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Title: Interactive Effects of Silvicultural Herbicides and Cervid Herbivory on Early Seral Plant Communities of the Northern Oregon Coast Range

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ABSTRACT

Intensive forest management (IFM, dense conifer plantings and herbicide applications) may alter the characteristics of early seral plant communities that function as major habitat resources for a host of wildlife species, including cervid herbivores such as *Cervus elaphus* and *Odocoileus hemionus*. Such large herbivores can also substantially affect plant community characteristics and succession, especially in disturbed early seral habitats. I hypothesized that the effect of cervid herbivory on early seral plant communities is mediated by the effect of silvicultural herbicide treatments. If that is the case, intensively treated stands with low plant cover and diversity should be most susceptible to herbivory, as cervids are less selective and herbivory impacts are highly concentrated where forage has been diminished.

To test this hypothesis, I experimentally established paired 225 m^2 cervid Exclusion and Open-Herbivory treatment plots in 28, 12-15 ha early seral plantation stands throughout the northern Oregon Coast Range, USA, representing a gradient in IFM. The gradient included three herbicide treatments and a no-spray Control applied at the stand scale and replicated using a randomized complete block design. I compared estimates of cover, height and diversity for entire

plant communities and specific functional groups among herbivory and herbicide treatments using mixed-effects models with a blocked split-plot design.

I found convincing evidence that the effect of herbivory was mediated by herbicide treatment. No-spray Control stands were too vigorous, diverse and rich with native perennial herb and deciduous shrub forage to be substantially impacted by cervid herbivory. The herbaceous specific, Light herbicide treatment reduced Shannon diversity and the cover and richness of native-perennial herbs, releasing deciduous shrub height growth where cervids where excluded. Highly selective herbivory suppressed the shrub height response by 20.5 cm, increasing the abundance and richness of introduced herb species. The broad spectrum, Moderate herbicide treatment reduced diversity, forage cover and diminished the cover and richness of deciduous shrubs and native-perennial herbs, favoring the dominance of introduced-ruderal herbs. Herbivory in the Moderate treatment reduced total cover by 17.7 percent cover, moderate-quality forage cover by 13.2 percent cover and native perennial herb richness by 1.5 species, while suppressing the cover of introduced-ruderal herbs by 4.58 percent cover and reducing the height of ferns and introduced-perennial herbs by 19.9 and 17.3 cm, respectively. Plant communities subject to the Heavy treatment were the most depauperate of all and herbivory exacerbated the effect of this treatment on native-perennial herbs only. Average height of dominant vegetation was consistently lower with cervid access across all stands, especially with Moderate herbicide treatment.

My results provide evidence that by reducing diversity and the abundance of native forage species, herbicide treatments altered herbivory selectivity and pressure. The alteration of herbivory pressure in turn influenced the outcome of herbicide treatments, resulting in an exacerbated effect with Moderate and Heavy treatments. The effect of herbivory in controlling vegetation in managed stands may have positive implications for conifer seedling growth, constituting a possible ‘ecosystem service’ by cervids in the Pacific Northwest. This ‘service’ may be to the detriment of biodiversity and other early seral associates when coupled with common intensive forest management practices.

Interactive Effects of Silvicultural Herbicides and Cervid Herbivory on Early Seral Plant Communities of the Northern Oregon Coast Range

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

Thomas D. Stokely, Author

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CHAPTER 1: INTERACTIONS BETWEEN LAND MANAGEMENT, KEYSTONE HERBIVORY AND BIODIVERSITY: A LITERATURE REVIEW

The purpose of this review is to provide background into the theories revolving around disturbance ecology and biodiversity functioning, particularly in the context of forest management and keystone herbivory. The theoretical context involves many facets of ecology and forest management pertaining to terrestrial ecosystems throughout the world with a focus on heavily disturbed landscapes. Though the context is broad in scope, the application of this review is specific to intensively managed forest landscapes of the Pacific Northwest (PNW). This review should provide sufficient background into the ecology, management and history of PNW forests, which will lead into Chapter 2, an experimental approach to understanding the interactions between intensive forest management and cervid herbivory.

DISTURBANCE ECOLOGY AND MANAGEMENT

Disturbances influence the successional dynamics of ecosystems by altering community characteristics and competitive interactions between species (Halpern 1989, Collins et al. 1995). There are many types of disturbances with varying intensities, durations, frequencies and degrees of selectivity. These factors and processes determine the extent of alteration induced, how often such alteration occurs and which organisms are affected in a given community (Collins et al. 1995, Dale et al. 2000, Svensson et al. 2009). With agricultural land management, altering competitive interactions and community characteristics is generally achieved by reducing the abundance of species intolerant to disturbance impacts, favoring those that are resilient or resistant (Halpern and Franklin 1990, Hobbs and Huenneke 1992, Augustine and McNaughton

1998). The effects of disturbance on biodiversity can be highly variable, having detrimental impacts in some cases and positive impacts in others (Hobbs and Huenneke 1992, Collins et al. 1995). Under certain conditions, scientists have hypothesized and observed that diversity, as a function of disturbance, follows a unimodal relationship in which diversity peaks at moderate levels of disturbance (i.e., Intermediate Disturbance Hypothesis, Connell 1979, Collins et al. 1995). However, teasing out the effect of a specific disturbance on plant communities can be difficult, given that disturbances generally occur in the context of other ecological processes and interactions.

Disturbances rarely occur in spatiotemporal isolation and are often interactive; meaning the effect of one is influenced by the effect of another (Hobbs and Huenneke 1992, Wisdom et al. 2006). For instance, a few experiments have demonstrated the outcomes of disturbances such as fire are greatly influenced by the biological disturbance of ungulate herbivory (Hobbs and Huenneke 1992, Royo et al. 2010, Collins and Calabrese 2012). It is therefore likely that the ecological outcomes of anthropogenic stand-replacing disturbances are mediated by ungulate herbivores which benefit from the resultant early seral conditions (Augustine and McNaughton 1998, Wisdom et al. 2006). Similarly, the competitive characteristics of early seral plant species associated with those disturbances often have long-lasting effects on community assembly and succession (Halpern 1989, Halpern and Franklin 1990, Collins et al. 1995). Such interacting processes should therefore have substantial influences on the biodiversity associated with natural and anthropogenic disturbance (Augustine and McNaughton 1998, Royo et al. 2010).

Vegetation management selectively controls plant life-forms, including forage, and should therefore have a marked effect on cervid foraging and the subsequent impact of herbivory in given plant communities (Augustine and McNaughton 1998). If vegetation management improves biodiversity and forage production, then managed plant communities may be buffered from herbivory impacts where foraging pressure is satiated (Cardinale et al. 2011). Conversely, large herbivores may have substantial concentrated impacts when the production and diversity of forage is diminished by management practices (Augustine and McNaughton 1998). The exacerbated effect of management and herbivory on forage could shift communities and cause herbivores to be less selective. Experimental studies involving these interactions are essential to understanding the role that humans play in nature by influencing the processes and functions associated with disturbances, herbivory and biodiversity (Hobbs and Huenneke 1992, Chapin et al. 1997, Wisdom et al. 2006, Turner 2010).

For millennia, humans have caused and utilized disturbances to extract resources and to promote the growth of selected species through the reduction of their competitors (i.e. vegetation management). In many areas throughout the world, disturbances such as timber felling, fire, cultivation and herbicide applications are used to clear land and create vast tracts of monoculture crops, often resulting in habitat loss and subsequent biodiversity reductions (Dale et al. 2000). In fact, approximately one-third of the world’s terrestrial net primary productivity and the majority of habitable land area is now appropriated to the production of goods for socio-economic systems, posing serious threats to global ecosystem functioning (Chapin et al. 2000, Dale et al. 2000, Imhoff et al. 2004).

That being said, anthropogenic disturbances can also be used in biodiversity conservation and restoration (Dale et al. 2000). Many conservation management activities use disturbances and vegetation management (e.g., timber felling, fire and herbicides) to reduce the abundance of dominant or invasive species and promote diverse plant communities that function as essential habitat for certain wildlife species (Fleming et al. 2009, Franklin and Johnson 2012). Some postulate that active management for biodiversity and wildlife habitat conservation is essential (Franklin and Johnson 2012), not only to ecosystem functioning, but to the ecological services that socio-economic systems receive from the natural world (Chapin et al. 1997, Chapin et al. 2000, Dale et al. 2000, Cardinale et al. 2011).

Disturbances and vegetation management can therefore be used as tools to manage land for two major sets of outcomes: (A) intensive management of ecosystems to guide succession towards the productivity of desired crop species (Wagner et al. 2006); or (B) conservation management of ecosystems to guide succession towards functional biodiversity (Dale et al. 2000). On one hand, intensive management can provide greater production of resources on less amount of land, freeing up natural areas for biodiversity conservation (Wagner et al. 2004, Paquette and Messier 2010). On the other hand, as we utilize more landmass for resource production, the integration of conservation management into heavily managed and disturbed landscapes will be essential for the functioning of the ecosystems on which we depend (Chapin et al. 2000, Dale et al. 2000).

INTENSIVE FOREST MANAGEMENT & EARLY SERAL COMMUNITIES

Forest ecosystems provide global markets with the timber used for wood products, which substantially contribute to economic and infrastructural development of socio-economic systems (Noble and Dirzo 1997). Forest management causes and utilizes disturbances for the extraction of timber (i.e. timber felling) as well as vegetation management (e.g. broadcast burning, soil scarification, herbicide application) for reforestation and plantation management efforts (Wagner et al. 2006). As the global demand of wood rises, more productive forestland will be utilized as intensively managed plantations (Stephens and Wagner 2007, Paquette and Messier 2010). The goal of intensive forest management (IFM) is to hasten forest succession and reduce timber harvest return intervals (i.e. rotation ages) through dense plantations of nursery seedling stock wherein competing vegetation is managed following timber harvests (Wagner et al. 2006). A timber harvest is in itself the initial disturbance that improves growing conditions for shade-intolerant crop trees. However, such a disturbance also benefits a diverse suite of early seral plant species, evolved to rapidly take advantage of increased resource availability (Halpern and Spies 1995). These species are viewed as competition with crop trees, so foresters prescribe a secondary disturbance, in the form of selective herbicides, to reduce their abundance and promote the rapid growth of crop seedlings (Maguire et al. 2009). Such compounding disturbances results in rapid succession of early seral into mid-seral forests which reduces rotational ages, increases profitability of timber harvests, and provides a steady and stable flow of timber for global wood markets (Wagner et al. 2006).

Early Seral Plant Communities of the Pacific Northwest

IFM is ubiquitous in the Pacific Northwest (PNW), especially in the Coast Range Ecoregion, which supports one of the world’s most productive forest ecosystems (Van Tuyl et al. 2005, Spies et al. 2007) and provides the highest volume of timber in the United States (Adams and Latta 2007). Without the secondary disturbance of herbicide application, harvested stands in the PNW may exist in an early seral state of succession for decades, with herbaceous dominance 0-15 years and shrub dominance 10-20 years post-harvest, depending on initial vegetation characteristics and disturbance intensity (Halpern and Franklin 1990). Early seral communities are known for high levels of plant diversity (Halpern and Spies 1995), consisting of native herbs, grasses and deciduous shrubs which take advantage of the open growing conditions that follow stand-replacing disturbances (Halpern 1989, Halpern and Spies 1995). These early seral communities tend to be floristically diverse (Halpern and Spies 1995), providing a higher richness and abundance of forage for herbivorous wildlife compared to closed-canopy forests (Cook et al. *in press*, Hagar 2007).

In the Pacific Northwest, the immediate flush of vegetation post-disturbance is mostly characterized by ruderal herbs, perennial herbs, grasses, ferns and understory shrubs and saplings; the latter of which are often legacies from the previous forested stands (Halpern 1989). Ruderal herbs consist of such genera as native *Epilobium, Galium* and *Claytonia,* as well as introduced *Crepis, Senecio,* and *Hypochaeris* which originate from the seed bank or wind-blown sources. Legacy, understory perennial herbs, graminoids and ferns are often composed of native genera such as *Viola, Iris, Actaea, Dicentra, Hieracium, Maianthemum, Trillium, Lilium, Lupinus, Lotus, Luzula, Pteridium, Polystichum,* and others, many of which sprout from underground vegetative bodies that survive stand replacing disturbances. Deciduous broadleaf shrubs and trees such as *Sambucus, Corylus, Cornus, Holodiscus* and *Acer* as well as evergreen broadleaf shrubs such as *Rhododendron, Gaultheria* and *Mahonia* comprise legacy/early seral shrubs, whereas *Acer, Tsuga, Picea* and *Abies* comprise understory saplings and trees (see appendix F for complete plant list). Many of the mature deciduous broadleaf shrub and tree species coppice sprout (sprout from basal epicormic buds) after being cut down and therefore vigorously compete for resources, quickly overtopping the herb layer and other understory shrubs and saplings. As succession proceeds, many of the legacy species spread vegetatively and/or set seed while other herbs, grasses and shrubs fill in the voids from the seed bank or outside sources.

In general, initial community structure and composition is determined by the disturbance intensity and the understory legacy species that survive the given disturbance (Halpern 1989, Collins et al. 1995). The competitive characteristics of the legacy or immigrant species then determines the successional dynamics and characteristics of early seral communities (Halpern and Franklin 1990). Moisture is often the most important limiting resource, given that rainfall typically ceases during the summer growing season in the PNW (Dinger and Rose 2009). Therefore, early seral species that are both competitive and stress tolerant are able to dominate later stages of early seral (10-20 years), eventually giving way to conifer trees such as *Pseudotsuga menziesii*, the major crop tree of the region. As a generalist, *P. menziesii* is well suited to both compete and tolerate stressful growing conditions, being able to opportunistically photosynthesize and grow at rates of over a vertical meter per year after escaping competition (Dinger and Rose 2009). However, the degree and timing of competition limit whether or not individual *P. menziesii* seedlings can become established during early seral stages (Halpern and Spies 1995, Maguire et al. 2009). In the absence of active management, legacy deciduous and evergreen broadleaves often limit growth of *P. menziesii* through direct competition, resulting in a lengthened early seral stage (Rose et al. 2006).

The functional attributes of early seral plants makes them particularly important for successional dynamics and ecosystem functioning (Swanson et al. 2011). Many studies on succession in the PNW show that through competitive interactions, diverse early seral characteristics can translate to higher physiognomic and structural diversity in later stand ages

(Halpern and Franklin 1990). The competitive and disturbance-adapted characteristics associated with early seral plants are also related to other characteristics such as forage quality and palatability as well as contributions to habitat structure for wildlife (Swanson et al. 2011). For instance, highly competitive plants are often highly palatable as the plants invest more energy in growth and less in chemical and mechanical defense (Mattson 1980, Augustine and McNaughton 1998). Coppicing of deciduous shrubs and trees, associated with physical disturbance, often promotes the abundant growth of numerous apical stems, with high densities of foliage and branching, providing abundant nutrition and habitat cover for wildlife (Best et al. 2003, Pelc et al. 2011, Kersch-Becker and Lewinsohn 2012). The diversity and abundance of various early seral life-forms provide a wide variety of forage resources for wildlife such as cervids. Forage resources such as herbaceous tissues, woody meristems, buds, catkins, deciduous foliage, hard and soft mast are all more common in early compared to closed-canopy, mid-seral forest understories (Hagar 2007). In essence, early seral plant communities serve as an important basal trophic level in forested ecosystems. A review by Hagar (2007) highlights the importance of deciduous shrub vegetation for wildlife species of the PNW, suggesting that many forest wildlife species are either dependent on or associated with these vegetation types.

Intensive Forest Management

The ecological importance of early seral communities has been overlooked in the past century of forest management in the PNW, despite their importance for many wildlife species (Swanson et al. 2011). Following over a century of harvest of primary-forest and salvage logging, fire suppression and extensive vegetation management/reforestation efforts on federal lands, the Northwest Forest Plan (NWFP) was enacted, predominately in response to declines of old growth forests and associated obligate species such as the Northern Spotted Owl (*Strix occidentalis caurina*) (Northwest Forest Plan 1994). The NWFP halted clear-cut timber harvesting on federal lands with the intention of promoting the restoration of late seral forests, although much of the regenerating forests had been replanted and intensively managed using chemical and mechanical methods (USFS 1973, BLM 1989). Along with fire suppression, such land management has favored the dominance of dense, mid seral forests throughout PNW landscapes, with very little functional early seral habitat (Swanson et al. 2011). As a result, much of the remaining early seral habitat occurs primarily on private, industrial forest lands of the Oregon Coast Range and parts of the Cascade Foothills, where short-rotation intensive forest management is common practice (Spies et al. 2007). The Oregon Forest Practices Act (OFPA) requires forest landowners to maintain 200 seedlings per acre, which are 'free to grow' over undesired competing plants (ODF 1994). In order to ensure planted seedlings maintain dominance, landowners often perform vegetation management in the form of silvicultural herbicide treatments (Maguire et al. 2009).

Intensive forest management and plantation-style forestry is becoming more controversial in the PNW as stigmas relating to herbicides arise within society and environmental groups throughout the nation (McBroom et al. 2013). Irrespective of public concerns, there is very little evidence of acute toxicological effects of silvicultural herbicide prescriptions on wildlife or humans, given EPA application rate standards (McComb et al. 2008). Much less well known are the indirect effects of silvicultural herbicides and vegetation management on biodiversity and wildlife through habitat modifications and bottom-up plant community alterations (Stephens and Wagner 2007).

There are three major types of broad silvicultural herbicide applications utilized in the PNW. These are often used in succession and with varying combinations of chemicals during the critical threshold period of seedling development (Maguire et al. 2009): (1) post-harvest site preparation (broad spectrum, post-emergent, pre-planting), (2) 1st year spring herbaceous (herbaceous/graminoid specific, pre-emergent), (3) 2nd year fall woody (broadleaf hardwood specific, post-emergent), and subsequent spring herbaceous or fall broadleaf woody treatments if needed. The immediate effects of herbicide application are generally a severe reduction in the cover and richness of early seral perennial plants followed by a spike in introduced ruderals, especially during the second growing season (Dinger and Rose 2009). Such a reduction in shrub and perennial herbaceous cover is greatly beneficial to planted seedling growth and survival, giving them a head start on the competition (Dinger and Rose 2009, Maguire et al. 2009). However, the invasion by introduced-ruderals can be a problem for plantations success, generally addressed with additional spring herbaceous treatments (Dinger and Rose 2009, Devine et al. 2011). Shortly after the cessation of herbicide treatments (within 3-5 years), the plant community begins to reestablish, giving way to a flush of herbaceous vegetation (native and introduced), and gradually shrubs (Miller et al. 1999, Rose and Rosner 2005, Rose et al. 2006). In general, the selectivity of chemicals used and timing of application have great influence on how the plant community responds to treatments (Newton 2006, Maguire et al. 2009). The effects can range from a positive effect on diversity and forage to a dramatic loss in native plant diversity and dominance (Wagner et al. 2004, Stephens and Wagner 2007)

With certain herbicide prescriptions, treated stands have developed higher plant diversity than untreated stands, as untreated deciduous shrubs can close canopies 10-15 years post-harvest, reducing understory herbaceous diversity (Lindgren and Sullivan 2001, Iglay et al. 2010). However, broad spectrum treatments can facilitate the invasion by introduced species which take advantage of the exposed resources, often maintaining dominance along with planted seedlings (Dinger and Rose 2009). Therefore, herbicide induced disturbance can cause a shift in plant community composition, with little perceived effects on diversity *per se* (Sullivan et al. 1996). Essentially, herbicide induced disturbance is used to truncate early succession, promoting conifer canopy closure within 15 years and reducing rotation ages down to ~40 years (Wagner et al. 2006, Maguire et al. 2009). Though the early seral stage is maintained on private industrial forestlands, it is both truncated and functionally altered, thus failing to provide suitable habitat for some wildlife species (Hagar 2007, Spies et al. 2007, Swanson et al. 2011).

CERVID FORAGING ECOLOGY

Unmanaged early seral habitats are now considered to be the scarcest forest habitat type in the PNW (Spies et al. 2007, Swanson et al. 2011), leading to concern for the wildlife that rely on these habitats. The two native cervid species *Odocoileus hemionus columbianus* (black-tailed deer) and *Cervus elaphus roosevelti* (Roosevelt elk or Wapiti) are among those species that are considered to be strongly associated with early seral habitats (Hagar 2007). Both species have made tremendous comebacks since the early 1900’s when they were hunted to near extinction in many areas (Ogara & Dundas 2002). Black-tailed deer populations actually spiked during the federal timber harvests of the 1970’s and 80’s, likely because early seral habitat was abundant during those periods (ODFW 2008). However, black-tailed deer, and some Roosevelt elk populations have been on the decline since the 1980-90’s possibly as a partial result of declines in high quality early seral habitat associated with land management practices (ODFW 2008, ODFW 2003).

Cervid Habitat Requirements

Both cervids share similar habitats, though elk have a broader diet and are able to digest less palatable plants (Stewart et al. 2011). Compared to most ungulates, cervids are highly selective regarding the forage species they consume. They generally require plants with high concentrations of digestible proteins and sugars and low concentrations of lignin and digestion-inhibiting compounds such as phenols (Cook 2002, Cook et al. *in press*). Foraging selectivity is often focused on plant species that are highly competitive and which invest much energy into growth and less into chemical or physical defense (Augustine and McNaughton 1998). The competitive nature of early seral vegetation, especially coppice sprouting shrubs and many perennial herbs, also make them high quality sources of energy and protein for cervids (Best et al. 2003). Plants are temporally variable in palatability and nutrient quality, depending on phenotypic characteristics (Mattson 1980). Thus floristically diverse early seral communities serve as an essential source of year-round forage for cervids. These communities provide deciduous stems and cold-hardy forb and grass foliage in the winter, palatable evergreen, deciduous and herbaceous foliage and stems in spring, abundant deciduous and herbaceous foliage and seeds in summer and mast and apical meristems of shrubs in the fall (ODFW 2003, ODFW 2008). Although much research and management has focused on winter and spring forage (i.e. critical for body maintenance and lactation in females, respectively), summer and fall forage has been recently recognized as being functionally important for building fat reserves, crucial for overall fitness (winter survival, mating and fecundity) (Cook et al. 2013).

