

## AN ABSTRACT OF THE THESIS OF

Joshua P. Averett for the degree of Master of Science in Rangeland Science presented on June 30, 2014.

Title: Non-native and Native Plant Species Distributions and Variability along an Elevation Gradient in the Wallowa Mountains, Oregon.

Abstract approved:

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Invasion by non-native plants into natural areas is an important component of global change that threatens biodiversity and ecosystem structure and function. Mountains are currently among the least invaded ecosystems, however, these biodiversity hotspots are increasingly under threat of exotic plant invasion. Evaluation of plant species distribution patterns in mountain ecosystems can provide insight into dominant processes of plant invasion and inform management to reduce the spread of non-native plants in mountains. The objectives of this study were to: 1) evaluate the main drivers of plant invasions in the Wallowa Mountain Range of northeastern Oregon, and the extent patterns of native species distributions and their causes differed from non-native species along an elevation gradient; and 2) investigate inter- and intra-annual understory vascular plant species variability along an elevation gradient to inform long-term monitoring of plant invasion dynamics in the Wallowa Mountains.

We sampled understory vascular plant communities in summer 2012 along three forest roads in the Wallowa Mountains. Transects ( $n=20$ ) were evenly stratified by elevation (60 meters) along each road. Indicator species analysis (ISA) was used to identify habitat tendencies for non-native species. Non-metric multidimensional scaling (NMS) related community composition to environmental and species trait factors. Predictors of non-native and native species abundance and richness were evaluated using Non-parametric multiplicative regression (NPMR). Canopy openness and elevation niche widths were modeled for all common species and evaluated for evidence of high elevation or closed canopy specialization.

Non-native species richness decreased continuously with increasing elevation. In contrast, native species richness displayed a unimodal distribution with maximum richness at the mid-elevations. According to NMS and NPMR, elevation, canopy openness, and disturbance were the strongest correlates of non-native species abundance. Non-native species were concentrated in low elevation bunchgrass, roadside, and open forest habitats with high canopy openness, and moderate to high disturbance intensity. Overlays of species trait factors onto ordinations revealed that the transition into the subalpine community and over-story canopy closure exceeding approximately 60 percent were potential barriers to non-native species establishment.

Vegetation sampling was repeated three times (June, July, and August 2013) during the growing season in summer 2013 for a subset ( $n=10$ ) of our transects. Blocked Multi Response Permutation Procedure (MRBP) was used to test the hypothesis of no change in species composition between years (summer 2012 and summer 2013) and between each sampling period (June, July, and August) within one

growing season. NMS related community composition at different times to environmental and trait category factors. Blocked Indicator Species Analysis was used to identify species with tendencies towards specific sampling periods. Important predictors of vegetation change were identified and indicator species distributions were related to NMS axes using NPMR.

Vegetation composition changed both between years and between each sampling period within one growing season. Species richness increased with sampling effort, dominant species were consistently found throughout all sampling periods and rare species showed the highest rate of turnover between sampling periods. The highest species richness and greatest number of indicator species were associated with the early summer (June) sampling period. Approximately 25% of all non-native species showed tendencies towards a specific sampling period where greater than half favored the June sampling period within lowland bunchgrass communities. Annual species including the most dominant non-native species within the lowland and montane zones showed the highest inter- and intra-annual variability compared to other trait categories. Total species richness was positively related to turnover and was the most important predictor of relative abundance change between all sampling periods. Species turnover was highest in species rich montane plots; however, trait abundance and richness did not statistically differ in montane plots.

These data suggest that elevation, canopy, openness, and disturbance are important factors structuring non-native plant distributions in the Wallowa Mountains. Our findings that non-native species tended to be concentrated in low-elevation, early successional habitats coupled with a lack of high elevation or closed

canopy specialization indicates that non-native plants that occur at the highest elevations are likely generalist species that depend on disturbance (primarily open over-story canopy) for spread into higher elevation sites until they are eventually filtered out by harsh environmental conditions coincident with the subalpine transition zone. Collectively these results suggest that interactions between introduction pathways that favor human assisted dispersal into the low-elevations where ruderal species are favored and environmental filters (elevation, canopy openness, and disturbance) are the dominant factors structuring non-native plant distributions in the Wallowa Mountains.

Our results also indicate that long-term monitoring of vegetation change in the Wallowa Mountains will be improved through periodic sampling during each growing season. Sampling once during the spring or early summer and then again coincident with peak biomass should improve estimates of species distributions and diversity patterns by capturing both vernal and late season species. Early season sampling may be particularly important for monitoring non-native plants in the Wallowa Mountains as most non-natives were concentrated in low elevation semi-arid bunchgrass communities where spring and early summer specialization is common.

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Non-native and Native Plant Species Distributions and Variability along an Elevation  
Gradient in the Wallowa Mountains, Oregon

by  
Joshua P. Averett

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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.

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Joshua P. Averett, Author

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## CONTRIBUTION OF AUTHORS

Dr. Bruce McCune contributed to the entire thesis through guidance and editing. Dr. McCune also provided technical support regarding analytical approaches and implementation of Non-metric multidimensional scaling, Non-parametric multiplicative regression, Blocked Multi-response Permutation Procedures, and Blocked Indicator Species Analysis using HyperNiche 2.0 and PC-Ord 6.0. Dr. Catherine Parks provided guidance regarding research questions, provided edits, and assisted in the development of the sampling protocol for both chapters. Bridgett Naylor contributed to chapters 2 and 3 through support of data extraction, data-base management, and assisted with the development of the sampling protocol. Dr. Ricardo Mata-González provided guidance and editing for the entire thesis.

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# Non-native and Native Plant Species Distributions and Variability along an Elevation Gradient in the Wallowa Mountains, Oregon

## Chapter 1 Introduction

Invasion into natural areas by introduced plant species is considered one of the most significant threats to global biodiversity and ecosystem structure and function (Chapin et al. 2000; Levine et al. 2003; and Scherer-Lorenzen 2007). Invasive plants can influence community structure by decreasing local plant diversity (Vila et al. 2006; Powell et al. 2011), altering species composition of both flora (Brooks and Pyke 2001; Adams and Engelhardt 2009) and fauna (Slobodchikoff and Doyen 1977; Simao et al. 2010), and by out-competing native species for resources including water (Gordon et al. 1989; D'Antonio and Mahall 1991), light (Van Auken and Bush 1990; Dyer and Rice 1999), and nutrients (Caldwell et al. 1985; D'Antonio and Vitousek 1992). The most problematic invasive plants are often referred to as “transformer species” for their ability to alter ecosystem processes (D'Antonio and Vitousek 1992; Rejmanek et al. 2013). Invasive “transformer” plant species influence ecosystem processes in two primary ways: 1) invaders can alter system level resource availability through mechanisms such as excessive use of water (Scott and Lesch 1996; Levine et al. 2003), increased nitrogen fixation (Stock et al. 1995; Liao et al. 2007), accumulation of litter (Farrer and Goldberg 2009), and accumulation and redistribution of salt within the soil profile (Ladenburger et al. 2006); and 2) plant invasions can result in changes to disturbance regimes including increased frequency of fire (Brooks et al. 2004; Balch et al. 2013) and alterations to rates of nutrient cycling (Vitousek and Walker 1989; Ehrenfeld et al. 2010).

Researchers have identified important factors that drive plant invasions including disturbance (Hobbs and Huenneke 1992; Burke and Grime 1996; Davis et al. 2000), altered disturbance regimes (Hobbs and Huenneke 1992; Theoharides and Dukes 2007); increased resource availability (Davis et al. 2000; Rejmanek et al. 2013), higher propagule pressure (Simberloff 2009; Rejmanek et al. 2013), and greater residency time of introduced species (Thuiller et al. 2006; Pyšek et al. 2011). Still, attempts to develop general theories that explain inherent differences in invasibility between plant communities have been unsuccessful (Davis et al. 2000; Dietz and Edwards 2006; Jeschke et al. 2012). Ecologists recognize that a full understanding of plant invasion biology is not likely unless researchers begin to address the spatial and temporal complexity of plant invasions (Pyšek and Hulme 2005; Seipel et al. 2011; Rejmanek et al. 2013). Uncertainties regarding plant invasion dynamics over multiple spatial and temporal scales have heightened interest in the development of long-term, multi-scale monitoring projects (Burt 1994; Pyšek and Hulme 2005; Dietz and Edwards 2006; Rejmanek et al. 2013).

The Mountain Invasion Research Network (MIREN), a global consortium focused on facilitating research and monitoring efforts related to plant invasions in mountain ecosystems has recently established permanent vegetation transects along elevation gradients in eleven mountain ranges around the globe (Dietz et al. 2006; McDougall et al. 2009). MIREN's primary goals are to facilitate multi-scale (spatial and temporal) invasive plant research and monitoring in mountain environments in order to improve the understanding of plant invasion dynamics in mountains including drivers of species



spread and subsequent impacts to different plant communities, and to inform invasive plant management and control efforts in mountain ecosystems (McDougall et al. 2009). Mountain environments are currently among the least invaded ecosystems, however these biodiversity hotspots are increasingly under threat of exotic plant invasions (Pauchard et al. 2009; McDougall et al. 2011). The resistance of mountain environments to exotic species invasions is likely due to a combination of low anthropogenic disturbance, low propagule supply, and extreme environmental conditions (Barni et al. 2012). Two emergent themes in mountain plant invasion research are: non-native species richness tends to decrease strongly at high elevations (high elevations are defined as subalpine and alpine communities in this paper) (Alexander et al. 2011; Seipel et al. 2011; Barni et al. 2012); and high elevation, non-native plant communities consist of generalist species that are also found at low elevations (Becker et al. 2005; Alexander et al. 2011; Marini et al. 2013). Researchers have recently proposed the “directional ecological filtering hypothesis” as an explanation for patterns of high elevation generalist species and declining species richness with increasing elevation (Alexander et al. 2011). The main idea behind this theory is that historical introduction pathways are critical for shaping non-native plant distributions in mountain ecosystems. The directional ecological filtering hypothesis assumes that non-native plants are preferentially introduced into low elevations, pre-adapted species establish, species are filtered out along an elevation gradient, and generalist species end up occupying the broadest elevation range (Alexander et al. 2011). The dominant factors related to ecological filtering of non-natives along elevation gradients are less understood and likely to change over time

(Dietz and Edwards 2006; Alexander et al. 2011; Pyšek et al. 2011; Barni et al. 2012).

Similar patterns of non-native species distributions in multiple mountain ranges suggest that common mechanisms are responsible for limiting the establishment of non-native species in high elevation environments (Pauchard et al. 2009; McDougall et al. 2011; Seipel et al. 2011).

According to McDougall et al. (2011), the most damaging plant invasions in mountain ecosystems have occurred relatively recently and are expected to increase in the future. Changing land use patterns in mountains have resulted in an increased introduction rate of non-native species that are pre-adapted to subalpine and alpine environments. Direct introductions of pre-adapted high elevation invaders such as *Pinus contorta* in Chile (Langdon et al. 2010), *Pinus radiata* in Hawaii (Daehler 2005), and *Pinus pinaster* in South Africa (Richardson et al. 1990) have resulted in complete shifts from herbaceous to tree dominated communities. Other recent high elevation adapted species including *Hieracium auranticum*, *Juncus effuses*, and *Cytisus scoparius* which are some of the most aggressive invaders in the Australian Alps are thought to have spread from ski-resort gardens (Williams et al. 2008). Upward expansion of non-native species ranges have also been observed in mountains. Pyšek et al. (2011) reported that 65 non-native vascular plant species in the Czech Republic showed an average altitudinal increase of approximately 2 meters per year between 1738 and 1986.

Evidence of increasing plant invasion into mountain environments is particularly disconcerting given the important roles of mountains as harbors of high biodiversity and protected areas, and providers of important ecosystem services such as clean water

storage and delivery to low lying areas (Araujo and Williams 2001; Korner 2004; Gret-Regamey et al. 2012). Although mountains occupy less than one quarter of all terrestrial land area, more than half of the world's population depends on clean water that is captured and supplied by mountain ecosystems (Becker and Bugmann 2001; Beniston 2003; Gret-Regamey et al. 2012). The maintenance of healthy vegetation communities is critical to insure efficient hydrologic cycling in mountain systems. Plant invasions in mountains environments have also reduced vegetation productivity resulting in losses to livestock production, decreased recreational value, and threaten biodiversity in habitats with a high proportion of endemic species (D'Antonio and Vitousek 1992; Irwin et al. 1994; Olson 1999). It is important to understand what drives the spread of non-native plant species in mountain environments so that management and restoration actions can be developed to reduce the expansion of non-native plants in these environments.

Our study focusses on non-native plant distributions in the Blue Mountains (Wallowa Mountain Range) located in northeastern Oregon. The Wallowa Mountains are included within MIREN's Pacific Northwest Core Region. The Wallowa Mountains are part of the Middle Rocky Mountain Range and consist of approximately 4,700 square kilometers of deeply dissected topography. The presence of extreme elevation gradients, high geologic and topographic variability, and the Wallowa Mountains' position at the extreme western edge of the Cascade Range's rain shadow have resulted in highly variable plant communities ranging from semi-arid bunchgrass and shrub dominated habitats in the low lying valleys to moist, closed canopy conifer forests within the

montane zone, and alpine tundra at the highest elevation sites (Johnson 1994; Anderson et al. 1998; U.S. Department of Agriculture 2014).

Human induced changes to disturbance regimes including widespread overgrazing in the late 1800's and early 1900's, suppression of fire over the last 150 years, past logging practices, and the introduction of non-native species have resulted in substantial shifts in vegetation community composition and structure in the Wallowa Mountains that threaten the future provisioning of ecosystem services to multiple users in the region (Johnson 1994; Quigley et al. 1997; Youngblood et al. 2006; U.S. Department of Agriculture 2014). The Wallowa Mountains provide important ecological, economic, and cultural services to society including: traditional hunting, fishing, and spiritual resources for Native American tribes; trees for lumber, wood products, and fuel; clean water for irrigation, hydropower, and domestic usage in the lowlands; abundant and cool water that supports federally endangered salmonid populations; forage for livestock; recreational opportunities; and harbors of local biodiversity, endemic species, and protected wilderness and National Forest lands (Johnson 1994; Quigley 1997; U.S. Department of Agriculture 2014). According to local land managers, the capacity of the Wallowa Mountain's vegetation communities to support ecosystem services has been diminished by post Euro-American land management practices coupled with the introduction of non-native plant species (Johnson 1994; Quigley 1997; U.S. Department of Agriculture 2014). The majority of rangelands and dry montane forests in the Wallowa's are considered to be in "poor" health and most cold forests, subalpine, and

alpine communities show substantial departure from natural conditions (Johnson 1994; Quigley et al. 1997; Youngblood et al. 2006; U.S. Department of Agriculture 2014).

Current land management goals in the region include the restoration of vegetation communities back towards pre Euro-American settlement conditions by using tools such as prescribed fire, and alterations of logging and grazing practices to more closely mimic the natural disturbance regime of the area (Quigley et al. 1997; U.S. Department of Agriculture 2014). Land managers do recognize that restoring disturbance regimes may not result in desired plant community trajectories in some areas. The major concern is that response potentials of many communities have also been altered by the introduction of non-native plants, erosion, pollution, grazing by non-native herbivores, increased populations of wild herbivores, and loss of functional predator populations (Irwin et al. 1994; Quigley et al. 1997). Invasion by non-native plants has been identified as a major factor contributing to the loss of ecosystem integrity in the Wallowa Mountains and restoration of native communities, control of current invasions, and identification of future invaders are important priorities for the region (Quigley et al. 1997; Johnson and Swanson 2005; U.S. Department of Agriculture 2010a).

Pacific Northwest bunchgrass communities have proven particularly susceptible to non-native plant invasions in the Blue Mountain Region (Mack and Thompson 1982; Johnson and Swanson 2005; Parks et al. 2005). Some bunchgrass sites particularly benches (gentle slopes < 20%), streamside terraces, meadows, and ridge tops have been converted over to non-native annual grass and non-native perennial grass dominated communities (Johnson 1994; Quigley et al. 1997; U.S. Department Agriculture 2014).

These sites have likely crossed thresholds into alternative stable states where reversal back to desired native communities may be impossible (Laycock 1991; Quigley 1997; Johnson and Swanson 2005; U.S. Department of Agriculture 2014). Local land managers have also identified low elevation dry forests as highly susceptible to invasion by non-native species (Quigley et al. 1997; U.S. Department of Agriculture 2014). Subalpine and alpine communities in the Wallowa Mountains are scarcely invaded and are generally thought to be relatively resilient to plant invasions (Quigley et al. 1997; Parks et al. 2005; U.S. Department of Agriculture 2014). However, several established species in and around the Blue Mountain region including *Cirsium arvense*, *Cirsium vulgare*, *Leucanthernum vulgare*, *Carduus nutans*, *Lythrum salicaria*, and *Centaurea diffusa* have been identified as potential invaders of the subalpine and alpine communities (Quigley et al. 1997; Parks et al. 2005). Additionally, recent non-native introductions into the Wallowa Mountains include *Hieracium aurantiacum* and *Hieracium caespitosum*. These two hawkweed species have proven invasive in subalpine communities in other mountain ranges (Williams et al. 2008), and have shown some evidence of spread in the Wallawas (Parks et al. 2005).

Past investigations into drivers of plant invasions in the Blue Mountains region have focused on targeted species and have primarily occurred in invaded bunchgrass and sagebrush dominated communities. The tendency for researchers to focus on grass and shrubland communities has undoubtedly resulted from the high invasion status of these communities. Invasions by non-native annual grasses have been extensively studied in the area. The apparent high invasibility of pacific northwest bunchgrass communities to

annual grass invasions is thought to be related to early overgrazing practices in the late 1800's and early 1900's coupled with the introductions of pre-adapted species that are able to capitalize on early season moisture (Mack and Thompson 1982; Johnson and Swanson 2005). Past land use, human disturbance, allelopathy, and grazing by domestic and wild ungulates have also been identified as factors that influence non-native species invasion into grass and shrub communities in the Wallowa Mountain region. Endress et al. (2007) found that *Potentilla recta* spread was most associated with abandoned fields within bunchgrass communities. Interactions between agricultural practices and allelopathic properties of *Cardaria pubescens* have resulted in substantial spread of this species into rangelands on the western flank of the Wallowa Mountain Range (Kiemnec and McInnis 2002). Researchers have also shown that cattle and wild ungulate grazing and movement influence both the production and dispersal of non-native seeds in bunchgrass and open conifer forests in the Blue Mountains (Bartuszevige and Endress 2008; Parks et al. 2008).

Few studies have evaluated non-native species distributions and potential to spread in subalpine communities. One study specifically investigated the dominant factors that restrict distributions of eight *Asteraceae* forbs along an elevation gradient in the Wallowa Mountains. Alexander et al. (2009) found that adaptation and propagule pressure were not limiting factors to species spread in the introduced range as all observed *Asteraceae* species occupied comparable elevation ranges in their home and introduced ranges. Thus far, no attempt has been made to evaluate dominant abiotic factors related to non-native and native species distributions along an elevation gradient

in the Wallowa Mountains. Additionally, MIREN's initiative is the first effort to establish permanently located plots along an elevation gradient in the Wallowa Mountains for the purpose of monitoring non-native and native species distribution changes over time.

The Wallowa Mountains provide an ideal system for studying plant invasion dynamics. Because of steep elevation gradients in the Wallowas, most species are likely to encounter distribution limitations and multiple community types are encountered over short geographical distances. This provides an excellent opportunity to study non-native species colonization at an invasion front. The current status of high elevation communities in the Wallowa Mountains also provide researchers and land managers with the rare opportunity of getting ahead of the invasion front. Evidence of increasing invasion risk for mountain ecosystems coupled with the identification of potential subalpine and alpine invaders already established in the area suggest that plant invasion into high elevations of the Wallowa Mountains is imminent. Failure to identify dominant drivers of non-native plant invasion into high elevations, problematic species, and impacts on native communities may result in future conversion of mid- and high elevation communities to alternative states and irreversible impacts on ecosystem processes similar to conditions currently encountered in low elevation grass and shrub communities. Evaluation of non-native and native species distributions and how they relate to abiotic and biotic factors along an elevation gradient can provide insight into important factors and processes related to non-native species distribution in the Wallowa Mountains. This approach can also help managers identify problematic species and



compare the invasion status of different communities. Combining analyses of species distributions with long-term monitoring will allow researchers to identify factors related to non-native species establishment and spread and subsequent impacts on native communities. In order for vegetation sampling to accurately capture true species abundance, distribution, and change over time, sampling methodology must take into account annual and seasonal variability of species abundance and community composition.

### Objectives

This study has two specific objectives that are addressed in separate chapters: 1) evaluate the main drivers of plant invasions in the Wallowa Mountain Range of northeastern Oregon, and explore the extent patterns of native species distributions and their causes differ from non-native species along an elevation gradient (as described in Chapter 2); and 2) investigate inter- and intra-annual changes in understory vascular plant species composition along an elevation gradient in the Wallowa Mountains (as described in Chapter 3).

Chapter 2 uses complementary community analyses techniques to address the following questions: 1) which are the most common non-native species in the study area; 2) what habitats are most invaded; 3) how does native and non-native species composition relate to environmental and disturbance factors along the elevation gradient; 4) what are the most important predictors of native and non-native species richness and abundance; and 5) is there evidence for non-native species specialization at high elevations or in closed canopy forests?

