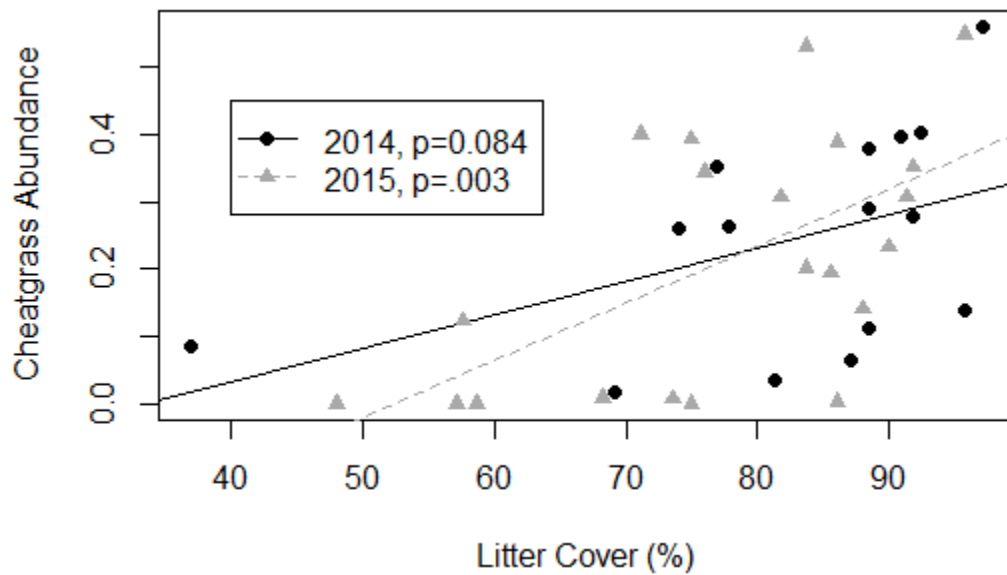


Figure 11. (a) Cheatgrass abundance versus litter cover at Red Bluff in 2014 (circles) and 2015 (triangles).

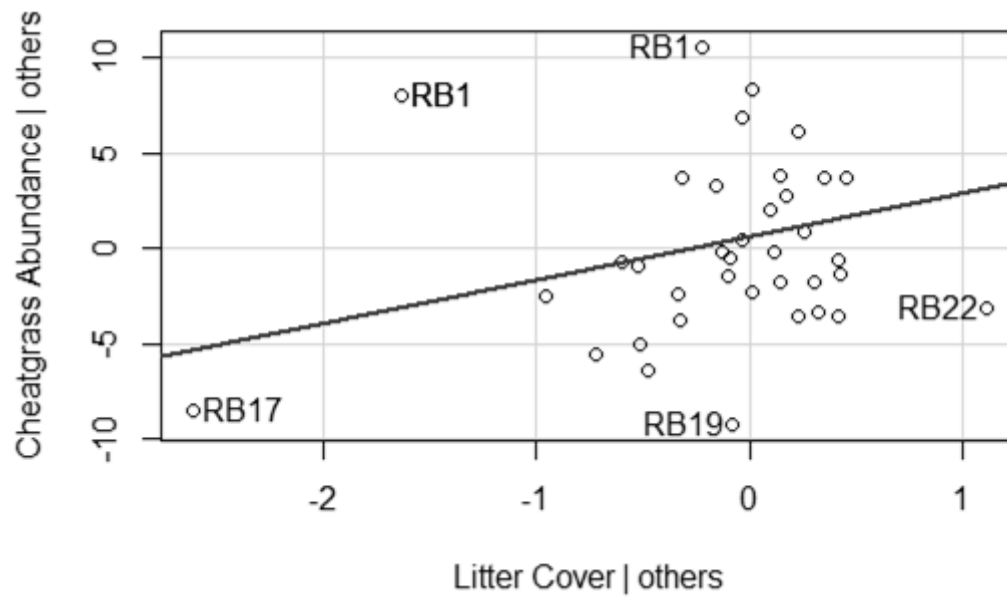


Figure 11. (b) Partial regression plot for cheatgrass abundance versus litter cover at Red Bluff when all other variables are accounted for. Plots RB17, 19, and 22 are all zero plots.