The availability of high-quality forage needed to sustain desired cervid populations in the PNW is generally low (Cook et. al 2013). It is possible that IFM and silvicultural herbicide applications contribute to the lack of high quality forage by truncating the early stages of succession and reducing the abundance and diversity of early seral vegetation during those shortened stages. A long-term study in western Alberta, Canada demonstrated that hexazinone herbicide treatment caused an overall reduction in forage for *Cervus*, *Alces* & *Odocoileus* up to 20 years following harvest, compared to unsprayed harvest units, thus negating the benefit of clear-cutting for cervid forage production (Strong and Gates 2006). However, cervids utilize even the most heavily treated plantations (OFRI 2013) and summer forage can rebound with a flush of herbaceous growth following the cessation of herbicide treatments (Iglay et al. 2010). Still, young industrial plantations serve as an important source of forage for cervids compared to the relatively depauperate conditions of mid-seral closed canopy forests in the PNW (OFRI 2013). As a result, cervid browsing in plantations often results in damage to crop seedlings, adding to conflict between management goals for wildlife and economic objectives (ODFW 2008, OFRI 2013). Less well known is the role that cervid foraging plays in influencing the early seral plants that are targeted by herbicide prescriptions.

Cervid Herbivory Impacts

Due to the highly selective nature of cervid foraging and the sheer biomass required to maintain such large mammals, cervids are considered keystone herbivores in many ecosystems throughout the world (Hobbs 1996, Putman 1996, Cote et al. 2004). Their foraging tendencies can exert strong top-down pressure on plant communities, often altering the characteristics and successional dynamics of ecosystems (Augustine and McNaughton 1998). These herbivores can be thought of as a biological disturbance, which trample vegetation and selectively remove aboveground tissues of highly palatable and competitive plants (Wisdom et al. 2006). Cervid exclusion and density manipulation experiments have revealed that these top-down biological disturbances reduce the sprouting of many palatable shrubs and trees (both evergreen and deciduous), favoring communities dominated by non-palatable woody and herbaceous vegetation (Rambo and Faeth 1999, Bailey and Whitham 2002, Horsley et al. 2003). At high cervid densities, herbivory can cause local extinction of native herb species, intolerant to repeated above ground tissue loss (Knight et al. 2009).

At moderate cervid densities, however, infrequent foraging can stimulate apical shoot growth and the diversity of herbaceous vegetation, increasing alpha diversity and forage abundance (Augustine and McNaughton 1998, Stewart et al. 2006, Royo et al. 2010). Therefore, cervid foraging resembles the characteristics other disturbances in which selective, moderate intensities of foraging can promote diversity (i.e. Intermediate Disturbance Hypothesis) (Connell 1979, Hobbs and Huenneke 1992, Nuttle et al. 2013). That said, the diversity of forage available and the amount of foraging pressure on palatable plants influences the degree of foraging selectivity (Augustine and McNaughton 1998). For instance Stewart et al. (2011) found that high densities of elk reduced the richness and abundance of high quality forage, causing both deer and elk to consume a wider variety of less palatable plants. Augustine & McNaughton (1998) suggest that with moderate cervid densities, the abundance and variety of forage limits the impact that cervid foraging can have on plant communities. With high levels of forage abundance and diversity, herbivory impacts become saturated, whereas the same animal densities will have a disproportionate effect on habitats that contain lower abundance and variety of forage resources.

It is quite likely that cervid herbivory interacts with disturbances involved in land management activities (Wisdom et al. 2006). In other words, the effects of disturbance on plant communities should influence forage abundance and richness, thus altering foraging intensity and degree of selectivity. As previously suggested, stand-replacing disturbances such as timber harvesting generally favor a flush of early seral vegetation, which is often composed of high quality forage. The initial disturbance of the timber harvest may facilitate the secondary disturbance of cervid herbivory, which in turn mediates the successional trajectory of those stands (Stromayer and Warren 1997, Rooney and Waller 2003). Highly diverse early seral plant communities with an abundance of forage should be relatively buffered from cervid herbivory as foraging is dispersed across a wide variety of forage species (Augustine and McNaughton 1998). Alternatively, stands subjected to intensive, repeated disturbances which diminish forage may be less resilient to herbivory impacts as foraging pressure is concentrated on the few remaining forage plants. Cervids may also have to consume a wider variety of less palatable plants to meet nutritional demands (Stewart et al. 2011). If management practice alters the relative abundances of different competing plants, then selective foraging pressure on the more nutritious species should influence competitive interactions among those species and thus succession dynamics (Augustine and McNaughton 1998).

Variable forest retention harvesting and cervid density and/or exclusion experiments in the eastern United States have shown that the effect of harvest on understory vegetation and stand regeneration is heavily influenced by the density or presence/absence of deer (Horsley et al. 2003, Rooney and Waller 2003). In many cases, cervid browsing in thinned units has inhibited understory seedling growth and diversity of hardwood species (Horsley et al. 2003, Rooney and Waller 2003, Nuttle et al. 2013). In other cases, moderate densities of cervids, in combination with prescribed fire and selective timber felling, contributed towards the restoration of the diverse herbaceous understories associated with deciduous woodland habitats (Horsley et al. 2003, Royo et al. 2010, Nuttle et al. 2013).

Studies involving other ungulates such as cattle and American bison (*Bison bison*) also suggest that grazing in combination with moderate fire frequency serve to promote the diversity that is historically associated with tallgrass prairie ecosystems (Veen et al. 2008, Collins and Calabrese 2012). Likewise, cervid foraging in semi-arid forested ecosystems is thought to mediate fire behavior by influencing surface and ladder fuels (Hobbs 1996, Augustine and McNaughton 1998). Augustine and McNaughton (1998) hypothesized that the selective pressures of both fire and herbivory have influenced disturbance tolerance traits such as coppice sprouting in some hardwood species, which suggests that these plant species evolved under the interactive pressure of both disturbances. Though coppicing feeds back to promote an abundance of forage in harvested timber stands, vegetation management practices heavily focus on the control of coppice sprouting species, which should influence disturbance-herbivory interactions (Best et al. 2003, Rose and Rosner 2005, Pelc et al. 2011).

Many of these studies have been conducted in mesic and arid ecosystems with overabundant white-tail deer (*Odocoileus virginianus*) populations (Stromayer and Warren 1997), cattle (*Bos spp)* (Hobbs and Huenneke 1992), bison (*Bison bison)* (Collins and Calabrese 2012) and rocky mountain elk (*Cervus elaphus nelsoni)* (Stewart et al. 2006*)* Less well known, are the interactions between cervid herbivory and intensive management of moist-temperate conifer plantations via silvicultural herbicide applications, especially in the PNW with black-tailed deer and Roosevelt elk (OFRI 2003). Considering the extent of managed forest landscapes and cervid populations in the Oregon Coast Range, it is likely that the effects of silvicultural herbicide applications on early seral plant communities are influenced by selective cervid herbivory. Many experimental studies on vegetation management and plantation development have controlled for the confounding effects of herbivory by building exclosures around study areas (Rose et al. 2006, Dinger and Rose 2009, Dinger and Rose 2010) or overlook the effect of herbivory when cervid exclusion was not available (Sullivan et al. 1996, Maguire et al. 2009)). Likewise, many studies and management efforts focus on the relative impacts of cervids on plant communities and agricultural systems, ignoring the role that management has on influencing foraging behavior (Wisdom et al. 2006). In general, little experimental information on the interactive effects of herbicides and herbivory exists. A detailed experimental assessment of the range of operational herbicide treatments, with and without cervids, is warranted to better understand the interactive effects of both disturbance types on early seral characteristics.

QUESTION AND HYPOTHESES

With this thesis, I seek to answer the following research question: How does cervid herbivory affect early seral plant communities across a gradient of intensive forest management? I hypothesized that the effect of cervid herbivory is mediated by the effect of silvicultural herbicide treatment on early seral plant community characteristics. Treated stands with low plant cover and diversity should be most heavily impacted by herbivory as cervids become less selective where forage has been diminished. The few, rebounding life-forms within intensively treated stands will be more heavily impacted by concentrated herbivory pressure, regardless of forage quality characteristics. Therefore, cervid herbivory may exacerbate the effect of herbicide application by suppressing the regeneration of those plant communities. As a corollary, untreated stands with high plant cover and diversity should be highly buffered against cervid herbivory, because forage is abundant and rich. As predicted by the Intermediate Disturbance Hypothesis (Connell 1979), selective herbivory is expected to increase diversity by reducing the dominance of palatable herbs and shrubs.

The objective of this study is to test the overarching hypothesis of an interaction between herbicide and herbivory treatments with two major response groups: community characteristics and functional groups. Community characteristics include plant cover, species richness, height of dominant vegetation and Shannon and Simpson diversity and evenness indices. Functional group responses include the cover, richness and average height by life-form and cover of three forage quality categories.

If the effect of herbivory is mediated by herbicide treatment, then cover, richness, diversity and dominant vegetation height should be lowest with cervid access in heavily treated stands, which have low diversity and forage cover, and thus low tolerance to herbivory. The cover and richness of forage species, including deciduous hardwoods and native herbs, should be lowest with cervid access in heavily treated stands where those rebounding plants are most susceptible to selective herbivory. The abundance of low quality forage, such as ferns and some introduced-ruderal herbs should be impacted by cervid herbivory where higher quality forage has been diminished and cervids are less selective. Cover and richness of introduced-ruderal herbs should spike with cervid access in moderately treated stands as they replace of locally extirpated native flora.

CHAPTER 2: INTERACTIVE EFFECTS OF SILVICULTURAL HERBICIDES AND CERVID HERBIVORY ON EARLY SERAL CHARACTERISTICS

INTRODUCTION

Understanding how different disturbances interact to influence plant communities is crucial to the effective conservation and management of heavily disturbed ecosystems (Hobbs and Huenneke 1992, Dale et al. 2000, Turner 2010). As an important component to ecosystem functioning, disturbances mediate plant community characteristics by altering the competitive dynamics between species and functional groups (Halpern 1989, Hobbs and Huenneke 1992). Disturbances act as both an ecological filter and floodgate, reducing the abundance of intolerant organisms while releasing environmental resources for the benefit of others. The effects of disturbances on plant communities can be profound (Hobbs and Huenneke 1992), which has major implications for functional biodiversity (Chapin et al. 1997). For instance, stand replacing disturbances in forested ecosystems are well known to promote the productivity and diversity of understory, early-seral plant communities (Halpern and Spies 1995). These diverse plant communities function to provide a variety of floristic resources to a variety of herbivorous fauna, inducing positive bottom-up trophic cascades (Hagar 2007, Swanson et al. 2011).

Globally, large ungulate herbivores utilize disturbed plant communities where forage is highly abundant and diverse (Hobbs 1996, Augustine and McNaughton 1998) and in many regions, ungulates have dramatic effects on plant communities and ecosystems (Cote et al. 2004, Putman 1996). Ungulates, especially cervids, can be highly selective, generally foraging on palatable herbs, grasses and deciduous shrubs, as many of these plants invest more energy into growth and competition than chemical defense (Cook et al. 2013). This selectivity can result in dominance by non-palatable species, which has a cascading effect throughout the food web and ecosystem as a whole (Hobbs 1996, Augustine and McNaughton 1998). Foraging selectivity can also be highly plastic in which ungulates may consume a wider variety of forages, including low quality species, where high quality forage is less abundant (Augustine and McNaughton 1998, Stewart et al. 2011).

Theoretically, the characteristics of plant communities govern the relative impacts that selective foraging may have (Augustine and McNaughton 1998). For instance, diverse plant communities with high forage availability can be buffered from moderate levels of herbivory because herbivory pressure is distributed among palatable species (Augustine and McNaughton 1998). Browsed plants are then able to rebound rapidly or are replaced by other competitive species. On the other hand, heavily disturbed communities with low diversity and forage availability can be more susceptible to herbivory as foraging pressure is concentrated on the remaining forage species. As forage species are diminished, cervids may then become less selective, foraging on a wider variety of plants to meet nutritional requirements (Stewart et al. 2011).

The effects of herbivory may be dependent on the effects of the primary disturbance (Augustine and McNaughton 1998, Royo et al. 2010, Beguin et al. 2011). Likewise, the effects of the primary physical or chemical disturbance can be highly mediated by the secondary biological disturbance, herbivory. These interactions are presumed to be integral to the characteristics of native plant communities and ecological functioning of many regions (Royo et al. 2010, Augustine and McNaughton 1998, Collins 2012). However, anthropogenic disturbances and non-native invasive species have altered the relationships between natural disturbances and plant community characteristics (Hobbs and Huenneke 1992, Chapin et al. 1997), therefore altering interactions with herbivory (Hobbs and Huenneke 1992, Augustine and McNaughton 1998).

Humans have utilized disturbances for millennia in an attempt to promote the growth of selected species over natural assemblages. With the advent of modern management techniques and a growing human population, more land is being utilized and intensively managed at the cost of native biodiversity and ecosystem functioning (Chapin et al. 2000, Dale et al. 2000, Tilman and Lehman 2001). For example, mechanical harvesting and chemical site preparation has enabled the establishment of vast monoculture crops, which has led to habitat loss and altered natural disturbance regimes (Dale et al. 2000, Turner 2010). In many cases, the management of these plantations facilitates the co-dominance of exotic invasive species that thrive in the wake of human-induced disturbance, further exacerbating biodiversity loss (Hobbs and Huenneke 1992, Tilman and Lehman 2001, Tilman 2004).

In order to meet the growing global demand for wood products, more forestland is being utilized as intensively managed plantations (Wagner et al. 2004). Intensive forest management practices (IFM) include large (>10 ha) clearcut timber harvesting, followed up by chemical vegetation management (i.e. silvicultural herbicide treatments) and dense plantings of nursery seedling stock (Wagner et al. 2006, Maguire et al. 2009). These practices ensure the survival and rapid growth of crop trees, resulting in decreased rotation ages, increased investment returns and steady timber supplies (Wagner et al. 2006, Maguire et al. 2009).

In the Pacific Northwest (PNW), intensively managed plantations are ubiquitous throughout the Coast Range and Cascade Foothills ecoregions, which constitute some of the most productive forest ecosystems in the world (Van Tuyl et al. 2005, Spies et al. 2007). Without the site preparation, timber harvesting promotes a diverse flush of early seral species that have evolved to take advantage of stand replacing disturbances and dominate stands for up to 20 years (Halpern and Franklin 1990, Rose et al. 2006). Therefore, production foresters must prescribe a suite of herbicides to effectively and efficiently ensure plantation establishment as per state regulations (ORS 526.490) and anticipated investment returns (Wagner et al. 2006, Maguire et al. 2009). These herbicide treatments generally result in an immediate reduction of early seral shrubs and herbs, a spike in exotic-ruderal herb cover and rapid seedling growth (Dinger and Rose 2009). Eventually, early seral species do rebound; although the early seral stage is truncated because conifer canopy closure occurs from 10-15 years post-harvest (Wagner et al. 2006).

Most studies on intensive forest management have focused on competition between early seral plants and planted seedlings, and less so on the ecological processes that pertain to functional biodiversity and interacting disturbances (Stephens and Wagner 2007). In some cases, experiments were conducted in fenced areas, thus reporting on the effects of herbicide alone, without accounting for the effect of herbivory (Rose et al. 2006, Dinger and Rose 2009, Dinger and Rose 2010). To my knowledge, no published studies have investigated the role of cervid herbivores in mediating the effect of the intensive forest management practices, especially in the PNW. Likewise, few experimental studies have investigated the ecological effects of disturbances and land management practices on the impacts of cervid herbivory (Wisdom et al. 2006).

Black-tailed deer and Roosevelt elk are ubiquitous throughout the region and rely heavily on harvested units for year-round forage (ODFW 2008). More importantly, these disturbed stands provide cervids with crucial spring, summer and fall nutrition, important for lactation, breeding and winter survival (Cook et al. 2004, Cook et al. 2013). Though ubiquitous, populations of black-tailed deer have declined steadily since the 1980's and elk are beginning to decline in some areas, potentially as a result of inadequate forage availability at landscape scales (Cook et al. 2013, Cook et al. *in press*). Though vegetation management practices can reduce forage availability (Strong and Gates 2006) and truncate early seral stages, these cervids utilize even the most heavily treated stands (OFRI 2003), foraging on rebounding flora and planted seedlings. In forestry, cervids are considered pests as they damage and depredate planted seedlings, in some cases causing plantation failure (ODFW 2008, ODFW 2003). Much less attention has been given to the 'ecosystem services' role that cervids may have in controlling competition and in mediating the effect of vegetation management. Considering that herbicide treatment immediately reduces plant diversity and alters the composition of early seral plants, it is likely that cervids have a disproportionate effect on recovering communities in intensively treated stands compared to naturally regenerating stands.

I hypothesized that the effect of cervid herbivory is mediated by the effect herbicide treatment on plant community characteristics. Treated stands with low plant cover and diversity should be most heavily impacted by herbivory because cervids become less selective where forage has been diminished. Furthermore, cervid herbivory may exacerbate the effect of herbicide treatment by concentrating foraging pressure on the remaining flora, regardless of forage quality. Alternatively, untreated stands should be buffered against herbivory because foraging pressure is distributed among a variety of high quality forage species where early seral diversity is high. Herbivory may increase diversity within untreated stands as cervids selectively forage on dominant high quality forage, thus releasing rare or suppressed species. The objectives of this study are to test these hypotheses by comparing broad community characteristics (vegetation cover, dominant vegetation height and diversity metrics) and specific functional group responses (cover of three forage groups; cover, richness and height of eight life-forms) between cervid exclusion treatments among a gradient in herbicide application intensity.

METHODS

In order to test these hypotheses, we established a large-scale Intensive Forest Management experiment throughout the northern Oregon Coast Range, USA (Betts et al. 2013).

Study Area

The study sites were located within the northern Oregon Coast Range along a 100 km longitudinal gradient from the Luckiamute and Siletz river watersheds to the Wilson river watershed (Figure 1). The average annual precipitation for easterly sites was approximately 180 cm in 2011 and 160 cm in 2012, and average annual precipitation for westerly sites was approximately 250 cm for 2011 and 220 cm for 2012; the majority of rainfall occurred from November to May for all sites (NOAA 2014). The average minimum temperature was approximately 5.2º C and average maximum temperature was approximately 15º C across the Coast Range (NOAA 2014). The topographic features of the Coast Range consisted of highly dissected, low mountains with steep slopes (Spies et al. 2007). The sites varied in elevation from 184 to 756 m, ranged from 1 to 30 degree slopes and reflected aspect in all cardinal and intercardinal directions. Geologic parent material consisted of basalts, sandstones and siltstones with soils being characterized as deep, well-drained silt loams, clay loams and sandy loams with high organic matter content and deep O horizons (Personal observations, NRCS Soil Survey). All blocks existed in the *Tsuga heterophylla* vegetation zone, which is dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* with scattered stands of *Alnus rubra* and intermediate *Acer macrophyllum* (Franklin and Dyrness 1988). *Gautheria, Polystichum, Pteridium, Rhamnus, Mahonia, Acer, Rhododendron, Corylus* and *Holodiscus* characterize the understory and early seral hardwood community types (Franklin and Dyrness 1988). Landownership of the Coast Range is dominated by private industrial (41%) with co-dominant private non-industrial (22%), USDI Bureau of Land Management (15%), Oregon State Department of Forestry (12%), USDA Forest Service (10%) and Indian Tribal Lands (<1%) (Spies et al. 2007). Cervid populations are spatially variable throughout the region, but are relatively consistent year round, as neither elk nor deer migrate to winter range in the region (ODFW 2003, ODFW 2008).

Study Design

In collaboration with forest industry partners and the Oregon Department of Forestry, we designed the experimental IFM units using a replicated block design, with 7 distinct study blocks, spanning approximately 100 km (N-S) and 45 km (E-W) . Within each block, we established four ~13 ha herbicide treatment stands, each of which were located within larger harvested units (15 - 20 ha). All harvest units were cut within 1 year of each other. We selected 4 harvest units that were between 1 and 5 km from each other within each of the 7 blocks. We used this distance criterion for stand selection to reduce within-block variability (avoid stands too far apart) and also reduce confounding influences of animal movement (avoid stands too close, where the effect of one treatment on animal behavior may influence the others). With seven blocks (total N=28) distributed along a 100 km geographic gradient, to our knowledge this constitutes one of the largest single experimental studies on IFM globally.

Vegetation Management Intensity Experiment

All blocks underwent commercial clear-cutting operations during fall 2009. Starting fall of 2010, we randomly assigned each of the four stands within each block to one of four treatments, which represent a gradient in vegetation management intensity with varying chemical mixtures and treatment timing: (1) no-spray Control; (2) Light herbicide treatment; (3) Moderate herbicide treatment; (4) Heavy herbicide treatment (See appendix A for a list of chemicals, rates and timing). In early spring of 2011, all stands were planted by reforestation professionals with nursery stock, bare root *Pseudotsuga menziesii* seedlings, the major commercial species in the region. The no-spray served as our Control (reference treatment), representing conditions where landowners harvest and plant but do not treat vegetation with herbicides. These conditions are rare in the Oregon Coast Range due to the Northwest Forest Plan, the Oregon Forest Practices Act and common intensive forest management practices. The Light herbicide treatment consisted of a Velpar (Hexazinone) and 2,4-D, a spring application which primarily targeted herbaceous vegetation. This treatment represented a very light treatment, more common on small scale private lands and Oregon Department of Forestry lands than on large-scale, private industrial operations. The Moderate treatment was sprayed with a broad spectrum, fall 2010 site preparation treatment which consisted of Escort (Metsulfuron-methyl), Accord (Glyphosate), Chopper (Imazapyr), Oust (Sulfometuron-methyl) and MSO (methylated seed oil, surfactant) followed by a spring 2011 herbaceous treatment (same chemicals and rates as Light herbaceous treatment). This treatment represented an operational standard most common on industrial forest lands throughout the region. The Heavy treatment was sprayed with a fall 2010 site preparation treatment (same as chemicals and rates as Moderate site preparation treatment) and spring 2011 and 2012 herbaceous treatments (same chemicals and rates as Light and Moderate spring herbaceous treatments). This treatment represented a more extreme operational standard, common on industrial lands only when needed to control heavy invasion by ruderals.

Herbivory Treatments

In each of the experimental units, we constructed one 15x15x2.4 m cervid exclosure fence which served as our cervid Exclusion treatment plot which was paired with an adjacent Open-Herbivory treatment plot of the same size (Figure 2). To ensure longevity and durability, we constructed the exclosures with metal braided wire, wood H-brace corners and steel t-posts for the sides. The cervid exclosures were paired with bird exclosures of the same size, as part of a companion study on songbird trophic cascades. I based the size of the exclosures on feasible construction, rather than plant species area curves. However, I used a stratified-random approach in locating each exclosure to ensure that the herbivory treatments would be applied to a random sample from the broader community of each stand. The stratification attempted to avoid roads, stand edges, riparian areas, large skid roads, slash piles and burn piles to maintain a representative vegetation sample of the stand, while also avoiding slopes over 30 degrees and extreme surface undulations to maintain feasible construction. The fence mesh size was large enough (10x8 cm) to allow access by the other herbivorous mammals in the region. See detailed protocols of exclosure placement in Appendix B and construction in Appendix C. I confirmed that cervids foraged in all stands via camera traps located in Open-Herbivory plots.