In Chapter 3 we investigate the variability of vegetation composition change between two years (summer 2012 and summer 2013) and between three sampling periods (June, July, and August 2013) within the same growing season. The motivation behind this study is to inform the development of methodology to improve sampling techniques that will increase the capture of plant invasion dynamics across multiple plant communities and assure repeatable measurements over long-term monitoring so that true vegetation change can be separated from measurement error associated with natural inter- and intra-annual variability of species abundance. We address the following questions in Chapter 3: 1) how did sampling date influence changes in native and non-native species composition; 2) which species varied the most as a function of sampling date; 3) what are the most important predictors of understory vegetation change; and 4) how does temporal vegetation change relate to environmental and species trait factors along an elevation gradient?

Lastly, Chapter 4 presents our major findings, management implications, future research directions, and a synthesis that ties the results together thematically.

Chapter 2 Non-native and native plant distributions along an elevation  
gradient in the Wallowa Mountains, Oregon

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## ABSTRACT

Mountain environments are currently among the least invaded ecosystems, however, these biodiversity hotspots are increasingly under threat of exotic plant invasion. The resistance of mountain ecosystems to exotic plant invasions is likely due to a combination of low anthropogenic disturbances, low propagule supply, and extreme environmental conditions. The importance of any one of these factors is highly debated and likely ecosystem dependent. The objectives of this study were to evaluate the main drivers of plant invasions in the Wallowa Mountain Range of northeastern Oregon and explore to what extent patterns of non-native species distributions and their causes differ from native species along an elevation gradient. We conducted a complete understory vascular plant inventory in summer 2012 along three roads located in the Wallowa Mountain Range of northeastern Oregon. Transects ( $n=20$ ) were evenly stratified by elevation (60m) along each road. All vascular plants were identified to the species level and species abundance, herbivory, and environmental parameters were measured. Non-native species richness decreased linearly with increasing elevation. In contrast, native species richness displayed a unimodal distribution with maximum richness occurring at the mid-elevations. As shown by non-metric multidimensional scaling (NMS), species composition was strongly related to elevation and canopy openness. Non-natives were concentrated in low elevation sites with high canopy openness and moderate to high disturbance. Overlays of trait and environmental factors onto ordinations identified the transition into the subalpine community and over-story canopy closure exceeding approximately 60 percent as potential barriers to non-native species establishment. Non-

parametric multiplicative regression modeling (NPMR) indicated that elevation and canopy openness were the most important predictors of non-native species abundance, and elevation and disturbance related factors were the strongest predictors of non-native species richness. Unlike native species, non-native species showed no evidence for high elevation or closed canopy specialization. These data suggest that interactions between introduction pathways that favor the introduction of species pre-adapted to low elevation early successional habitats and environmental factors (increasingly harsh climatic conditions particularly at the subalpine transition zone, and disturbance that increases over-story canopy openness) are likely the dominant factors that structure non-native plant distribution patterns in the Wallowa Mountains. Additionally, the lack of high elevation and closed canopy specialization suggests that non-native species that occur at high elevations are generalist species that also occur at low elevations and are dependent on disturbance (canopy openness) for spread into higher elevations.

## INTRODUCTION

Invasions into natural areas by introduced plant species are considered one of the most significant threats to global biodiversity and ecosystem structure and function (Chapin et al. 2000; Levine et al. 2003; Scherer-Lorenzen 2007). Mountain environments are currently among the least invaded ecosystems, however, these biodiversity hotspots are increasingly under threat of exotic plant invasions. Over one thousand naturalized non-native species have been identified at high elevations worldwide, and there is increasing evidence for upward range expansions of long

established non-native species in some mountain environments (Pauchard et al. 2009; Pyšek et al. 2011). According to McDougall et al. (2011), the most damaging non-native plant invasions at high elevations have occurred relatively recently, coincident with climate change and shifting anthropogenic land use from agriculture to recreation and tourism. Evidence of increasing plant invasion into mountain environments is particularly disconcerting given the important roles of mountains as harbors of high biodiversity and protected areas, and providers of important ecosystem services such as clean water storage and delivery to low lying areas (Araujo and Williams 2001; Korner 2004; Gret-Regamey et al. 2012). It is important to understand what drives the spread of non-native plant species in mountain environments so that management and restoration actions can be developed to reduce the expansion of non-native plants in these environments.

Because most species encounter distribution limitations along steep elevation gradients, invasion ecology research in mountain environments has provided researchers with a unique opportunity to explore non-native species colonization at an invasion front (Alexander et al. 2009). Two emergent themes in mountain plant invasion research are: 1) non-native species richness tends to decrease strongly at high elevations (Alexander et al. 2011; Seipel et al. 2011; Barni et al. 2012); and 2) high elevation, non-native plant communities are typically comprised of generalist species that also occur at the lowest elevations (Becker et al. 2005; Alexander et al. 2011; Marini et al. 2013). Although declines in non-native plant species richness at high elevations appears to be a rather universal trend, low to mid-elevation responses have varied. Most studies, particularly in

temperate mountains, have reported continuous declines in non-native species richness with increasing elevation (Daehler 2005; Alexander et al. 2011; Seipel et al. 2011; Marini et al. 2013). Other research, primarily in tropical mountains, have revealed hump-shaped responses where non-native richness peaked at mid-elevations similar to the common mid-elevation peaked responses for native plant richness in mountain environments (Arevalo et al. 2005; Becker et al. 2007; Haider et al. 2010; Seipel et al. 2011).

Native and non-native plant distributions in mountains are thought to be driven by different processes. Native species distributions have been shaped by long histories of evolutionary adaptation to changing biotic and abiotic conditions resulting in high levels of habitat specialization particularly in high elevation areas where abiotic conditions are harsh and reproductive isolation is common (Hadley 1987; Becker et al. 2007; Price and Kirkpatrick 2009). Mid-elevation native species richness peaks are thought to be largely related to a “range overlap effect” where mild climatic conditions related to mesic soil conditions and moderate temperatures coupled with high microhabitat heterogeneity maximizes range overlaps of species from different life zones (Korner et al. 2004; Oommen and Shanker 2005; Becker et al. 2007; Lee et al. 2013). Non-native plant distributions are thought to be less related to evolutionary factors and be more strongly influenced by site preadaptation, dispersal limitations, disturbance, climate barriers, and introduction pathways (Haider et al. 2010; Alexander et al. 2011; Pollnac et al. 2012). Researchers have recently proposed the “directional ecological filtering hypothesis” as an explanation for patterns of high elevation generalist species and declining species richness with increasing elevation (Alexander et al. 2011). The main idea behind this

theory is that historical introduction pathways are critical for shaping non-native plant distributions in mountain ecosystems. This hypothesis assumes that non-native species are preferentially introduced into low elevation sites. Pre-adapted species are able to establish at introduced sites, and those with wide elevation ranges spread up the elevation gradient while species with narrow altitudinal ranges are sequentially filtered out along the elevation gradient resulting in generalist non-native species occupying the broadest elevation ranges in mountain environments (Alexander et al. 2011). Several recent studies have supported the directional ecological filtering hypothesis (Pollnac et al. 2012; Marini et al. 2013). Global similarity of non-native plant species distributions in mountains implies that common factors are responsible for filtering non-native species in mountain environments (Alexander et al. 2011). The dominant factors related to ecological filtering of non-natives along elevation gradients are less understood and likely to change over time (Dietz and Edwards 2006; Alexander et al. 2011; Pyšek 2011; Barni et al. 2012).

Four major factors that affect non-native plant species abundance and richness with elevation are: 1) climate (temperature and precipitation); 2) disturbance; 3) soil and topographical characteristics; and 4) propagule pressure (Barni et al. 2012). All of these factors are often highly correlated with elevation and difficult to separate from an overall elevation effect. Several studies have focused on non-native species distributions along mountain roads in attempts to control for disturbance and propagule pressure (Pauchard and Alaback 2004; Arevalo et al. 2005; Daehler 2005; Haider 2010). Road networks provide excellent conditions for evaluating non-native species distributional responses



along elevation gradients due to efficient anthropogenic seed dispersal and the presence of continuous disturbed habitat along the entire elevation gradient (Alexander et al. 2009; Mortensen et al. 2009; Haider et al. 2010). Most studies along mountain roads have led researchers to believe that decreased anthropogenic disturbance and increased climatic stress with increasing elevation interact to filter non-native species along elevation gradients (Pauchard and Alaback 2004; Arevalo et al. 2005; Kalwij et al. 2008; Mallen-Cooper and Pickering 2008; Haider et al. 2010). However, less studied factors including propagule pressure, potential changes in habitat resilience, and gradients of soil characteristics with increasing elevation may shape non-native distributions in mountains (Parks et al. 2005; Ross et al. 2008; Pauchard et al. 2009; Haider et al. 2010).

Current patterns of non-native species distributions are directly related to the pool of species available for introduction. Most reported non-native species in mountain environments are early successional, herbaceous species of Eurasian descent (Pickering and Hill 2007; Seipel et al. 2011). Some researchers suggest that the lack of late successional invasive species is less a result of invasion potential and more reflective of past human activities and priorities (Mack and Lonsdale 2001; Martin et al. 2009; Pyšek and Richardson 2007). Increased global trade and shifts in land use from agriculture to recreation and tourism are expected to increase the introduction of high elevation and closed canopy adapted species to mountain environments (Martin et al. 2009; Pauchard et al. 2009; McDougall et al. 2011). Additionally, range expansion of current invaders into undisturbed areas is expected to increase over time due climate change and localized species adaptation (Dietz and Edwards 2006; Pyšek 2011). Several studies have reported

rapid local adaptation of introduced species, and time since introduction has often proven an important predictor for species spread into high elevations and undisturbed areas (Dietz and Edwards 2006; Thuiller et al. 2006; Alexander et al. 2009; Pyšek 2011). Non-native species capable of invading undisturbed habitats, specifically high elevations and closed canopy forests may be particularly destructive to mountain systems as they are not dependent on disturbance for spread (Martin et al. 2009; McDougall et al. 2011). Early identification of these species will be critical for successful control in mountain environments.

The Blue Mountains (Wallowa Mountain Range) of Oregon has been identified as a mountain range of interest, where non-native vascular plant species distributions are thought to be shaped by directional ecological filtering processes (Alexander et al. 2011; Seipel 2011). Thus far, no attempt has been made to evaluate dominant abiotic factors related to non-native and native species distributions along an elevation gradient in the Wallowa Mountain Range. Determination of common non-native species, important correlates of non-native species distributions, and how they differ from native species patterns in this region will assist local management and conservation efforts as well inform the broader context of non-native species assembly processes in mountain environments.

The objectives of this study were to evaluate the main drivers of plant invasions in the Wallowa Mountain Range of northeastern Oregon, and explore to what extent patterns of native species distributions and their causes differ from non-native species along an elevation gradient. This study will specifically address the following questions:

1) which are the most common non-native species; 2) what habitats are most invaded; 3) how does native and non-native species composition relate to environment and disturbance along the elevation gradient; 4) what are the most important predictors of native and non-native species richness and abundance; and 5) is there evidence for non-native species specialization at high elevations or in closed canopy forests?

## METHODS

### Study site and site selection

Complete understory (vascular plant) community data were collected in summer 2012 along 97 km of gravel forest roads located in the Wallowa Mountain Range of northeastern Oregon. Three roads identified for this survey were Mt. Harris road (Union County, OR), Moss Spring road (Union County, OR), and Fish Lake road (Baker County, OR) (Figure 2.1). These roads were selected based on the following criteria: 1) open to general vehicular traffic at least part of the year; 2) covered the broadest elevation range in their respective region; and 3) captured typical geographical and environmental variation in each region. Survey sites along each road traversed lowland, montane, and subalpine vegetation zones (Federal Geographic Data Committee 1997).

The Wallowa Mountains encompass approximately 4,700 square kilometers of steep, deeply dissected topography. The majority of land area in the Wallowa Mountains is publicly owned and administered by the Wallowa Whitman National Forest. The highest elevations lie within the 150,219 hectare Eagle Cap Wilderness area (Johnson 2004). Private land ownership is concentrated in the lower elevation valleys and slopes where dominant land uses include cattle ranching, agriculture, and scattered human

settlement. Land use at the mid and high elevations includes timber harvest, recreation, and widespread livestock grazing on both public and private lands (Parks et al. 2005). Study site elevations ranged between 902 to 2,264 meters. Mean annual precipitation increased with elevation from 608 to 1,460 mm (Daly et al. 2002). Approximately 60% of the precipitation occurs between November and April and the remaining 40% occurs between May and October. The tendency for winter dominated precipitation and dry summers are intensified with decreasing elevation towards the semi-arid valleys in this system. Temperatures in the Wallowa Mountains are warmer when compared to more easterly ranges within the middle Rocky Mountain Ecoregion because of close proximity to the ocean (Anderson et al. 1998; and Parks et al. 2005). Mean summer temperatures ranged from 11.3 to 19.1 °C and mean winter temperatures ranged from 0.3 to -5.4 °C across the study area (Table 2.1).

Vegetation communities were highly variable at the low elevations with a mixture of grass and shrub habitats and open mixed conifer forest sites. Dominant vegetation in grass and shrub habitats included non-native annual and perennial grasses including *Ventenata dubia*, and *Poa compressa* with remnant populations of native bunchgrasses including *Festuca idahoensis* and *Pseudoroegneria spicata*. Open forest sites consisted of *Pinus ponderosa* and *Pseudotsuga menziesii* in the over-story with associated grasses, sedges, forbs and shrub species including *Carex geyeri* and *Symphoricarpos albus*. At the mid elevations, closed canopy mixed *Abies grandis*, *Pseudotsuga menziesii*, and *Larex occidentalis* dominated the over-story with understory species including *Calamagrostis rubescens*, *Vaccinium membranaceum*, and other shade tolerant forbs and

shrub species. High elevation sites varied due to differences in geographic and physical characteristics such as aspect, soil depth, and disturbance history. High elevation sites along Fish Lake road were subjected to a stand replacing fire in 1994, resulting in abundant standing dead wood, regenerating *Abies lasiocarpa* and *Pinus contorta* with an understory of *Anaphalis margaritacea*, *Chamerion angustifolium*, *Lupinus caudatus* and other early successional high elevation species. High elevation sites along Mt. Harris and Moss Springs roads consisted of a mixture of closed canopy *Tsuga mertensiana* dominated forests on north slopes, open forests exposed to wind-throw with an *Abies lasiocarpa* and *Picea engelmannii* over-story on gentle slopes, and south facing, shallow soil sites with a wide variety of sedges, shrubs, and forbs including *Valeriana sitchensis*, *Hieracium scoulerii*, and *Polygonum phytolaccifolium*.

### Sampling design

Belt transects (n=20) were evenly stratified by elevation (60 m) along each road. Transects were subdivided into three (50 m x 2 m) plots with one plot parallel to the road edge and the other two plots perpendicular to the road plot, together forming a “T” and extending 100 meters from the road (Figure 2.2). Plots were further subdivided into 25 frames (2 m x 2 m) for a total of 75 frames within the “T”. All vascular plants present within frames were identified to the species level and species abundance and environmental parameters were measured. Measurements recorded at transect, plot, and frame levels are indicated in Table 2.2.

Transect locations were geo-referenced using a GEO-Explorer Trimble 3 hand-held geographic positioning system. Plots were permanently located by driving bent iron

rods (0.64 cm diameter) into the ground at the center (25 m), at both ends of plot 1 (parallel to the road), and at the ends of plot 2 (50m from the road) and plot 3 (100 m from the road) (Figure 2.2).

### *Biological variables*

All vascular understory (height  $\leq 2$  m) plants within observational units (2 m x 2 m sub-plot) were identified to the species level when possible. Several species were lumped into groups based on genus where specimens lacked phenologic development or structures necessary for identification to the species level. Species abundances were estimated using canopy cover. Within each observational unit, percent canopy cover for identified species were classified into one of eight categories: zero (0%); one (1%); two (1-5%); three (5-25%); four (25-50%); five (50-75%); six (75-95%); seven (95-99%); and eight (99-100%).

Herbivory was assessed by visually estimating the percentage of vegetation removed for each species within a sampling unit (2 m x 2 m sub-plot). Intact plants within or nearby sampling units were used to provide a reference of comparison for damaged plants. Herbivory was classified into one of five categories: very minor ( $< 1\%$ ); very light (1-10%); light (10-25%); moderate (25-50%); heavy (50-75%); and severe ( $> 75\%$ ).

### *Environmental variables*

Canopy openness was measured as the mean of four measurements taken in the cardinal directions using a spherical densitometer. Canopy openness measurements were taken at ten meter increments along each transect. A clinometer was used to measure

slope for each plot. Disturbance intensity was assessed for each 50 m x 2 m plot. For analysis purposes, disturbance intensity was assigned to smaller subplots (2 m x 2 m) based on the classification of the larger plot in which they were nested. Disturbance observations were qualitatively evaluated and classified into one of three categories: one (low); two (moderate); and three (high). Low disturbance was defined as no to little visual impact to vegetation or soil from a recent disturbance (affecting < 10% of plot area). Disturbance intensity was considered moderate if moderate amounts of disturbance resulted in vegetation loss and soil exposure (affecting 10 to 40% of plot area). This includes past disturbances that may have been severe however, vegetation appeared to be recovering. A high level of disturbance was noted where there were signs of a recent disturbance that resulted in major removal event of vegetation cover and exposure of bare soil (affecting greater than 40% of plot area). Disturbances were further classified into disturbance type categories including: none (no visible sign of disturbance of any kind, vegetation was intact); human (signs that humans have recently influenced the vegetation, these included agriculture, forestry, mowing, digging, and road maintenance); animal (grazing, trampling or disturbance caused by wild or domesticated animals); and environmental (include geomorphologic processes such as flooding, rock slides, erosion, fire).

Plots were classified into habitat types including: roadside (plots parallel to roads, located within 2 meters of road adjacent vegetation boundary); grass-shrubland (dominant species include grasses, forbs, and shrubs up to five meters tall, trees were mostly absent); open forest (montane forest with an open canopy, where large gaps

existed between trees); closed forest (montane forest where canopy cover was high with few small gaps in the over-story canopy); subalpine (vegetation over-story dominated by *Abies lasiocarpa* in our study area).

Climate variables were extracted from the PRISM model (Daly et al. 2002), including: mean spring and summer precipitation, number of frost free days in the spring and summer, mean frost free period, mean frost free period start and end dates, temperature difference between the mean warmest month temperature and the mean coldest month temperature (continentality), mean annual precipitation, mean summer precipitation, extreme minimum temperature over a 30 year period, mean annual maximum temperature, mean annual minimum temperature, and Hargreaves climate moisture deficit. Topographic variables including elevation, aspect index (Roberts et al. 1989), and slope were extracted from digital elevation models (DEM) accessible through the Malheur, Umatilla, Wallowa-Whitman National Forest GIS Data Library (U.S. Department of Agriculture 2013). Elevation was acquired at 60 m resolution at the transect origin along the roadside. We then used the average slope and distance from road to estimate elevation change at a two meter resolution consistent with vegetation sampling. Soil variables including available water capacity (fraction of soil water available), available water supply (0-25 cm), percent clay-sand-silt, depth to restrictive layer, and percent organic matter were extracted from the Natural Resources Conservation Service Web Soil Survey (Soil Survey Staff 2012).



## Statistical analysis

### *Plots used in analysis*

Analyses were performed on 20 m<sup>2</sup> plots (10 m x 2 m). Plots were obtained by averaging species abundance (midpoint of cover class) for each set of five consecutive subplots (2 m x 2 m) within each transect. The primary reason for combining subplots was to reduce noise by improving local estimates of abundance, while maintaining resolution necessary to detect finer scaled gradients such as distance from roadsides. Ten plots that were logged less than one week before field sampling were excluded from the data analysis. The remaining species matrix consisted of 890 plots by 385 species prior to any transformations and data modifications.

### *Dominant non-native species*

We identified the most common non-native understory vascular plant species based on frequency of occurrence within all plots sampled. Non-native species frequency of occurrence was further evaluated based on habitat type. Because frequency of occurrence does not provide information regarding the dominance of any particular species within a specific habitat, species observed abundances were also plotted for each habitat type. Observed abundances were calculated by summing the total canopy cover for each species across all plots within a given habitat.

Indicator species analysis evaluated habitat tendencies for each of the common non-native species identified (Dufrene and Legendre 1989; McCune and Mefford 2011). Indicator species analysis generates indicator values (IV) that describe the tendencies for species to occur in specific a priori groups. Indicator values were tested for statistical

significance using a technique with 10,000 iterations. Species were considered common if they occurred in more than 5% of all plots sampled.

### *Community gradients*

Non-metric multidimensional scaling (NMS; McCune and Mefford 2011) using a Euclidean distance measure was utilized to extract gradients in community composition. We used the “slow and thorough” NMS autopilot setting and Kruskal’s strategy 2 for penalization for ties in the distance matrix. There was no expectation that species percent cover would respond in a linear fashion over the large environmental distances sampled. Therefore, NMS was selected because this ordination method is ideally suited to recover the nonlinear structure common in ecological community data (McCune and Grace 2002). A Euclidean distance measure was used to retain information related to the absolute differences in species percent cover between sample units. Species data were transformed using a generalized  $\log_{10}$  transformation, and species occurring in  $< 5\%$  of sample units were excluded from each analysis. Deletion of rare species was chosen to decrease noise and thus enhances any signal relating community composition with environmental factors (McCune and Grace 2002). A log transformation was selected to enhance the signal of less frequent species while maintaining monotonicity with the raw data. A generalized log transformation,  $(b = \log(x+x_{\min}) - \log(x_{\min}))$ , where  $x_{\min}$  is the smallest nonzero value in the matrix, was used because the smallest non-zero numbers were much less than one. No relativizations were required because comparisons of absolute abundances between sample units and between species were considered

important information for this analysis. Multivariate analyses were performed on a species matrix with final dimensions of 890 plots by 141 species.