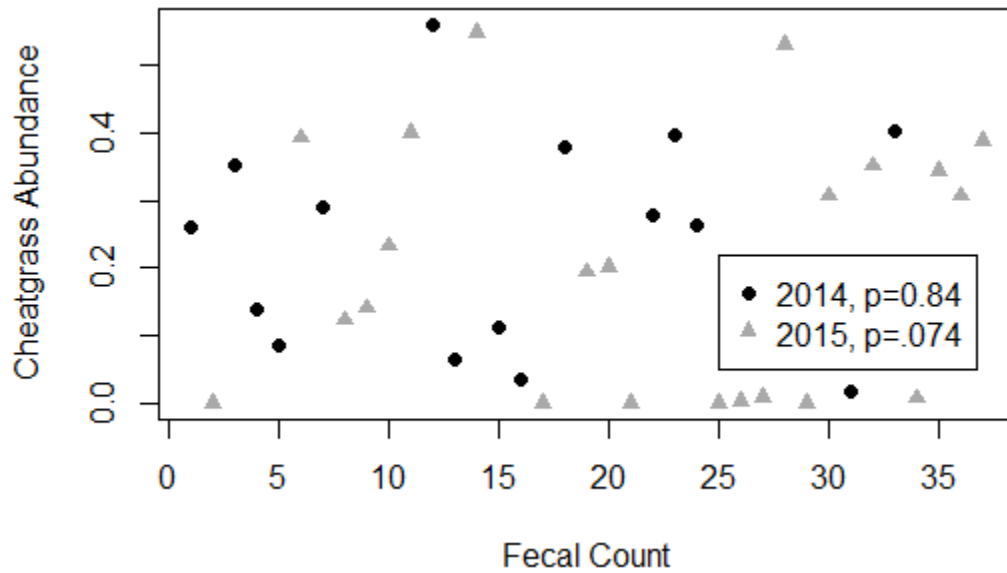


Figure 12. (a) Cheatgrass abundance versus livestock fecal count in 2014 (circles) and 2015 (triangles).

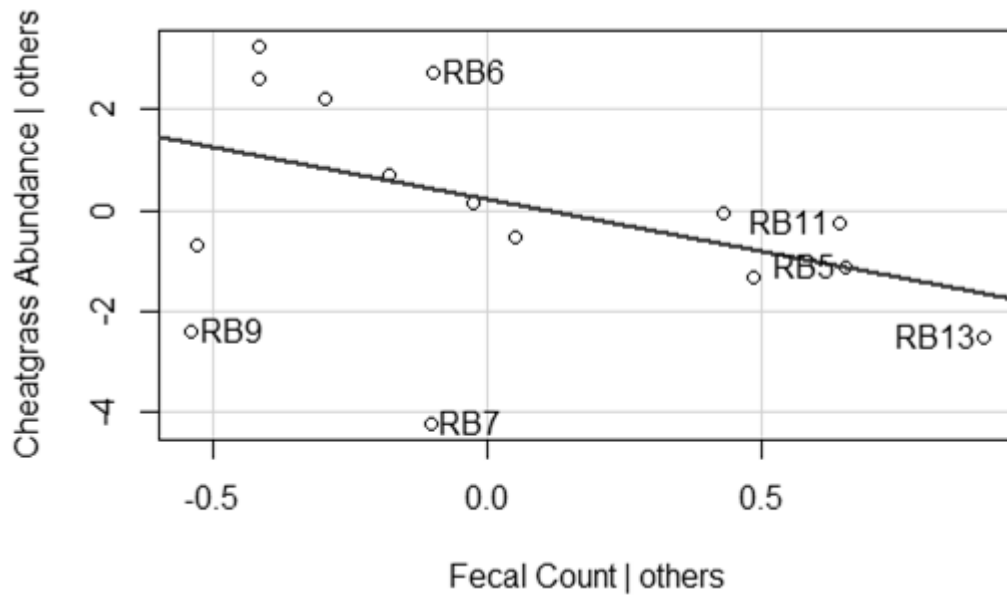


Figure 12. (b) Partial regression plot showing the relationship between fecal count and cheatgrass abundance at Red Bluff in 2014 once all other variables are accounted for. Several plots with unusual values may cause the apparent trend here, but fecal count was not important in Red Bluff's top 2014 models.