Vegetation Measurements

During the mid-summer (July-August) of 2011 and 2012, I estimated percent cover and height by species as well as total plant cover using 12, 1x1 m permanently located quadrats systematically placed throughout each herbivory treatment plot. I identified each vascular plant species which had any tissue within or over the quadrat to species level and recorded with an ocular percent cover estimate from 1 to 100 (Helm and Mead 2004, Wilson 2011). Ocular cover estimates were made by one observer and calibrated based on the scale of 10x10 cm being 1% cover in a 100x100 cm quadrat. I estimated cover at 1% increments from 1 to 15% and at 5% increments from 15 to 100%. Species with cover values lower than 1% were recorded as 0.5%. I also estimated maximum height of each species to the nearest cm (Cadenasso et al. 2002) by measuring from the base of the plant to the highest part of each species that fell within or directly over the quadrat. For total cover estimates, I made an ocular measurement of all plants in one horizontal plane, regardless of species or height and recorded from 0 to 100%. To obtain herbivory treatment plot level estimates, I averaged cover values of each species across the 12 quadrats sampled and averaged height per species across the number of quadrats for which each species existed (1 to 12). For the purposes of diversity and richness metrics, I retained rare species by rounding to the nearest hundredth of a percent, rather than to the whole percent.

Plant Community Response Variables

Using information previously highlighted in literature pertaining to plant community characteristics and forage quality for cervids, I came up with a set of response variables to test the stated hypotheses.

Vegetation Cover

This metric is a simplified approach to determining how much vegetation covers the ground, and can be thought of as a broad measurement of vegetation density and competition with crop-trees. Cumulative cover, on the other hand, is the summed horizontal projections of all species in a plot. This metric reflects horizontal layering of species in vertical profile, in which short species under tall species are given the same weight in sampling. Therefore, cumulative cover can exceed 100 %, which indicates multiple layers of canopies and structural diversity.

Diversity

I used species richness (or the total number of species sampled from quadrats) as the simplest species diversity metric. For more complex diversity measures, I chose to use both Shannon and Simpson's diversity and evenness indices because each provides an alternative characterization of the alpha diversity of a given plant community (Onaindia et al. 2004). Simpson's diversity index (1-D) gives greater weight to common species and quantifies how dominated a community is. As the value of the index rises, dominance decreases and diversity increases. (Magurran 2009). Simpson's evenness ($E_{1/D}$) is a very similar metric, but uses species richness to quantify how evenly distributed relative abundance is across all species. As the index increases, the distribution of cover among species in the community becomes more even. Shannon diversity ($e^{H'}$) gives greater weight to rare species and quantifies the number of species that would have been found in a sample given that all species were common. As the value increases, diversity increases (Magurran 2009). Shannon evenness, or Pielou's evenness, (J') measures the ratio of observed diversity to a maximum diversity that can be possible where all species have equal abundances, and as the value increases, evenness increases (Pielou 1969, 1975, Magurran 2009). All four indices provide different interpretations of the effects of the treatments on the plant communities (i.e. dominance of common versus prevalence of rare species, respectively). See appendix D for technical definitions and formulas for diversity indices.

Growth forms

Using a plant database from Niell (2012), I identified 8 growth-form functional groups: deciduous trees, deciduous shrubs, evergreen shrubs, native-perennial herbs, native-ruderal herbs, introduced-perennial herbs, introduced-ruderal herbs and native-ferns (see Appendix E for definitions of each group and Appendix F for species list). For each group, I calculated cumulative cover, average height and richness among the species within each group. I excluded height estimates of deciduous trees over 2m as those individuals escaped typical browse height before the establishment of the exclosures. I excluded evergreen trees (predominately planted seedlings) from this set of response variables, because they had consistently low cover and richness values across all stands, although they were present in each plot. A preliminary analysis indicated that they did not respond to any treatments; specific volume metrics are more appropriate than cover values for seedling response. I also excluded fern richness from analysis as there were generally only two species (*Polystichum* and *Pteridium*) across all stands. It is important to note that I included graminoids (*Poaceae, Juncaceae and Cyperaceae*) in the herb groups as they represent species of the herbaceous layer targeted by herbicides and selective herbivory. These families primarily belonged to native-perennial and introduced-perennial life-forms.

Forage Classes

I used information from Cook (*in press*) as well as Neill (2012) and the USDA Plants Database to group each species into one of three forage groups: high quality, moderate quality and non-forage. Non-forage refers to forage avoided by tame Roosevelt elk and which do not provide nutrition to either cervid species, whether consumed or not (Cook et al. *in press*). Moderate quality forage refers to plant species selected by tame Roosevelt elk which provide sufficient, but not substantial, nutrition to deer and elk. High quality forage refers to plant species highly that are selected by tame Roosevelt elk and which provide substantial nutrition to both cervid species. The quality categories should not be confused with quantitative nutritional forage quality metrics; rather, they represent qualitative categories of cervid forage selection preferences and potential forage quality which is consistent across a wide geographic area (Cook et al. *in press*).

Statistical Analysis

Data from 2011 served as an herbivory exclusion baseline and were primarily used to assess the initial effects of herbicide treatment and any immediate effects of cervid exclusion. Data from 2012 were used to test hypotheses and represented at least one full year of cervid exclusion treatment and 1.5 years after initiation of the vegetation management treatments.

To test the hypotheses pertaining to the interactive effects of herbivory and herbicide for each response variable, I fit linear mixed-effects models with 2 fixed effects (herbicide and herbivory treatment) and 3 random effects (block, stand, herbivory plot) using the R statistical program (R Core Team 2012) and lme function of the nlme package (Pinheiro et al.2011). For all models, herbicide treatment stands were nested within block and herbivory treatment plots within herbicide treatment stands. The equation for the general model is as follows:

$$Y_{ijk} = \beta_0 + \beta_1 I_{HbivOpen} + \beta_2 I_{HcidL} + \beta_3 I_{HcidM} + \beta_4 I_{HcidH} + \beta_5 I_{HbivOpen} I_{HcidL} +$$

$$\beta_6 I_{HbivOpen} I_{HcidM} + \beta_7 I_{HbivOpen} I_{HcidH} + b_k + c_{ij} + \varepsilon_{ijk}$$

Y_{ijk} is the response variable in the *ith* herbicide treatment of the *jth* herbivory treatment in the *kth* block. β refers to the fitted coefficients under *I* treatment; *HbivOpen* is the Open herbivory treatment and *Hcid* refers to the herbicide treatments: L = Light, M = Moderate, H = Heavy. *IHbiv* x *IHcid* refers to the interactive effect of herbivory and herbicide. The Excluded no-spray Control treatment (1 per block, n = 7) served as the reference level (Control) for testing for an interaction. The Excluded treatment (4 per block, n = 28) was the reference level for testing the overall herbivory effect and the no-spray Control treatment (1 per block, n = 7) was the reference level for testing an overall herbicide effect. b_k is the random effect of blocks on the response variables; c_{ij} is the random effect of the ~13 ha stands, nested within blocks, on the response variables, and $\varepsilon_{ijk}$is the random effect of the 225 m^2 herbivory plots, nested within stands.

To test the overarching hypothesis of an interactive effect of herbivory and herbicide on plant community characteristics, I assessed the ANOVA output of each model for a statistical interaction at the 0.05 alpha level. To test for the magnitude in which herbicide mediated the effect of herbivory, I compared the Open herbivory treatment plots to the Excluded herbivory treatment plots within each herbicide treatment using multiple comparisons. If I found evidence of an interaction, and/or an herbivory effect at the 0.05 alpha level, I compared each herbivory*herbicide treatment plot to the Excluded no-spray Control treatment plot. This tested for the magnitude in which herbivory mediated the effects of herbicide treatment. If there was no evidence of an interaction or herbivory effect, and the ANOVA output indicated evidence of an herbicide effect, then I compared each herbicide treatment stand to the Control stand, independent of herbivory treatment (averaged over Excluded and Open treatment plots). This tested the magnitude in which herbicide treatment affected plant community characteristics, without accounting for herbivory treatment. If both ANOVA output and herbivory treatment comparisons indicated a consistent herbivory effect across all stands, then I compared the average of all Open treatment plots to the average of all Excluded treatment plots. This tested for the magnitude of an overall herbivory effect, without accounting for herbicide treatment.

I used the ‘estimable’ function of the gmodels package (Gregory et al. 2013) in R for multiple comparisons. In attempt to avoid Type-I error, I used Bonferroni corrected 95% confidence intervals, accounting for the multiple comparisons made for each set of treatment comparisons (i.e. 4 comparisons for Excluded versus Open per herbicide treatment; 7 comparisons for the Excluded-Control versus all treatment combinations; and 3 for the overall effect of herbicide treatments). In some cases, the corrected confidence intervals overlapped with zero, although the p-value of the comparison were below 0.05, indicating only slight evidence of a difference. For comparison of cover values between 1 and 15%, any differences in cover greater than 1% should be ecologically meaningful as low cover values were estimated to the whole percent. For cover values between 15 and 100%, differences greater 5% are most ecologically meaningful. For richness, a difference of less than one species can be thought of as diminutive, especially for species rich stands.

I confirmed that each model was an appropriate fit for the data by checking the assumptions of normality and equal variance. Mixed effects models are generally robust to non-normality and unequal variances and can be corrected for unequal variances if specified

(Pinheiro et al.2011). If the variance of residuals were not equal across herbicide treatments, then I specified unequal variances (allows for weighting of unevenly distributed residuals) in the lme function, which generally corrected the issue of unequal variance. Though my design was balanced, specifying unequal variances mimics lack of balance in the model, and I therefore used the Type III Sum of Squares F-test to test for the herbivory effect only (Pinheiro et al. 2011). If specifying unequal variances did not help to achieve equal variances and normality of residuals, I used natural-log transformation of the response variable + 1, as summed cover estimates can be considered continuous data (not bound by 100). I added 1 to the value of the response variable, because there were often 0's in the data set for heavier herbicide treatments. I back-transformed the log transformed data to present the effect sizes as multiplicative effects of the median.

For true graphical representation of the data, I presented raw cover and height data using boxplots (Gregory 2013). The horizontal bar represents the median of the data, the diamond represents the mean, the box represents the first and third quartiles (i.e. interquartile range), the "whiskers" (vertical bars) are 1.5 times the interquartile range (upper and lower extremes) and the dots represent data points beyond the extremes (i.e. outliers). Overlap of whiskers does not indicate a lack of difference because mixed effects models compare the mean of the treatment differences among blocks rather than the differences between treatment means. Because the species richness data were not well represented by boxplots, I presented those data in tables with median, mean and two times the standard error (i.e. approximation of the 95% confidence interval). I report ANOVA output and treatment comparisons in a table which includes the interaction, herbicide and herbivory tests as well as mean treatment differences and corrected

95% Confidence Intervals. When stating the mean value of the reference group (i.e. Control or Excluded-Control), I present the mean (+/- two times the standard error) in bold.

RESULTS

Initial Treatment Effects: 2011

In the first growing season after treatment application, the effects of herbicide treatments on plant community characteristics were strong. Overall, richness, cover and diversity declined with increasing herbicide application as most life-forms were diminished. The Control stands had the highest total cover, cumulative cover, richness and diversity (Figure 4). Those stands were dominated by a diverse assemblage of native-perennial herbs, deciduous shrubs, native-ferns, and introduced-ruderal herbs; abundance of all other life-forms was low (Figure 5).

The Light herbicide treatment had similar total cover as the Control but with about 25.3 pc lower cumulative cover (95% CI = [-43.8, -6.74]), 13 fewer species (95% CI = [-19.6, -6.53]), a 0.09 lower Simpson’s diversity (95% CI = [-0.18, -0.008]) and a 4.68 lower Shannon diversity (95% CI = [-8.14, -1.21]) (Figure 4 - A, B, C, E, F). Though total cover was similar between those treatments, the Light treatment was much more variable, having very low cover in some stands (Figure 4 - A). The differences between Light and Control treatments were driven primarily by the reduced cover and richness of native-perennial and introduced-ruderal herbs with that herbaceous-specific herbicide treatment (Figure 5, Table 1). Consequently, the cover of high quality forage was 12.8 pc lower with the Light treatment (95% CI = [-21.7, -3.91]) (Figure 7 - A) and moderate quality forage about 0.62 times lower, although the latter effect was relatively weak (95% CI = [-0.87, 0.12]) (Figure 7 - B). I found very slight evidence that

Simpson's evenness was higher with Light treatment (95% CI = [-0.04, 0.275]), showing that the effect of that treatment evened out dominance of those stands slightly.

As of 2011, the Moderate and Heavy treatment stands had received the same herbicide prescriptions (see Appendix A). Both of these treatments had substantially diminished plant community structure and composition, having very low total and cumulative cover (~6 pc), richness (~5 species) and diversity, which contrasted starkly to the Control (Figure 4). The cover and richness of each life-form was reduced down to trace amounts (< 1 pc and 0-1 species), with the exception of deciduous trees, which maintained at approximately 4.8 pc for only 1 species on average (Figure 5, Table 2). Although the diversity indices of those stands were lower, the heavier two treatments had higher Simpson's evenness than the lighter two treatments (Figure 4 - G), suggesting a lack of dominance among the variety of plants that remained.

The 2011 herbivory treatment baseline data revealed no interactive effects of herbivory and herbicide treatment on any of the response variables I considered. This is most likely due to the short time period between exclosure construction and vegetation sampling in 2011. I did, however, find weak evidence that dominant vegetation height was an average of 6.37 cm taller in the Open-Control treatment (95% CI [-1.83, 14.6]) compared to Excluded-Control treatment (Figure 4 - D). There was also slight evidence that moderate quality forage cover was 0.36 times lower (95% CI = [-0.64, 0.12]) with Open-Light compared to Excluded-Light treatment (Figure 7 - B). In both cases, the corrected confidence intervals of the comparisons overlap with 0, so the effects can only be considered weak baseline differences which did not translate into herbivory treatment differences in 2012.

Second Season Treatment Effects: 2012

In 2012, herbicide treatments continued to exert a strong influence on plant community characteristics, although plant communities in the Moderate treatments began to rebound with cervid exclusion and communities in the Heavy treatment remained suppressed. Diversity of no-spray Control treatments was similar to 2011, but those naturally regenerating stands had higher total cover, cumulative cover, richness (Figure 8 - A, B, C) and cover of forage (Figure 11 - A, B). The greater values for broad community characteristics was mostly likely due to an increase in cover and richness of deciduous shrubs, introduced-perennial herbs, native-ruderal herbs and the cover of native ferns (Figure 9 - A, C, G, H, Table 2). The Control remained the most diverse and vigorous treatment, with the highest cover of forage of all treatments (Figure 11, Figure 3).

The Light treatment remained similar to the Control in terms of cover, vegetation height and evenness, although there were 10.9 fewer species (95% CI = [-20.0, -1.90]), a 4.70 lower Shannon diversity (95% CI = [-8.61, -0.78] (Figure 8 - C,F, Table 3) and native-perennial herbs remained at about 14.0 pc less cover (95% CI = [-26.3, -1.67]) with 5 fewer species (95% CI = [-10.3, 0.33]) (Figure 9 - B, Table 4; Table 2, Table 5). Moderate-quality forage rebounded within the Light treatment, becoming similar to the control while high-quality forage remained suppressed by 22.0 pc (95% CI = [-41.5, -2.55]) (Figure 11 - A, B, Table 7). With cervid exclusion, the herbaceous-specific, Light herbicide treatment had a positive effect on deciduous shrub height growth by about 17.1 cm (95% CI = [-6.05, 40.3]), although this effect was highly variable (Figure 10-A, Table 6).

The Moderate treatment stands began to rebound with cervid exclusion, although total cover was still 27.0 pc lower than the control (95% CI = [-50.7, -3.19]), cumulative cover was -

53.5 pc lower (95% CI = [-99.4, -7.69]), and there were 10.9 fewer species (95% CI = [-20.0, -1.90]) (Figure 8 - A, B, C, Table 3; Figure 3). With cervid exclusion, the cover and richness of introduced-ruderal herbs increased by about 14.9 pc (95% CI = [1.30, 28.4]) to dominate Moderate treatments at 21.9 pc (+/- 8.5) (Figure 9 - D, Table 4; Table 2, Table 5), resulting in lower Simpson diversity and Shannon evenness than the control (Figure 8 - G, H, Table 3). Although the moderate treatment stands became dominated by introduced-ruderals, with little abundance of any other functional group, the cover and richness of native-perennials and ruderals rebounded slightly from 2011 (Figure 9 - B, H, Table 4, Table 2, Table 5). The cover, richness and heights of deciduous shrubs, ferns and evergreen shrubs still remained suppressed compared to the control (Figure 9 - A, C, F, Table 4; Table 2, Table 5; Figure 10 - A, C, F, Table 6). All forage groups (including non-forage) rebounded slightly from 2011, although moderate and high-quality forage remained suppressed by about 15.1 pc (95% CI = [-38.2, 7.95]) and 30.9 pc (95% CI = [-50.4, -11.4]) compared to the Excluded-Control, respectively (Figure 11 - A, B, Table 7).

In 2012, the Heavy treatment prescription deviated from the Moderate as the result of an additional herbicide treatment designed to control invading herbaceous vegetation. Very little vegetation recovered from this treatment rendering it the most species depauperate treatment across all functional groups, with only introduced-ruderal herb cover recovering slightly (Figure 6, Table 4; Figure 3).

I found convincing evidence of an interaction between herbicide and herbivory in which the effects of herbivory treatment were mediated by the effects of herbicide treatment across numerous response variables. The effect of herbivory was strongest with Moderate herbicide treatment, in which cervid herbivory exacerbated the effect of herbicides on total cover (F = 3.00, p = 0.05), further reducing it by 17.7 pc (95% CI = [-31.3, -4.15]) (Figure 8 - A, Table 3, Figure 3). Similarly, cumulative cover was 23.3 pc lower (95% CI = [-41.6, -4.95]) with cervid access compared to exclusion, although there was no evidence of a statistical interaction (Figure 8 - B, Table 3). Of the forage groups, moderate quality forage was most heavily impacted by cervid herbivory within the Moderate herbicide treatment only (F = 3.27, p = 0.04), where cervids reduced the forage cover by 13.2 pc (95% CI = [-27.2, 0.73]) (Figure 11 - B, Table 7). There was a similar effect size for high quality forage although the relationship was weak and variable (Table 7).

As cervids diminished the abundance of moderate quality forage, they also browsed down the height of ferns by about 19.9 cm (95% CI = [-38.6, -1.07]), which are generally non-palatable species (Figure 10 - C, Table 6). It also appeared as if the cover of introduced-ruderal herbs in Moderate treatment stands was reduced by an average of 4.58 pc (95% CI = [-10.5, 1.3]) with cervid foraging, although the effect was relatively weak (Figure 9 - D, Table 4). Cervids more strongly reduced the height of introduced-perennial herbs by about 7.33 cm (95% CI = [-13.1, -1.6]) (Figure 10 - G, Table 6). Cervid herbivory also exacerbated the effect of the Moderate treatment on native-perennial herbs by about 1.57 species (95% CI = [-3.26, 0.12]) (Table 2, Table 5). The magnitude and direction of an herbivory effect in the Moderate herbicide treatment was sufficient to result in similar vegetation structure and composition as the Heavy treatment (Figure 3). However, with cervid exclusion, plant communities in the Moderate treatment stands began to rebound to more closely resemble the Light and Control treatments.

The vegetation community in the Light treatment, though vigorously rebounding by 2012, was also measurably affected by cervid herbivory. With cervid exclusion, deciduous shrubs in the light treatment stands grew taller than those in the Control treatment stands (Figure 10 - A, Table 6). However, cervids suppressed this height-growth response, browsing shrubs 20.5 cm shorter than in the Excluded-Light treatment (95% CI = [-31.8, -9.20]). As shrub height was suppressed with herbivory access, introduced-ruderal herb cover was stimulated slightly, by about 2.80 pc (95% CI = [0.46, 5.13]) (Figure 9 - D, Table 4). Interestingly, the richness of deciduous shrubs and introduced-perennial herbs was also higher by about one species in both cases, although these effects were relatively weak (Table 2, Table 5).

With the Heavy herbicide treatment, there was only an average of one less native-perennial herb species with cervid access compared to exclusion (95% CI = -2.01, 0.01) (Table 2, Table 5). In general, these stands were too species poor, due to direct effects of herbicide, to be heavily impacted by cervids. Conversely, the only observable effect of cervid herbivory in the no-spray Control was with Shannon evenness, which was about 10% higher with cervid access compared to exclusion (Figure 8 - H, Table 3), although the positive effect was relatively weak.

The overall effect of herbivory, across herbicide treatments, was most apparent for dominant vegetation height ($F = 7.62$, $p = 0.01$). Browsing reduced height of dominant plants by an average of 6.54 cm across all stands (95% CI = -12.3, -0.74) (Figure 8 - D, Table 3). This effect was greatest with Moderate herbicide treatment where cervids reduced the height of those plants by 11.8 cm (95% CI = -23.5, -0.13). This result further demonstrates the stronger influence that cervid herbivory had in mediating the effects of herbicide in the Moderate treatment compared to the other treatments. I also found some evidence of an herbivory effect on high quality forage cover across herbicide treatment stands (F = 5.29, p = 0.03), although there was only very weak evidence that forage cover was 5.5 pc lower with cervid access (95% CI = [-18.5, 7.5]).

DISCUSSION

Herbivory-Herbicide Interactions

In this study, I tested the interactive effects of herbivory and herbicide on early seral plant communities in young forest plantations of the Oregon Coast Range. Specifically, I tested the hypothesis that silvicultural herbicide treatments mediate the effect of cervid herbivory and that cervid herbivory exacerbates the effects of herbicide treatments. Using a fully experimental approach, I found convincing evidence that herbicide treatment interacted with cervid herbivory to mediate plant community characteristics.

The interactive effects were greatest with Moderate herbicide treatment, which represents a commonly prescribed treatment in the PNW. In these stands, cervid herbivory exacerbated the effect of herbicide treatment on total cover, cumulative cover, moderate quality forage cover, native-perennial herb richness and fern and introduced-perennial herb heights. Stands in this treatment were particularly susceptible to cervid herbivory because herbicide initially reduced available forage, which concentrated herbivore pressure on the residual recovering plants. Though this treatment released introduced-ruderal herbs, cervids helped to mitigate the spike in their abundance. The herbaceous-specific, Light herbicide treatment reduced the richness and cover of native-perennial herbs and released deciduous shrub height with a net reduction of high quality forage cover. With that alteration in community structure, cervids had a strong negative effect on the height of deciduous shrubs, the main forage constituent remaining in those stands, while releasing introduced herbs. Very little vegetation regenerated with the Heavy treatment, rendering those stands generally too depauperate to be substantially impacted by cervid herbivory. Cervid herbivory did exacerbate the effect of that treatment on the remaining, yet diminished, native-perennial herbs. Conversely, as hypothesized, the no-spray Control stands were too vigorous and diverse with high abundances of deciduous shrub and native-perennial herb forage to be heavily impacted by cervid herbivory; although I found some evidence of a positive herbivory effect on evenness of rare species.