Three dimensional ordinations were produced with a random starting configuration and a maximum of 500 iterations. Rotation by orthogonal principal axes was selected to load the greatest amount of variance represented by the ordination on axis 1 and ensure that axes 1 and 2 were independent of one another. Environmental parameters were overlaid on the ordination to investigate relationships between species composition and environmental factors. Species traits were also overlaid on the ordination to determine how particular traits were related to both environmental parameters and sample units in species space. The ordination was rotated to load axis 1 on canopy openness (strongest abiotic correlate with axis 1) to allow for an easy visual comparison between species traits and environmental parameters. Three traits of particular interest were: 1) non-native species status, where a binary value was used to indicate status (0 = native, 1 = non-native); 2) abundance potential for a particular species; and 3) observed abundance for a particular species. The abundance potential of a species was defined as the maximum percent cover observed in a plot for that particular species, and was calculated as the maximum value found within each column of the species matrix (**A**). The observed abundance for each species was defined as the total percent cover observed for a particular species in all plots, and was simply the sum total of each column in the species matrix. These values were obtained for each species from the row and column summary available in PC-ORD, and added to a matrix (**S**) that included other species traits of interest. The trait matrix used as an overlay for this

analysis was created by multiplying the species matrix by the transposed species trait matrix ( $AS'$ ).

Non-parametric multiplicative regression (NPMR) was performed using Hyperniche 2.0 (McCune and Mefford 2009) to evaluate how species distributions were related to the strongest NMS community gradients. NPMR implements an iterative kernel smoothing process that requires no assumptions regarding the relationship between response and predictor variables, automatically models interactions among predictors, and has built in over-fitting protection (McCune 2006). We used a local mean estimator, Gaussian kernel, and automatic average minimum neighborhood size option in HyperNiche 2.0 corresponding to 27 for our dataset (the average number of data points bearing on the estimate of the response at each point). Cross-validated  $R^2$  ( $xR^2$ ) was used to evaluate model fit. This differs from the conventional  $R^2$  based on the exclusion of each data point from the estimate of the response at that point. This results in a more conservative estimate of the variability captured by a given model, more closely approximating the true prediction error (McCune 2011).

Two-dimensional NPMR response curves were generated using HyperNiche 2.0 to evaluate the distributional responses of target non-native and native species to the strongest NMS community gradients. An initial screening indicated that most species were non-linearly related to both NMS axes indicating complex interactions across community gradients. In order to estimate species optima along each axis, we needed to first control for the interaction with the other axis. To model species responses for axis 1, we sliced three dimensional responses for each species according to axis 2 scores. For a

given species, this resulted in a two-dimensional plot with axis 1 scores along the x-axis, species abundance along the y-axis, and multiple response curves corresponding to differing axis 2 scores. The optimum (highest abundance) response curve along axis 1 was selected as the distribution of a particular species along that axis as it represented an estimated distribution of that species along axis 1 when optimal conditions along axis 2 were met. This procedure was repeated for optima on axis 2, thus fitting response curves for each species for each axis while controlling for the other axis (Jovan and McCune 2005).

### *Species richness patterns*

We used NPMR to explore relationships between native and non-native species richness and elevation and to identify important environmental and physical habitat predictors of non-native and native species richness and abundance. Models were generated in a stepwise procedure. We evaluated the best models for each response by balancing the number of predictors and each predictor's contribution to the overall cross-validated  $R^2$  ( $xR^2$ ) value. A predictor was added to the model if it increased the  $xR^2$  by at least 0.03. Sensitivity was calculated to evaluate the importance of each predictor in a model, based on its influence on species richness and proportional abundance. Sensitivity is the ratio of the relative mean difference in response to the relative mean difference of the predictor, in both cases relative to the range of the variable. For example, if a predictor has a sensitivity of 1.0, we would expect that a 5% change in the predictor would elicit on average a 5% change in the response (McCune 2006).

### *Non-native high elevation and understory specialization*

To investigate the potential of specialized high elevation and closed canopy invaders, scatterplots of minimum and maximum elevation and canopy openness occurrences were generated for all non-native and native species. NPMR was used to estimate species elevation and canopy openness ranges. Maximum and minimum elevation occurrences were calculated using two-dimensional NPMR response curves for each of the 141 species represented in the ordination. Each species range was determined as the 95% central range of that species' elevation distribution defined as the range between the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles. We excluded the extreme 5% of each species' distribution because we considered these as atypical representations of a species range. Canopy openness ranges were calculated in the same fashion. Species ranges for both elevation and canopy openness were calculated twice. The first range was calculated from estimated species responses to the "true" measured elevation (extracted from DEM), and canopy openness (field measurements). The second range for elevation and canopy openness was calculated from the estimated species response to ordination axis 2 (strongly correlated to elevation,  $r = 0.629$ ), and axis 1 (strongly correlated to canopy openness,  $r = 0.596$ ) respectively. Because NMS ordination procedures recover the structure of plots in species space based on species composition information, the order of plots along ordination axes are likely better representations of the elevation gradient and canopy openness as experienced by species than the actual measured values. Species axis ranges along axis 2 can be thought of as the "effective elevation" range for a species. Species responses to actual elevation may be misleading, since south facing slopes are

occupied by lower elevation species and higher elevation communities extend lower on north facing slopes. Likewise, overstory canopy openness measurements fail to capture topographic shading information and may misrepresent the effective shading at particular plots. Species scores along axis 1 may better represent species responses to the “effective canopy openness” gradient when compared to actual overstory canopy openness measurements. Scatterplots of species elevation and canopy openness range patterns and variability were examined for evidence of niche specialization.

## RESULTS

### Dominant non-native species

A total of 385 understory vascular plant species were recorded within 890 plots sampled in the Wallowa Mountains. Approximately 19% (72) of the total understory species pool consisted of non-natives. Of the 72 non-native species observed, only 24 (34%) of these species occurred in at least 5% of the plots, and were thus considered common species in the area sampled (Table 2.3). The percentage (38%) of the native species pool that occurred in at least 5% of the plots was similar to non-natives with 118 out of the total 314 represented (Table 2.3). Non-natives were found most frequently in grassland habitats, where they occurred in 100 percent of sites sampled, followed by roadside plots (85.3%), open montane forests (66.7%), closed montane forests (34.1%), and subalpine habitats (12%) (Table 2.4). Eight of the common non-natives identified in the Wallowa Mountain system are listed as invasive species by the U.S. Forest Service in the region (region six), including *Bromus tectorum*, *Cynoglossum officinale*, *Dactylis glomerata*, *Lactuca serriola*, *Plantago lanceolata*, *Cirsium arvense*, *Verbascum Thapsus*

and *Ventenata dubia* (U. S. Department of Agriculture 2010b; Table 2.4). *Cynoglossum officinale* was the most common invasive species, occurring in 22% of all plots. Only *Taraxacum officinale* (27%) and *Poa compressa* (23%) were more frequently observed non-natives in this study. *Cynoglossum officinale* was also the most common non-native found in closed canopy forests, where this species was present in 29 out of 185 (16%) of the closed forest sites sampled. Subalpine habitats were the least invaded by non-natives with 12 out of 100 (12%) sites being occupied. *Taraxacum officinale* with seven occurrences and *Poa compressa* with three occurrences were the most common non-natives observed in subalpine habitats (Table 2.4).

### Invaded habitats

Grass and shrubland habitats showed the highest potential to harbor dominant non-native species (Figure 2.3). Six out of the ten most abundant species observed in grass and shrubland plots were non-native species. *Ventenata dubia* (VEDU) and *Taeniatherum caput-medusae* (TACAC) had the highest rank abundance for all species in grass and shrubland habitats (Figure 2.3). Native species were dominant in closed canopy forests and subalpine habitats. Non-native abundance was scant in closed canopy forests and subalpine habitats where *Thinopyrum intermedium* (THIN6) with a rank abundance of 81, and *Taraxacum officinale* (TAOF) with a rank abundance of 82 were the most abundant species found in closed canopy forested and subalpine habitats respectively (Figure 2.2). *Ventenata dubia*, *Thinopyrum intermedium*, and *Trifolium repens* were among the most abundant non-native species in several habitat types (Figure 2.3).



Indicator species analysis revealed that all but one common non-native species have tendencies for roadside and grass/shrub dominated habitats (Table 2.4). Only *Arrhenatherum elatius*, a perennial grass widely used for post disturbance seeding showed a slight ( $IV = 4.5$ ,  $p=0.046$ ) tendency towards open forest sites (Table 2.4).

### Community gradients

The three dimensional NMS ordination of sample units in species space represented 74.7% of the variation in the distance matrix with 31.1%, 28.9%, and 14.7% represented by axis 1, 2, and 3 respectively (final stress = 17.8, final instability  $< 10^{-5}$ , iterations = 115) (Figure 2.4). The randomization test indicated that the three-dimensional NMS ordination was extracting stronger axes than would be expected by chance ( $p = 0.004$ ). The strongest correlations with respect to environmental variables were found along axis 2. Elevation (0.629), and mean annual precipitation (0.560) exhibited strong positive correlations with axis 2 (Table 2.5). Mean annual minimum temperature (-0.624), mean annual maximum temperature (-0.619), and number of frost free days in the summer (-0.601) showed strong negative correlations with axis 2 (Table 2.5). Canopy openness (-0.596), soil available water capacity (0.457), available water supply (0-25cm) (0.447), and percent clay (-0.445) were the most highly correlated environmental variables with axis 1. Most environmental variables were weakly to moderately correlated with axis 3 (Table 2.5). Slope (0.404) was the primary environmental correlate with axis 3. Because axis 3 explained little variation in the distance matrix and showed primarily weak correlations with species and environmental variables, only axes 1 and 2 will be discussed further. Elevation was the most highly

correlated variable with axis 2 (0.629) and will be referred to as the primary gradient along axis 2 with an understanding that changes in elevation are implicit with variations in precipitation and temperature. Two gradients are evident in Figure 2.4: 1) along axis 1, there is a canopy openness gradient where sunny plots are located low on axis 1, and plots exposed to deep shade are located high on axis 1; and 2) there is a strong elevation gradient from low elevation plots low on axis 2 to high elevation plots high on axis 2. Consistent with field observations, sample units at low elevations show a wide variation in canopy openness and disturbance, plots at mid elevations had primarily low disturbance levels and moderate to high shading (absence of plots low on axis 1 and centered along axis 2), and the high elevation sites experienced variable disturbance and shading due to localized wind throw events along Mt. Harris and Moss Springs roads, and a high elevation fire approximately 18 years prior to sampling along Fish Lake road. According to nonparametric multiplicative regression (NPMR), most species were weakly to moderately associated with the first two ordination axes (Table 2.6). Cross validated R-squared values ranged from 0.03 (*Cryptantha affinis*) to 0.779 (*Vaccinium membranaceum*). Species abundance responses to ordination axes were variable and nonlinear (Figures 2.5 and 2.6). Common non-native species had abundance maxima at low scores along axis 1. This is consistent with linear species correlations where all 24 non-native species represented in the ordination had negative correlations with axis 1. *Dactylis glomerata*, a fairly shade tolerant, introduced grass species had a maximum abundance at higher axis 1 scores when compared to other dominant non-native species (Figure 2.5B). In contrast, native species showed variable responses to axis 1. For

example, early successional, shade intolerant species like *Epilobium brachycarpum* and *Madia glomerata* had maxima at low scores along axis 1 and were rare to nonexistent high along axis 1, similar to most observed non-native species distributions (Figure 2.5A). Consistent with field observations, *Leptosiphon harknessii* and *Polygonum douglasii* were most abundant at low to mid values along axis 1 corresponding to plots found at transitions between open and forested areas (Figure 2.5A). Shade tolerant species such as *Thalictrum occidentale* and *Melica subulata* were most abundant at high values along axis 1 (Figure 2.5A). Species correlations with NMS axis 2 indicate that most (21 out of 24) non-natives were negatively correlated with axis 2 indicating a propensity for non-natives at low values along axis 2. NPMR results show that optimum non-native species distributional responses along axis 2 after accounting for axis 1 were actually quite variable with maximum abundances ranging from low to moderate scores along axis 2 (Figure 2.6B). *Trifolium repens* had maximum abundance low along axis 2 (Figure 2.6B). Perennial and annual grasses (*Poa compressa*, *Thinopyrum intermedium*, *Bromus arvensis*, *Bromus tectorum*, and *Ventenata dubia*) showed bimodal responses with well-defined peaks in abundance mid-way along axis 2 (Figure 2.6B). *Poa pratensis* and *Cynoglossum officinale* had broad response curves and were only excluded from the highest ranges along axis 2 (Figure 2.6B). *Taraxacum officinale* and *Rumex acetosella* were the only species that did not show significant declines in abundance at high values along axis 2. Native species also varied widely in their responses along axis 2 (Figure 2.6A). A pattern unique to native species was depicted by high elevation

species like *Epilobium minutum* and *Anaphalis margaritacea* where estimated maxima occurred at high axis 2 values (Figure 2.6A).

Non-native species status was positively correlated (0.540) with axis 1 and negatively correlated (-0.451) with axis 2, indicating that non-native species status was associated with low elevation sites with open canopy and moderate to high disturbance (Figure 2.7A). Species abundance and abundance potential were positively associated with each other and negatively correlated with axis 1 (-0.700 and -0.452 respectively) indicating that species with high abundance potential were associated with closed canopies and low disturbance (Figure 2.7A). The rotated ordination plot shows a clear segregation of plots containing a high abundance of non-natives to the lower right quadrant, and along the boundary separating the lower and upper right quadrants (Figure 2.7A). There appears to be abrupt shifts in non-native abundance near the center of the ordination, indicating potential barriers to non-native species establishment in sites that have negative axis 1 scores or positive axis 2 scores. The abrupt decrease of non-native richness and abundance at positive values along axis 2 appears to corresponds to both a paucity of open canopy plots just above the origin along axis 2 (Figure 2.7A), and to a transition into subalpine habitat and the lower range of key subalpine indicator species (Figures 2.7B & D). Two dimensional non-linear response curves reveal that non-native species richness and abundance declines coincided with the subalpine habitat transition along each of the three roads sampled (Figure 2.8). Non-native richness and abundance decreased with canopy openness along axis 1. Negative axis 1 values are associated with canopy openness values less than 36% (Figure 2.7C).

### Species abundance and richness

Non-native species richness decreased continuously with increasing elevation. Native species richness displayed a unimodal distribution with maximum richness observed at mid-elevations (Figure 2.9). Elevation, percent slope, and disturbance intensity were the strongest predictors of non-native species richness, explaining 75% of the variation in non-native species richness, based on the best NPMR model. Elevation was the most important predictor (sensitivity = 0.588) followed by slope (0.0819), and disturbance (0.010). Non-native species richness was inversely related to slope, and increased with disturbance intensity (Figure 2.10A). Non-native richness declined more abruptly with increasing elevation at lower disturbance intensities (Figure 2.10B). Extreme minimum temperature over a 30 year period (EMT), aspect, and available soil water capacity were the most important predictors of native species richness. These three factors explained 45% of the variation in native species richness across the 890 plots sampled. Sensitivity analysis indicated that EMT (sensitivity = 0.4338) was the most important predictor followed by aspect (0.1390), and available water capacity (0.0462). Sliced response curves reveal complex interactions among predictors with respect to native species richness (Figure 2.10E and F). Canopy openness, elevation, and slope were the best predictors of non-native species abundance, and explained 71% of the variation in non-native abundance. Elevation was the most important predictor (sensitivity = 0.265) followed by canopy openness (0.220) and slope (0.075). Non-native abundance was inversely related to slope, and increased with canopy openness over most of the

elevation range (Figure 2.10C and D). Non-native abundance was highest for moderate canopy openness (50-75%) at the highest elevations (Figure 2.10D).

### Non-native high elevation and closed canopy specialization

There was an approximately linear relationship between non-native species elevation range and upper elevation occurrences (Figure 2.11B). This pattern is similarly strong when species ranges are predicted using “true” elevation or NMS axis 2 scores (Figures 2.10B and D). The high variability in minimum elevation range for native species indicates specialization at different elevation ranges (Figure 2.11A and C). Native elevation range predictions based on “true” elevation were more variable for lower elevation species when compared to estimates derived from ordination scores (Figure 2.11A and C).

All non-native species had maximum canopy openness occurrences over 85%. Similar to native species distributions, non-native species minimum canopy openness values grade from approximately 30 to around 0 % (Figure 2.11E to H). Native species occurred at a broader range of maximum canopy openness than non-native species. Estimates derived from “true” canopy openness resulted in 12 out of 118 (10%) of natives having maximum canopy openness occurrences below 85% (Figure 2.11E). Native species canopy openness range variability increased dramatically when estimated from axis 1 scores, suggesting that shade specialization by native species was common (Figure 2.11G).

## DISCUSSION

Non-native species were widely distributed across the study area. Approximately one third of all non-natives observed were common and collectively occurred in greater than 60% of the plots sampled. Previous research suggests that mountain invaders are typically ruderal species that rely on disturbance for establishment and persistence in mountain environments (Petryna et al. 2002; Pickering and Hill 2007; Kalwij et al. 2008; McDougall et al. 2011). We detected a similar pattern, as most non-natives showed tendencies for roadside and heavily disturbed grass and shrub dominated sites. Grass and shrub dominated habitats had the highest occurrence of non-native species and were the sites most likely to harbor dominant introduced annual grasses (Table 2.4 and Figure 2.3). Consistent with previous plant invasion studies, closed canopy forests and subalpine sites were the least invaded sites (Parendes and Jones 2000; Godfree et al. 2004; Chytry et al. 2008; Martin et al. 2009; Pauchard et al. 2009).

Introduced annual grasses including *Ventenata dubia* (ventenata) and *Taenatherum caput-medusae* (medusahead) had the highest potential to dominate sites when compared to other non-native species (Figure 2.3). Annual grass invasions were concentrated in low elevation grass and shrubland sites occurring primarily within fenced cattle pastures. These sites were located along benches (gentle slopes < 20%) above the Grande Ronde River Valley. Historically, these “benchlands” would have likely been dominated by native perennial bunch grasses including *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Poa secunda* (Johnson 1994). Our observations indicate that native perennial bunchgrasses are a minor component of these communities compared to non-native

species, accounting for less than 7% of the understory canopy cover in plots sampled. Pacific Northwest bunchgrass communities have proven particularly susceptible to annual grass invasions in the Blue Mountain Region (Mack and Thompson 1982; Johnson and Swanson 2005; Parks et al 2005). Researchers attribute the apparent high invasibility of these systems to early overgrazing practices coupled with a high influx of pre-adapted non-native winter annual grasses (Mack 1981; Mack and Thompson 1982; Johnson 1994; Wisdom and Chambers 2009). Previous observations revealed that the most heavily disturbed “benchlands” in the Blue Mountain region were initially colonized by winter annual *Bromus* species that were able to out-compete stressed bunchgrasses and their offspring for the abundant winter and early spring water available in the clayey upper soil layers (Lichthardt and Moseley 1997; Johnson and Swanson 2005). Our findings that *ventenata* and *medusahead* were the most abundant species in grassland areas support Johnson and Swanson’s (2005) suspicions that these recently introduced species may have the potential to outcompete *Bromus* annuals on some sites. *Medusahead* is thought to be somewhat limited in distribution to sites with the presence of heavy clay soil in our region (Johnson and Swanson 2005). Our observations support this, as the range of *medusahead* was constrained to grass and shrub habitat along Mt. Harris road where high clay content is characteristic of the shallow soil layers (Soil Survey Staff 2012). According to our data, *ventenata* is a dominant species in disturbed grass/shrubland, and roadside habitats, and is one of the most abundant non-native species in open forest habitats (Figure 2.3). Due to its relatively recent introduction (~1956) into the Pacific Northwest, little is known about the potential spread and



associated ecological consequences of *ventenata* in the region (Northam and Callihan 1994; James 2008). Regional observations, suggest that *ventenata* is currently expanding its range at an alarming rate along road networks and into undisturbed areas (Noon et al. 2013).

It is important to note that nine of the most common non-natives observed, including all perennial grass species (*Poa compressa*, *Trifolium repens*, *Poa pratensis*, *Dactylis glomerata*, *Thinopyrum intermedium*, *Poa bulbosa*, *Trifolium pratense*, *Bromus inermis*, and *Arrhenatherum elatius*), were intentionally introduced for soil stabilization following disturbances such as road construction, fire, timber harvest, and heavy grazing. Therefore, it is unsurprising that these species are primarily found in disturbed sites. Widespread distributions of Eurasian perennial grasses and legumes is a familiar pattern in mountain non-native flora around the world, and likely reflective of past land use priorities related to agriculture and pastoralism coupled with low elevation species introductory pathways (Daehler 2005; Pickering and Hill 2007; McDougall et al. 2011). The U.S. Forest Service has abandoned the practice of seeding non-native species in the Wallowa Whitman National Forest with hopes that native vegetation will out-compete the introduced non-natives over time (Aric Johnson, personal communication, July 17, 2013). However, private land owners at the low and mid elevations continue to seed these species for post disturbance soil stabilization and livestock forage (Brooks et al. 2011).