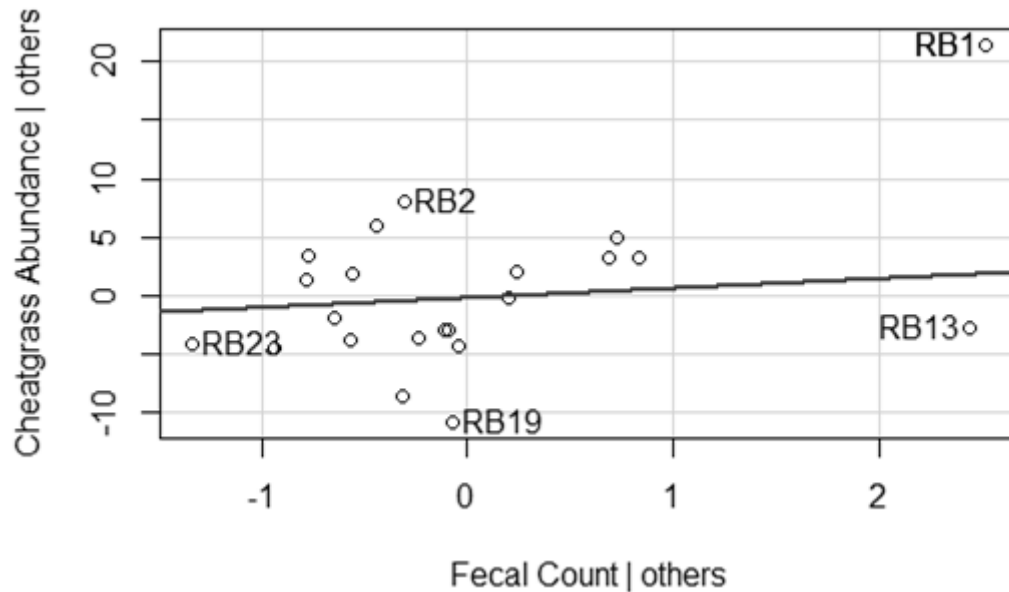


Figure 12. (c) Partial regression plot showing the relationship between fecal count and cheatgrass abundance at Red Bluff in 2015 once all other variables in the top 2015 models are accounted for. Note the strong impact of plot 1 on the otherwise trendless scatterplot.

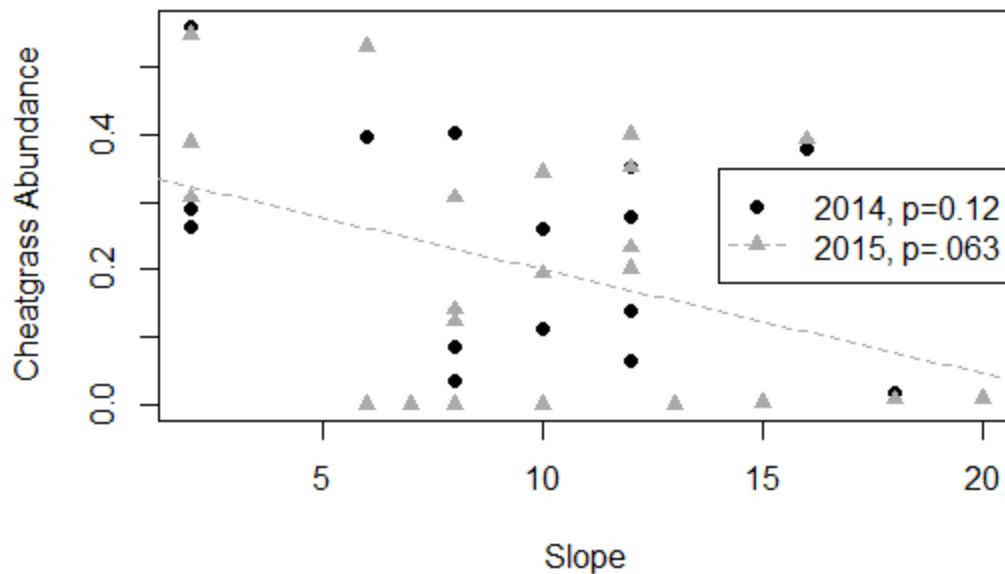


Figure 13. Cheatgrass abundance versus slope at Red Bluff in 2014 (circles) and 2015 (triangles). Slope was not ultimately important in any Red Bluff models.