Community Characteristics and Herbivory Effects

The variable impacts of cervid herbivory across herbicide treatments becomes clearer in the context of plant life-form characteristics as well as community structure and composition across treatments. No-spray Control stands had the highest plant diversity and forage abundance, which was mostly due to the high abundance and richness of native-perennial herbs and deciduous shrubs. The large difference between total cover (cannot exceed 100 pc) and cumulative cover (sum of species cover, can exceed 100 pc) shows that these stands had high amounts of overlap between species canopies which can be interpreted as high structural diversity. Such structural and compositional diversity could have buffered these plant communities against herbivory-induced disturbance impacts (Augustine and McNaughton 1998, Tilman et al. 2012). I found slight evidence that cervids increased species evenness in these untreated stands, which is likely due to selective herbivory pressure on dominant, high quality shrub and herb species, thus releasing rarer, slower growing species. Regardless, the vigor and diversity of naturally regenerating stands buffered them from negative impacts of herbivory, consistent with the findings of Tilman et al. (2012). The high amounts of forage available to cervids should have served to attract higher cervid densities and thus greater amounts of foraging overall, although I found no evidence of this (Kuijper et al. 2009). It may be that cervid populations are at moderate enough levels in the region to keep local cervid densities and foraging pressure relatively low, even where forage resources are abundant (ODFW 2003, ODFW 2008).

Overall, my findings are consistent with the review by Augustine & McNaughton (1998) which suggests that communities dominated by a diverse assemblage of high quality forage species are more resilient to moderate levels of herbivory pressure. This is partly because forage species are often highly competitive, being able to rapidly replace lost tissues following herbivory damage. That said, these relationships have not been widely tested across large spatial scales, especially in the USA, as they have in this study. In the Oregon Coast Range, native forage species are predominately comprised of deciduous shrubs and perennial herbs, many of which are highly adapted to disturbance and herbivory. It is quite possible that other diverse, disturbance adapted native plant communities in the region may respond similarly; in some cases such plant communities may be positively influenced by herbivory induced disturbance (Collins and Calabrese 2012, Wisdom et al. 2006).

Interestingly, the higher the diversity of forage available to cervids, the lower selective pressure may be on any particular species or functional group. When foraging pressure on dominant species is greater than on rare species, moderate levels of herbivory can stimulate diversity (Augustine and McNaughton 1998). Such a relationship is consistent with the

Intermediate Disturbance Hypothesis (Connell 1979), where moderate foraging pressure, coupled with high productivity and initial floristic diversity, acts as a secondary disturbance to allow rare species to fill in where dominant ones were heavily browsed (Collins et al. 1995, Adler et al. 2011, Collins and Calabrese 2012, Borer et al. 2014). I found some evidence of this relationship, where cervid herbivory increased Shannon evenness, showing that rare species where more evenly represented where cervids where allowed to forage.

When the diversity of forage is missing, the effects of herbivory are amplified (Bracken and Low 2012). The Light treatment targeted herbaceous vegetation, having the greatest impact on native-perennial herb richness and cover, with little effect on other life-forms. The lack of herbicide treatment effect on total vegetation cover, but strong effects on richness and diversity, indicate that rare or less abundant herb species were the most heavily impacted components of the community. The loss of those herbs in lightly treated stands may have resulted in altered competition-herbivory dynamics between herbs and shrubs (Augustine and McNaughton 1998). For instance, the decline in native herb cover I observed, was associated with stimulated deciduous shrub height growth, likely via competitive release. This release, combined with a reduced abundance of herbaceous forage, resulted in greater cervid herbivory pressure on vigorously growing deciduous shrubs. The lack of native herbs in combination with herbivory pressure on shrubs may then have facilitated the invasion of introduced herbs in the Light treatment. The selective herbivory pressure on deciduous shrubs may also have permitted the release of other rare or less abundant deciduous shrubs. These complex, cascading effects of disturbance and herbivory are consistent with similar studies in other systems. For instance, Beguin et al. (2011) found that in *Betula* plantations, soil scarification and selective herbivory pressure released non-palatable introduced herbs when shrubs were controlled by herbivory. Royo et al. (2010) also found that a combination of fire, canopy gap creation and *Odocoileus virginianus* herbivory increased richness of herbs and some shrubs, compared to any particular disturbance alone. A review by Hobbs & Huenneke (1992) highlighted the interactive effects of disturbance, herbivory and invasion, suggesting that herbivory can facilitate invasion by exotics when coupled with land-use disturbances that reduce the diversity of native plants.

With extreme loss of native diversity, the effects of herbivory on community structure and composition can exacerbate the destabilization of communities (Rzanny and Voigt 2012). In my study, the Moderate herbicide treatment removed the primary forage base for cervids, deciduous shrubs and native-perennial herbs, thus favoring the abundance of introduced-ruderal herbs. With cervid exclusion, moderate quality forage rebounded slightly from 2011, becoming similar to the Control. This can be attributed to the substantial increase in the introduced-ruderal, *Crepis capiliaris*. However, the main constituent of introduced-ruderals was *Senecio sylvaticus* a non-forage ruderal-herb. Cervids curbed the invasion of introduced-ruderals by browsing *Crepis,* but in doing so diminished the main forage resource in those stands. This may have caused cervids to have a disproportionate effect on the remaining flora across life-forms. The exacerbated effect of herbivory was greatest on total vegetation cover and height, indicating that herbivory pressure was distributed across the residual recovering flora. This provides evidence that when forage resources are diminished, cervids become less selective, which is further confirmed by the browsing of ferns in the Moderate treatment, generally *Pteridium aquilinium,* a low-quality forage. The only life-form to be specifically diminished from such an interactive effect of herbicide and herbivory were native-perennial herbs, further confirming the susceptibility of these species to repeated disturbance impacts.

These interactive processes align well with those highlighted by Augustine & McNaughton (1998) who reported that ungulate herbivory effects are mediated by the availability and diversity of forage. With extremely high forage availability, foraging impacts become saturated, meaning there is more forage available than can be substantially consumed, and thus herbivory has little impact. With lower forage availability, the same densities of cervid herbivores can have disproportionate negative effects. In this experiment, it is apparent that the effect of herbicides on forage availability caused cervids to have disproportionate effect on broad plant community characteristics. Plant diversity appears to have played a major role in the effects of foraging selectivity. Rzanny & Voigt (2012) found that in grassland communities, less diversity was related to greater community instability, altered trophic interactions, and decreased ecosystem functioning and lower tolerance to disturbance. The negative effects of herbicide on plant community characteristics, diversity and forage availability could therefore have reduced the tolerance of moderately treated communities to selective herbivory.

In the most intensive treatment (Heavy), reductions in plant cover and species richness caused by herbicide treatment were so extreme that there remained few plants for cervids to consume. However, even the few remaining native-perennial herbs were diminished by cervid herbivory. It is quite possible that there was insufficient forage to provide incentive for cervids to spend much time foraging in these stands, thus having an impact on only native herbs, the most susceptible functional group to herbicide and herbivory treatments. The consistent effects of herbivory on the richness of native-perennial herbs with both Moderate and Heavy treatments suggests that the site-preparation treatment reduced the abundance and richness of these herbs to the point where cervids could cause local extirpation. Such an effect of cervids on native herbs is consistent with the findings of other studies such as Knight et al. (2009) and Rambo & Faeth (1999) although these researchers did not take prior management history or compounding disturbances into account. In my study, native-perennial herbs were buffered in highly diverse communities but became susceptible to herbivory as herbicide treatments reduced their resilience and concentrated herbivory pressure on the few remaining native species.

Conservation and Management Implications

The immediate flush of early seral shrubs and herbs demonstrates how quickly plant communities can establish following timber harvest in the Pacific Northwest. Such vigorous and diverse characteristics contribute a substantial source of forage for cervids. So much so, that in the Control and Light treatments, herbivory pressure appears to be saturated, meaning there was more forage than cervids could substantially consume. Therefore, the plant communities I observed were relatively buffered from intensive, selective foraging by cervids, which contrasts with many forest management studies conducted in the eastern United States (Horsley et al. 2003, Rooney and Waller 2003, Nuttle et al. 2013) and Europe (Putman 1996, Kuijper et al. 2010). As the highly diverse communities in this study were buffered from herbivory, they were also buffered from introduced plant species, consistent with other studies investigating invasion, biodiversity and land management (Hobbs and Huenneke 1992). This provides evidence that management for early seral plant communities may be optimal for impeding invasive species in managed landscapes.

Although early seral plant communities of the Pacific Northwest are sources of high quality forage, forage species are also substantial competitors with planted seedlings. The vigorously establishing native plants within Control stands may be an incompliance with the ‘free to grow’ standards mandated by the Oregon Forest Practices act (ORS 526.490). For those reasons, these native plants are typically controlled via herbicide treatment with most forest management operations on state and private forestlands. Nevertheless, my results show substantial differences between Herbivory-Excluded and Open-Herbivory treatments, providing strong evidence that industrial forest lands are being heavily used by deer and elk in the Oregon Coast Range. In fact, intensive forest management is not new to cervid herbivores in the region (USFS 1973). It is quite likely that cervids are able to cope with the effects of vegetation management by adjusting foraging behavior within intensively managed landscapes (Cook et al. *in press*). That is not to say that cervid body condition and fitness is equal between heavily managed landscapes and landscapes with high proportions of naturally regenerating early seral plant communities (ODFW 2003, ODFW 2008, Cook et al. 2013, Hagar 2007).

Depending on the treatment applied, managed stands appear to provide several key attributes of early seral habitats (e.g., native herbs and shrubs), which often rebound following initial herbicide treatment, especially following light management regimes (Rose and Rosner 2005, Rose et al. 2006, Dinger and Rose 2009). With the spring-herbaceous application, only the richness and cover of native-perennial herbs was reduced, providing a viable light-handed approach for private land managers interested in maintaining early seral characteristics.

The results presented here provide important evidence that cervids provide an ‘ecosystem service’ to lightly managed plantations by intensively foraging on highly competitive deciduous shrubs. If cervids browse shrubs more intensively than planted conifers, then cervids would contribute to a conifer release, benefiting plantation management. Furthermore, the effect of herbivory in moderately treated stands was similar to that of the additional herbaceous application with the Heavy herbicide treatment. This provides evidence that cervids provide competition control equivalent to a spring treatment of 2,4-D and hexazinone. This interactive disturbance reduce vegetation cover down to 25 pc, which is the target of most silvicultural herbicide treatments, sufficient for rapid seedling growth within the critical period of seedling establishment (Maguire et al. 2009). Therefore, the ‘ecosystem services’ role that cervids played in the Light treatment was even more pronounced in the Moderate treatment. However, this benefit of cervids to vegetation management may come at the expense of native plant communities. Given that the Moderate treatment was a representative prescription in the Coast Range, the effects of vegetation management throughout the region seem to be highly contingent on the effect of cervid herbivory. Results from vegetation management studies that exclude cervids to control compounding effects of herbivory are therefore likely liberal in terms of the amount of herbicides required to control competing vegetation. Foresters may not need to apply such an intensive treatment when herbivores control the rebound of competitors. Though cervids controlled competition, they may have also intensively browsed planted seedlings once high-quality forage had been consumed. More investigation is needed to draw conclusions regarding the tradeoffs between this potential ‘ecosystem service’ and conifer seedling growth.

If the heaviest herbicide treatment reduced the overall utilization of plantations by cervids, it is possible that the conflicts between cervids and plantation management may be mitigated by reducing forage availability. However, it is also possible that cervids still heavily utilize those stands, intensively foraging on planted seedlings where they cannot find sufficient forage. From an ecological perspective, these heavily treated stands are likely too species poor to be considered a viable option for habitat management throughout the region, at least within the early stages of succession. Longer-term studies, incorporating seedling growth are needed to fully understand the tradeoffs between habitat management and intensive forest management.

Conclusions

Studies incorporating the interactions between disturbance, herbivory and plant community characteristics are essential to understanding how these components influence ecosystem functioning (Hobbs and Huenneke 1992, Augustine and McNaughton 1998, Wisdom et al. 2006). Furthermore, it is critical to understand how large herbivores influence management practices in order to determine the role of management-induced disturbance in structuring ecosystems. To my knowledge, this is the first study to investigate how cervid herbivores influence intensive forest management practices across a large, heavily managed region.

I found that the effects of common vegetation management practices (i.e. herbicide treatments) on plant communities were highly influenced by native cervid herbivores. The effects of cervid herbivory on plant community characteristics were mediated by the effect of herbicide treatment on plant cover, diversity and both native and introduced forage species. As native forage richness and abundance declined, the buffering capacity of plant communities was diminished, allowing cervids to have a detrimental effect on the recovering flora, especially in heavily invaded stands. With even a light management approach, foraging selectivity was altered, increasing the browsing effect on deciduous shrubs, thereby affecting competitive interactions among species. With a heavier management approach, forage declined and cervids had a disproportionate negative effect on the remaining palatable species. Experiments with longer time periods are necessary to draw broader conclusions about how intensive management and herbivory interact across the entire early seral stage. These results provide important information regarding the initial effects of cervid herbivores on stand initiation and early succession across a gradient in intensive forest management.

FIGURES

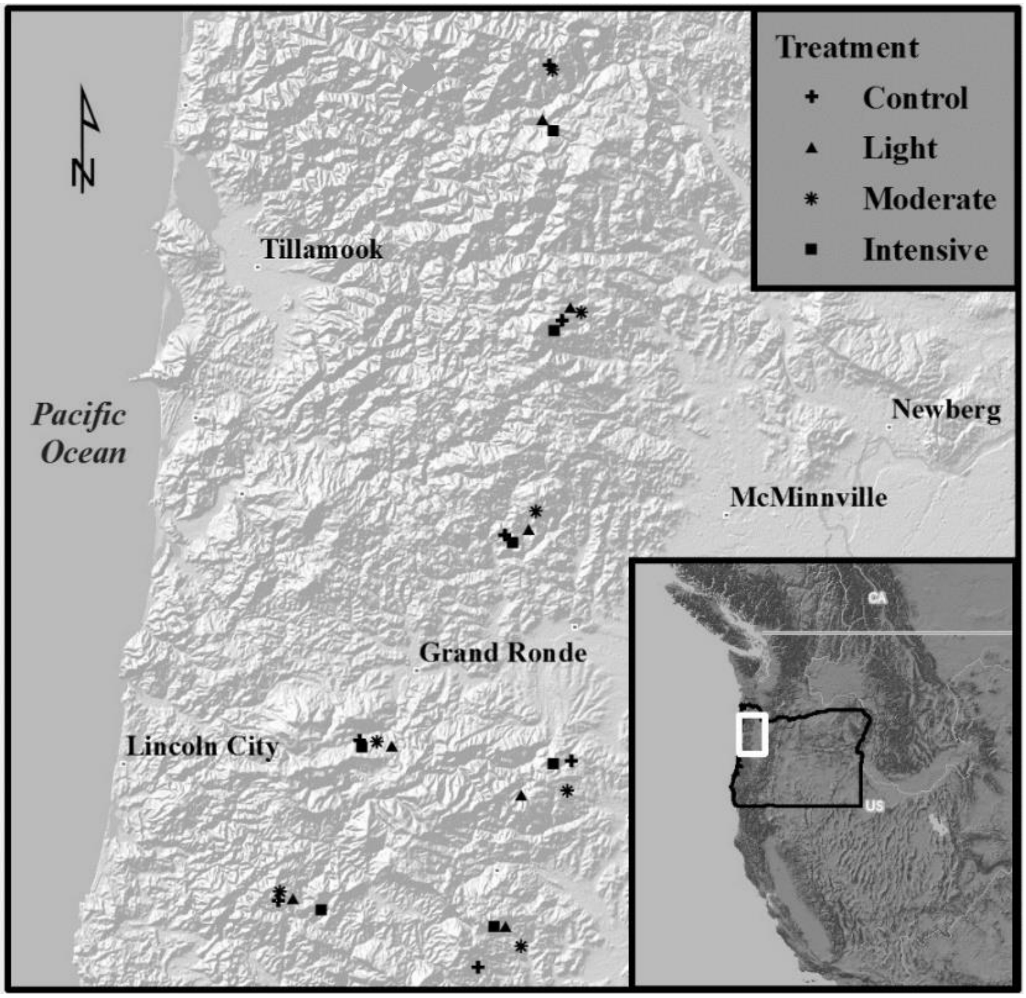


Figure 1. Study extent, Oregon Coast Range, USA: Each cluster of stands (shapes, herbivory treatments) equals one block.

Figure 2. Cervid exclosure (Excluded treatment, foreground) paired with bird exclosure for companion study (background); adjacent Open-Herbivory treatment plot was located 15 m from fence with the same size, shape and orientation.

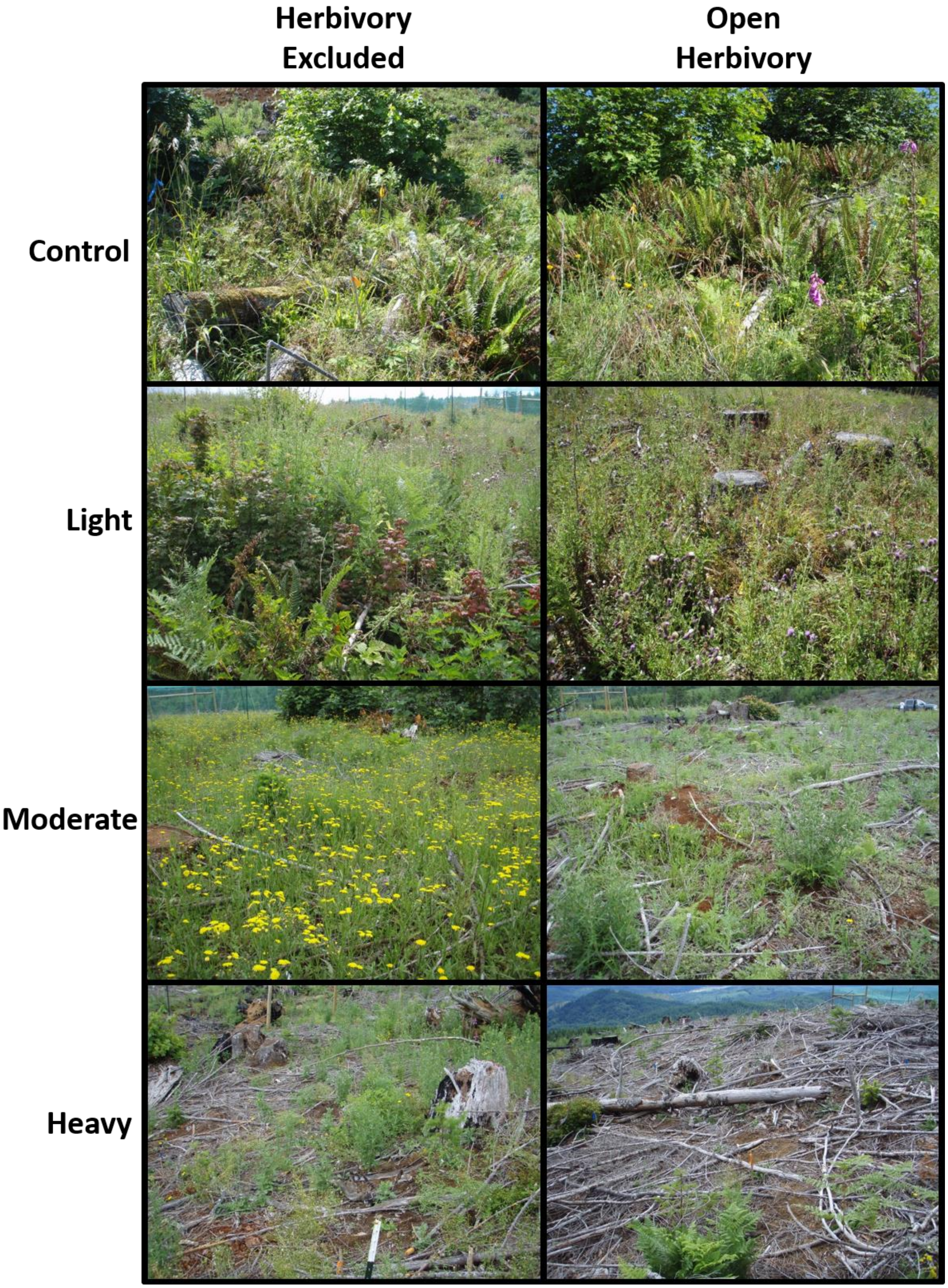


Figure 3. Increasingly intensive herbicide treatments (top to bottom) with Herbivory-Excluded (left column) and Open-Herbivory treatments (right column).