As shown by NMS, species composition was strongly related to elevation and canopy openness gradients (Figure 2.4). Consistent with other studies, non-native species

abundance increased with decreasing elevation and increasing canopy openness and disturbance (Parendes and Jones 2000; Haider et al. 2010; Barni et al. 2012). Although canopy openness and disturbance were strongly related to non-native species abundance at low to mid-elevation sites, elevation was the strongest correlate of non-native species distributions along an elevation gradient in the Wallowa Mountains. Unlike non-native species patterns, native species abundance was associated with increasing elevation and decreased canopy openness. Consistent with field observations, the highest observed dominance and potential dominance by a single understory species were both associated with closed canopy, mid-elevation sites with a high abundance of native species. This ordination result likely reflects the dominant understory stands of *Vaccinium membranaceum* (huckleberry) present at the mid-elevation sites.

Despite the presence of high canopy openness and disturbance at high elevation sites due to a recent stand replacing fire along Fish Lake road and wind-throw along Moss Springs and Mt. Harris roads, non-native species were primarily concentrated at the low to mid-elevation sites with high canopy openness and moderate to high disturbance levels. NMS ordination results indicated potential barriers to non-native species spread along both the elevation and canopy openness gradients (Figures 2.7A through D). An abrupt decline in non-native species abundance and richness was observed midway along the elevation gradient and corresponded to a paucity of open canopy habitat as well as a transition boundary into the subalpine community. These results suggest that several mechanisms could be responsible for reduced non-native plant invasions in the subalpine zone of the Wallowa Mountains.

Ordination results suggest that reductions in propagule pressure at subalpine sites may be responsible for reduced non-native abundance in subalpine habitats. While propagule pressure was not directly measured, the disconnect of suitable (disturbed, open canopy) habitat for non-native species at the mid elevations may act as a propagule buffer for the subalpine zone through reductions of non-native abundance and richness in the montane forest zone. Researchers have generally considered there to be little decrease in propagule pressure along mountain road networks due to well documented accounts of efficient seed dispersal along road networks (Gelbard and Belnap 2003; Alexander et al. 2009; Haider et al. 2010). The role of roads as efficient corridors of seed dispersal of early successional non-native species is largely related to the presence of a suitable habitat corridor along the entire length of the road network (Gelbard and Belnap 2003; Mortenson et al. 2009). Our ordination results suggest that the upper montane forest and lower subalpine transition zone may not provide suitable habitat for non-natives in our study area due to closed canopy forests and increased topographical shading of roadside habitat. We suspect that a decline of non-native species abundance in this zone will decrease propagule transport to higher elevations.

Although the reduction of propagule pressure at high elevations is likely in our study area, we believe that factors associated with the transition into subalpine communities are more important for limiting non-natives at high elevations in the Wallowa Mountains. This hypothesis is based on the comparable decline of non-native species at the same community transition (subalpine) along all three roads. If dispersal limitations were truly the barrier to high elevation spread of non-native species, we would

expect non-native declines to manifest within different vegetation communities along different roads because of variations in geographical distances between vegetation zones, traffic volumes, and disturbance histories.

The occurrence of common non-native species only in subalpine plots that were highly disturbed by a stand replacing fire along Fish Lake road indicates that disturbed subalpine sites are more prone to establishment. However, the low richness and abundance of species in these burned sites, despite almost two decades of exposed bare ground, suggest that subalpine sites in the Wallowa Mountains are relatively resistant to invasions by low-land adapted species. Climate variables associated with high elevation subalpine and alpine mountain zones have been considered a significant barrier to non-native spread into mountain systems (Ross et al. 2008; Haider et al. 2010; Barni et al. 2012). Cold temperatures, decreased growing season length, and increased precipitation influence transitions from montane to subalpine plant communities in the Wallowa Mountains (Johnson 2004). We suspect that the same harsh conditions that trigger native species transitions at the lower subalpine zone may also act to filter out lowland adapted non-native species.

Consistent with many studies in temperate mountain ecosystems, non-native species richness decreased continuously with increasing elevation and native species richness peaked at the mid-elevations sites (Korner et al. 2004; Seipel et al. 2011). Native species richness was associated with extreme minimum temperature (over a 30 year period), available soil water capacity, and aspect and showed common high elevation and closed canopy specialization. In contrast, NMS and NPMR revealed that

elevation, disturbance, and canopy openness, were the most important factors structuring non-native species distributions along an elevation gradient in the Wallowa Mountains. Additionally, non-native species elevation and canopy openness ranges showed no evidence of high elevation or closed canopy specialization for non-native species in this system. Our results indicate that non-native species abundance and richness decreased with increasing elevation and increasing canopy openness and disturbance, and that high elevation non-native species communities consisted of generalist species that also occur at the low elevation sites. These findings support the directional ecological filtering hypothesis.

### Management Implications

The results of our study demonstrated that common non-native species in the Wallowa Mountain Range of northeastern Oregon are primarily lowland adapted species that are dependent on disturbance and open forest canopies for persistence and spread. Many non-native species in our study can thrive at mid-elevations with increased canopy openness and disturbance, however, subalpine habitats proved largely uninvaded, even with high disturbance intensity. Land management activities such as timber harvest, road construction, and prescribed fire may promote increased invasion potential at low to mid elevation sites due to increased canopy openness, release of resources, and exposure of bare ground. Increased canopy openness and disturbance at mid-elevation sites will also provide more connectivity of suitable habitat for non-native species spread between the low and high elevations. Invasion potential will likely be highest at the lowest elevation sites that are adjacent to heavily invaded grass-shrubland and roadside habitats. In

contrast, our data suggest that subalpine communities may be more resistant to high disturbance events and will require less effort for control of non-native species establishment and spread.

Grass and shrubland communities were the most invaded habitats in our study area. The apparent high invasibility of these sites are largely due to past overgrazing, the persistence of early successional conditions, and introductions of pre-adapted ruderal species at low elevation sites. The dominant land use in these communities is cattle grazing. Pacific Northwest bunch grasses have a short evolutionary history with large ungulate grazers and are extremely sensitive to heavy grazing pressure (Mack and Thompson 1982; Milchunas et al. 1988; Belsky and Blumenthal 1997). Land managers consider light to moderate grazing of Pacific Northwest bunchgrasses to be a sustainable practice for maintaining healthy bunch grass communities (Mack 1981; Milchunas et al. 1988; Johnson and Swanson 2005; Davies et al. 2014). Timing of grazing is also extremely important in already invaded areas. Researchers suggest that early grazing coinciding with the “green up” of non-native annual grasses and prior to native bunchgrass growth can shift the competitive advantage to desired native species because livestock will preferentially select annual grasses at this time when nutritional content and sensitivity to grazing is greatest for species like cheatgrass (*Bromus tectorum*) and medusahead. Mid to late season grazing in invaded areas can have the opposite effect and result in increased dominance of annual grasses because once the desired perennial native grasses initiate growth, they become preferred to livestock and are extremely sensitive to grazing at this point (Smith et al. 2012). However, the overall effect of

grazing on non-native species spread in western rangelands is largely unexplored (Vavra et al. 2007). Grazing by large ungulates can influence non-native plant invasion dynamics through alteration of plant species composition and competitive interactions, establishment of seed beds, soil disturbance, alterations to nutrient dynamics, and transportation of seeds to un-infested sites (Vavra et al. 2007). Research regarding the effects of grazing in Pacific Northwest bunchgrass and forested ecosystems is needed to inform non-native species management in the region.

Past research suggests that disturbance is often necessary for non-native establishment in native bunchgrass communities; however, once non-native annual grass species are dominant, continued disturbance may not necessarily be required for their persistence. Managers suspect that many annual grass invaded bunchgrass communities have crossed thresholds into alternative stable states where reversal back to desired native communities have proven difficult (Laycock 1991; Johnson and Swanson 2005). At this point, restoration often requires much money and labor. It is important to note that non-native species control of low elevation grass and shrub communities in the Wallowa Mountains will require ongoing and active management, particularly with persistent disturbed habitat, efficient seed dispersal along roadsides, and high disturbance potential from livestock and human activities.

Little is known about the long term effects of seeded perennial grasses in native mountain ecosystems or their ability to spread into undisturbed sites. Previous work in mountain ecosystems indicate that post disturbance seeded grasses and legumes are generally relegated to early successional sites where they can suppress re-colonization by

native species and persist on the landscape for long periods of time (Keeley 2006; Pickering and Hill 2007; Beyers 2009; McDougall 2011). Our data suggest that “human assisted” species, while common, show little evidence of spread into undisturbed sites, particularly closed canopy forests and subalpine environments. The ability of these introduced species to persist in disturbed sites and their relative abundance in roadside, grass-shrubland, and open forest habitats in our study area suggest that threat of spread into undisturbed habitats will be higher in early successional, low elevation environments. Keeley (2003) found that post disturbance seeding of non-native species has little effect on short term erosion control and may actually result in decreased erosion control over the long term because of the loss of functional diversity. Post disturbance seeding efforts that use native species mixes will help to reduce the spread and persistence of non-native species in the Wallowa Mountains and may provide improved long term erosion control.

With the exception of grass and shrub dominated habitats, current non-native plant distributions indicate that non-native species will likely decrease in abundance and richness with increased succession in natural areas. We feel that this can lead to a false sense of complacency regarding the potential spread of non-native species into mid and high elevation forests in the Wallowa Mountains. Species invasions occur in stages and causal processes are documented to change through time (Dietz and Edwards 2006). Colonization and spread along disturbance corridors are common for early stages of introduction. The initial rapid rate of spread is usually followed by a period of slow population growth and spread called the “lag phase”. The lag phase can last for many



decades and is site and species specific (Mack et al. 2000; Crooks 2005; Dietz and Edwards 2006). Some species are able to transition into a second phase of spread into lower resource available natural areas. This last phase requires species to expand their ecological range and has been observed in several invasion studies (Dietz and Edwards 2006). There is also evidence that multiple introductions of non-native species into new geographic areas can result in rapid evolutionary adaptation and range expansion that is not expressed in the species home range (Edwards and Dietz 2006; Alexander 2009; Pyšek et al. 2011). Therefore, it is probable that longer retention times of non-natives in this system could lead to increased invasion of undisturbed and different habitat types over time. Recent research suggests that species with wide ecological ranges, like those common in mountains, may have a higher capacity for range expansion, resulting in uncertainties regarding the potential for future species spread (Owens et al. 1999; Cardillo et al. 2003).

The fact that non-native species are filtering in from the lowlands, and that high elevation and closed canopy specialists are not yet common in the Wallowa Mountains, provides land managers with a unique opportunity to develop management plans to buffer mid and high elevation sites before these ecosystems are compromised by damaging plant invasions. Effective management activities should focus on the reduction of non-native species richness and abundance at the source (low-lying areas), disconnection of dispersal corridors along elevation gradients (road networks, disturbance, high canopy openness), and the minimization of direct introduction of species into mid and high elevation sites.

## ACKNOWLEDGEMENTS

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## FIGURES

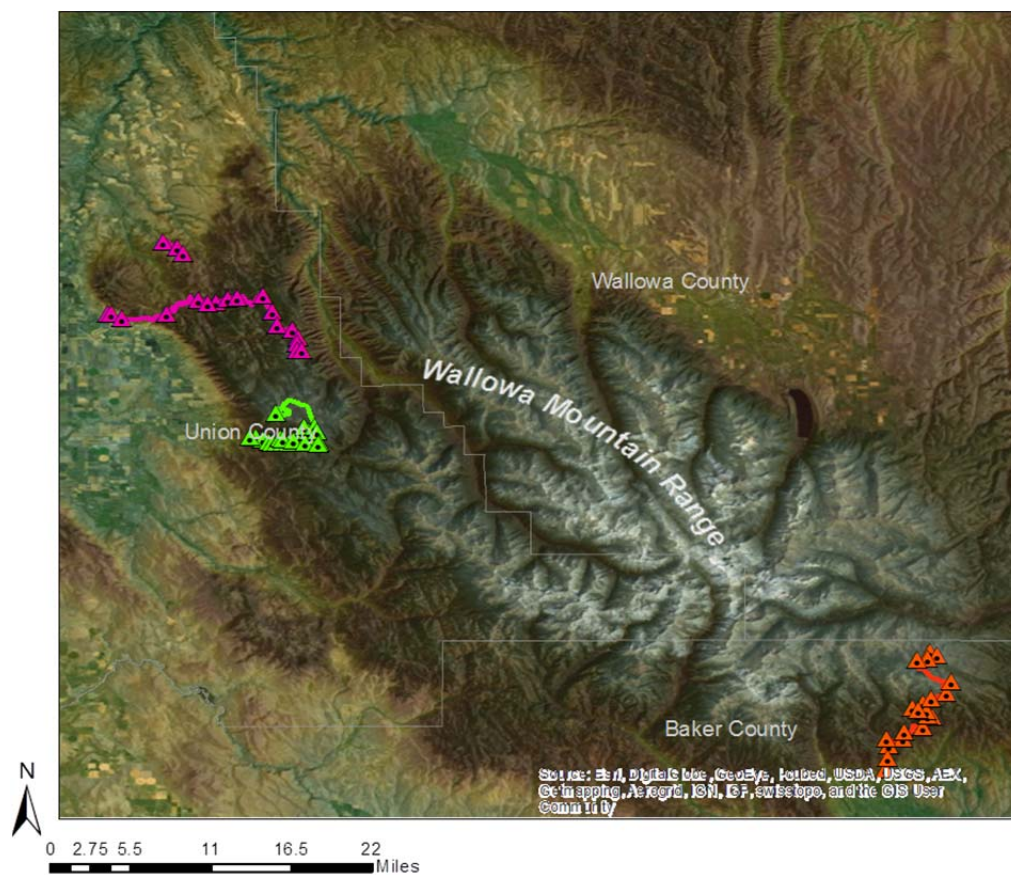


Figure 2.1: Wallowa Mountain study area. Colored lines represent roads. Orange, Fish Lake road; pink, Mt. Harris road; green, Moss Springs road. Symbols indicate locations of transects.

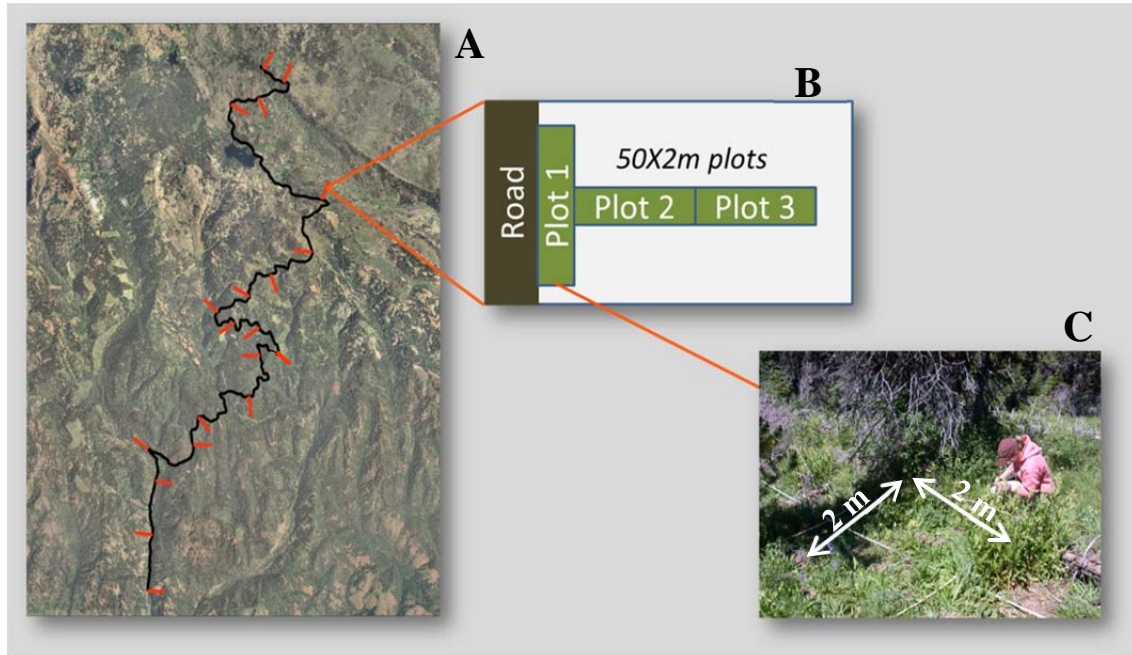


Figure 2.2: Depiction of A) Road transects subdivided into; B) three (50m x 2m) plots with one plot parallel to the road edge and the other two plots perpendicular to the road plot, together forming a “T” and extending 100m from the road. C) Plots were further subdivided into 25 subplots (2m x 2m) for a total of 75 frames within the “T”.

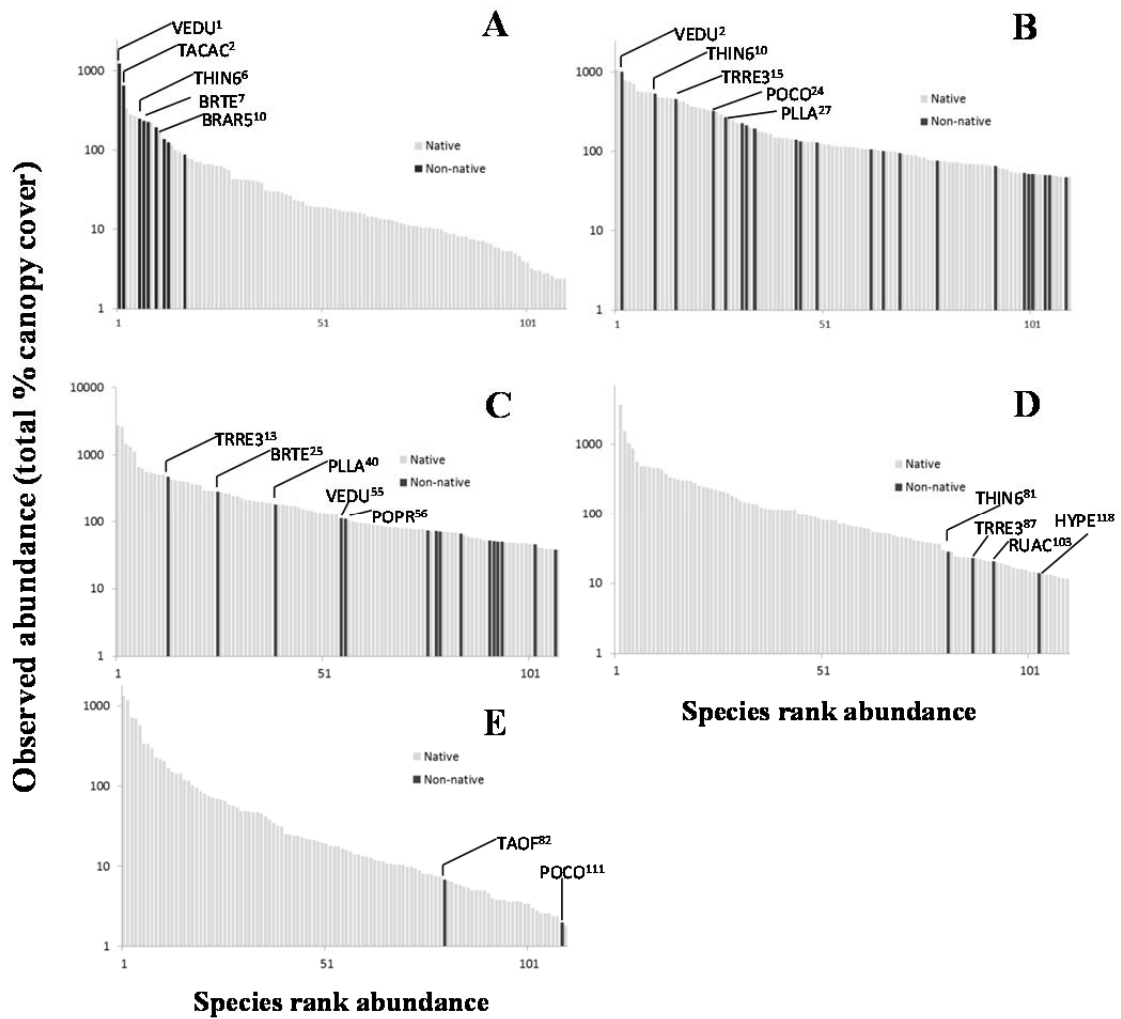


Figure 2.3: Observed species abundance by habitat type; calculated as the sum total canopy cover for a specific species in all plots within a particular habitat: A) grass-shrubland, B) roadsides, C) open canopy, montane forest, D) closed canopy, montane forest, and E) subalpine. Species number along the x-axis was cutoff at 111 species to allow for depiction of at least two non-native species in each habitat. BRAR<sup>5</sup>, *Bromus arvensis*; BRTE, *Bromus tectorum*; HYPE, *Hypericum perforatum*; PLLA, *Plantago lanceolata*; POCO, *Poa compressa*; POPR, *Poa pratensis*; RUAC, *Rumex acetosella*; TACAC, *Taeniatherum caput-medusae*; TAOF, *Taraxacum officinale*; THIN<sup>6</sup>, *Thinopyrum intermedium*; TRRE<sup>3</sup>, *Trifolium repens*; VEDU, *Ventenata dubia*. Superscript indicates rank abundance within habitat type.