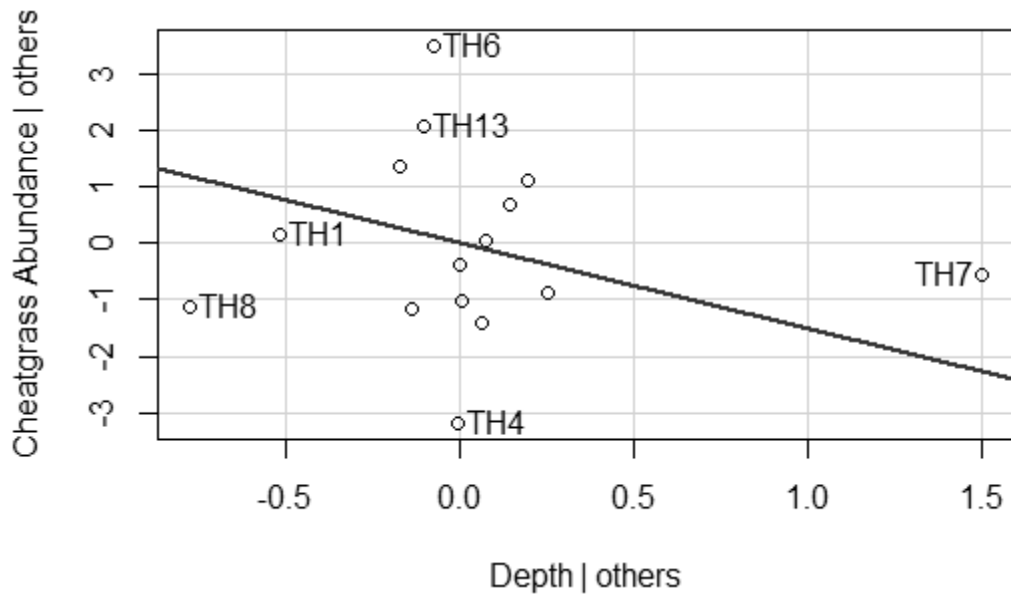


Figure 16. (b) Partial regression plot showing the relationship between soil depth and cheatgrass abundance at Thackeray in 2014 once all other variables are accounted for. Note the influence of widely spread values and lack of strong trend in any direction.

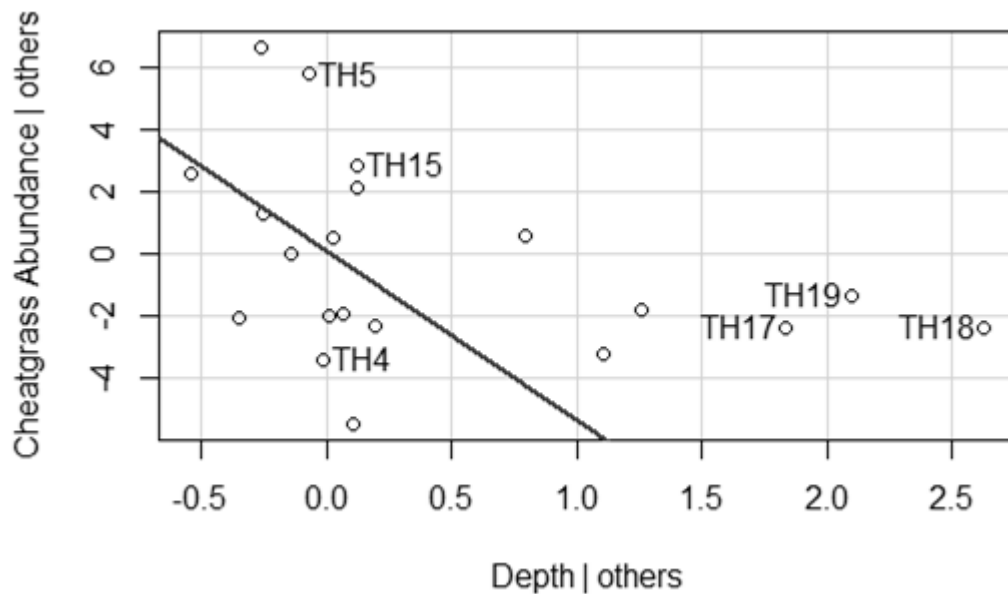


Figure 16. (c) Partial regression plot showing the relationship between soil depth and cheatgrass abundance at Thackeray in 2015 once all other variables are accounted for. A high value indicates shallow (from the original variables, shallow = “1”, deep = “0”) soil.