BROAD COMMUNITY CHARACTERISTICS: 2011

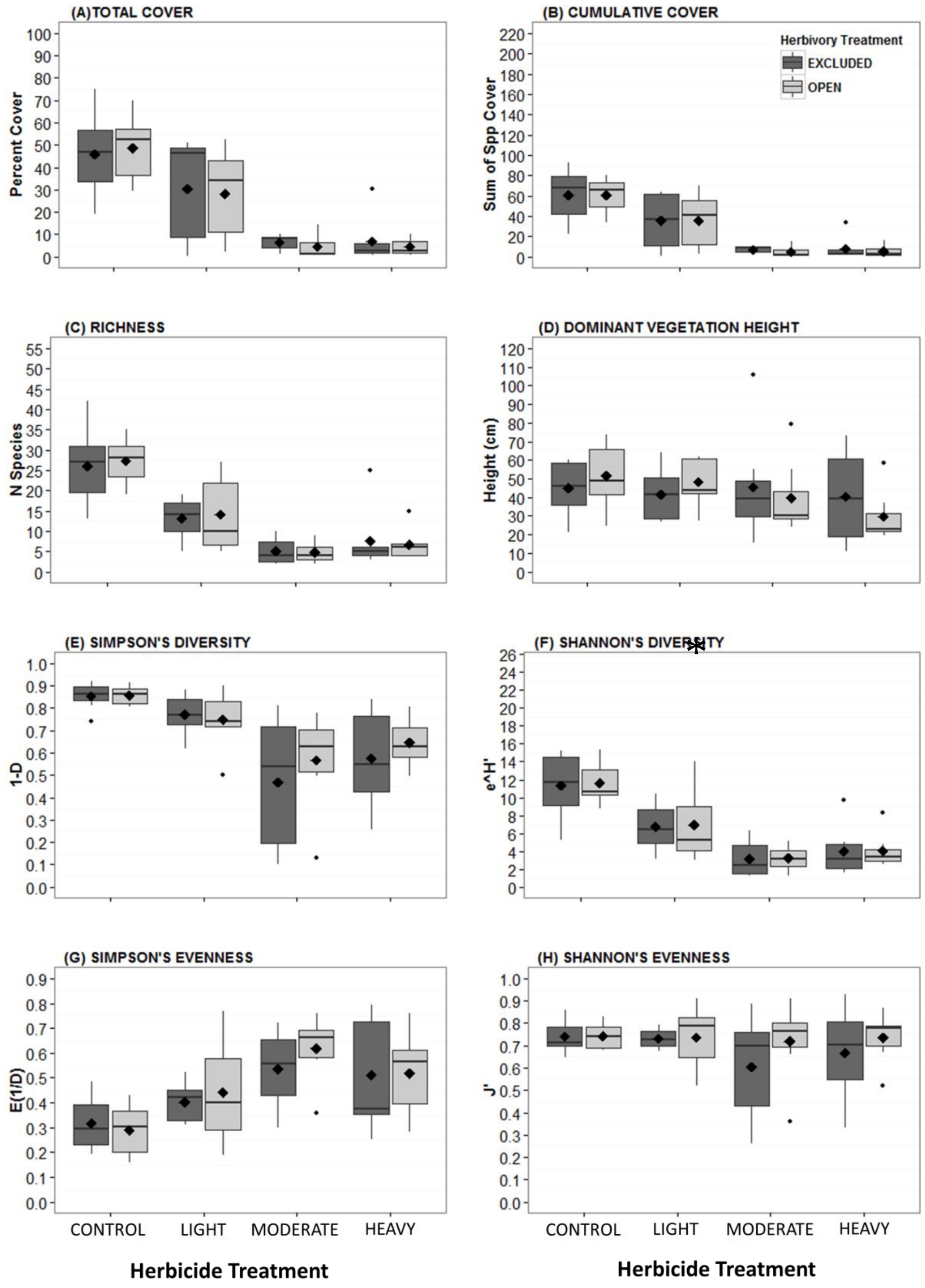


Figure 4. Boxplots of 2011 broad community characteristics with herbivory and herbicide treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots are outlying data.* signifies an herbivory effect at $p < 0.05$.

COVER OF LIFE-FORMS: 2011

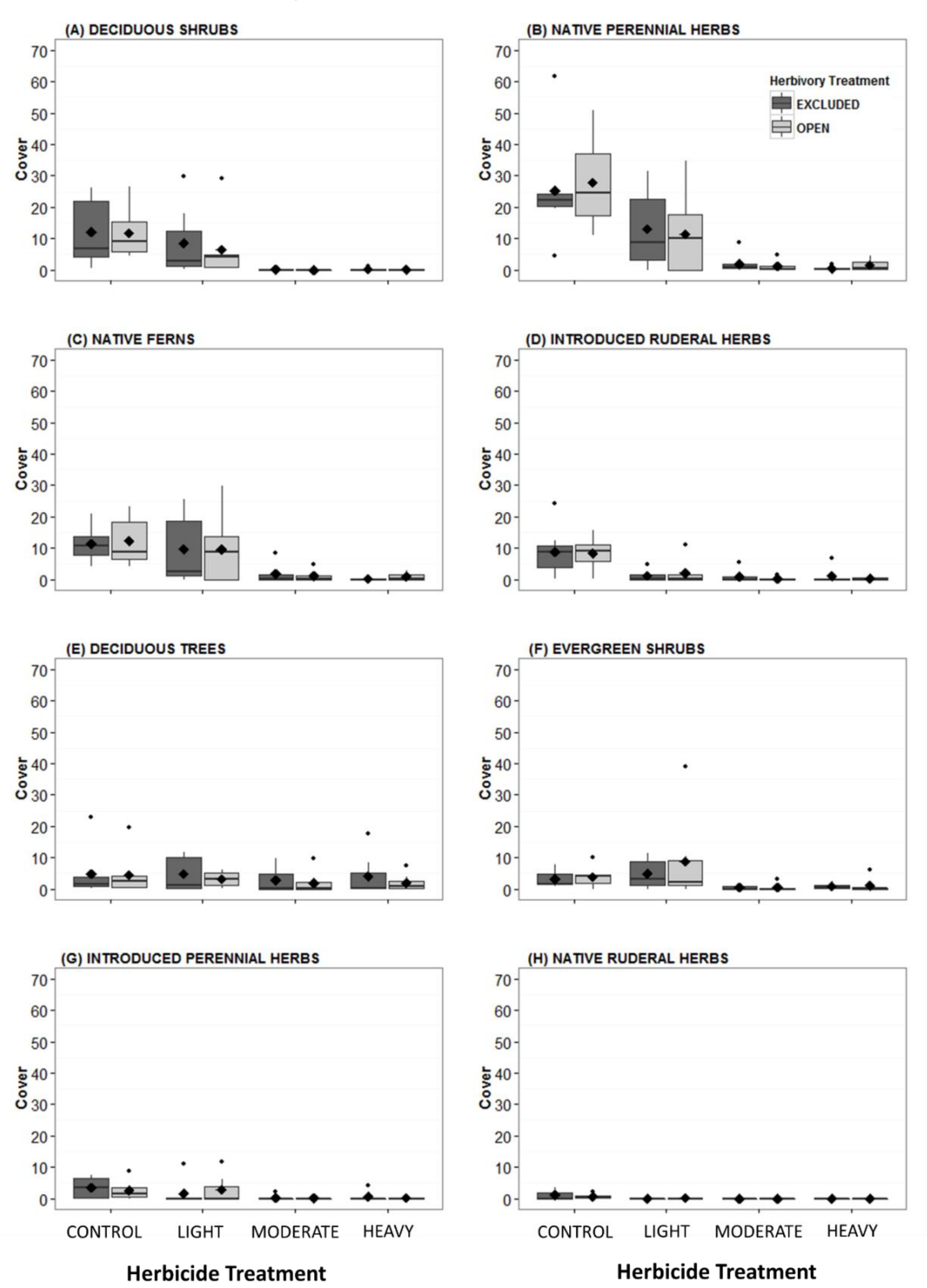


Figure 5. Boxplots of 2011 cover by life-form with herbivory and herbicide treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots are outlying data.

HEIGHT OF LIFE FORMS: 2011

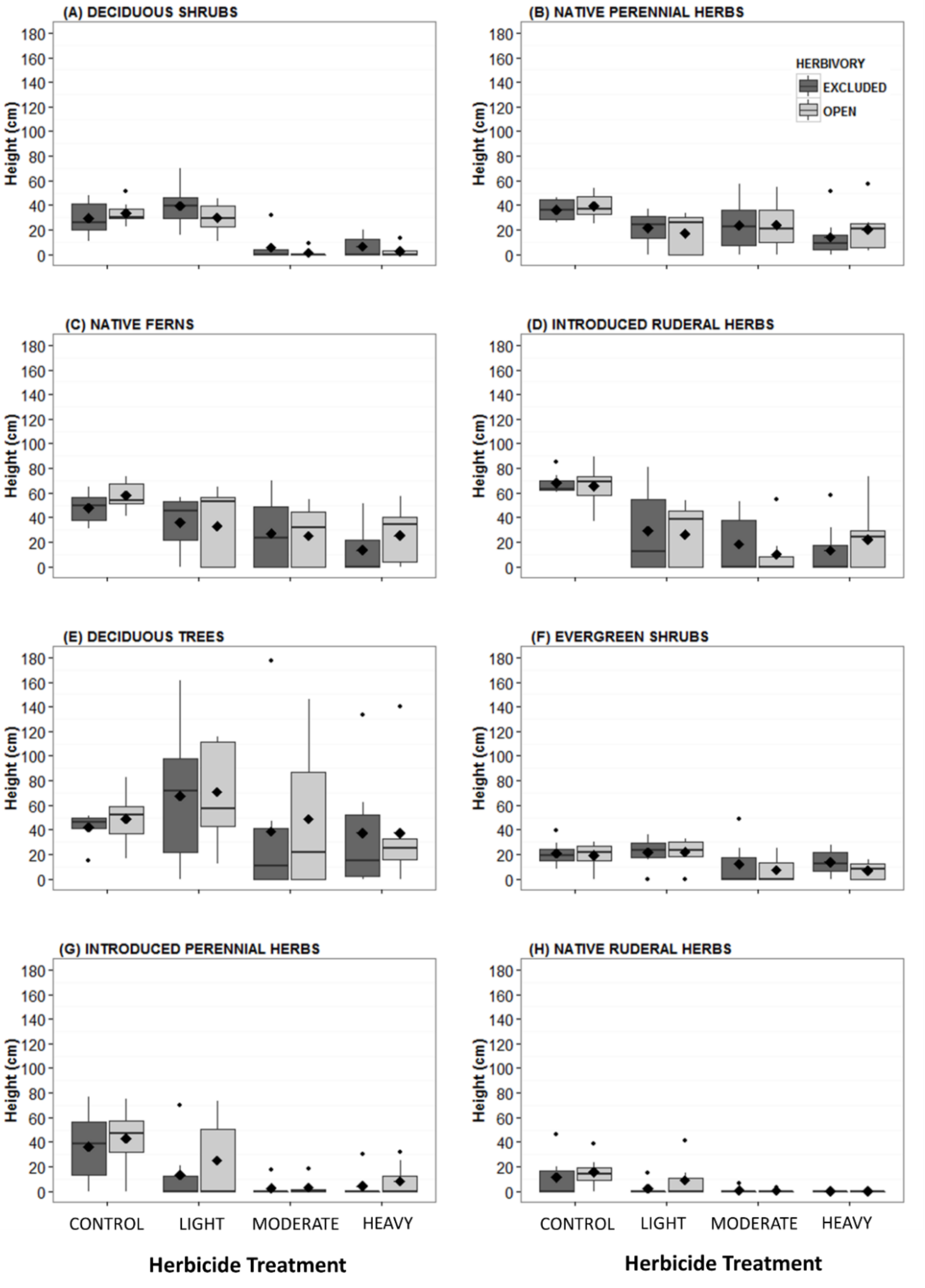


Figure 6. Boxplots of 2011 average height by life-form with herbicide and herbivory treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity, left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots are outlying data.

COVER OF FORAGE GROUPS: 2011

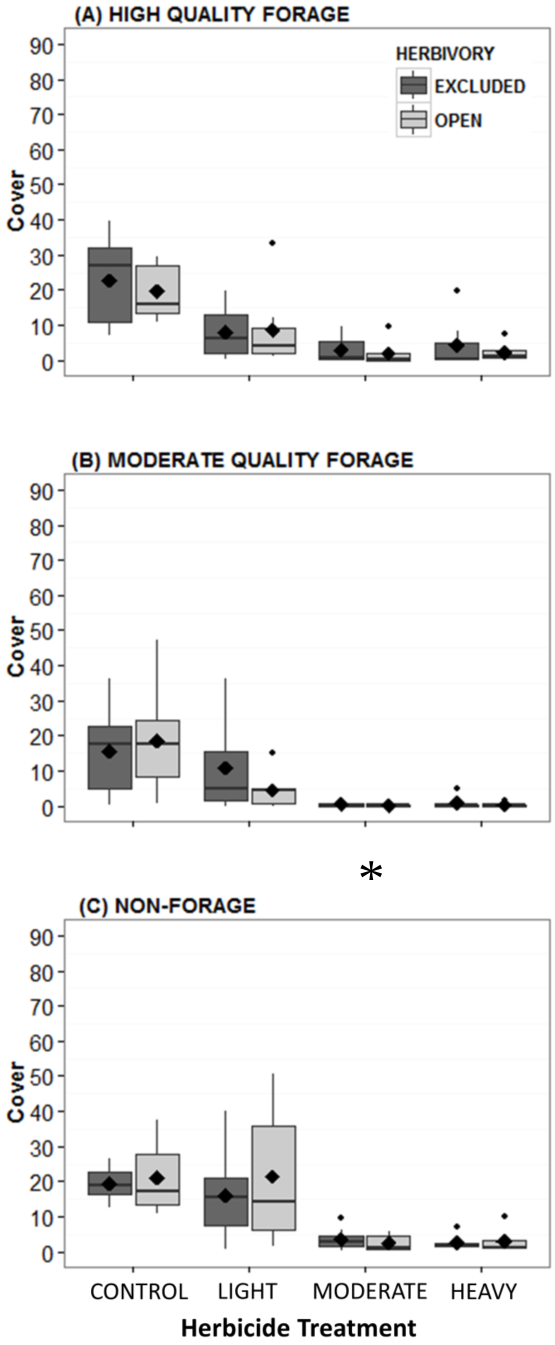


Figure 7. Boxplots of 2011 cover by forage quality group with herbicide and herbivory treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity, left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots are outlying data.* signifies an herbivory effect at $p < 0.05$.

BROAD COMMUNITY CHARACTERISTICS: 2012

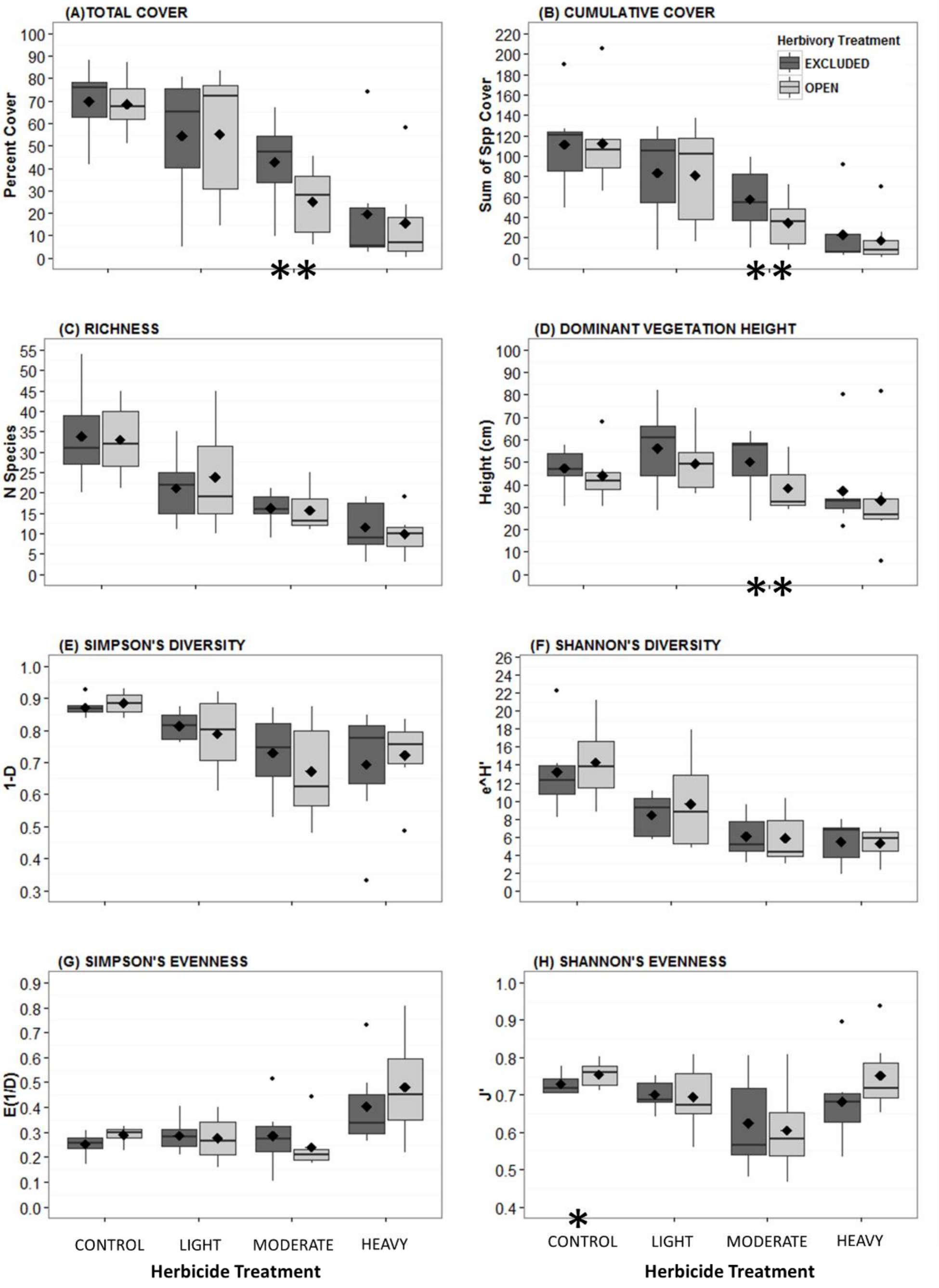


Figure 8. Boxplots of 2012 broad community characteristics with herbicide and herbivory treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity, left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots are outlying data.* signifies an herbivory effect at $p < 0.05$, **$p < 0.01$.

COVER OF LIFE-FORMS: 2012

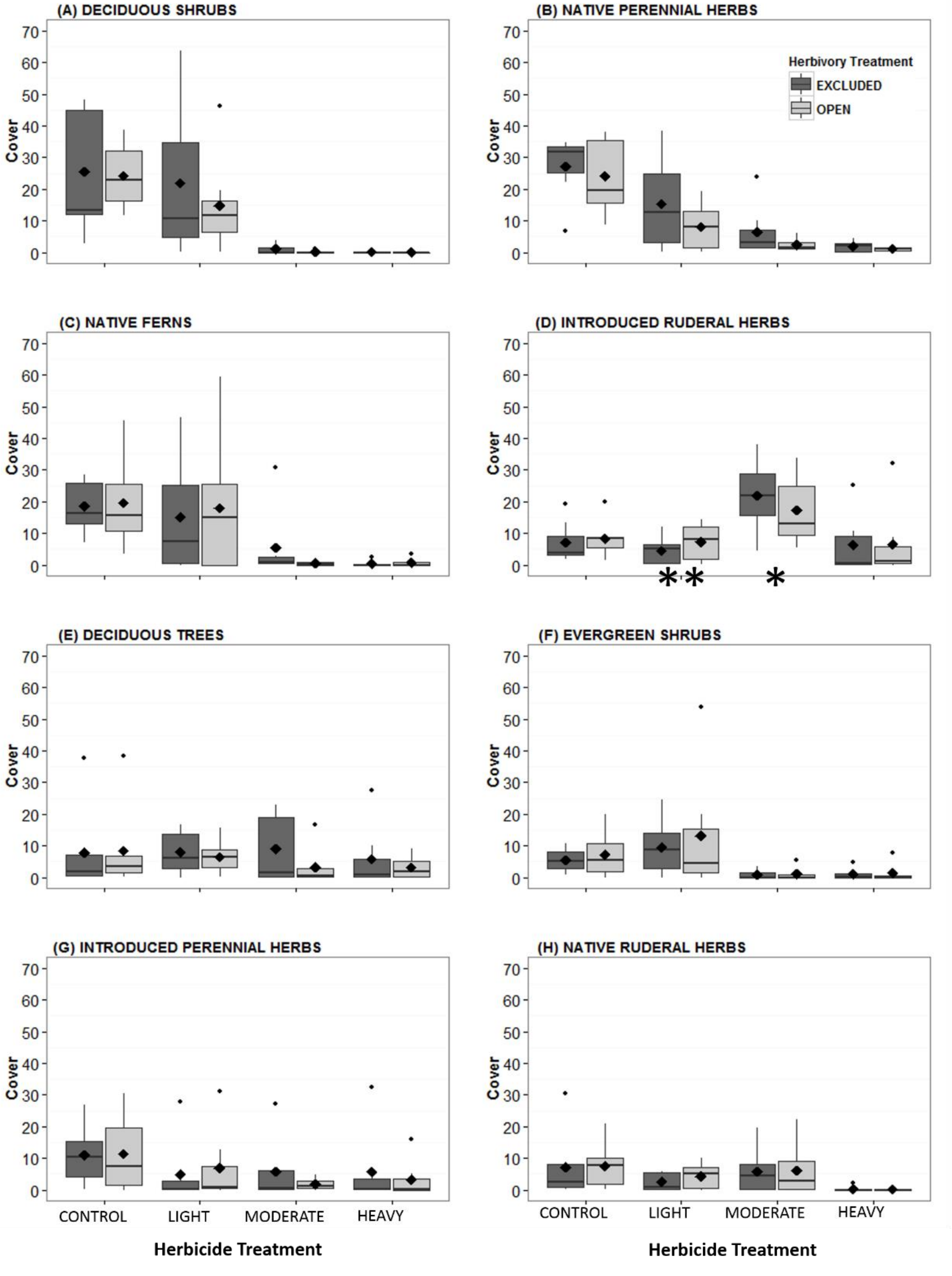


Figure 9. Boxplots of 2012 cover by life-form with herbivory and herbicide treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity, left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots are outlying data.* signifies an herbivory effect at $p < 0.05$, **$p < 0.01$.