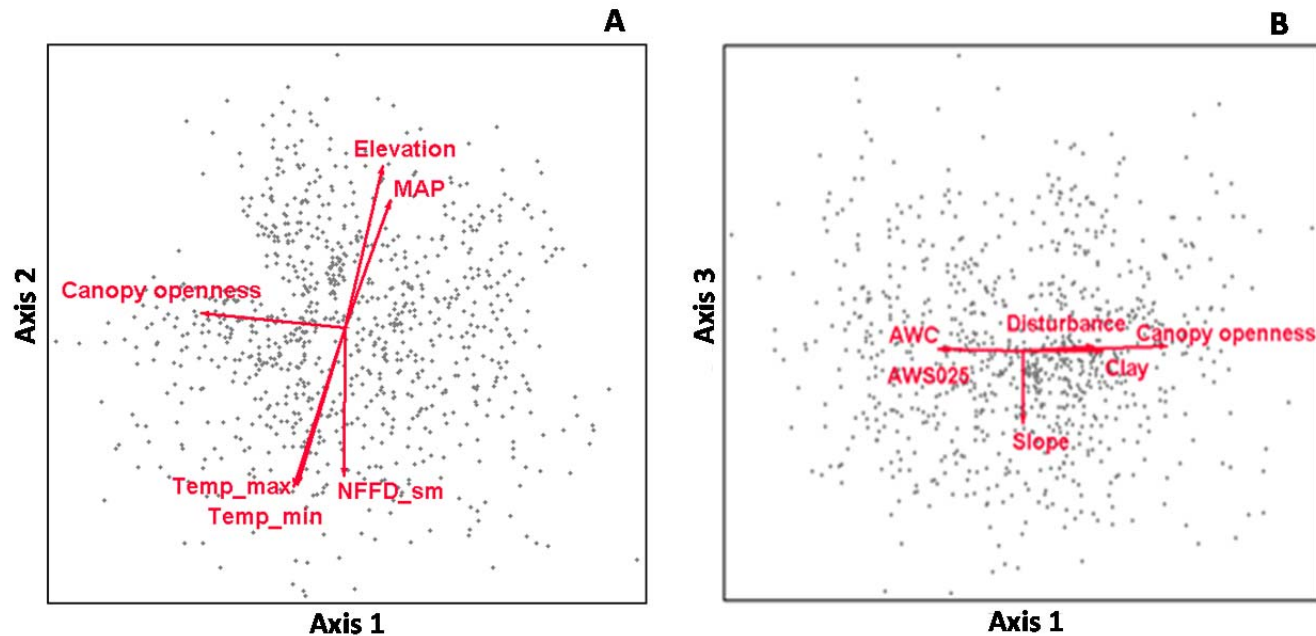


Figure 2.4: Three-dimensional NMS ordination of sample units in species space (rotated by orthogonal principal axes). Sample units that are closer together are more similar in species composition than those farther apart. Vectors indicate direction and magnitude (length) of correlation between sample units in species space and environmental parameters. The total combined distance matrix variance represented by three axes is 74.7%, with 31.1%, 28.9% and 14.7% being represented on axis 1, 2, and 3 respectively. A) Relationships between environmental variables and axes 1 and 2. B) Relationships between environmental variables and axes 1 and 3. Abbreviations for environmental variables include: MAP (mean annual precipitation), Temp\_max (mean annual maximum temperature), Temp\_min (mean annual minimum temperature), NFFD\_sm (mean number of frost free days during the summer), AWC (available soil water capacity), and AWS025 (available water supply 0-25cm)

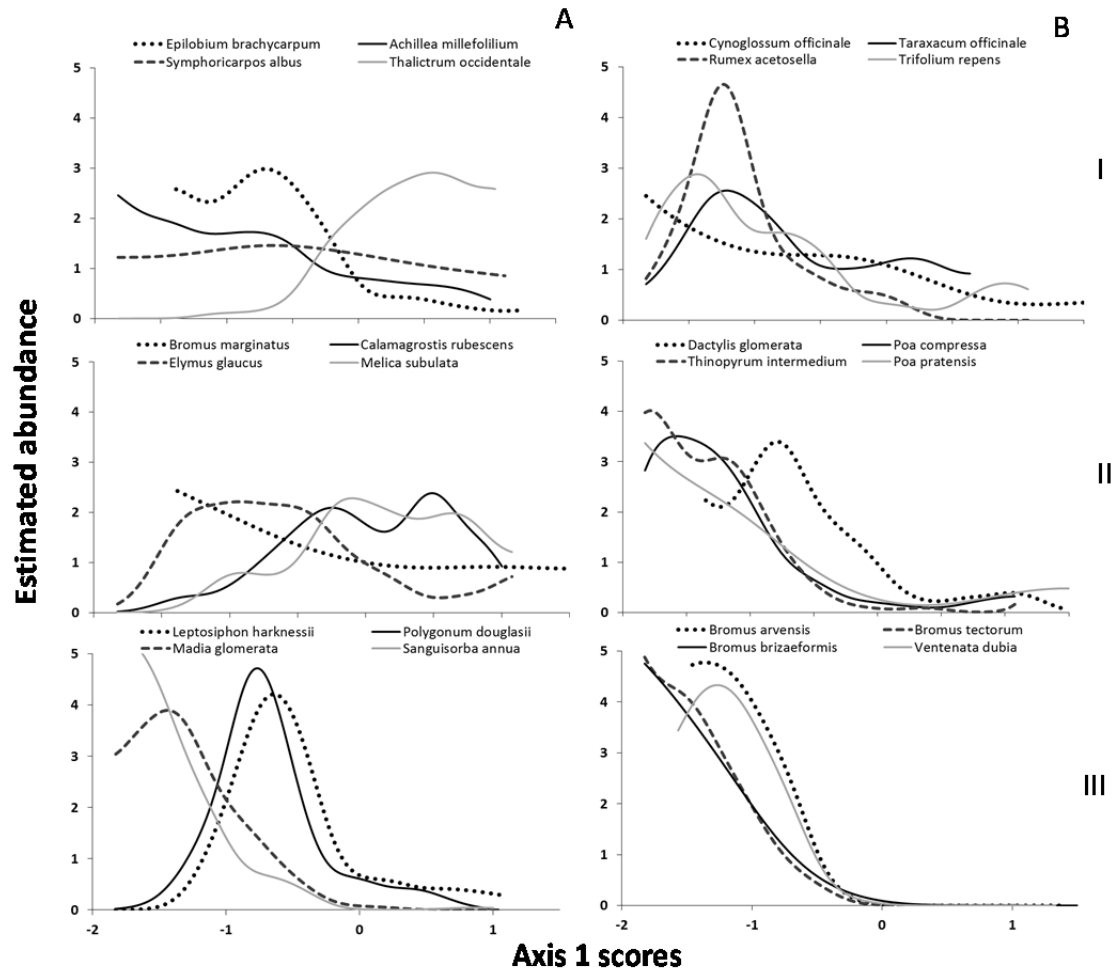


Figure 2.5: Nonparametric multiplicative regression response curves for native and non-native understory species along NMS ordination axis 1 (axis most correlated with canopy openness). A) Native species responses to axis 1; B) non-native species responses to axis 1; I) Forbs with multi-year life cycle; II). Perennial grass species; III; species with annual life cycle.

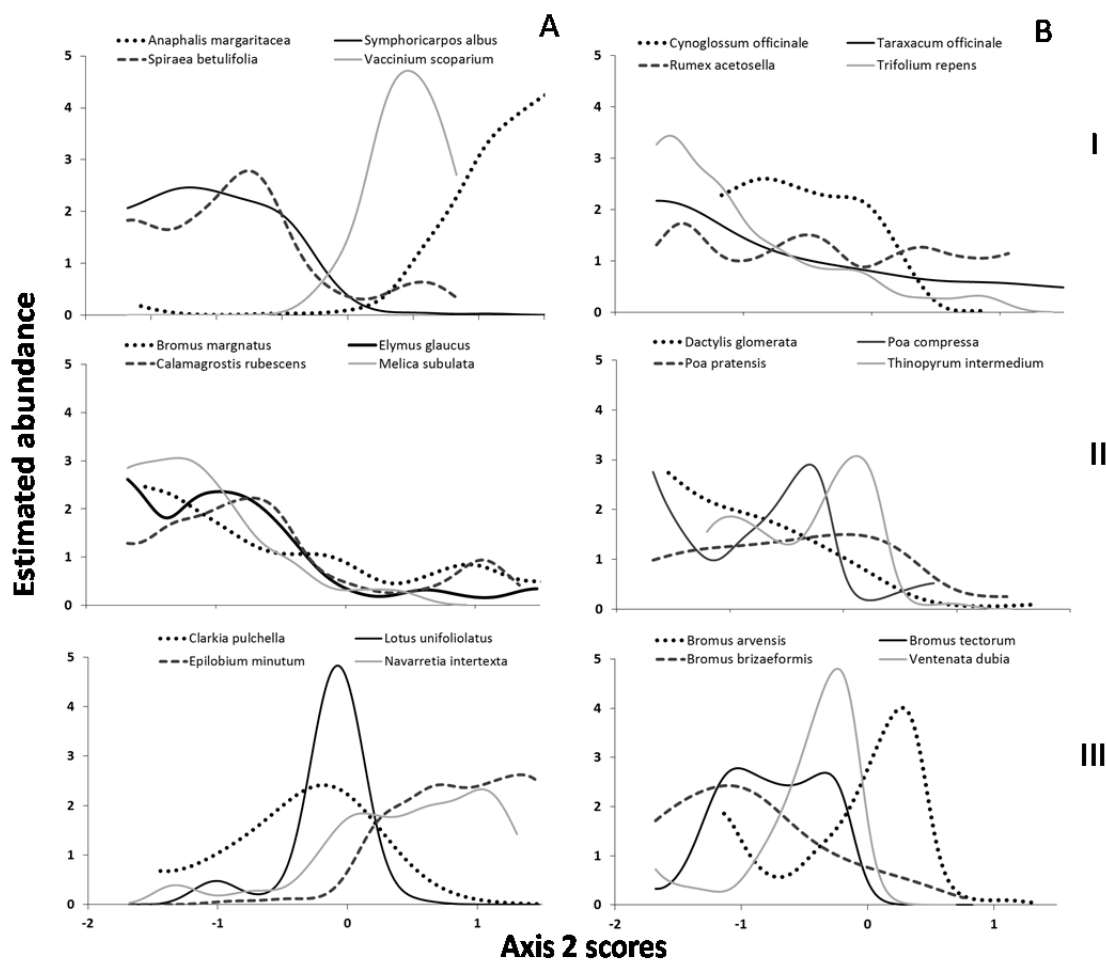


Figure 2.6: Nonparametric multiplicative regression response curves for native and non-native understory species along NMS ordination axis 2 (axis most correlated with elevation). A) Native species responses to axis 2; B) non-native species responses to axis 2; I) forbs with multi-year life cycle; II) perennial grass species; III) species with annual life cycle.



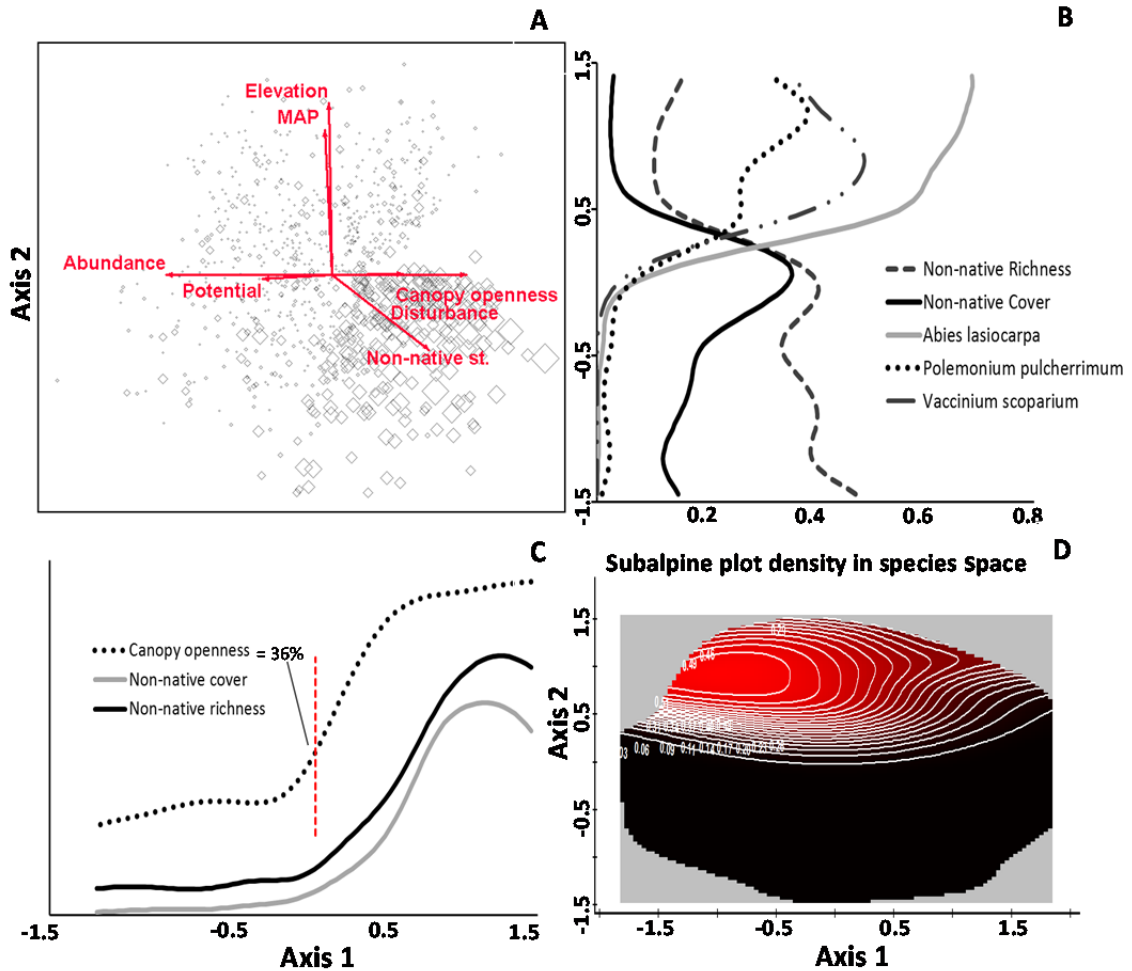


Figure 2.7: A) NMS ordination of sample units (open diamonds) in species space (rotated to load canopy openness on axis 1). Traits were combined with environmental parameters and overlaid on the ordination. Sample units are represented by open diamonds; the size of these symbols corresponds to the relative percent cover of non-native species found in that sample unit. The combined distance matrix variance represented by both axes is 60%, with 30.6% and 29.4% being represented by axis 1 and 2, respectively. B) subalpine indicator species and non-native richness and abundance NPMR estimated relationships with NMS ordination axis 2; C) canopy openness and non-native richness and abundance NPMR estimated relationships with NMS ordination axis 1; B and C) Response variables were relativized by maximum values to allow for pattern comparisons of variables with different units and scales. D) NPMR derived 3-dimensional contour plot depicting density of subalpine plot sampling in species space. MAP, mean annual precipitation; Non-native st, non-native status (trait factor representing non-native abundance in species space); Abundance and Potential, trait factors representing the observed abundance and potential abundance of species in species space.

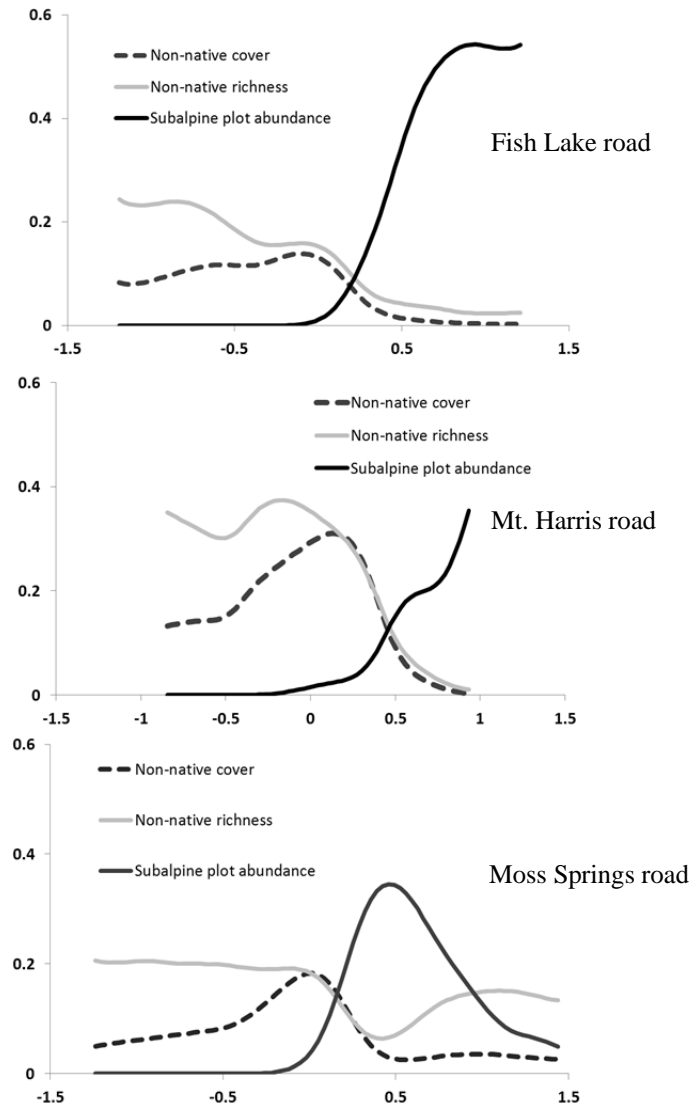


Figure 2.8: Non-native percent canopy cover, non-native richness, and subalpine plot sampling density non-linear relationships with NMS ordination axis 2 for different roads sampled (Fish Lake, Mt. Harris, Moss Springs). All response variables were relativized by their maximum values.