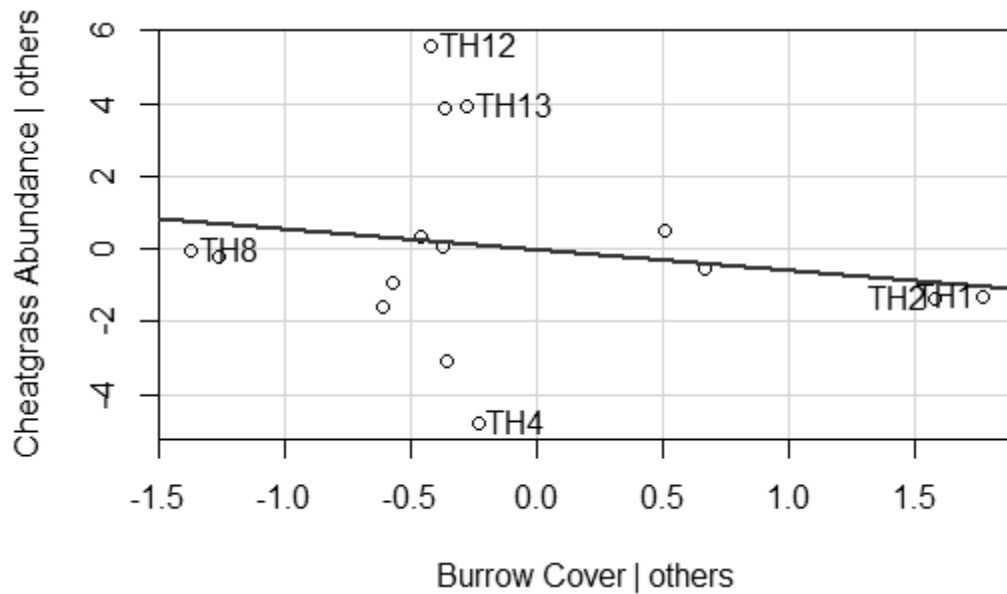


Figure 17. (b) Partial regression plot showing the relationship between burrow cover and cheatgrass abundance at Thackeray in 2014 once all other variables are accounted for. Note the influence of plots 1 and 2 (TH2, TH1) on an otherwise trendless scatterplot.

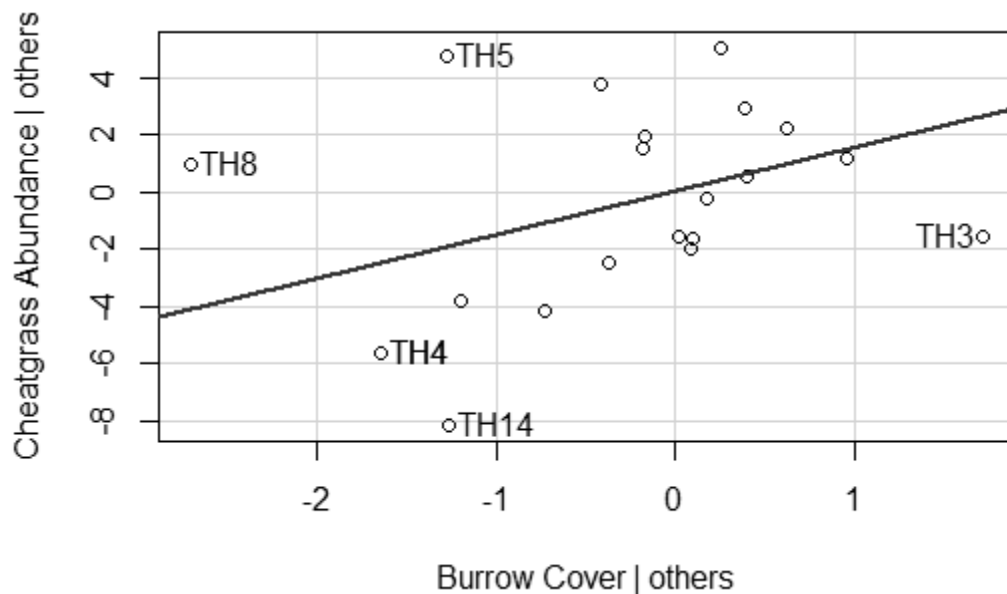


Figure 17. (c) Partial regression plot showing the relationship between burrow cover and cheatgrass abundance at Thackeray in 2015 once all other variables are accounted for. Relative outliers in this plot appear to have little impact on the overall trend.