HEIGHT OF LIFE-FORMS: 2012

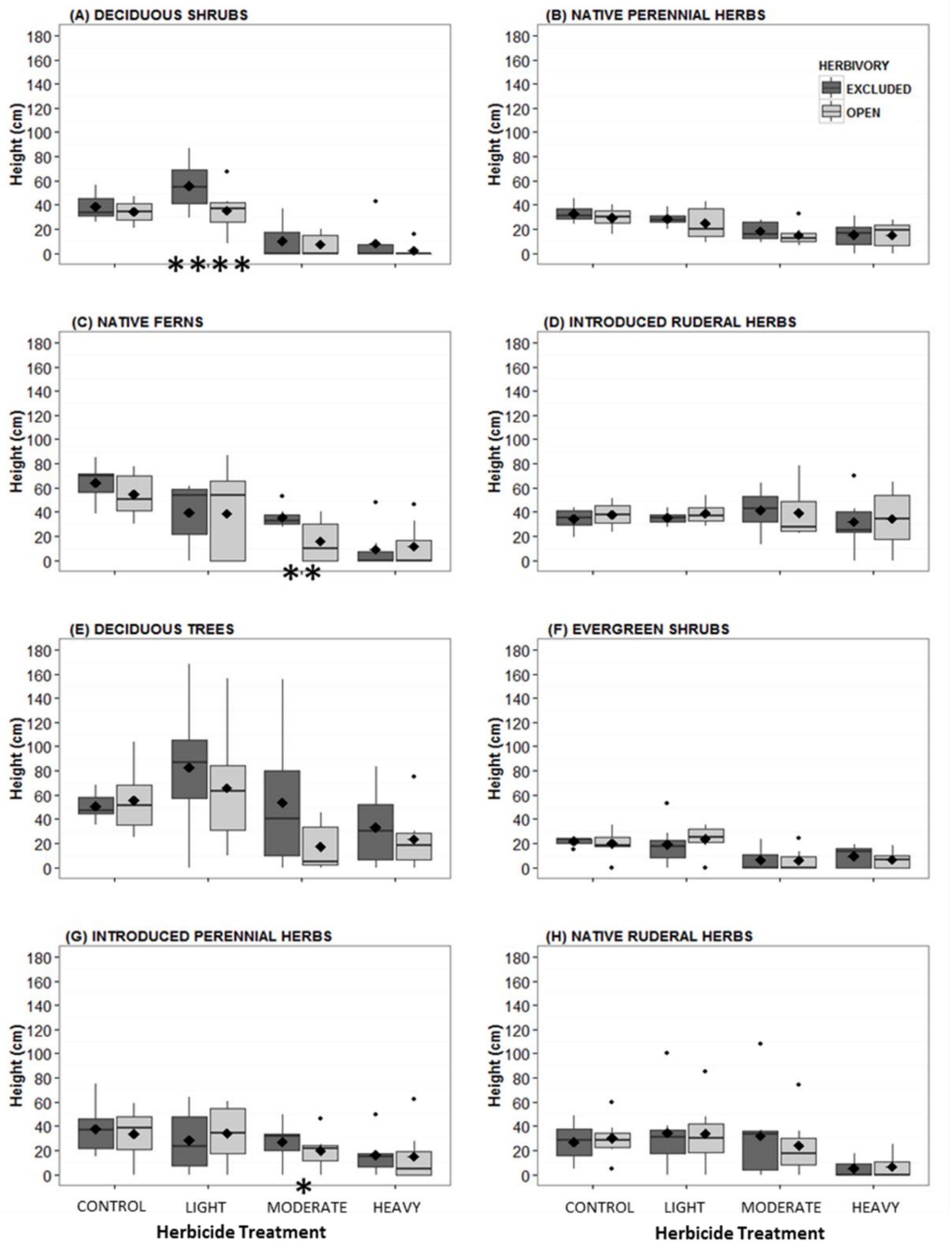


Figure 10. Boxplot of 2012 average height by life-form with herbicide and herbivory treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity, left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots represent outlying data.* signifies an herbivory effect at $p < 0.05$, **$p < 0.01$, ****$p < 0.0001$.

COVER OF FORAGE GROUPS: 2012

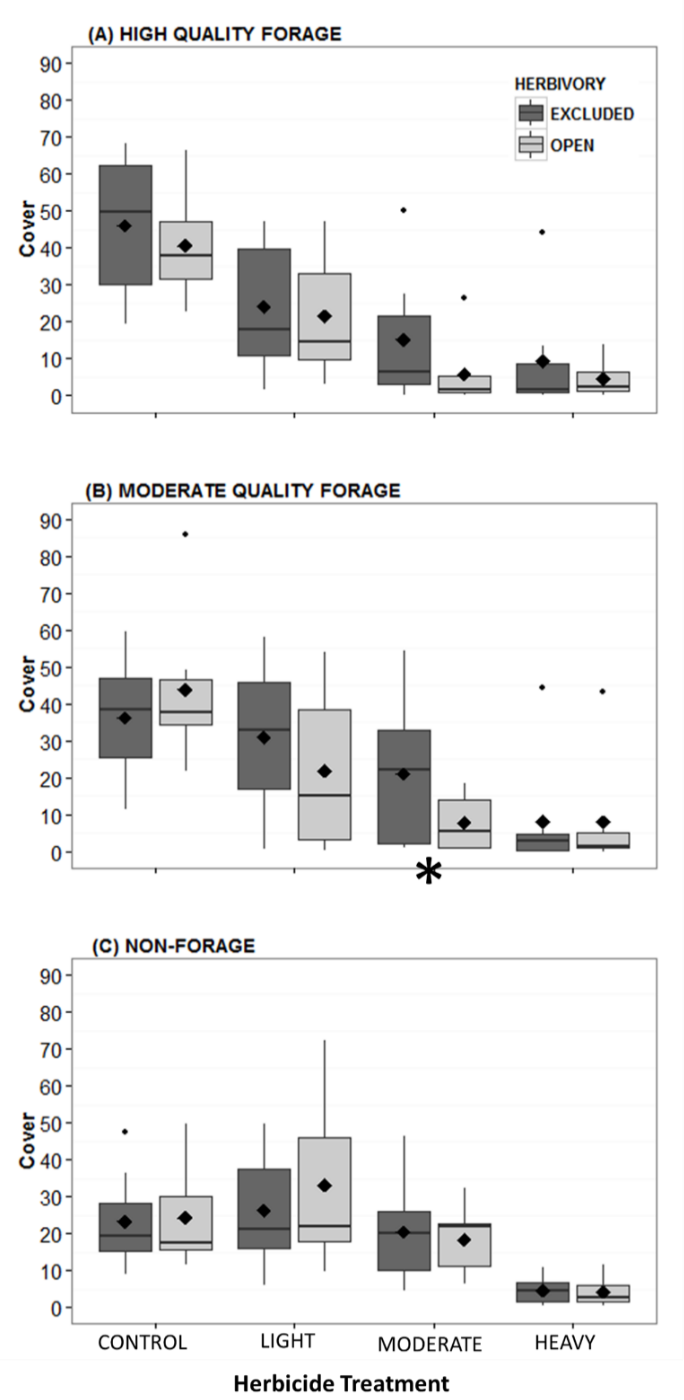
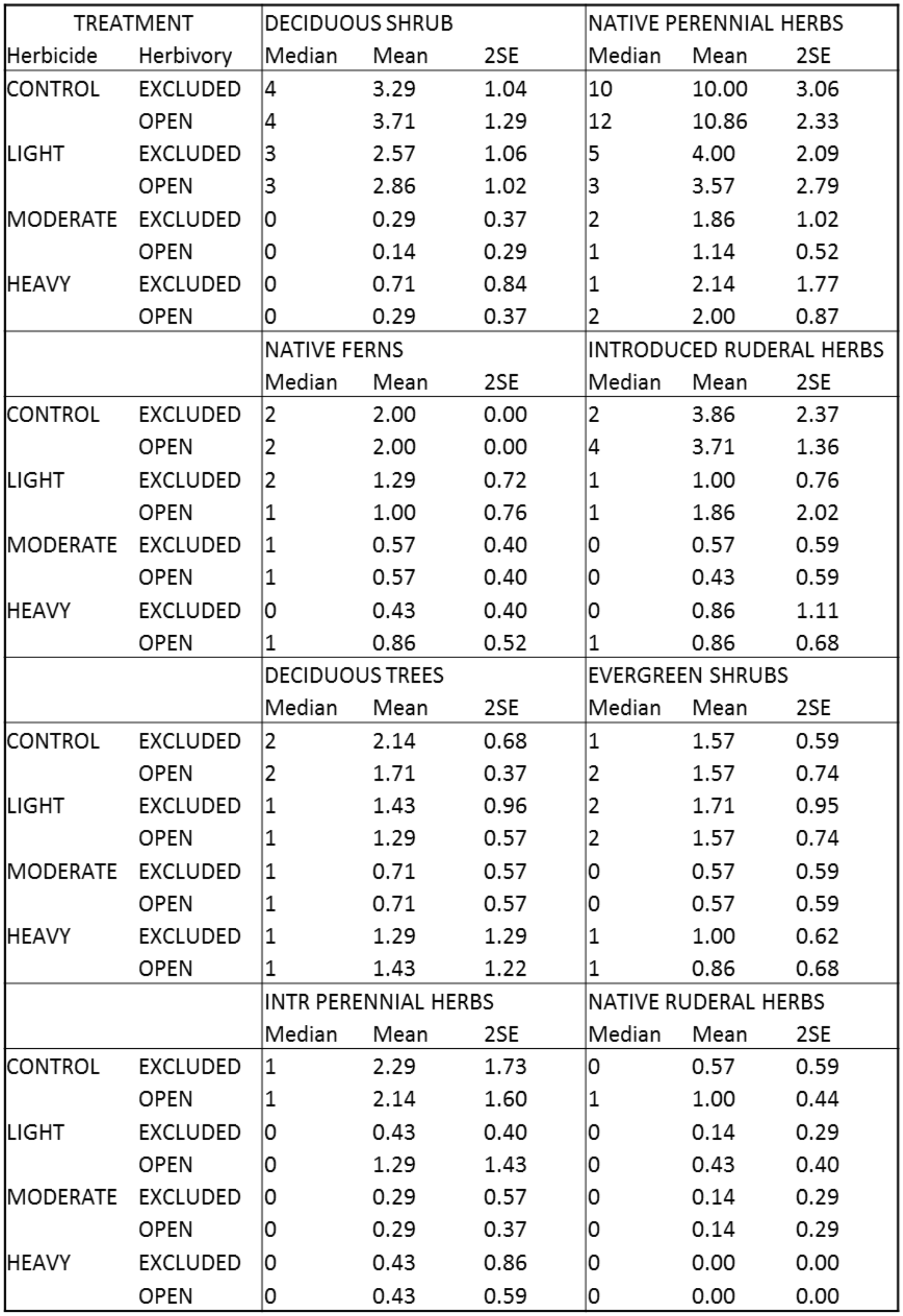


Figure 11. Boxplots of 2012 cover by forage group with herbivory and herbicide treatments. Each dark grey (Herbivory-Excluded) and light grey (Open-Herbivory) treatment is nested within each herbicide treatment (increasing intensity, left to right). Diamonds are treatment means, bars are medians, boxes are interquartile ranges, whiskers are 1.5(interquartile range) and dots are outlying data.* signifies an herbivory effect at $p < 0.05$.

Table 1. 2011 Richness (number of species) by life-form with herbivory and herbicide treatments.



TREATMENT		DECIDUOUS SHRUB			NATIVE PERENNIAL HERBS		
Herbicide	Herbivory	Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	4	3.29	1.04	10	10.00	3.06
	OPEN	4	3.71	1.29	12	10.86	2.33
LIGHT	EXCLUDED	3	2.57	1.06	5	4.00	2.09
	OPEN	3	2.86	1.02	3	3.57	2.79
MODERATE	EXCLUDED	0	0.29	0.37	2	1.86	1.02
	OPEN	0	0.14	0.29	1	1.14	0.52
HEAVY	EXCLUDED	0	0.71	0.84	1	2.14	1.77
	OPEN	0	0.29	0.37	2	2.00	0.87
		NATIVE FERNS			INTRODUCED RUDERAL HERBS		
		Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	2	2.00	0.00	2	3.86	2.37
	OPEN	2	2.00	0.00	4	3.71	1.36
LIGHT	EXCLUDED	2	1.29	0.72	1	1.00	0.76
	OPEN	1	1.00	0.76	1	1.86	2.02
MODERATE	EXCLUDED	1	0.57	0.40	0	0.57	0.59
	OPEN	1	0.57	0.40	0	0.43	0.59
HEAVY	EXCLUDED	0	0.43	0.40	0	0.86	1.11
	OPEN	1	0.86	0.52	1	0.86	0.68
		DECIDUOUS TREES			EVERGREEN SHRUBS		
		Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	2	2.14	0.68	1	1.57	0.59
	OPEN	2	1.71	0.37	2	1.57	0.74
LIGHT	EXCLUDED	1	1.43	0.96	2	1.71	0.95
	OPEN	1	1.29	0.57	2	1.57	0.74
MODERATE	EXCLUDED	1	0.71	0.57	0	0.57	0.59
	OPEN	1	0.71	0.57	0	0.57	0.59
HEAVY	EXCLUDED	1	1.29	1.29	1	1.00	0.62
	OPEN	1	1.43	1.22	1	0.86	0.68
		INTR PERENNIAL HERBS			NATIVE RUDERAL HERBS		
		Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	1	2.29	1.73	0	0.57	0.59
	OPEN	1	2.14	1.60	1	1.00	0.44
LIGHT	EXCLUDED	0	0.43	0.40	0	0.14	0.29
	OPEN	0	1.29	1.43	0	0.43	0.40
MODERATE	EXCLUDED	0	0.29	0.57	0	0.14	0.29
	OPEN	0	0.29	0.37	0	0.14	0.29
HEAVY	EXCLUDED	0	0.43	0.86	0	0.00	0.00
	OPEN	0	0.43	0.59	0	0.00	0.00

Table 2. 2012 Richness (number of species) by life-form with herbicide and herbivory treatments. .* signifies an herbivory effect at $p < 0.05$.

TREATMENT		DECIDUOUS SHRUB			NATIVE PERENNIAL HERBS		
Herbicide	Herbivory	Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	4	4.29	0.72	12	11.14	3.79
	OPEN	3	4.00	1.38	10	11.00	3.85
LIGHT	EXCLUDED	2	2.29 *	0.84	4	6.14	3.22
	OPEN	3	3.43	1.50	4	6.00	3.57
MODERATE	EXCLUDED	0	0.57	0.59	5	5.71 *	1.21
	OPEN	0	0.43	0.40	4	4.14	1.02
HEAVY	EXCLUDED	0	0.71	0.72	3	2.57 *	1.30
	OPEN	0	0.29	0.57	2	1.57	0.74
		NATIVE FERNS			INTRODUCED RUDERAL HERBS		
		Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	2	1.86	0.29	4	4.57	1.62
	OPEN	2	2.00	0.00	4	4.71	1.21
LIGHT	EXCLUDED	2	1.29	0.72	3	3.14	1.48
	OPEN	1	1.00	0.76	3	3.43	1.68
MODERATE	EXCLUDED	1	1.00	0.00	3	2.86	0.81
	OPEN	1	0.57	0.40	3	3.14	1.19
HEAVY	EXCLUDED	0	0.29	0.37	2	2.00	1.23
	OPEN	0	0.43	0.59	2	1.86	1.02
		DECIDUOUS TREES			EVERGREEN SHRUBS		
		Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	2	2.29	0.84	2	1.86	0.81
	OPEN	2	2.14	0.52	2	1.71	0.84
LIGHT	EXCLUDED	2	2.00	0.98	2	1.57	0.86
	OPEN	2	2.43	0.96	2	1.71	0.84
MODERATE	EXCLUDED	1	1.00	0.44	0	0.71	0.84
	OPEN	1	1.43	0.74	0	0.57	0.59
HEAVY	EXCLUDED	1	1.71	1.36	1	0.86	0.68
	OPEN	1	1.57	1.22	2	1.14	0.81
		INTR PERENNIAL HERBS			NATIVE RUDERAL HERBS		
		Median	Mean	2SE	Median	Mean	2SE
CONTROL	EXCLUDED	3	3.29	1.78	1	2.29	1.67
	OPEN	3	3.29	2.17	2	2.14	1.02
LIGHT	EXCLUDED	1	1.00 *	0.62	2	2.14	1.27
	OPEN	1	2.29	2.03	2	1.71	0.84
MODERATE	EXCLUDED	1	1.29	0.72	1	1.43	0.96
	OPEN	2	1.71	0.84	2	1.86	1.34
HEAVY	EXCLUDED	2	1.29	0.72	0	0.71	0.84
	OPEN	1	1.00	0.87	0	0.57	0.59

Table 3. 2012 Broad Plant Community Characteristics. ANOVA output (left column) and treatment comparisons (right column) of broad community characteristics among herbicide and herbivory treatments. Herbivory effect is the difference between Open and Excluded herbivory treatments. Herbicide effect is the difference between each herbicide treatment and Control, accounting for herbivory treatment in the case of a significant herbivory effect. Bold values are the means of the Control treatments (reference) and bold values in parentheses are 2(SE) of the Control. Non-bold values are mean differences between treatments and non-bold values in parentheses are Bonferonni-corrected 95% confidence intervals. * signifies a treatment effect at $p < 0.05$, **$p < 0.01$, ***$p<0.001$, ****$p<0.0001$.

Table 3. 2012 Broad Community Characteristics

RESPONSE	ANOVA OUTPUT	HERBICIDE TRT	HERBIVORY TRT	HERBIVORY EFFECT		HERBICIDE EFFECT	
TOTAL COVER	Interaction	Control	Excluded	-1.01	(-8.78, 6.75)	**69.7**	**(12.6)**
	F = 3.00, p = 0.05		Open				
	Herbivory	Light	Excluded	0.50	(-17.6, 18.7)	-15.1	(-40.7, 10.5)
	F = 5.86, p = 0.02		Open			-14.6	(-40.2, 11.0)
	Herbicide	Moderate	Excluded	-17.7	(-31.3, -4.15)**	-27.0	(-50.7, -3.19)**
	F = 20.8, p < 0.0001		Open			-44.7	(-68.4, -20.9)****
		Heavy	Excluded	-4.09	(-10.7, -2.49)	-50.2	(-72.0, -28.4)****
			Open			-54.3	(-76.1, -32.4)****
CUMULATIVE COVER	Interaction	Control	Excluded	1.27	(-16.0, 18.5)	**111**	**(24.1)**
	F = 2.61, p = 0.07		Open				
	Herbivory	Light	Excluded	-2.29	(-30.6, 26.1)	-27.7	(-76.7, 21.2)
	F = 4.29, p = 0.05		Open			-30.0	(-79.0, 18.9)
	Herbicide	Moderate	Excluded	-23.3	(-41.6, -4.95)**	-53.5	(-99.4, -7.69)**
	F = 16.1, p < 0.0001		Open			-76.8	(-123, -31.0)****
		Heavy	Excluded	-5.53	(-14.0, 2.89)	-88.4	(-132, -44.4)****
			Open			-93.9	(-138, -49.9)****
TOTAL RICHNESS	Interaction	Control	Excluded	-0.86	(-5.64, 3.93)	**33.4**	**(5.36)**
	F = 1.20, p = 0.33		Open				
	Herbivory	Light	Excluded	2.71	(-2.07, -7.50)	-10.9	(-20.0, -1.90)**
	F = 0.01, p = 0.90		Open				
	Herbicide	Moderate	Excluded	-0.57	(-5.36, 4.21)	-17.4	(-26.4, -8.40)***
	F = 18.1, p <.0001		Open				
		Heavy	Excluded	-1.71	(-6.50, 3.07)	-22.7	(-31.7, -13.7)****
			Open				
VEGETATION HEIGHT	Interaction	Control	Excluded	-3.46	(-13.12, 6.21)	**47.3**	**(7.04)**
	F = 0.86, p = 0.48		Open				
	Herbivory	Light	Excluded	-6.66	(-25.1, 11.8)	8.74	(-13.7, 31.2)
	F = 7.62, p = 0.01		Open			2.09	(-20.4, 24.6)
	-6.54 (-12.3, -0.74)*	Moderate	Excluded	-11.8	(-23.5, -0.13)**	2.80	(-17.1, 22.7)
	Herbicide		Open			-9.00	(-28.9, 10.9)
	F = 2.14, p = 0.13	Heavy	Excluded	-4.26	(-13.6, 5.04)	-10.0	(-29.3, 9.25)
			Open			-14.3	(-33.6, 4.99)
SIMPSONS DIVERSITY	Interaction	Control	Excluded	0.014	(-0.013, 0.041)	**0.872**	**(0.021)**
	F = 1.70, p = 0.19		Open				
	Herbivory	Light	Excluded	-0.025	(-0.097, 0.047)	-0.077	(-0.187, 0.032)
	F = 0.44, p = 0.51		Open				
	Herbicide	Moderate	Excluded	-0.057	(-0.161, 0.047)	-0.178	(-0.293, -0.062)**
	F = 8.62, p < 0.001		Open				
		Heavy	Excluded	0.029	(-0.064, 0.122)	-0.171	(-0.284, -0.058)**
			Open				
SIMPSONS EVENNESS	Interaction	Control	Excluded	0.038	(-0.019, 0.094)	**0.270**	**(0.0236)**
	F = 2.42, p = 0.09		Open				
	Herbivory	Light	Excluded	-0.010	(-0.099, 0.078)	0.010	(-0.095, 0.116)
	F = 0.41, p = 0.52		Open				
	Herbicide	Moderate	Excluded	-0.045	(-0.113, 0.023)	-0.009	(-0.111, 0.093)
	F = 4.01, p = 0.02		Open				
		Heavy	Excluded	0.079	(-0.145, 0.302)	0.171	(0.022, 0.321)**
			Open				
SHANNON DIVERSITY	Interaction	Control	Excluded	1.13	(-3.99, 6.25)	**13.2**	**(3.40)**
	F = 0.49, p = 0.70		Open				
	Herbivory	Light	Excluded	1.27	(-2.42, 4.97)	-4.70	(-8.61, -0.78)**
	F = 0.73, p = 0.40		Open				
	Herbicide	Moderate	Excluded	-0.15	(-1.61, 1.31)	-7.80	(-11.3, -4.30)****
	F = 17.9, p < 0.0001		Open				
		Heavy	Excluded	-0.17	(-1.21, 0.86)	-8.38	(-11.8, -4.92)****
			Open				
SHANNON EVENNESS	Interaction	Control	Excluded	0.026	(-0.008, 0.060)*	**0.742**	**(0.017)**
	F = 2.23, p = 0.11		Open				
	Herbivory	Light	Excluded	-0.007	(-0.067, 0.053)	-0.044	(-0.153, 0.064)
	F = 2.03, p = 0.17		Open				
	Herbicide	Moderate	Excluded	-0.019	(-0.074, 0.036)	-0.127	(-0.235, -0.019)**
	F = 3.91, p = 0.03		Open				
		Heavy	Excluded	0.070	(-0.029, -0.169)	-0.025	(-0.141, 0.091)
			Open				

Table 4. 2012 Cover of Life-Forms. ANOVA output (left column) and treatment comparisons (right column) of cover by life-form among herbicide and herbivory treatments. Herbivory effect is the difference between Open and Excluded herbivory treatments. Herbicide effect is the difference between each herbicide treatment and Control, accounting for herbivory treatment in the case of a significant herbivory effect. Bold values are the means of the Control treatments (reference) and bold values in parentheses are 2(SE) of the Control. Non-bold values are mean differences between treatments and non-bold values in parentheses are Bonferonni-corrected 95% confidence intervals. * signifies a treatment effect at $p < 0.05$, **$p < 0.01$, ***$p<0.001$, ****$p<0.0001$.

Table 4. 2012 Cover of Life-Forms.