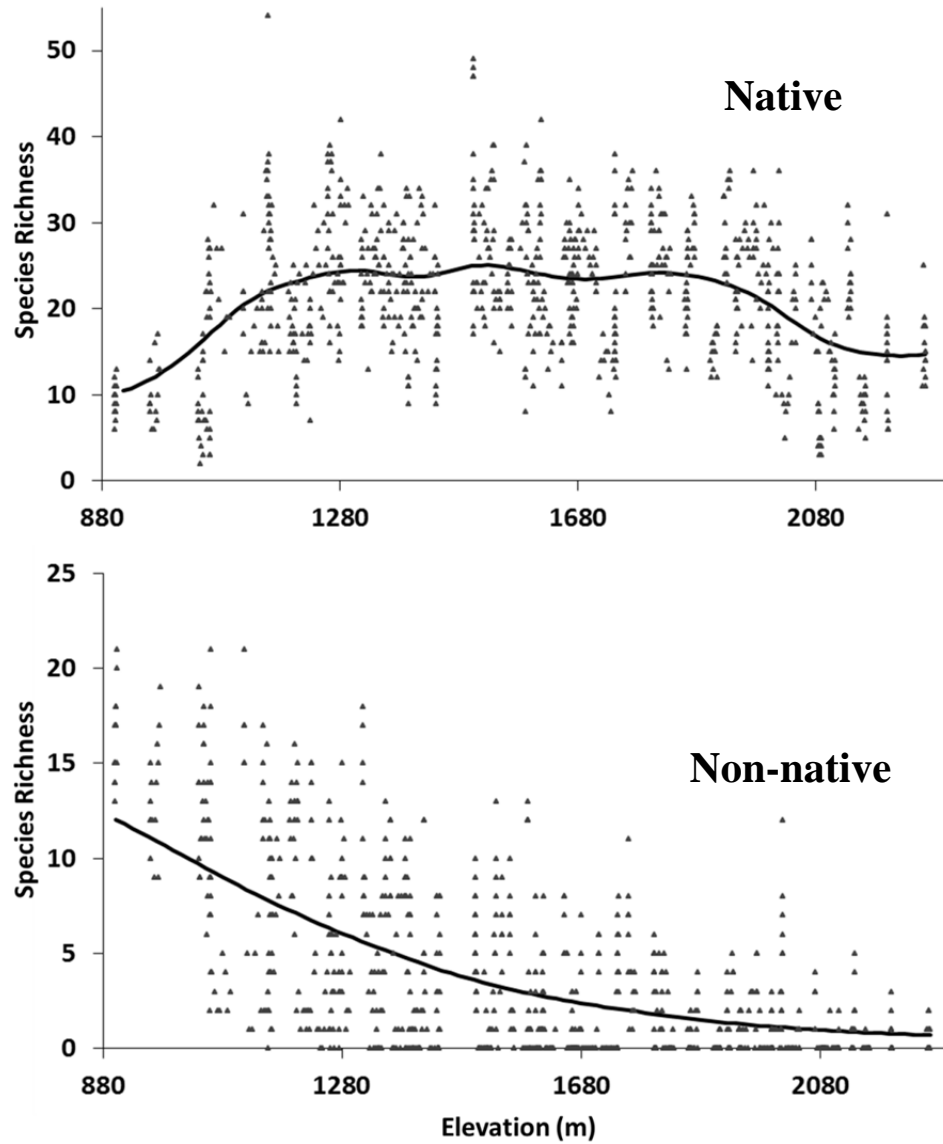


Figure 2.9: Native and non-native species richness as a function of elevation along three mountain roads in the Wallowa Mountain Range of northeastern Oregon. Model fits were generated using nonparametric regression with a local mean estimator, Gaussian kernel function, and automatic average minimum neighborhood size ( $890 \text{ plots} \times 0.03 = 26.7$ )

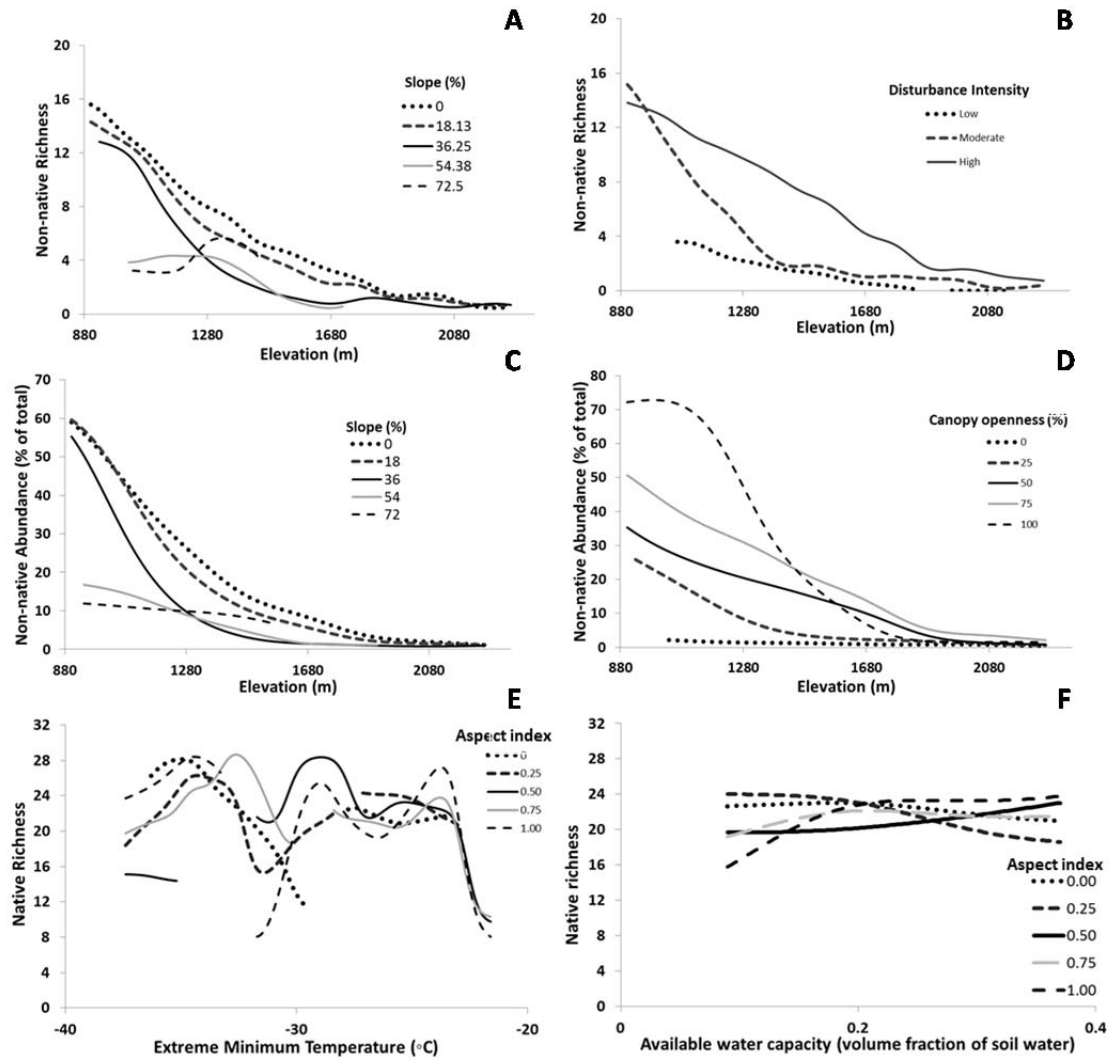


Figure 2.10: NPMR response curves for native and non-native species abundance and richness as a function of the most important predictors.

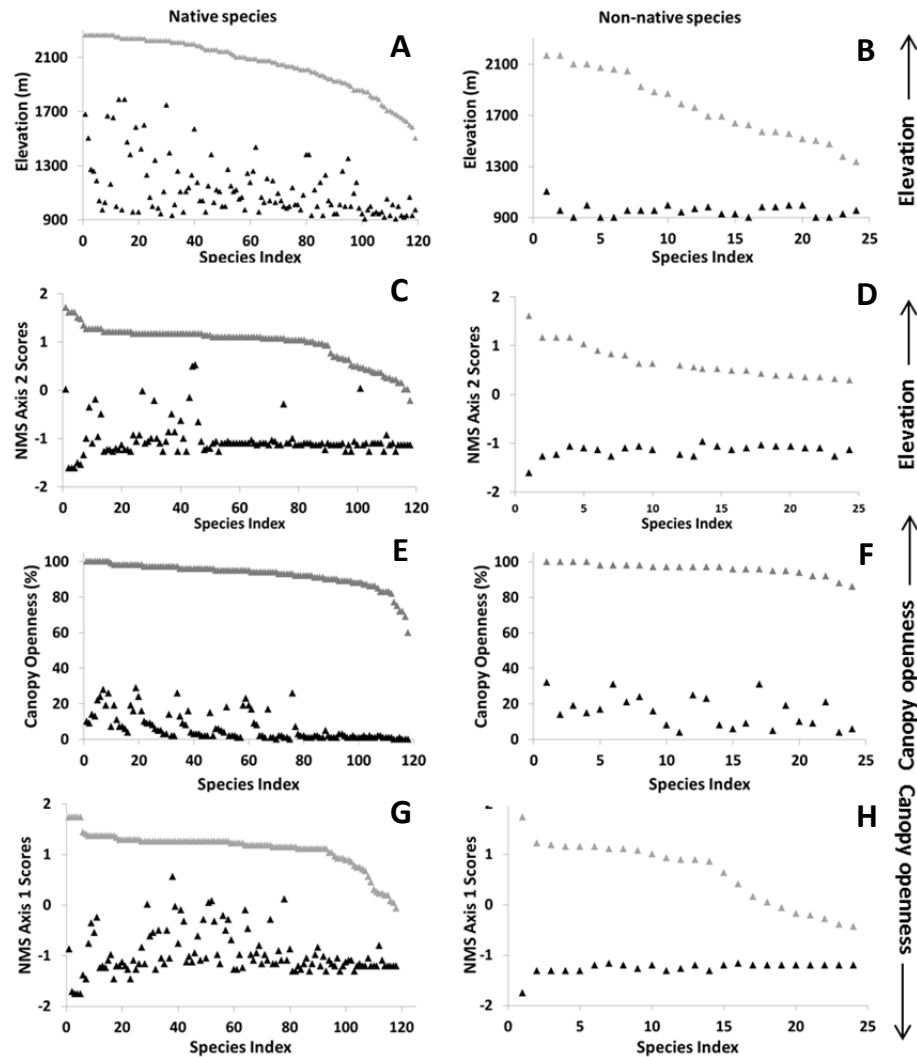


Figure 2.11: Maximum and minimum elevation and canopy openness range limits for native and non-native species included in NMS ordination analyses ( $n=141$ ). Maximum and minimum range occurrences were calculated from the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of species ranges estimated from NPMR models. Elevation ranges are depicted for “true” measured elevation and “effective” species ranges along NMS axis 2 (most correlated with elevation). Canopy openness ranges are depicted for “true” canopy openness from densitometer measurements and for “effective” species ranges along NMS axis 1 (most correlated with canopy openness). Maximum (grey symbols) and minimum (dark symbols) range occurrences are depicted for A) native “true” elevation ranges; B) non-native “true” elevation ranges; C) native axis 2 ranges; D) non-native axis 2 ranges; E) native “true” canopy openness ranges; F) non-native “true” canopy openness ranges; G) native axis 1 ranges; and H) non-native axis 1 ranges. In each plot, species indices are ordered by maximum value rank order (largest to smallest)

## TABLES

Table 2.1: Climatic ranges for roads surveyed in the Wallowa Mountain Range of northeastern Oregon. Precipitation and temperature ranges represent values at the lowest to highest elevation for each road.

<b>Road</b>	<b>Elevation Range (m)</b>	<b>Precipitation Range (mm)</b>	<b>Average Summer Temperature Range (°C)</b>	<b>Average Winter Temperature Range (°C)</b>
Fish Lake	1051 to 2264	694 to 1460	19.1 to 11.3	-2.3 to -5.4
Moss Springs	1161 to 2163	883 to 1375	16.2 to 11.6	0.3 to -3.3
Mt. Harris	902 to 2046	608 to 1356	18.5 to 12.8	-0.9 to -4.1

Table 2.2: Hierarchical sample unit structure and measurements recorded at each level for transects along an elevation gradient in the Wallowa Mountains, Oregon.

<b>Sample Unit</b>	<b>N</b>	<b>Measurements/Observations</b>
Transect	60	Longitude (degrees); Latitude (degrees); Elevation (m)
Plot	180	Elevation (m); Canopy Openness (%); Slope (%); Aspect; Precipitation (mm); Temperature max. & min. (°C); Disturbance Intensity (3 levels); Habitat Type (5 categories)
Subplot	4500	Species; Canopy Cover (%); Abundance (3 levels); Herbivory (%); Herbivore (2 categories); Bareground Cover (%); Rock Cover (%); (Moss/Lichen Cover (%); Coarse Woody Debris Cover (%); Litter Cover (%))

Table 2.3: List of species found in more than 5% (44 out of 890) of plots sampled along an elevation gradient in the Wallowa Mountains, Oregon. Non-native species are depicted in bold.

Species	Ave	Freq	Rnk	Species	Ave	Freq	Rnk
<i>Abies grandis</i>	9.0	404	6	<i>Epilobium ciliatum</i>	1.7	69	111
<i>Abies lasiocarpa</i>	12.6	210	26	<i>Epilobium minutum</i>	1.9	110	65
<i>Acer glabrum</i>	7.6	94	84	<i>Eurybia conspicua</i>	3.7	77	102
<i>Achillea millefolium</i>	2.2	511	1	<i>Festuca idahoensis</i>	4.8	46	132
<i>Achnatherum occidentale</i>	2.7	106	68	<i>Fragaria vesca</i>	3.9	412	4
<i>Adenocaulon bicolor</i>	4.8	198	31	<i>Fragaria virginiana</i>	3.7	225	23
<i>Agoseris heterophylla</i>	0.8	57	121	<i>Galium aparine</i>	1.7	158	40
<i>Agastache urticifolia</i>	3.8	58	119	<i>Galium bifolium</i>	1.1	69	112
<i>Amelanchier alnifolia</i>	3.6	133	54	<i>Galium boreale</i>	1.2	245	19
<i>Anaphalis margaritacea</i>	4.7	198	30	<i>Geranium viscosissimum</i>	1.7	44	140
<i>Anemone piperi</i>	1.1	242	20	<i>Goodyera oblongifolia</i>	0.9	88	90
<i>Antennaria rosea</i>	1.4	82	97	<i>Helianthella uniflora</i>	3.1	46	134
<i>Antennaria stenophylla</i>	3.9	63	113	<i>Hieracium albertinum</i>	1.3	334	10
<i>Apocynum androsaemifolium</i>	4.0	98	79	<i>Hieracium cynoglossoides</i>	1.9	84	95
<i>Aquilegia flavescens</i>	0.7	44	138	<i>Holodiscus discolor</i>	10.4	92	86
<i>Arenaria aculeata</i>	4.3	49	128	<i>Hydrophyllum capitatum</i>	0.9	96	80
<i>Arnica cordifolia</i>	4.2	317	12	<i>Kelloggia galioides</i>	1.5	48	130
<b><i>Arrhenatherum elatius</i></b>	<b>2.1</b>	<b>44</b>	<b>141</b>	<i>Larix occidentalis</i>	3.7	49	129
<i>Arctostaphylos uva-ursi</i>	3.8	60	116	<b><i>Lactuca serriola</i></b>	<b>1.4</b>	<b>130</b>	<b>56</b>
<i>Astragalus canadensis</i>	1.7	76	103	<i>Leptosiphon harknessii</i>	2.4	148	44
<b><i>Bromus arvensis</i></b>	<b>3.5</b>	<b>101</b>	<b>73</b>	<i>Linnaea borealis</i>	14.7	105	70
<b><i>Bromus brizaeformis</i></b>	<b>2.2</b>	<b>46</b>	<b>131</b>	<i>Lotus purshianus</i>	7.4	83	96
<b><i>Bromus inermis</i></b>	<b>1.6</b>	<b>59</b>	<b>117</b>	<i>Lonicera utahensis</i>	6.6	101	72
<i>Bromus marginatus</i>	1.5	435	3	<i>Lupinus sp.</i>	9.2	157	41
<b><i>Bromus tectorum</i></b>	<b>5.5</b>	<b>112</b>	<b>64</b>	<i>Lupinus polyphyllus</i>	4.0	90	88
<i>Bromus vulgaris</i>	1.7	95	82	<i>Madia glomerata</i>	1.6	140	49
<i>Carex geyeri</i>	7.8	476	2	<i>Madia gracilis</i>	1.3	71	110
<i>Aster modestus</i>	2.6	54	126	<i>Mahonia repens</i>	3.5	96	81
<i>Carex sp.</i>	4.3	411	5	<i>Maianthemum stellatum</i>	2.9	142	46
<i>Calamagrostis rubescens</i>	10.0	205	27	<b><i>Medicago lupulina</i></b>	<b>1.4</b>	<b>58</b>	<b>118</b>
<i>Castilleja sp.</i>	2.9	45	136	<i>Melica subulata</i>	1.4	159	39
<i>Ceanothus velutinus</i>	19.3	57	120	<i>Phlox gracilis</i>	0.8	185	34
<i>Chamerion angustifolium</i>	3.7	136	51	<i>Microseris nutans</i>	0.7	78	100
<i>Chimaphila umbellata</i>	2.9	134	52	<i>Mitella stauropetala</i>	1.7	183	35
<b><i>Cirsium arvense</i></b>	<b>1.3</b>	<b>81</b>	<b>98</b>	<i>Arenaria macrophylla</i>	1.5	398	7
<i>Claytonia perfoliata</i>	1.4	71	109	<i>Navarretia intertexta</i>	1.2	129	57
<i>Clarkia pulchella</i>	1.8	114	62	<i>Orthilia secunda</i>	1.9	134	53
<i>Clarkia rhomboidea</i>	0.7	112	63	<i>Osmorhiza berteroi</i>	1.9	373	9
<i>Clintonia uniflora</i>	3.8	87	92	<i>Paxistima myrsinites</i>	2.5	99	77
<i>Collomia grandiflora</i>	0.7	147	45	<i>Physocarpus malvaceus</i>	7.7	44	139
<i>Collomia linearis</i>	0.8	192	33	<i>Pinus contorta</i>	4.9	157	42
<i>Collinsia parviflora</i>	0.9	301	13	<i>Picea engelmannii</i>	6.2	124	59
<i>Epilobium densiflorum</i>	0.6	75	104	<i>Pinus ponderosa</i>	4.2	75	105
<i>Cryptantha affinis</i>	0.6	98	78	<b><i>Plantago lanceolata</i></b>	<b>4.4</b>	<b>105</b>	<b>69</b>

Table 2.3: continued: List of species found in more than 5% (44 out of 890) of plots sampled along an elevation gradient in the Wallowa Mountains, Oregon. Non-native species are depicted in bold.

Species	Ave	Freq	Rnk	Species	Ave	Freq	Rnk
<b><i>Cynoglossum officinale</i></b>	<b>1.1</b>	<b>197</b>	<b>32</b>	<b><i>Poa bulbosa</i></b>	<b>1.8</b>	<b>101</b>	<b>74</b>
<b><i>Dactylis glomerata</i></b>	<b>1.9</b>	<b>141</b>	<b>47</b>	<b><i>Poa compressa</i></b>	<b>2.7</b>	<b>201</b>	<b>29</b>
<i>Deschampsia elongata</i>	1.4	94	85	<i>Polygonum douglasii</i>	0.6	160	38
<i>Elymus glaucus</i>	2.2	219	25	<i>Potentilla glandulosa</i>	2.4	284	14
<i>Epilobium brachycarpum</i>	1.0	234	22	<i>Polemonium micranthum</i>	0.5	80	99
<i>Polygonum phytolaccifolium</i>	11.5	45	137	<b><i>Spergularia rubra</i></b>	<b>1.1</b>	<b>54</b>	<b>124</b>
<i>Polygonum polygaloides</i>	0.6	74	107	<i>Symphoricarpos albus</i>	11.8	377	8
<b><i>Poa pratensis</i></b>	<b>2.4</b>	<b>155</b>	<b>43</b>	<i>Symphyotrichum cusickii</i>	3.5	107	66
<i>Polemonium pulcherrimum</i>	4.4	173	36	<b><i>Taraxacum laevigatum</i></b>	<b>0.7</b>	<b>102</b>	<b>71</b>
<i>Poa secunda</i>	5.2	221	24	<b><i>Taraxacum officinale</i></b>	<b>1.3</b>	<b>241</b>	<b>21</b>
<i>Prunella vulgaris</i>	1.5	57	122	<b><i>Thinopyrum intermedium</i></b>	<b>8.1</b>	<b>107</b>	<b>67</b>
<i>Pseudotsuga menziesii</i>	3.8	264	18	<i>Thalictrum occidentale</i>	4.3	267	17
<i>Pteridium aquilinum</i>	9.3	55	123	<b><i>Tragopogon dubius</i></b>	<b>1.0</b>	<b>99</b>	<b>76</b>
<i>Ranunculus uncinatus</i>	1.1	202	28	<b><i>Trifolium pratense</i></b>	<b>4.0</b>	<b>62</b>	<b>114</b>
<i>Ribes lacustre</i>	2.9	45	135	<b><i>Trifolium repens</i></b>	<b>5.8</b>	<b>165</b>	<b>37</b>
<i>Ribes viscosissimum</i>	3.6	87	93	<i>Tsuga mertensiana</i>	7.6	54	125
<i>Rosa gymnocarpa</i>	4.1	139	50	<i>Vaccinium membranaceum</i>	26.5	274	16
<i>Rosa woodsii</i>	2.6	72	108	<i>Vaccinium scoparium</i>	16.5	128	58
<b><i>Rumex acetosella</i></b>	<b>1.6</b>	<b>141</b>	<b>48</b>	<i>Valeriana sitchensis</i>	6.6	87	94
<i>Rudbeckia occidentalis</i>	5.7	118	61	<b><i>Ventenata dubia</i></b>	<b>26.4</b>	<b>89</b>	<b>89</b>
<i>Sanguisorba annua</i>	1.7	101	75	<b><i>Verbascum thapsus</i></b>	<b>1.0</b>	<b>74</b>	<b>106</b>
<i>Salix lasiolepis</i>	6.9	46	133	<i>Viola adunca</i>	1.7	327	11
<i>Salix scouleriana</i>	8.4	95	83	<i>Vicia americana</i>	1.4	87	91
<i>Sedum stenopetalum</i>	3.0	92	87	<i>Viola glabella</i>	0.7	50	127
<i>Sidalcea oregana</i>	1.9	61	115	<i>Viola nuttallii</i>	0.9	132	55
<i>Sorbus scopulina</i>	2.1	78	101	<i>Viola orbiculata</i>	1.4	119	60
<i>Spiraea betulifolia</i>	5.0	283	15				



Table 2.4: Frequency of occurrence by habitat type for common (occurring in  $\geq 5\%$  of all plots) non-native plant species. Species indicator values (IV) are reported along with specific habitat tendencies and statistical significance for each species.