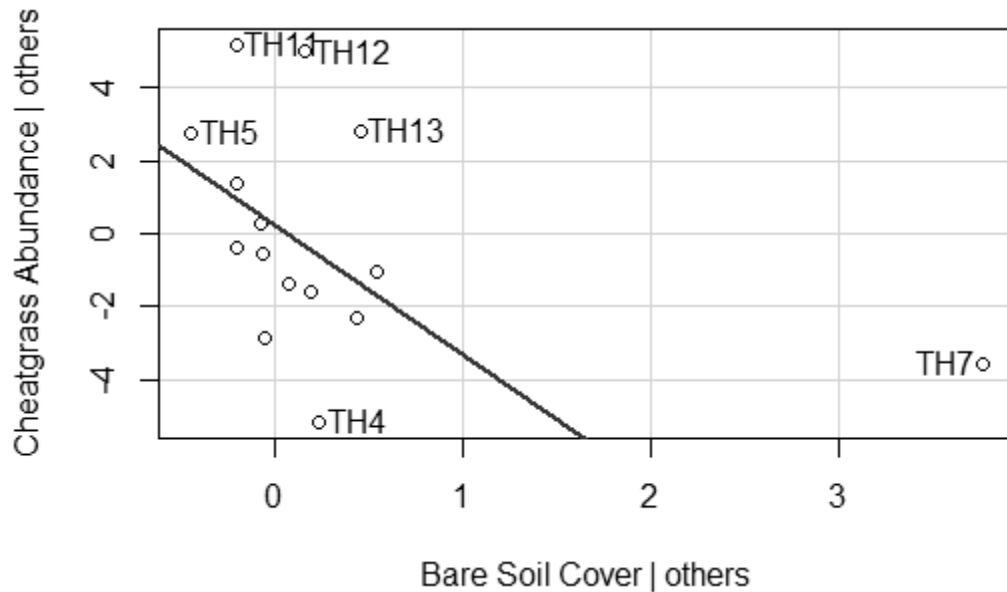


Figure 18. (b) Partial regression plot showing the relationship between bare soil cover and cheatgrass abundance at Thackeray in 2014 once all other variables in the top 2014 models are accounted for.

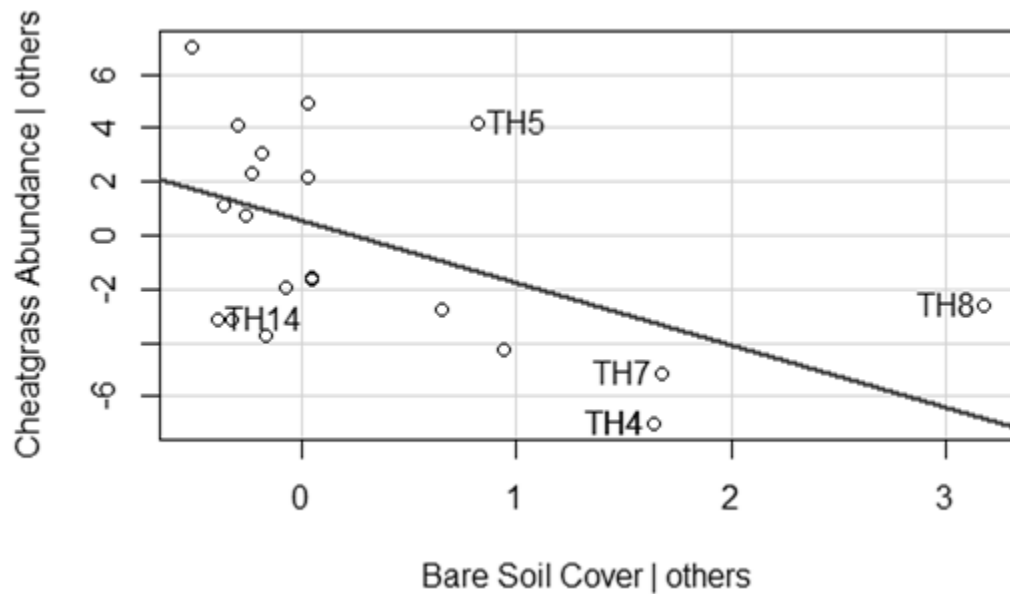


Figure 18. (c) Partial regression plot showing the relationship between bare soil cover and cheatgrass abundance at Thackeray in 2015 once all other variables in the top 2015 models are accounted for.