RESPONSE	ANOVA OUTPUT	HERBICIDE TRT	HERBIVORY TRT	HERBIVORY EFFECT		HERBICIDE EFFECT	
DECIDUOUS SHRUBS	Interaction F = 0.84, p = 0.48 Herbivory F = 0.47, p = 0.50 Herbicide F = 16.8, p < 0.0001	Control	Excluded Open	-1.24	(-23.8, 21.3)	**24.9**	**(8.07)**
		Light	Excluded Open	-7.13	(-35.6, 21.3)	-6.53	(-25.2, 12.2)
		Moderate	Excluded Open	-0.83	(-2.27, 0.61)	-24.3	(-35.9, -12.7)****
		Heavy	Excluded Open	-0.05	(-0.28, 0.18)	-24.8	(-36.4, -13.2)****
DECIDUOUS TREES log transformed	Interaction F = 0.68, p = 0.57 Herbivory F = 0.63, p = 0.43 Herbicide F = 1.29 , p = 0.31	Control	Excluded Open	0.23	(-0.63, 3.04)	**8.15**	**(6.94)**
		Light	Excluded Open	-0.02	(-0.50, 0.92)	0.26	(-0.61, 3.05)
		Moderate	Excluded Open	-0.49	(-0.85, 0.81)	-0.29	(-0.80, 1.58)
		Heavy	Excluded Open	-0.08	(-0.42, 0.48)	-0.35	(0.79, 1.02)
EVERGREEN SHRUBS log transformed	Interaction F = 0.01, p = 0.99 Herbivory F = 0.01, p = 0.98 Herbicide F = 5.39, p = 0.01	Control	Excluded Open	0.003	(-0.46, 0.87)	**6.34**	**(3.00)**
		Light	Excluded Open	0.05	(-0.62, 1.88)	0.17	(-0.68, 3.34)
		Moderate	Excluded Open	-0.003	(-0.23, 0.30)	-0.72	(-0.92, -0.05)*
		Heavy	Excluded Open	-0.04	(-0.66, 1.73)	-0.69	(-0.92, 0.13)*
NATIVE PERENNIAL HERBS	Interaction F = 0.72, p = 0.55 Herbivory F = 2.62, p = 0.12 Herbicide F = 25.9, p < 0.0001	Control	Excluded Open	-3.08	(-18.9, 12.7)	**25.7**	**(5.73)**
		Light	Excluded Open	-7.31	(-25.3, 10.7)	-14.0	(-26.3, -1.67)***
		Moderate	Excluded Open	-4.14	(-12.7, 4.40)	-21.2	(-30.5, -12.0)****
		Heavy	Excluded Open	-0.75	(-2.54, 1.04)	-24.1	(-32.3, -15.9)****
NATIVE RUDERAL HERBS log transformed	Interaction F = 1.29, p = 0.30 Herbivory F = 2.84 , p = 0.10 Herbicide F = 4.79, p = 0.01	Control	Excluded Open	0.28	(-0.16, 0.96)	**7.39**	**(4.73)**
		Light	Excluded Open	0.42	(-0.25, 1.67)	-0.36	(-0.79, 0.96)
		Moderate	Excluded Open	-0.007	(-0.32, 0.45)	-0.23	(-0.74, 1.29)
		Heavy	Excluded Open	-0.03	(-0.26, 0.28)	-0.75	(-0.92, -0.26)**
INTRODUCED PERENNIAL HERBS	Interaction F = 1.01, p = 0.41 Herbivory F = 0.54, p = 0.47 Herbicide F = 1.73, p = 0.20	Control	Excluded Open	0.50	(-6.82, 7.83)	**11.2**	**(5.60)**
		Light	Excluded Open	1.97	(-5.35, 9.30)	-5.32	(-16.9, 6.27)
		Moderate	Excluded Open	-4.03	(-11.4, 3.29)	-7.36	(-18.9, 4.23)
		Heavy	Excluded Open	-2.42	(-9.75, 4.90)	-2.42	(-18.2, 4.92)
INTRODUCED RUDERAL HERBS	Interaction F = 3.56, p = 0.03 Herbivory F = 0.006, p = 0.94 Herbicide F = 4.92 , p = 0.01	Control	Excluded Open	1.29	(-4.69, 7.29)	**7.04**	**(5.01)**
		Light	Excluded Open	2.80	(0.46, 5.13)**	-2.54 0.25	(-15.4, 10.3) (-12.6, 13.1)
		Moderate	Excluded Open	-4.58	(-10.5, 1.3)*	14.9 10.3	(1.30, 28.4)** (-3.28, 23.9)*
		Heavy	Excluded Open	0.20	(-4.22, 4.62)	-0.69 -0.48	(-13.9, 12.5) (-13.7, 12.7)
NATIVE FERNS log transformed	Interaction F = 1.64, p = 0.21 Herbivory F = 8.52, p = 0.001 Herbicide F = 1.64 , p = 0.21	Control	Excluded Open	-0.08	(-0.49, 0.65)	**19.1**	**(6.04)**
		Light	Excluded Open	0.003	(-0.37, 0.60)	-0.61	(-0.91, 0.74)
		Moderate	Excluded Open	-0.54	(-0.85, 0.43)	-0.87	(-0.98, -0.41)**
		Heavy	Excluded Open	0.19	(-0.19, 0.74)	-0.92	(-0.98, -0.66)***

Table 5. 2012 Richness of Life-Forms. ANOVA output (left column) and treatment comparisons (right column) of richness by life-form among herbicide and herbivory treatments. Herbivory effect is the difference between Open and Excluded herbivory treatments. Herbicide effect is the difference between each herbicide treatment and Control, accounting for herbivory treatment in the case of a significant herbivory effect. Bold values are the means of the Control treatments (reference) and bold values in parentheses are 2(SE) of the Control. Non-bold values are mean differences between treatments and non-bold values in parentheses are Bonferonni-corrected 95% confidence intervals. * signifies a treatment effect at $p < 0.05$, **$p < 0.01$, ***$p<0.001$, ****$p<0.0001$.

Table 5. 2012 Richness of Life-Forms.

RESPONSE	ANOVA OUTPUT	HERBICIDE TRT	HERBIVORY TRT	HERBIVORY EFFECT		HERBICIDE EFFECT	
DECIDUOUS SHRUBS log transfomed	Interaction F = 3.15, p = 0.04 Herbivory F = 0.34, p = 0.57 Herbicide F = 30.6, p < 0.0001	Control	Excluded	-0.08	(-0.28, 0.18)	**4.29**	**(0.72)**
			Open				
		Light	Excluded	0.30	(-0.03, 0.76)*	-0.40	(-0.66, 0.04)
			Open			-0.22	(-0.55, 0.36)
		Moderate	Excluded	-0.06	(-0.20, 0.11)	-0.72	(-0.84, -0.54)****
			Open			-0.74	(-0.85, -0.57)****
		Heavy	Excluded	-0.23	(-0.51, 0.23)	-0.71	(-0.84, -0.46)****
			Open			-0.78	(-0.88, -0.58)****
DECIDUOUS TREES	Interaction F = 0.86, p = 0.47 Herbivory F = 0.65, p = 0.43 Herbicide F = 2.33, p = 0.12	Control	Excluded	-0.14	(-1.10, 0.82)	**2.2**	**(0.48)**
			Open				
		Light	Excluded	0.43	(-0.53, 1.39)	0.00	(-1.25, 1.25)
			Open				
		Moderate	Excluded	0.43	(-0.53, 1.39)	-1.00	(-2.25, 0.25)
			Open				
		Heavy	Excluded	-0.14	(-1.10, 0.82)	-0.57	(-1.82, 0.68)
			Open				
EVERGREEN SHRUBS	Interaction F = 0.45, p = 0.72 Herbivory F = 0.03, p = 0.87 Herbicide F = 2.98, p = 0.06)	Control	Excluded	-0.14	(-1.18, 0.89)	**1.79**	**(0.56)**
			Open				
		Light	Excluded	-0.14	(-0.59, 0.88)	-0.14	(-1.39, 1.11)
			Open				
		Moderate	Excluded	-0.14	(-0.84, 0.55)	-0.14	(-2.39, 0.10)*
			Open				
		Heavy	Excluded	0.29	(-0.67, 1.24)	-0.78	(-2.08, 0.50)
			Open				
NATIVE PERENNIAL HERBS	Interaction F = 1.16, p = 0.34 Herbivory F = 2.54 , p = 0.12 Herbicide F = 1.17, p = 0.34	Control	Excluded	-0.14	(-4.33, 4.04)	**11.1**	**(3.80)**
			Open				
		Light	Excluded	-0.14	(-1.57, 1.28)	-5.00	(-10.3, 0.33)**
			Open			-5.14	(-10.5, 0.19)**
		Moderate	Excluded	-1.57	(-3.26, 0.12)*	-5.43	(-10.8, -0.05)**
			Open			-7.00	(-12.4, -1.62)***
		Heavy	Excluded	-1.00	(-2.01, 0.01)*	-8.57	(-13.8, -3.3)****
			Open			-9.57	(-14.8, -4.3)****
NATIVE RUDERAL HERBS	Interaction F = 0.94, p = 0.44 Herbivory F = 0.15, p = 0.70 Herbicide F = 2.22, p = 0.12	Control	Excluded	-0.14	(-1.13, 0.86)	**2.21**	**(0.94)**
			Open				
		Light	Excluded	-0.43	(-1.43, 0.57)	-0.29	(-2.09, 1.52)
			Open				
		Moderate	Excluded	-0.43	(-0.57, 1.43)	-0.57	(-2.38, 1.23)
			Open				
		Heavy	Excluded	-0.14	(-1.45, 0.86)	-1.57	(-3.38, 0.23)
			Open				
INTRODUCED PERENNIAL HERBS	Interaction F =1.56 , p = 0.23 Herbivory F = 1.69 , p = 0.21 Herbicide F = 5.06, p = 0.01	Control	Excluded	0.00	(-1.48, 1.48)	**3.28**	**(1.78)**
			Open				
		Light	Excluded	1.29	(-0.20, 2.77)*	-2.29	(-4.45, -0.12)**
			Open			-1.00	(-3.16, 1.16)
		Moderate	Excluded	4.28	(-1.05, 1.91)	-2.00	(-4.16, 0.16)*
			Open			-1.57	(-3.73, 0.59)*
		Heavy	Excluded	-2.86	(-1.77, 1.20)	-2.00	(-4.16, 0.16)*
			Open			-2.29	(-4.45, -0.12)**
INTRODUCED RUDERAL HERBS	Interaction F = 0.14, p = 0.93 Herbivory F = 0.29, p = 0.59 Herbicide F = 5.32, p = 0.01	Control	Excluded	0.14	(-1.28, 1.56)	**4.64**	**(0.97)**
			Open				
		Light	Excluded	0.28	(-1.14, 1.71)	-1.34	(-3.26, -0.54)
			Open				
		Moderate	Excluded	0.28	(-1.13, 1.71)	-1.64	(-3.54, -0.26)*
			Open				
		Heavy	Excluded	-0.14	(-1.56, 1.27)	-2.71	(-4.62, -0.81)**
			Open				

Table 6. 2012 Height of Life-Forms. ANOVA output (left column) and treatment comparisons (right column) of height by life-form among herbicide and herbivory treatments. Herbivory effect is the difference between Open and Excluded herbivory treatments. Herbicide effect is the difference between each herbicide treatment and Control, accounting for herbivory treatment in the case of a significant herbivory effect. Bold values are the means of the Control treatments (reference) and bold values in parentheses are 2(SE) of the Control. Non-bold values are mean differences between treatments and non-bold values in parentheses are Bonferonni-corrected 95% confidence intervals. * signifies a treatment effect at $p < 0.05$, **$p < 0.01$, ***$p<0.001$, ****$p<0.0001$.

Table 6. 2012 Height of Life-Forms.

RESPONSE	ANOVA OUTPUT	HERBICIDE TRT	HERBIVORY TRT	HERBIVORY EFFECT		HERBICIDE EFFECT	
DECIDUOUS	Interaction	Control	Excluded	-4.20	(-14.9, 6.45)	**38.6**	**(8.54)**
SHRUBS	F = 4.36, p = 0.01		Open				
	Herbivory	Light	Excluded	-20.5	(-31.8, -9.20)****	17.1	(-6.05, 40.3)*
	F = 15.9, p = 0.0005		Open			-3.38	(-26.5, 19.8)
	Herbicide	Moderate	Excluded	-3.00	(-10.5, 4.54)	-28.4	(-50.6, -6.27)***
	F = 16.4, p < 0.0001		Open			-31.4	(-53.6, 9.27)***
		Heavy	Excluded	-5.86	(-15.6, 3.87)	-30.4	(-53.1, -7.74)***
			Open			-36.6	(-59.0, -13.6)***
DECIDUOUS	Interaction	Control	Excluded	4.30	(-25.6, 34.2)	**53.0**	**(11.1)**
TREES	F = 1.07, p = 0.38		Open				
	Herbivory	Light	Excluded	-17.0	(-87.8, 53.8)	21..2	(-27.5, 70.0)
	F = 2.67, p = 0.12		Open				
	Herbicide	Moderate	Excluded	-36.4	(-93.4, 20.7)	-17.6	(-61.3, 26.1)
	F = 3.12, p = 0.05		Open				
		Heavy	Excluded	-9.79	(-27.0, 7.40)	-24.8	(-58.4, 8.81)
			Open				
EVERGREEN	Interaction	Control	Excluded	-2.18	(-12.2, 7.87)	**20.7**	**(4.26)**
SHRUBS	F = 0.36, p = 0.78		Open				
	Herbivory	Light	Excluded	4.69	(-14.7, 24.1)	0.52	(-14.3, 15.4)
	F = 0.005, p = 0.94		Open				
	Herbicide	Moderate	Excluded	-0.31	(-5.13, 4.51)	-14.6	(-25.9, -3.29)**
	F = 6.38, p = 0.004		Open				
		Heavy	Excluded	-2.86	(-13.3, 7.60)	-12.9	(-25.2, -0.69)*
			Open				
NATIVE	Interaction	Control	Excluded	-3.53	(-11.1, 4.03)	**31.2**	**(4.25)**
PERENNIAL	F = 0.10, p = 0.96		Open				
HERBS	Herbivory	Light	Excluded	-3.73	(-18.4, 10.9)	-4.60	(-13.5, 4.36)
	F = 1.58, p = 0.22		Open				
	Herbicide	Moderate	Excluded	-3.45	(-10.1, 3.24)	-14.6	(-20.5, -8.68)****
	F = 18.7, p < 0.0001		Open				
		Heavy	Excluded	-0.21	(-15.5, 15.1)	-16.2	(-25.4, -6.95)****
			Open				
NATIVE	Interaction	Control	Excluded	-3.53	(-11.1, 4.03)	**28.5**	**(8.49)**
RUDERAL	F = 0.63, p = 0.60		Open				
HERBS	Herbivory	Light	Excluded	-3.73	(-18.4, 10.9)	-4.59	(-13.5, 4.36)
	F = 0.12, p = 0.73		Open				
	Herbicide	Moderate	Excluded	-3.45	(-10.1, 3.24)	-14.6	(-20.5, -8.68)
	F = 3.01, p = 0.06		Open				
		Heavy	Excluded	-0.21	(-15.5, 15.1)	-16.2	(-25.4, -6.95)
			Open				
INTRODUCED	Interaction	Control	Excluded	-3.84	(-17.6, 9.92)	**35.6**	**(11.3)**
PERENNIAL	F = 1.19, p = 0.33		Open				
HERBS	Herbivory	Light	Excluded	5.94	(-20.6, 32.4)	-4.41	(-27.6, 18.6)
	F = 0.28, p = 0.60)		Open				
	Herbicide	Moderate	Excluded	-7.33	(-13.1, -1.60)*	-12.2	(-31.1, 6.68)
	F = 3.19, p = 0.05		Open				
		Heavy	Excluded	-1.05	(-11.2, 9.14)	-20.1	(-39.6, -0.73)*
			Open				
INTRODUCED	Interaction	Control	Excluded	3.59	(-7.71, 14.9)	**35.9**	**(5.06)**
RUDERAL	F = 0.11, p = 0.95		Open				
HERBS	Herbivory	Light	Excluded	3.76	(-4.60, 12.1)	1.21	(-6.03, 8.44)
	F = 0.22, p = 0.64		Open				
	Herbicide	Moderate	Excluded	-2.30	(-29.8, 25.2)	4.29	(-11.0, 19.6)
	F = 0.36, p = 0.78		Open				
		Heavy	Excluded	2.56	(-28.1, 33.2)	2.81	(-19.6, 14.0)
			Open				
NATIVE FERNS	Interaction	Control	Excluded	-9.86	(-29.2, 9.47)	**64.2**	**(12.8)**
	F = 2.16, p = 0.12		Open				
	Herbivory	Light	Excluded	-0.64	(-40.5, 39.3)	-24.9	(-65.5, 15.8)
	F = 2.21, p = 0.15		Open			-25.5	(-66.2, 15.2)
	Herbicide	Moderate	Excluded	-19.9	(-38.6, -1.07)**	-28.6	(-58.2, 0.92)**
	F = 12.7, p = 0.0001		Open			-48.5	(-78.1, -18.9)**
		Heavy	Excluded	2.50	(-13.1, 18.1)	-55.4	(-83.7, -27.0)****
			Open			-52.9	(-81.2, -24.5)****

Table 7. 2012 Cover of Forage Groups. ANOVA output (left column) and treatment comparisons (right column) of cover by forage group among herbicide and herbivory treatments. Herbivory effect is the difference between Open and Excluded herbivory treatments. Herbicide effect is the difference between each herbicide treatment and Control, accounting for herbivory treatment in the case of a significant herbivory effect. Bold values are the means of the Control treatments (reference) and bold values in parentheses are 2(SE) of the Control. Non-bold values are mean differences between treatments and non-bold values in parentheses are Bonferonni-corrected 95% confidence intervals. * signifies a treatment effect at $p < 0.05$, **$p < 0.01$, ***$p<0.001$, ****$p<0.0001$.

RESPONSE	ANOVA OUTPUT	HERBICIDE TRT	HERBIVORY TRT	HERBIVORY EFFECT		HERBICIDE EFFECT	
HIGH QUALITY FORAGE	Interaction	Control	Excluded	-5.52	(-18.5, 7.51)	**46.1**	**(14.7)**
	F = 0.35, p = 0.79		Open				
	Herbivory	Light	Excluded	-2.52	(-15.5, 10.5)	-22.0	(-41.5, -2.55)**
	F = 5.29, p = 0.03		Open			-24.6	(-44.1, -5.08)**
	Herbicide	Moderate	Excluded	-9.41	(-22.4, 3.62)	-30.9	(-50.4, -11.4)***
	F = 18.2, p < 0.0001		Open			-40.3	(-59.8, -20.9)****
		Heavy	Excluded	-4.73	(-17.8, 8.29)	-36.8	(-56.4, -17.4)****
			Open			-41.6	(-61.1, -22.1)****
MODERATE QUALITY FORAGE	Interaction	Control	Excluded	7.67	(-6.27, 21.6)	**36.3**	**(12.6)**
	F = 3.27, p = 0.04		Open				
	Herbivory	Light	Excluded	-9.03	(-23.0, 4.92)	-5.32	(-28.4, 17.8)
	F = 2.01, p = 0.17		Open			-14.3	(-37.4, 8.75)
	Herbicide	Moderate	Excluded	-13.2	(-27.2, 0.73)*	-15.1	(-38.2, 7.95)
	F = 8.84, p = 0.001		Open			-28.4	(-51.5, -5.27)**
		Heavy	Excluded	-0.09	(-14.0, 13.9)	-28.0	(-51.1, -4.93)**
			Open			-28.1	(-51.2, -5.02)**
NON-FORAGE	Interaction	Control	Excluded	0.99	(-12.6, 14.5)	**23.2**	**(10.4)**
	F = 0.62, p = 0.61		Open				
	Herbivory	Light	Excluded	6.90	(-6.65, 20.5)	-5.93	(-10.7, 22.5)
	F = 0.27, p = 0.61		Open				
	Herbicide	Moderate	Excluded	-2.17	(-15.7, 11.4)	-4.33	(-20.9, 12.3)
	F = 6.53, p = 0.004		Open				
		Heavy	Excluded	-0.53	(-14.1, 13.0)	-19.3	(-35.9, -2.75)**
			Open				

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APPENDICES

APPENDIX A: HERBICIDE PRESCRIPTIONS

Study treatment	Season & Year	Prescription	Chemical	Quantity/Acre
Control	Spring 2011	Planting	NA	None
Light	Spring 2011	Planting		
	Spring 2011	Herbaceous	Velpar 2-4-D	2.66 lbs 32 oz
Moderate	Late Summer 2010	Site Preparation	Escort Accord Chopper Oust MSO	1.5 oz 3 qts 24 oz 3 oz 24 oz
	Spring 2011	Planting		
	Spring 2011	Herbaceous	Velpar 2-4-D	2.66 lbs 32 oz
Heavy	Late Summer 2010	Site Preparation	Escort Accord Chopper Oust MSO	1.5 oz 3 qts 24 oz 3 oz 24 oz
	Spring 2011	Planting		
	Spring 2011	Herbaceous	Velpar 2-4-D	2.66 lbs 32 oz
	Spring 2012	Herbaceous	Velpar 2-4-D	2.66 lbs 32 oz

APPENDIX B: EXCLOSURE LOCATION PROTOCOLS

In order to reduce bias in site selection, but ensure selection of sites which are feasible for construction and that avoid edge effects, we identified 30 x 30 m locations that were 50 m from treatment edges and that were no steeper than 30 degrees slope using Geographic Information Systems. Within these constraints, we randomly assigned a single exclosure corner location in the center of one of the 30 x 30 m locations, randomly specified as NW, NE, SW, and SE. Since GIS is unable to adequately determine newly built forest roads, surface undulations, skid trails, landing sites, slash and burn piles, we used the following set of on-site criteria for selection of feasible exclosure construction: corner locations must be at least 30 m from roads and landings; not have extreme surface undulations; fence lines must be free of many large stumps; and exclosures cannot be built on large slash or burn piles. If randomized locations did not meet the specified criteria, then we (1) shifted the corners incrementally to avoid obstacles, (2) flipped the orientation of corner locations or (3) searched in concentric circles around the random location for the next available location that met the above criteria. We assigned an open herbivory control plots to one of twelve random locations 15 m from the exclosures, to avoid edge and drift fence effects. Open herbivory plots followed the same selection criteria as used in exclosure construction.

APPENDIX C: EXCLOSURE CONSTRUCTION PROTOCOLS

1. I used a compass with eye pin, and measuring tape with 2 people to delineate corner posts in a rectangular fashion. I used one corner as reference to make sure all corners were square.