Species	Road	Grass Shrub	Open Forest	Closed Forest	Subalpine	Total	% of sites	Habitat Tendency	IV	p-value
<i>Taraxacum officinale</i>	158	5	60	11	7	241	27.1	Road	34	0.0002
<i>Poa compressa</i>	123	37	32	6	3	201	22.6	Grass Shrub	48.7	0.0002
<i>Cynoglossum officinale</i> (I)	94	12	62	29	0	197	22.1	Road	13.8	0.0114
<i>Trifolium repens</i>	98	5	52	10	0	165	18.5	Road	14.3	0.0028
<i>Poa pratensis</i>	81	27	37	8	2	155	17.4	Grass Shrub	39.4	0.0002
<i>Dactylis glomerata</i> (I)	96	3	39	3	0	141	15.8	Road	22.2	0.0002
<i>Rumex acetosella</i>	82	0	46	12	1	141	15.8	Road	16.4	0.006
<i>Lactuca serriola</i> (I)	60	32	36	1	1	130	14.6	Grass Shrub	53.3	0.0002
<i>Bromus tectorum</i> (I)	40	44	25	3	0	112	12.6	Grass Shrub	66.9	0.0002
<i>Thinopyrum intermedium</i>	65	22	14	6	0	107	12.0	Grass Shrub	30.7	0.0002
<i>Plantago lanceolata</i> (I)	85	6	12	2	0	105	11.8	Road	14.9	0.0002
<i>Taraxacum laevigatum</i>	62	1	34	5	0	102	11.5	Road	13.4	0.0002
<i>Bromus arvensis</i>	48	32	19	0	2	101	11.3	Grass Shrub	56	0.0002
<i>Poa bulbosa</i>	64	18	15	4	0	101	11.3	Grass Shrub	22.8	0.0002
<i>Tragopogon dubius</i>	46	22	25	6	0	99	11.1	Grass Shrub	31.3	0.0002
<i>Ventenata dubia</i> (I)	45	28	16	0	0	89	10.0	Grass Shrub	48.4	0.0002
<i>Cirsium arvense</i> (I)	42	7	26	6	0	81	9.1	Grass Shrub	3.7	0.4153
<i>Verbascum Thapsus</i> (I)	41	6	25	2	0	74	8.3	Grass Shrub	6.2	0.0334
<i>Trifolium pratense</i>	47	4	11	0	0	62	7.0	Road	12.8	0.0006
<i>Bromus inermis</i>	30	0	21	7	1	59	6.6	Road	4.6	0.0802
<i>Medicago lupulina</i>	24	7	22	5	0	58	6.5	Grass Shrub	5.9	0.0344
<i>Spergularia rubra</i>	39	4	9	2	0	54	6.1	Grass Shrub	5.8	0.052
<i>Bromus brizaeformis</i>	19	21	5	1	0	46	5.2	Grass Shrub	38.6	0.002
<i>Arrhenatherum elatius</i>	23	1	20	0	0	44	4.9	Open Forest	4.5	0.0462
Number of sites with target sp	256	50	170	63	12	551	<b>61.9</b>			
Number of sites sampled	300	50	255	185	100	890				
%Habitats with target sp	<b>85.3</b>	<b>100.0</b>	<b>66.7</b>	<b>34.1</b>	<b>12.0</b>					

Notes: "(I)" means that species are considered invasive (U.S. Forest Service Pacific Northwest Region six invasive species list)

Table 2.5: Correlations between environmental variables/sample unit traits and NMS ordination axes.

Variable	r		
	Axis 1	Axis 2	Axis 3
<b>Spring precipitation</b>	0.34	0.53	-0.17
<b>Summer precipitation</b>	0.30	0.53	-0.14
<b>Frost free days -spring</b>	-0.25	-0.54	0.25
<b>Frost free days - summer</b>	-0.06	-0.60	0.20
Continentality	-0.15	-0.47	-0.11
<b>Mean annual precipitation</b>	0.33	0.56	-0.24
Mean summer precipitation	0.30	0.49	-0.08
<b>Frost free period start date</b>	0.17	0.52	-0.27
Frost free period end date	-0.06	-0.45	0.18
<b>Frost free period</b>	-0.14	-0.51	0.25
Extreme minimum temp (30 years)	-0.05	-0.14	0.32
Hargreaves climate moisture deficit	-0.33	-0.53	0.06
<b>Canopy openness (%)</b>	-0.60	0.20	0.12
<b>Elevation</b>	0.30	0.63	-0.20
Slope	-0.03	-0.25	-0.40
Aspect Index	0.12	0.06	0.03
Bare-ground (%)	-0.31	0.02	0.04
<b>Maximum average temperature</b>	-0.34	-0.62	0.13
<b>Minimum average temperature</b>	-0.36	-0.62	0.11
Distance to road	0.23	0.02	-0.21
Disturbance intensity	-0.42	0.20	0.12
AWC (Available water capacity)	0.46	0.44	0.08
Available water supply (0-25 cm)	0.45	0.43	0.08
Clay (%)	-0.45	-0.31	0.04
Depth to restrictive layer	0.16	0.02	0.08
Organic Matter	0.22	0.26	-0.04
Sand (%)	0.08	-0.31	-0.13
Silt (%)	0.19	0.50	0.10
<b>Non-native status</b>	-0.64	-0.27	0.39
Potential abundance	0.40	-0.26	0.13
<b>Observed Abundance</b>	0.67	-0.19	-0.01
Variables with $r > 0.5$ or $r < -0.5$ are bolded			

Table 2.6: Nonparametric multiplicative regression model summary for species abundance responses with first two NMS ordination axes scores as predictors.

Species	R <sup>2</sup>	Neighb	Axis 1		Axis 2	
			Tolerance	Sensitivity	Tolerance	Sensitivity
<i>Abies grandis</i>	0.35	66.3	0.18	0.91	0.34	0.35
<i>Abies lasiocarpa</i>	0.53	35.6	0.18	0.77	0.17	0.84
<i>Acer glabrum</i>	0.17	123.5	0.37	0.12	0.34	0.22
<i>Achillea millefolium</i>	0.26	35.6	0.18	0.90	0.17	0.49
<i>Achnatherum occidentale</i>	0.32	35.6	0.18	0.37	0.17	0.28
<i>Adenocaulon bicolor</i>	0.41	35.6	0.18	0.51	0.17	0.51
<i>Agoseris heterophylla</i>	0.07	65.7	0.37	0.12	0.17	0.16
<i>Agastache urticifolia</i>	0.05	109.7	0.73	0.03	0.17	0.13
<i>Amelanchier alnifolia</i>	0.21	174.1	Na	Na	0.17	0.39
<i>Anaphalis margaritacea</i>	0.39	65.7	0.37	0.14	0.17	0.54
<i>Anemone piperi</i>	0.39	35.6	0.18	0.68	0.17	0.35
<i>Antennaria rosea</i>	0.03	35.6	0.18	0.25	0.17	0.27
<i>Antennaria stenophylla</i>	0.11	66.3	0.18	0.18	0.34	0.15
<i>Apocynum androsaemifolium</i>	0.13	35.6	0.18	0.24	0.17	0.34
<i>Aquilegia flavescens</i>	0.07	66.3	0.18	0.13	0.34	0.08
<i>Arenaria aculeata</i>	0.12	35.6	0.18	0.15	0.17	0.16
<i>Arnica cordifolia</i>	0.27	35.6	0.18	0.68	0.17	0.14
<i>Arrhenatherum elatius</i>	0.05	65.7	0.37	0.09	0.17	0.15
<i>Arctostaphylos uva-ursi</i>	0.22	35.6	0.18	0.30	0.17	0.28
<i>Astragalus canadensis</i>	0.16	35.6	0.18	0.25	0.17	0.20
<i>Bromus arvensis</i>	0.59	35.6	0.18	0.44	0.17	0.24
<i>Bromus brizaeformis</i>	0.18	123.5	0.37	0.13	0.34	0.06
<i>Bromus inermis</i>	0.12	35.6	0.18	0.15	0.17	0.18
<i>Bromus marginatus</i>	0.12	65.7	0.37	0.18	0.17	0.43
<i>Bromus tectorum</i>	0.45	35.6	0.18	0.41	0.17	0.16
<i>Bromus vulgaris</i>	0.11	35.6	0.18	0.21	0.17	0.20
<i>Carex geyeri</i>	0.31	35.6	0.18	0.60	0.17	0.75
<i>Aster modestus</i>	0.17	123.5	0.37	0.07	0.34	0.14
<i>Carex sp.</i>	0.24	90.5	0.55	0.15	0.17	0.66
<i>Calamagrostis rubescens</i>	0.15	35.6	0.18	0.56	0.17	0.48
<i>Castilleja sp.</i>	0.04	66.3	0.18	0.14	0.34	0.08
<i>Ceanothus velutinus</i>	0.04	35.6	0.18	0.28	0.17	0.20
<i>Chamerion angustifolium</i>	0.14	35.6	0.18	0.16	0.17	0.31
<i>Chimaphila umbellata</i>	0.27	35.6	0.18	0.47	0.17	0.24
<i>Cirsium arvense</i>	0.05	66.3	0.18	0.14	0.34	0.08
<i>Claytonia perfoliata</i>	0.13	66.3	0.18	0.13	0.34	0.10
<i>Clarkia pulchella</i>	0.41	66.3	0.18	0.39	0.34	0.14
<i>Clarkia rhomboidea</i>	0.12	35.6	0.18	0.19	0.17	0.26
<i>Clintonia uniflora</i>	0.28	65.7	0.37	0.22	0.17	0.18
<i>Collomia grandiflora</i>	0.25	35.6	0.18	0.38	0.17	0.35
<i>Collomia linearis</i>	0.15	35.6	0.18	0.46	0.17	0.22
<i>Collinsia parviflora</i>	0.16	66.3	0.18	0.48	0.34	0.24

R<sup>2</sup>, cross-validated coefficient of determination; Neighb, average neighborhood size; Tolerance, bandwidth of the multiplicative kernel smoother in units of the predictor; Sensitivity, unitless measure of predictor importance (0 = no response, 1 = 1:1 change in predictor and response proportionally).

Table 2.6 continued: Nonparametric multiplicative regression model summary for species abundance.

Species	R <sup>2</sup>	Neighb	Axis 1		Axis 2	
			Tolerance	Sensitivity	Tolerance	Sensitivity
<i>Cryptantha affinis</i>	0.00	335.3	0.37	0.05	Na	Na
<i>Cynoglossum officinale</i>	0.15	65.7	0.37	0.13	0.17	0.31
<i>Dactylis glomerata</i>	0.23	66.3	0.18	0.34	0.34	0.22
<i>Deschampsia elongata</i>	0.03	35.6	0.18	0.23	0.17	0.19
<i>Elymus glaucus</i>	0.25	35.6	0.18	0.33	0.17	0.50
<i>Epilobium brachycarpum</i>	0.40	35.6	0.18	0.51	0.17	0.45
<i>Epilobium ciliatum</i>	0.10	35.6	0.18	0.15	0.17	0.20
<i>Epilobium densiflorum</i>	0.06	65.7	0.37	0.11	0.17	0.20
<i>Epilobium minutum</i>	0.45	35.6	0.18	0.46	0.17	0.25
<i>Eurybia conspicua</i>	0.10	35.6	0.18	0.19	0.17	0.27
<i>Festuca idahoensis</i>	0.18	35.6	0.18	0.15	0.17	0.18
<i>Fragaria vesca</i>	0.36	65.7	0.37	0.37	0.17	0.89
<i>Fragaria virginiana</i>	0.10	66.3	0.18	0.32	0.34	0.24
<i>Galium aparine</i>	0.22	65.7	0.37	0.16	0.17	0.33
<i>Galium bifolium</i>	0.07	90.5	0.55	0.05	0.17	0.14
<i>Galium boreale</i>	0.34	65.7	0.37	0.42	0.17	0.41
<i>Geranium viscosissimum</i>	0.04	35.6	0.18	0.16	0.17	0.16
<i>Goodyera oblongifolia</i>	0.14	66.3	0.18	0.23	0.34	0.06
<i>Helianthella uniflora</i>	0.01	123.5	0.37	0.06	0.34	0.06
<i>Hieracium albertinum</i>	0.26	35.6	0.18	0.65	0.17	0.37
<i>Hieracium cynoglossoides</i>	0.08	35.6	0.18	0.25	0.17	0.23
<i>Holodiscus discolor</i>	0.18	156.5	1.84	0.01	0.17	0.36
<i>Hydrophyllum capitatum</i>	0.03	123.5	0.37	0.07	0.34	0.13
<i>Kelloggia galioides</i>	0.03	65.7	0.37	0.09	0.17	0.20
<i>Larix occidentalis</i>	0.03	66.3	0.18	0.14	0.34	0.06
<i>Lactuca serriola</i>	0.30	35.6	0.18	0.34	0.17	0.14
<i>Leptosiphon harknessii</i>	0.07	35.6	0.18	0.36	0.17	0.31
<i>Linnaea borealis</i>	0.23	35.6	0.18	0.48	0.17	0.27
<i>Lotus purshianus</i>	0.19	35.6	0.18	0.24	0.17	0.35
<i>Lonicera utahensis</i>	0.13	35.6	0.18	0.42	0.17	0.25
<i>Lupinus sp.</i>	0.51	35.6	0.18	0.57	0.17	0.50
<i>Lupinus polyphyllus</i>	0.06	123.5	0.37	0.11	0.34	0.11
<i>Madia glomerata</i>	0.32	35.6	0.18	0.35	0.17	0.22
<i>Madia gracilis</i>	0.15	35.6	0.18	0.19	0.17	0.15
<i>Mahonia repens</i>	0.09	35.6	0.18	0.18	0.17	0.30
<i>Maianthemum stellatum</i>	0.28	91.5	0.18	0.34	0.51	0.22
<i>Medicago lupulina</i>	0.09	66.3	0.18	0.15	0.34	0.07
<i>Melica subulata</i>	0.17	35.6	0.18	0.30	0.17	0.37
<i>Microseris nutans</i>	0.13	65.7	0.37	0.14	0.17	0.20
<i>Microsteris gracilis</i>	0.18	65.7	0.37	0.23	0.17	0.22
<i>Mitella stauropetala</i>	0.41	35.6	0.18	0.52	0.17	0.34
<i>Moehringia macrophylla</i>	0.28	35.6	0.18	0.57	0.17	0.56

R<sup>2</sup>, cross-validated coefficient of determination; Neighb, average neighborhood size; Tolerance, bandwidth of the multiplicative kernel smoother in units of the predictor; Sensitivity, unitless measure of predictor importance (0 = no response, 1 = 1:1 change in predictor and response proportionally).

Table 2.6 continued: Nonparametric multiplicative regression model summary for species abundance.

Species	R <sup>2</sup>	Neighb	Axis 1		Axis 2	
			Tolerance	Sensitivity	Species	R <sup>2</sup>
<i>Navarretia intertexta</i>	0.19	35.6	0.18	0.42	0.17	0.27
<i>Orthilia secunda</i>	0.23	35.6	0.18	0.39	0.17	0.33
<i>Osmorhiza berteroi</i>	0.32	35.6	0.18	0.37	0.17	0.56
<i>Paxistima myrsinites</i>	0.18	123.5	0.37	0.20	0.34	0.14
<i>Physocarpus malvaceus</i>	0.06	35.6	0.18	0.14	0.17	0.15
<i>Pinus contorta</i>	0.24	65.7	0.37	0.15	0.17	0.43
<i>Picea engelmannii</i>	0.21	66.3	0.18	0.38	0.34	0.17
<i>Pinus ponderosa</i>	0.09	174.1	Na	Na	0.17	0.13
<i>Plantago lanceolata</i>	0.16	66.3	0.18	0.28	0.34	0.16
<i>Poa bulbosa</i>	0.32	35.6	0.18	0.38	0.17	0.18
<i>Poa compressa</i>	0.39	35.6	0.18	0.57	0.17	0.36
<i>Polygonum douglasii</i>	0.16	35.6	0.18	0.48	0.17	0.21
<i>Potentilla glandulosa</i>	0.04	123.5	0.37	0.14	0.34	0.19
<i>Polemonium micranthum</i>	0.02	179.9	0.18	0.15	Na	Na
<i>Polygonum phytolaccifolium</i>	0.13	123.5	0.37	0.05	0.34	0.15
<i>Polygonum polygaloides</i>	0.12	35.6	0.18	0.22	0.17	0.15
<i>Poa pratensis</i>	0.22	123.5	0.37	0.30	0.34	0.10
<i>Polemonium pulcherrimum</i>	0.22	35.6	0.18	0.34	0.17	0.46
<i>Poa secunda</i>	0.11	35.6	0.18	0.50	0.17	0.35
<i>Prunella vulgaris</i>	0.08	35.6	0.18	0.16	0.17	0.20
<i>Pseudotsuga menziesii</i>	0.20	35.6	0.18	0.47	0.17	0.68
<i>Pteridium aquilinum</i>	0.12	35.6	0.18	0.13	0.17	0.24
<i>Ranunculus uncinatus</i>	0.14	123.5	0.37	0.24	0.34	0.17
<i>Ribes lacustre</i>	0.06	151.8	0.18	0.09	1.36	0.00
<i>Ribes viscosissimum</i>	0.17	123.5	0.37	0.15	0.34	0.10
<i>Rosa gymnocarpa</i>	0.36	90.5	0.55	0.13	0.17	0.41
<i>Rosa woodsii</i>	0.08	123.5	0.37	0.09	0.34	0.13
<i>Rumex acetosella</i>	0.07	35.6	0.18	0.27	0.17	0.22
<i>Rudbeckia occidentalis</i>	0.15	65.7	0.37	0.15	0.17	0.33
<i>Sanguisorba annua</i>	0.34	35.6	0.18	0.30	0.17	0.21
<i>Salix lasiolepis</i>	0.14	35.6	0.18	0.23	0.17	0.21
<i>Salix scouleriana</i>	0.03	35.6	0.18	0.33	0.17	0.33
<i>Sedum stenopetalum</i>	0.20	35.6	0.18	0.34	0.17	0.25
<i>Sidalcea oregana</i>	0.14	123.5	0.37	0.14	0.34	0.07
<i>Sorbus scopulina</i>	0.06	111.2	0.18	0.19	0.68	0.03
<i>Spiraea betulifolia</i>	0.36	35.6	0.18	0.49	0.17	0.91
<i>Spergularia rubra</i>	0.02	65.7	0.37	0.07	0.17	0.07
<i>Symphoricarpos albus</i>	0.68	65.7	0.37	0.31	0.17	1.26
<i>Symphyotrichum cusickii</i>	0.19	90.5	0.55	0.05	0.17	0.39
<i>Taraxacum laevigatum</i>	0.04	35.6	0.18	0.23	0.17	0.28
<i>Taraxacum officinale</i>	0.06	66.3	0.18	0.41	0.34	0.21

R<sup>2</sup>, cross-validated coefficient of determination; Neighb, average neighborhood size; Tolerance, bandwidth of the multiplicative kernel smoother in units of the predictor; Sensitivity, unitless measure of predictor importance (0 = no response, 1 = 1:1 change in predictor and response proportionally).

Table 2.6 continued: Nonparametric multiplicative regression model summary for species abundance.

Species	R <sup>2</sup>	Neighb	Axis 1		Axis 2	
			Tolerance	Sensitivity	Species	R <sup>2</sup>
<i>Thinopyrum intermedium</i>	0.30	35.6	0.18	0.36	0.17	0.24
<i>Thalictrum occidentale</i>	0.40	35.6	0.18	0.69	0.17	0.39
<i>Tragopogon dubius</i>	0.22	65.7	0.37	0.18	0.17	0.13
<i>Trifolium pratense</i>	0.16	66.3	0.18	0.16	0.34	0.11
<i>Trifolium repens</i>	0.09	35.6	0.18	0.34	0.17	0.36
<i>Tsuga mertensiana</i>	0.12	35.6	0.18	0.21	0.17	0.21
<i>Vaccinium membranaceum</i>	0.78	35.6	0.18	1.21	0.17	0.53
<i>Vaccinium scoparium</i>	0.37	35.6	0.18	0.41	0.17	0.71
<i>Valeriana sitchensis</i>	0.24	35.6	0.18	0.30	0.17	0.28
<i>Ventenata dubia</i>	0.69	35.6	0.18	0.51	0.17	0.38
<i>Verbascum thapsus</i>	0.09	123.5	0.37	0.14	0.34	0.10
<i>Viola adunca</i>	0.17	35.6	0.18	0.42	0.17	0.38
<i>Vicia americana</i>	0.18	65.7	0.37	0.06	0.17	0.30
<i>Viola glabella</i>	0.07	123.5	0.37	0.10	0.34	0.06
<i>Viola nuttallii</i>	0.16	35.6	0.18	0.19	0.17	0.34
<i>Viola orbiculata</i>	0.24	35.6	0.18	0.28	0.17	0.30

R<sup>2</sup>, cross-validated coefficient of determination; Neighb, average neighborhood size; Tolerance, bandwidth of the multiplicative kernel smoother in units of the predictor; Sensivity, unitless measure of predictor importance (0 = no response, 1= 1:1 change in predictor and response proportionally).

Chapter 3 Intra- and Inter-annual Vegetation Change along an Elevation  
Gradient in the Wallowa Mountains, Oregon

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## ABSTRACT

Long-term monitoring of non-native plant distribution patterns in mountain environments can provide insight into drivers of plant invasions and subsequent impacts to non-native communities. In order for monitoring efforts to repeatedly and accurately capture vegetation change over time, protocols need to account for measurement variation associated with natural variability of species distributions that could otherwise be falsely interpreted as true community change over time. The objective of this study was to investigate changes in inter-annual understory vascular plant species composition between two years (summer 2012 and summer 2013), and intra-annual understory vascular plant species composition between three sampling periods (June, July, and August 2013) within one growing season. We used permanent plots to sample understory vascular plant composition during one date (July) in summer 2012, and three separate periods (June, July, and August) in summer 2013 along a forest road in the Wallowa Mountain Range of northeastern Oregon. Transects ( $n=10$ ) spanned an elevation range of 902 to 1981 meters. Vascular plant species composition changed both between years and between each sampling period within one growing season. Species turnover rates ranged from 20 to 32%. Species richness increased with sampling effort, common species were consistently found throughout all sampling periods and rare species showed the highest rate of turnover. Species richness and number of indicator species were greatest in early summer (June). Approximately 25% of non-native species showed peaks in abundance during a specific sampling period. More than half of non-native indicator species favored the early summer (June), and were located within lowland bunchgrass communities. Two



non-native June indicator species (*Taraxacum officinale* and *Veronica serpyllifolia*) were found in the subalpine community. Annual species including dominant non-native species within the lowland and montane zones showed the highest inter- and intra-annual variability. Total species richness was positively associated with and the most important predictor of relative abundance turnover for each sampling period transition. The greatest relative abundance turnover occurred within species rich montane plots, however, trait abundance and richness did not show statistical differences between sampling periods in the montane zone. These data indicated that both sampling error and true vegetation change were responsible for observed vegetation change over time. Sampling error was attributed to both overlooking and misidentification of species. Our results suggest that periodic sampling, once during the late spring or early summer and again coinciding with peak biomass will be necessary for accurate estimates of both early and late season species. Mid and late season sampling are likely to underestimate vernal species. This may be particularly important for monitoring non-native species in the Wallowa Mountains as most non-native species are concentrated in lowland bunchgrass communities where early growing season specialization is common.