2. We dug corner posts about 6-8 inches in diameter, using a 2 man power auger and posthole diggers, to 4 feet deep and sunk 12 foot treated posts. Have corners angled out slightly (about a degree or two) so that when the fence is pulled tight in both directions, the corner posts shifted upright. Gradually we filled in the hole, making sure that the posts did not shift and tamped down using sticks, rock bars or shovel handles.

3. We stretched a length of high tensile wire around perimeter and pulled tight to the reference corner using a come-along cinch. This served as a template for setting the H-braces strait.

4. We dug H-Brace holes, 8 feet from the corners in both directions and did not angle them but did sink them the same as the corners. To put the door on a short side of the fence, we dug two holes extra holes. The H-brace for the door was off-set from the corner so that the door was between two H-braces.

5. We drilled 2 holes pointed toward the H-brace about 5.5 ' high in the corner posts and one hole in the H-braces pointed towards the corner. We set an 8ft horizontal post (with holes drilled in the ends) between the corner post and H-brace post, align all the holes and had one person hammer in 10 inch metal spikes through the holes to the horizontal brace in between corner and H-brace posts. We had another person hold the opposite horizontal post steady while the metal spike was being driven.

6. We set a nail at the bottom of the corner posts and at the height of the horizontal brace on the H-brace post. We then stretched high tensile wire from nail to nail and back and connect to itself

(tight as possible) so that there are two wires going from bottom corner to high on the brace post. We then tightened the wires (brace wire) by twisting them together using a metal spike and set a stop (such as a stick or peice of wire) to keep it from unwinding (see our fence for refernce). We repeated for all braces.

7. We sunk 10 ft t-posts, 2 ft deep at a 10 ft spacing using a t-post driver.

10. We used layed out the braided wire, and attached a fence puller to one end by cinching two, two-by-fours together on either side of the braided wire and set the wire and fence puller up vertically.

11. We used two come-along cinches, attached to top and bottom of fence and attached to a loop that was fastened to the fence puller. We attached the opposite end of the fence to the opposite corner of the same side and then pulled the fence puller using the come-along cinches. We then sunk fence nails (u-nails) to attach horizontal wires to H-brace post. We let the come-along cinch loose and used the nail puller end of a hammer to lever-pull the wire (from bottom to top of fence) to the corner posts and sunk fence nails to attach the wire to the corner posts

12. We repeated the process for all sides.

13. We then left a length of fence across the door to serve as gate.

APPENDIX D: DIVERSITY INDICES DEFINED

The Simpson's index technically represents the compliment of the probability that two individuals from a community, drawn at random, will be the same species (Simpson 1949) and is calculated as:

$$1 – D = 1 - \sum p_i^2$$

Where p_i is the proportion of cover for the ith species out of the summed cover of all species. As 1 – D rises (bounded between 0 and 1), the community becomes more diverse as there is less dominance by common species. Overall, the Simpson's index gives weight to abundant species rather than richness per se (Magurran 2009).

As Simpson's index emphasizes dominance, rather than richness, it does not directly represent evenness. Therefore, Simpson's evenness can be calculated by dividing the reciprocal of the Simpson's diversity index by the species richness in a sample:

$$E_{1/D} = (1/D)/S$$

Where S is the number of species in a sample. Bounded between 0 and 1, higher values indicate higher levels of evenness between species, still giving weight to common species and less so to species richness.

The Shannon index quantifies the uncertainty of predicting the species pulled from a sample in a given community and thus is more weighted towards rare species (Magurran 2009) and is calculated as:

$$H' = -\sum p_i \ln p_i$$

However, interpretation of this index is typically difficult between communities, so Ecologists sometimes express the index as $e^{H'}$, which is an intuitively direct measurement of the number of species that would have been found in a sample given that all species were common (Magurran 2009). For this study, I use $e^{H'}$ rather than H'.

Shannon evenness J' measures the ratio of observed diversity to a maximum diversity that can be possible where all species have equal abundances (Pielou 1969, 1975, Magurran 2009) where:

$$J' = H'/\ln(S)$$

This index provides a more direct measure of evenness between species in a community than the Shannon Diversity Index.

APPENDIX E: LIFE-FORM DEFINITIONS

I formulated the life-form groups by investigating the overall community and literature pertaining to early seral plant communities. Deciduous trees refer to broadleaf trees and tall shrubs and deciduous shrubs refer to broadleaf shrubs and subshrubs, both with deciduous foliage longevity and which are predominately comprised of species with high coppice sprouting potential and native status. Evergreen trees refer to needle leaf conifers with evergreen foliage longevity and evergreen shrubs refer to broadleaf subshrubs, shrubs and shrub-trees with evergreen foliage longevity. Perennial herbs refers to forbs and grasses with perennial longevity, often with underground sprouting structures (rhizomes, corms, bulbs, etc.). Ruderal herbs refers to forbs with annual or biennial longevity, often sprouting from seeds or temporary underground structures. I included graminoids (*Poaceae*, *Juncaceae and Cyperaceae*) in the herb groups as they represent species of the herbaceous layer targeted by herbicides and selective herbivory. These families primarily belonged to native-perennial and introduced-perennial life-forms. Ferns refer to long-lived Pteridophytes that reproduce via spores and often sprout from underground vegetative structures. I separated ferns from herbaceous as there are only two predominate species in our study area which are generally of high abundance, in contrast to native herbaceous which are generally of high richness and more or less equivalent abundance. Native status, native or introduced, refers to whether or not the species originates the PNW or not, respectively. In general, all the deciduous and evergreen woodies, native herbs and ferns are of native status and can be thought of as representing the composition of native early seral plant communities.

I calculated cover values of each life-form group by adding up all the cover values of each species within a group, from each herbicide*herbivory treatment plot. For richness, of each group, I counted all of the species within each group from each treatment plot. I then calculated average height values of each life-form group by taking the average height between all species within each group, from each treatment plot. In order to avoid samples that exceeded browse line heights, I did not use species with heights over 2 m when averaging across species. I calculated the average height of the top-five abundant species by determining the five species with highest cover values and taking the average between all five heights.

APPENDIX F: SPECIES LIST

Scientific Name	Family	Origin	Perenniality	Life Form	Forage Quality	Nomenclature
Acer macrophyllum	Aceraceae	Native	Perennial	Deciduous Tree	High	Pursh
Toxicodendron diversilobum	Anacardiaceae	Native	Perennial	Deciduous Shrub	Moderate	(Torr. & A. Gray) Greene
Daucus carota	Apiaceae	Introduced	Ruderal	Herbaceous	Non-forage	L.
Osmorhiza berteroi	Apiaceae	Native	Perennial	Herbaceous	Non-forage	DC.
Perideridia parishii	Apiaceae	Native	Perennial	Herbaceous	Unknown	J.M. Coult. & Rose
Torilis arvensis	Apiaceae	Introduced	Ruderal	Herbaceous	Unknown	(Huds.) Link
Ilex aquifolium	Aquifoliaceae	Introduced	Perennial	Evergreen Broadleaf	Non-forage	L.
Oplopanax horridus	Araliaceae	Native	Perennial	Deciduous Shrub	High	(Sm.) Miq
Asarum caudatum	Aristolochiaceae	Native	Perennial	Herbaceous	Moderate	Lindl.
Adenocaulon bicolor	Asteraceae	Native	Perennial	Herbaceous	High	Hook.
Agoseris sp	Asteraceae	Native	Perennial	Herbaceous	Non-forage	Raf.
Agoseris grandiflora	Asteraceae	Native	Perennial	Herbaceous	Non-forage	(Nutt.) Greene
Anaphalis margaritacea	Asteraceae	Native	Perennial	Herbaceous	Moderate	(L.) Benth.
Cirsium arvense	Asteraceae	Introduced	Perennial	Herbaceous	Moderate	(L.) Scop.
Cirsium vulgare	Asteraceae	Introduced	Ruderal	Herbaceous	Moderate	(Savi) Ten.
Conyza canadensis	Asteraceae	Native	Ruderal	Herbaceous	Moderate	(L.) Cronquist
Crepis capillaris	Asteraceae	Introduced	Ruderal	Herbaceous	Moderate	(L.) Wallr.
Erechtites minima	Asteraceae	Introduced	Ruderal	Herbaceous	Non-forage	(Poir.) DC.
Hieracium albiflorum	Asteraceae	Native	Perennial	Herbaceous	Moderate	Hook.
Hypochaeris radicata	Asteraceae	Introduced	Perennial	Herbaceous	High	L.
Lactuca serriola	Asteraceae	Introduced	Perennial	Herbaceous	Moderate	L.
Lapsana communis	Asteraceae	Introduced	Ruderal	Herbaceous	Unknown	L.
Leucanthemum vulgare	Asteraceae	Introduced	Perennial	Herbaceous	Non-forage	Lam.
Madia gracilis	Asteraceae	Native	Ruderal	Herbaceous	Unknown	(Sm.) D.D. Keck
Mycelis muralis	Asteraceae	Introduced	Ruderal	Herbaceous	Moderate	(L.) Dumort.
Petasites palmatus	Asteraceae	Native	Perennial	Herbaceous	High	(Aiton) A. Gray
Senecio jacobaea	Asteraceae	Introduced	Perennial	Herbaceous	Non-forage	L.
Senecio sylvaticus	Asteraceae	Introduced	Ruderal	Herbaceous	Non-forage	L.
Senecio vulgaris	Asteraceae	Introduced	Ruderal	Herbaceous	Unknown	L.
Sonchus asper	Asteraceae	Introduced	Ruderal	Herbaceous	Moderate	(L.) Hill
Achlys triphylla	Berberidaceae	Native	Perennial	Herbaceous	High	(Sm.) DC
Mahonia nervosa	Berberidaceae	Native	Perennial	Evergreen Broadleaf	Non-forage	(Pursh) Nutt.
Vancouveria hexandra	Berberidaceae	Native	Perennial	Herbaceous	Moderate	(Hook.) C. Morren & Decne.
Alnus rubra	Betulaceae	Native	Perennial	Deciduous Tree	High	Bong.
Corylus cornuta	Betulaceae	Native	Perennial	Deciduous Tree	High	Marshall

Scientific Name	**Family**	**Origin**	**Perenniality**	**Life Form**	**Forage Quality**	**Nomenclature**
Campanula scouleri	Campanulaceae	Native	Perennial	Herbaceous	High	Hook ex. A. DC.
Linnaea borealis	Caprifoliaceae	Native	Perennial	Herbaceous	Moderate	L.
Sambucus racemosa	Caprifoliaceae	Native	Perennial	Deciduous Tree	Moderate	L.
Symphoricarpos albus	Caprifoliaceae	Native	Perennial	Deciduous Shrub	High	(L.) S. F. Blake
Symphoricarpos hesperius	Caprifoliaceae	Native	Perennial	Deciduous Shrub	High	G. N. Jones
Cerastium glomeratum	Caryophyllaceae	Introduced	Ruderal	Herbaceous	Moderate	Thuill.
Hypericum perforatum	Clusiaceae	Introduced	Perennial	Herbaceous	Moderate	L.
Cornus canadensis	Cornaceae	Native	Perennial	Evergreen Broadleaf	Moderate	L.
Scirpus sp	Cyperaceae	Native	Ruderal	Herbaceous	Unknown	Greene
Pteridium aquilinum	Dennstaedtiaceae	Native	Perennial	Fern	Non-forage	(L.) Kuhn
Polystichum munitum	Dryopteridaceae	Native	Perennial	Fern	Moderate	(Kaulf.) C. Presl
Arbutus menziesii	Ericaceae	Native	Perennial	Evergreen Broadleaf	Non-forage	Pursh
Gaultheria shallon	Ericaceae	Native	Perennial	Evergreen Broadleaf	Non-forage	Pursh
Rhododendron macrophyllum	Ericaceae	Native	Perennial	Evergreen Broadleaf	Non-forage	D. Don ex G. Don
Vaccinium oreophilum	Ericaceae	Native	Perennial	Deciduous Shrub	Moderate	L.
Vaccinium ovalifolium	Ericaceae	Native	Perennial	Deciduous Shrub	High	Sm.
Vaccinium parvifolium	Ericaceae	Native	Perennial	Deciduous Shrub	High	Sm.
Vaccinium sp	Ericaceae	Native	Perennial	Deciduous Shrub	Moderate	L.
Vaccinium ovatum	Ericaceae	Native	Perennial	Evergreen Broadleaf	High	Pursh
Lathyrus nevadensis	Fabaceae	Native	Perennial	Herbaceous	Moderate	S. Watson
Lotus crassifolius	Fabaceae	Native	Perennial	Herbaceous	Moderate	(Benth.) Greene
Lotus micranthus	Fabaceae	Native	Ruderal	Herbaceous	Unknown	Benth.
Lupinus arcticus	Fabaceae	Native	Perennial	Herbaceous	Moderate	S. Watson
Trifolium repens	Fabaceae	Introduced	Perennial	Herbaceous	High	L.
Vicia americana	Fabaceae	Native	Perennial	Herbaceous	High	Muhl. Ex Willd
Vicia sativa	Fabaceae	Introduced	Ruderal	Herbaceous	Moderate	L.
Dicentra formosa	Fumariaceae	Native	Perennial	Herbaceous	Non-forage	(Haw.) Walp.
Geranium bicknelli	Geraniaceae	Native	Ruderal	Herbaceous	Unknown	Britton
Geranium carolinianum	Geraniaceae	Native	Ruderal	Herbaceous	Unknown	L.
Geranium sp	Geraniaceae	Native	Ruderal	Herbaceous	Unknown	L.
Ribes lacustre	Grossulariaceae	Native	Perennial	Deciduous Shrub	Moderate	(Pers.) Poir.
Ribes lobbii	Grossulariaceae	Native	Perennial	Deciduous Shrub	Moderate	A. Gray
Ribes sanguineum	Grossulariaceae	Native	Perennial	Deciduous Shrub	High	Pursh
Nemophila parviflora	Hydrophyllaceae	Native	Ruderal	Herbaceous	Unknown	Douglas ex Benth.
Nemophila sp	Hydrophyllaceae	Native	Ruderal	Herbaceous	Unknown	Nutt.
Phacelia nemoralis	Hydrophyllaceae	Native	Ruderal	Herbaceous	Moderate	Greene
Iris sp	Iridaceae	Native	Perennial	Herbaceous	Unknown	L.
Iris tenax	Iridaceae	Native	Perennial	Herbaceous	Moderate	Douglas ex Lindl.

Scientific Name	**Family**	**Origin**	**Perenniality**	**Life Form**	**Forage Quality**	**Nomenclature**
Luzula parviflora	Juncaceae	Native	Perennial	Herbaceous	Moderate	(Ehrh.) Desv.
Clinopodium douglasii	Lamiaceae	Native	Perennial	Herbaceous	Unknown	(Benth.) Kuntze
Medicago lupulina	Lamiaceae	Introduced	Ruderal	Herbaceous	Unknown	L.
Prunella vulgaris	Lamiaceae	Native	Perennial	Herbaceous	Non-forage	L.
Stachys cooleyae	Lamiaceae	Native	Perennial	Herbaceous	Moderate	A. Heller
Lilium sp	Liliaceae	Native	Perennial	Herbaceous	Unknown	L.
Lilium columbianum	Liliaceae	Native	Perennial	Herbaceous	Moderate	Leichtlin
Maianthemum dilatatum	Liliaceae	Native	Perennial	Herbaceous	High	(Alph. Wood). elson & J.F. Macbr.
Maianthemum racemosum	Liliaceae	Native	Perennial	Herbaceous	Moderate	(L.) Link
Maianthemum stellatum	Liliaceae	Native	Perennial	Herbaceous	Moderate	(L.) Link
Prosartes hookeri	Liliaceae	Native	Perennial	Herbaceous	Non-forage	Torr.
Prosartes smithii	Liliaceae	Native	Perennial	Herbaceous	Non-forage	(Hook.) Utech.
Streptopus amplexifolius	Liliaceae	Native	Perennial	Herbaceous	Unknown	(L.) DC.
Trillium ovatum	Liliaceae	Native	Perennial	Herbaceous	Non-forage	Pursh
Veratrum californicum	Liliaceae	Native	Perennial	Herbaceous	Moderate	Durand
Fraxinus latifolia	Oleacea	Native	Perennial	Deciduous Tree	Unknown	Benth.
Epilobium brachycarpum	Onagraceae	Native	Ruderal	Herbaceous	Moderate	C. Presl
Epilobium ciliatum	Onagraceae	Native	Perennial	Herbaceous	Moderate	Raf.
Epilobium angustifolium	Onagraceae	Native	Perennial	Herbaceous	Moderate	L.
Oxalis oregana	Oxalidaceae	Native	Perennial	Herbaceous	High	Nutt.
Tsuga heterophylla	Pinaceae	Native	Perennial	Evergreen Tree	Moderate	(Raf.) Sarg.
Pseudotsuga menziesii	Pinaceae	Native	Perennial	Evergreen Tree	Non-forage	(Mirb.) Franco
Plantago major	Plantaginaceae	Introduced	Perennial	Herbaceous	Moderate	L.
Aira sp	Poaceae	Introduced	Ruderal	Herbaceous	Unknown	L.
Brachypodium sylvaticum	Poaceae	Introduced	Perennial	Herbaceous	Non-forage	(Huds.) P. Beauv.
Cinna latifolia	Poaceae	Native	Perennial	Herbaceous	Unknown	(Trevis. ex Goepp.) Griseb.
Elymus glaucus	Poaceae	Native	Perennial	Herbaceous	Moderate	Buckley
Holcus lanatus	Poaceae	Introduced	Perennial	Herbaceous	Moderate	L.
Lolium perenne	Poaceae	Introduced	Ruderal	Herbaceous	Moderate	L.
Phalaris arundinacea	Poaceae	Native	Perennial	Herbaceous	High	L.
Vulpia bromoides	Poaceae	Introduced	Ruderal	Herbaceous	Unknown	(L.) Gray
Agrostis exrata	Poaceae	Native	Perennial	Herbaceous	Moderate	Nutt.
Aira caryophyllea	Poaceae	Introduced	Ruderal	Herbaceous	Unknown	L.
Bromus orcuttianus	Poaceae	Native	Perennial	Herbaceous	Moderate	Vasey
Deschampsia danthoniodes	Poaceae	Native	Ruderal	Herbaceous	Non-forage	(Trin.) Munro
Lolium perenne	Poaceae	Introduced	Perennial	Herbaceous	Moderate	L.
Poa pratensis	Poaceae	Introduced	Perennial	Herbaceous	Moderate	L.

Scientific Name	**Family**	**Origin**	**Perenniality**	**Life Form**	**Forage Quality**	**Nomenclature**
Collomia heterophylla	Polemoniaceae	Native	Ruderal	Herbaceous	Unknown	Douglas ex Hook.
Rumex acetosella	Polygonaceae	Introduced	Perennial	Herbaceous	Moderate	L.
Botrychium sp	Polypodiaceae	Native	Perennial	Fern	Unknown	Sw.
Claytonia sibirica	Portulacaceae	Native	Ruderal	Herbaceous	High	L.
Lysimachia nummalaria	Primulaceae	Introduced	Perennial	Herbaceous	Unknown	L.
Trientalis borealis ssp. latifolia	Primulaceae	Native	Perennial	Herbaceous	Non-forage	Raf.
Actaea elata	Ranunculaceae	Native	Perennial	Herbaceous	Unknown	(Nutt.) Prantl
Actaea rubra	Ranunculaceae	Native	Perennial	Herbaceous	Moderate	(Aiton) Willd.
Anemone deltoidea	Ranunculaceae	Native	Perennial	Herbaceous	Moderate	Hook.
Anemone sp	Ranunculaceae	Native	Perennial	Herbaceous	Moderate	L.
Coptis laciniata	Ranunculaceae	Native	Perennial	Herbaceous	Unknown	A. Gray
Aquilegia formosa	Ranunculaceae	Native	Perennial	Herbaceous	High	Fisch ex DC.
Rhamnus purshiana	Rhamnaceae	Native	Perennial	Deciduous Tree	High	(DC.) A. Gray
Fragaria sp	Rosaceae	Native	Perennial	Herbaceous	Moderate	L.
Holodiscus discolor	Rosaceae	Native	Perennial	Deciduous Tree	Moderate	(Pursh) Maxim.
Oemleria cerasiformis	Rosaceae	Native	Perennial	Deciduous Shrub	Moderate	(Torr. & A. Gray ex Hook. & Arn.) Landon
Prunus emarginata	Rosaceae	Native	Perennial	Deciduous Tree	Moderate	(Douglas ex Hook.) D. Dietr.
Rosa gymnocarpa	Rosaceae	Native	Perennial	Deciduous Shrub	High	Nutt.
Rubus armeniacus	Rosaceae	Introduced	Perennial	Evergreen Broadleaf	Moderate	Focke
Rubus leucodermis	Rosaceae	Native	Perennial	Deciduous Shrub	Non-forage	Douglas ex Torr. & A. Gray
Rubus nivalis	Rosaceae	Native	Perennial	Evergreen Broadleaf	Moderate	Douglas ex Hook.
Rubus parviflorus	Rosaceae	Native	Perennial	Deciduous Shrub	High	Nutt.
Rubus spectabilis	Rosaceae	Native	Perennial	Deciduous Shrub	Moderate	Pursh
Rubus ursinus	Rosaceae	Native	Perennial	Deciduous Shrub	Moderate	Cham. & Schltdl.
Galium aparine	Rubiaceae	Native	Ruderal	Herbaceous	Non-forage	L.
Galium oreganum	Rubiaceae	Native	Perennial	Herbaceous	Moderate	Britton
Galium triflorum	Rubiaceae	Native	Perennial	Herbaceous	Moderate	Michx.
Salix sp	Salicaceae	Native	Perennial	Deciduous Tree	High	L
Salix lucida	Salicaceae	Native	Perennial	Deciduous Tree	High	Muhl
Tellima grandiflora	Saxifragaceae	Native	Perennial	Herbaceous	Non-forage	(Pursh) Douglas ex Lindl.
Digitalis purpurea	Scrophulariaceae	Introduced	Ruderal	Herbaceous	Non-forage	L.
Veronica arvensis	Scrophulariaceae	Introduced	Ruderal	Herbaceous	Non-forage	L.
Veronica serpyllifolia	Scrophulariaceae	Native	Perennial	Herbaceous	Moderate	L.
Vicia cracca	Scrophulariaceae	Introduced	Perennial	Herbaceous	Moderate	L.

Scientific Name	**Family**	**Origin**	**Perenniality**	**Life Form**	**Forage Quality**	**Nomenclature**
Viola sp	Violaceae	Native	Perennial	Herbaceous	Moderate	L.
Viola glabella	Violaceae	Native	Perennial	Herbaceous	Moderate	Nutt.
Viola sempervirens	Violaceae	Native	Perennial	Herbaceous	Moderate	Greene