## INTRODUCTION

Uncertainties regarding plant invasion dynamics over multiple spatial and temporal scales have heightened interest in the development of long-term, multi-scale monitoring projects (Burt 1994; Pyšek and Hulme 2005; Dietz and Edwards 2006; Rejmanek et al. 2013). The Mountain Invasion Research Network (MIREN), a global consortium focused on facilitating research and monitoring efforts related to plant invasions in mountain ecosystems, has recently established permanent vegetation transects along elevation gradients in eleven mountain ranges around the globe (Dietz et al. 2006; McDougall et al. 2009). Among MIREN's long-term goals, are to evaluate the dominant causal factors of non-native plant invasions into mountain environments, investigate how drivers change over different temporal and spatial scales, and to assess the impacts of non-native invasions on natural communities over time and across different geographic scales (Pauchard et al. 2009). In order to achieve these goals, long-term repeat monitoring protocols need to detect changes in non-native and native plant community composition. Successful protocols for repeatable and precise measurements will need to account for measurement variation to minimize error that could otherwise be falsely interpreted as true community changes over time.

Measurement variation in repeat vegetation monitoring can arise from both human error and natural variability of vegetation due to climatic fluctuations, herbivory, insects, and disease. Numerous studies have evaluated the role of sampling error in repeat vegetation measurements. Overlooking species is common, and it is estimated that even experienced observers often overlook greater than 20% of species in a given area (Nilsson and Nilsson 1983; Scott and Hallam 2002; Kery et al. 2006). Species

identification agreement between different observers has been well documented as a substantial source of error in repeat vegetation monitoring. Between-observer pseudo-turnover rates have been reported between 10 to 15% for both alpine and lowland meadow communities (Leps and Hadincova 1992; Vittoz and Guisan 2007). Higher turnover rates have been reported for studies covering large community gradients similar to mountain environments where an average of 24% pseudo-turnover was identified across a range of communities from open grasslands to forested woodlands in the United Kingdom (Scott and Hallam 2002), and 29 to 34% pseudo-turnover was reported across a broad range of forest types throughout Oregon (Gray and Azuma 2005). Even when observers agree on species identification, researchers rarely report coefficients of variation below 20% for between observer visual cover estimates (Kennedy and Addison 1987; Vittoz et al. 2010).

Natural variation of plant species composition due to seasonal and annual climatic fluctuations can also obscure results obtained from repeat vegetation sampling. Many researchers have documented changes in individual plant population abundance and species composition that corresponded to climatic events including annual changes in precipitation (Talbot et al. 1939; Silvertown et al. 1994; Herben et al. 2003; Legget et al. 2003; Levine et al. 2008), and timing of precipitation and temperature related events (Pitt et al. 1978; Fay et al. 2003; Levine et al. 2011). Annual plant populations within semi-arid climates are particularly sensitive to short-term variations in weather patterns (Talbot et al. 1939, Pitt et al. 1978; Legget et al. 2003; Levine et al. 2008). According to Levine et al. (2011), annual fluctuations in precipitation resulted in nine to 100 fold changes in

inter-annual density of annual forb populations in a California grassland community. Similarly, researchers have reported 10 fold changes in *Bromus tectorum* biomass in invaded Great Basin shrub communities as a function of inter-annual precipitation (Bradley and Mustard 2005). Researchers are often able to separate climate related community variability from general community trends by comparing long-term species responses to climate records (Turner 1990; Hobbs and Mooney 1995; Hobbs et al. 2007). Annual and seasonal variations in temperature and precipitation also affect the timing of plant development. In fact, plant phenology is often considered to be one of the most sensitive biological responses to changes in climate (Sparks and Menzel 2002). Temperature is the most important cue for initiating early season plant growth and fluctuations in early spring heat-load can result in substantial variation in the timing of plant development in many communities (Beaubien and Freeland 2000; Badeck et al. 2004 ). One of the most striking examples of shifting phenology with fluctuating climatic conditions is Sparks and Carey's (1995) discovery that inter-annual flowering timing for *Galanthus nivalis*, *Anemone nemorosa*, and *Crataegus monogyna* varied by as much as 89, 71, and 55 days, respectively, over more than a 140 year period. The literature documenting shifts in plant phenology as a result of climatic variation are vast and include individual species responses to annual weather patterns and snowmelt (Franks et al. 2007; Miller-Rushing and Primack 2008; Hulber et al. 2010; Lambert et al. 2010); annual variations in timing of green-up and interactions with ecosystem function (Richardson et al. 2009; Duparc et al. 2013); and shifts in plant phenology as a function of climate change (Badeck et al. 2004; Schwartz et al. 2006; Cleland et al. 2007).

Despite widespread recognition that plant phenology varies greatly from year to year in many ecosystems, few studies have explicitly investigated the implications of inter-annual variations in timing of plant development to repeat vegetation measurements. Some researchers that have considered phenology in their sampling protocols, recommend that year to year sampling be completed at the same phenological time each year, but indicate that timing of vegetation sampling is generally dictated by field crew and resource availability with little regard to plant phenology (Ristau et al. 2001; Pokorny et al. 2004; Korb and Fule 2008).

Intra-annual vegetation change is another important source of variability in many ecosystems. Most communities are sampled only one time during the growing season. Often sampling is timed to coincide with peak biomass, and other times, sampling efforts are dictated by resource and field crew availability (Pokorny et al. 2004; Korb and Fule 2008). Researchers have long recognized that herbaceous plant communities continuously change with the seasons where more stress tolerant and less competitive species are favored in the spring and highly competitive species are dominant later in the season (Grubb 1977). Additionally, conventional vegetation sampling that coincides with peak biomass may underestimate species richness and abundance particularly with regards to vernal species (Holland 1971; Ristau 2001; Tremblay and Larocque 2001; Pokorny et al. 2004). A few studies have explored multiple sampling efforts within one growing season to quantify changes in plant communities over time. Researchers reported significant shifts in species composition over one growing season, and found that: 1) sampling once during the growing season resulted in underestimation of species

abundances and decreased species capture (Ristau et al. 2001; Pokorny et al. 2004; Korb and Fule 2008); 2) sampling at least twice during the growing season, once in the spring and once during peak biomass, increased species capture and improved estimation of asynchronous species abundances (Ristau et al. 2001; Pokorny et al. 2004; Korb and Fule 2008); and 3) species richness tended to be highest in the spring and early summer (Ristau et al. 2001; Tremblay and Larocque 2001; Pokorny et al. 2004).

Several studies that have assessed vegetation change using aggregate community metrics such as species richness or trait group abundance typically report little to no change in vascular plant composition over the growing season. Korb and Fule (2008) observed clear shifts in individual understory species abundances over the growing season (June, July, and August), however, aggregate trait category richness and diversity (Simpson and Shannon indices) did not change significantly and total trait group absolute abundance only showed slight changes over the summer in a mixed conifer forest. Similarly, Carlsson et al. (2005) found that timing of measurements accounted for less than three percent of the variation in vascular plant species composition in European grasslands between three different sampling times (June, July, and August) during one growing season.

Mountain ecosystems experience high inter- and intra-annual climatic variability, and species phenology can vary widely over the strong environmental gradients that are typical in these systems (Hulber et al. 2010; Larson et al. 2011). Assessing the temporal variability of individual plant populations and communities in mountain ecosystems will inform the development of efficient vegetation monitoring protocols by identifying

highly variable communities and temporally specialized species that require unique sampling techniques, determining methods for selecting sampling timing on an inter-annual basis; and evaluating the optimal sampling time or times within one growing season.

The objective of this study was to investigate changes in inter-annual understory vascular plant species composition between two years (summer 2012 and summer 2013), and intra-annual understory vascular plant species composition between three sampling periods (June, July, and August, 2013) within the same growing season. We specifically explored the following questions: 1) how did sampling time influence changes in native and non-native species composition; 2) which species varied the most with regards to abundance and occurrence as a function of sampling time; 3) what were the most important predictors of understory vegetation change and 4) how did temporal vegetation change relate to environmental and species trait factors along an elevation gradient?

## METHODS

### Study site and site selection

This study was conducted in the Wallowa Mountains located in northeastern Oregon. The Wallowa Mountains are located within the Middle Rocky Mountain Ecoregion and encompass approximately 4,700 square kilometers of steep, deeply dissected topography. The majority of land area in the Wallowa Mountains is publicly owned and administered by the Wallowa Whitman National Forest. The highest elevations lie within the 150,219 hectare Eagle Cap Wilderness area (Johnson 2004). Private land ownership is concentrated in the lower elevation valleys and slopes where

dominant land uses include cattle ranching, agriculture, and scattered human settlement. Land uses at the mid and high elevations include timber harvest, recreation, and widespread livestock grazing on both public and private lands (Parks et al. 2005). Study site elevations ranged between 902 to 1,981 meters (Table 1). Mean annual precipitation increased with elevation from 608 to 1,356 mm (Daly et al. 2002; Table 1). Approximately 60% of the precipitation occurs between November and April and the remaining 40% occurs between May and October. The tendency for winter dominated precipitation and dry summers are intensified with decreasing elevation towards the semi-arid valleys in this system (Parks et al. 2005). Mean summer temperatures ranged from 13.3 to 18.5 °C and mean winter temperatures ranged from 0.3 to -2.9 °C across the study area (Daly et al. 2002; Table 3.1).

The lowest elevation sites (902 to 1,042 meters; lowland mountain zone) were located within fenced cattle pastures where the dominant vegetation included non-native annual and perennial grasses including *Ventenata dubia*, *Taeniatherum caput-medusae*, and *Poa compressa* with remnant populations of native bunchgrasses including *Festuca idahoensis* and *Pseudoroegneria spicata*. Thick stands of *Crataegus douglasii* with sparse understory vegetation bordered ephemeral streams at these sites. At the mid elevations (1,260 to 1,619 meters; montane mountain zone), closed canopy mixed *Abies grandis*, *Pseudotsuga menziesii*, and *Larix occidentalis* dominated the over-story with understory species including *Carex geyeri*, *Vaccinium membranaceum*, *Chimaphila umbellata* and other shade tolerant forbs and shrub species. The highest elevation sites (1,743 to 1,981 meters; subalpine mountain zone) consisted of a mixture of open forests



exposed to wind-throw with an *Abies lasiocarpa* and *Picea engelmannii* overstory on gentle slopes, and south facing, shallow soil sites with a wide variety of sedges, shrubs, and forbs including *Valeriana sitchensis*, *Hieracium scouleri*, and *Polygonum phytolaccifolium*.

Permanent vegetation plots were located along a 31 km stretch of gravel forest road (Mt. Harris road, Union County). Mt. Harris road was selected based on the following criteria: 1) open to general vehicular traffic at least part of the year; 2) covered a broad elevation range; and 3) captured typical geographical and environmental variation in the region. Survey sites traversed lowland, montane, and subalpine vegetation zones (Federal Geographic Data Committee 1997).

### Sampling design

Belt transects (n=10) were located along an elevation gradient (Table 3.1). Transects were subdivided into three (50 m x 2 m) plots with one plot parallel to the road edge and the other two plots perpendicular to the road plot, together forming a “T” and extending 100 m from the road. Plots were further subdivided into 25 frames (2 m x 2 m) for a total of 75 frames within the “T”.

Transect locations were geo-referenced using a GEO-Explorer Trimble 3 handheld geographic positioning system. Plots were permanently located by driving bent iron rods (0.64 cm diameter) into the ground at the center (25 m), at both ends of plot 1 (parallel to the road), and at the ends of plot 2 (50 m from the road) and plot 3 (100 m from the road) during July 2012. Plots were constructed by laying a 50 m transect line between the iron rods to establish the central line of each plot. Sampling was completed

over a two week period in July (2-16), 2012. The same plots were measured over a three week period in June and July (June 18-July 8), a two week period in July (18-31), and a two and a half week period in August (12-27), 2013. Six observers worked together to sample all of the plots in 2012. Three observers from the 2012 survey sampled all of the plots during the 2013 season.

### *Biological variables*

All vascular understory plants (height  $\leq 2$  m) present within subplots were identified to the species level and species abundance and environmental parameters were measured. Several species were combined into genus (*Carex*, *Juncus*, *Lomatium*, *Salix*) when phenological stage was not conducive for identification to the species level. Species abundances were estimated using canopy cover. Within each frame, percent canopy cover for identified species was classified into one of eight categories: zero (0%); one (1%); two (1-5%); three (5-25%); four (25-50%); five (50-75%); six (75-95%); seven (95-99%); and eight (99-100%).

### *Environmental variables*

Canopy openness was measured as the mean of four measurements taken in the cardinal directions using a spherical densitometer. Canopy openness measurements were taken at ten meter increments along each transect. A clinometer was used to measure slope for each plot. Disturbance intensity was assessed for each 50 m x 2 m plot. Disturbance observations were qualitatively evaluated and classified into one of three categories: one (low); two (moderate); and three (high). Low disturbance was defined as no to little visual impact to vegetation or soil from a recent disturbance (affecting  $< 10\%$

of plot area). Disturbance intensity was considered moderate if moderate amounts of disturbance resulted in vegetation loss and soil exposure (affecting 10 to 40% of plot area). A high level of disturbance was noted where there were signs of a recent disturbance that resulted in major removal event of vegetation cover and exposure of bare soil (affecting greater than 40% of plot area).

Plots were classified into mountain zones including: lowland (plots below the tree-line where the vegetation community was dominated by grasses, forbs, or shrubs with sparse to no tree cover); montane (open and closed canopy forest with over-story dominated by *Abies grandis*, *Pseudotsuga menziesii*, or *Pinus ponderosa*); and subalpine (vegetation over-story dominated by *Abies lasiocarpa* in our study area). Climate variables were extracted from the PRISM model (Daly et al. 2002), including: mean spring and summer precipitation, number of frost free days in the spring and summer, mean frost free period, mean frost free period start and end dates, temperature difference between the mean warmest month temperature and the mean coldest month temperature (continentality), mean annual precipitation, mean summer precipitation, extreme minimum temperature over a 30 year period, mean annual maximum temperature, mean annual minimum temperature, and Hargreaves climate moisture deficit. Topographic variables including elevation, aspect index (Roberts et al. 1989), and slope were extracted from digital elevation models (DEM) accessible through the Malheur, Umatilla, Wallowa-Whitman National Forest GIS Data Library (U.S. Department of Agriculture 2013). Elevation was acquired at 60 m resolution at the transect origin along the roadside. Soil variables including available water capacity (fraction of soil water

available), available water supply (0-25 cm), percent clay-sand-silt, depth to restrictive layer, and percent organic matter were extracted from the Natural Resources conservation Service Web Soil Survey (Soil Survey Staff 2012).

### Statistical analysis

#### *Non-native and native species pools*

Species lists were compared across sampling periods (July 2012; June 2013, July 2013; August 2013) to determine total non-native and native species richness for each sampling period and to identify species that were unique to specific sampling periods. Native and non-native species were classified as either common species (occurred in > 5% of subplots for at least one sample period) or rare species (occurred in  $\leq 5\%$  of subplots for all sample period). Subplots for this analysis were 20 m<sup>2</sup> (10 m x 2 m). Abundance values for subplots were calculated by averaging cover mid-points for species within each set of five consecutive frames (2 m x 2 m). Frames were combined to larger subplots to be consistent with subplot dimensions among all MIREN regions. Species that were persistent (recorded in all sampling periods), and unique (recorded in only one sampling period) were evaluated in context of their distribution (common or rare) to determine how species commonality was related to species capture across all sampling periods.

Apparent species turnover rates were also calculated for each sampling period transition as the percent of unpaired records between the two sampling periods being compared (Sorenson 1948; Nilsson and Nilsson 1983; Vittoz et al. 2010).

$$T = 100[(X + Y) / (S_x + S_y)] \quad (1)$$

Where  $T$  is the turnover rate (%),  $X$  and  $Y$  are the number of species recorded exclusively within one sampling period, and  $S_X$  and  $S_Y$  are the total number of species recorded for each sampling period.

### *Plots and data structure used in multivariate analyses*

Multivariate analyses were performed on 100 m<sup>2</sup> plots. Plot abundances were obtained by averaging species abundance (midpoint of cover class) for all frames within each larger plot. Combining subplots reduces noise and improves local estimates of species abundance. The final species matrix consisted of 120 plots (30 for each sampling period) by 326 species prior to any transformations and data modifications.

### *Community change over time*

Non-metric multidimensional scaling (NMS; McCune and Mefford 2011) using a Euclidean distance measure was used to extract gradients in community composition. We used the “slow and thorough” NMS autopilot setting, and Kruskal’s strategy 2 for penalization for ties in the distance matrix. There was no expectation that species percent cover would respond in a linear fashion over the large environmental distances sampled. Therefore, NMS was selected because this ordination method is ideally suited to recover the nonlinear structure common in ecological community data (McCune and Grace 2002). A Euclidean distance measure was used to retain information related to the absolute differences in species percent cover between sample units.

Species data were transformed using a generalized  $\log_{10}$  transformation to increase the contribution of subdominant species to the community structure (McCune and Mefford 2011). Species occurring in  $\leq 5\%$  of sample units for all sampling periods

were excluded. Species that were observed in > 5% of sample units for any given sampling period were retained because we expected and wanted to detect changes in species abundance that resulted from species being common during some sampling periods and rare in others. Deletion of rare species was chosen to decrease the bulk noise and thus enhance any signal relating community composition with environmental factors (McCune and Grace 2002). A generalized log transformation was chosen to increase the contribution of subdominant species to the community structure.

Two dimensional ordinations were produced with a random starting configuration and a maximum of 500 iterations. Rotation by orthogonal principal axes was selected to load the greatest amount of variance represented by the ordination on axis 1 and ensure independence of axes 1 and 2. Environmental parameters were overlaid on the ordination to investigate relationships between species composition and environmental factors. Species trait categories (growth form, duration, and native status), non-native richness, and native species richness variables were also overlaid on the ordination to determine how these biotic variables were related to both environmental parameters and sample units in species space. Species trait categories included: non-native annual forbs (IAF); non-native annual grasses (IAG); non-native perennial forbs (IPF); non-native perennial grasses (IPG); native annual forbs (NAF); native perennial forbs (NPF); native perennial grasses (NPG); and native shrubs (NPS).

Species trait categories were overlaid onto the ordination space by creating a plot x trait matrix, each element representing the abundance of each trait category within each plot. In order to create the trait matrix: 1) a species x trait matrix (**S**) was created with

trait categories as rows and species as columns; 2) a binary value indicated the trait category for each species (0/1 = species did not/did have that trait); and 3) the plot x trait matrix used as an overlay was created by matrix multiplication ( $\mathbf{AS}'$ ).

Vectors were used to connect plots as they moved through time in the ordination space. The relative magnitude and direction of community change was investigated for each plot by translating the tail of each vector to the origin (centroid of the ordination) and comparing vector length and trajectory (McCune and Grace 2002). One-way ANOVA procedures were performed in R to compare vector lengths between mountain zones for each sampling period transition and to compare vector lengths within mountain zones between sampling periods (R Development Core Team 2012).

We used both multivariate and univariate approaches to investigate changes in vegetation composition over time. Blocked Multi Response Permutation Procedure (MRBP; Mielke 1991; McCune and Mefford 2011) was used to test the null hypothesis of no change in understory plant species composition between sampling periods. We used a Euclidean distance measure and aligned the medians to zero for all blocks. Separate MRBP analyses were performed for the intra- and inter-annual datasets respectively (plots = blocks and sampling period = groups). Pairwise comparisons were made to test for differences in species composition between each intra- and inter-annual pair of sampling dates. We further explored between sampling period differences in trait category composition within each mountain zone using additional MRBP analyses for both intra-annual and inter-annual datasets in order to determine which trait categories had the most variation and where along the elevation gradient those changes were

occurring. One-way ANOVA was used in R to assess differences between sampling periods in trait abundances and richness, each mountain zone analyzed separately.

Variables with significant effects ( $p \leq 0.05$ ) were plotted and pairwise comparisons were made using a Tukey Kramer. Trait category mean abundance was  $\ln$  transformed to better match the normal distribution assumption required for ANOVA.

MRBP is a nonparametric procedure for testing of no difference between two or more a priori groups (McCune and Grace 2002). MRBP is a blocked version of Multi Response Permutation Procedure (MRPP; Mielke 1984) that focuses on within group differences after accounting for block differences, and was chosen because of large variation in biotic and abiotic characteristics across the study area (Mielke 1991). MRBP provides an effect size known as the chance-corrected within-group agreement (A) that indicates within group homogeneity compared to random expectation (McCune and Grace 2002). An A-value of one indicates that all components within a group are identical and an A-value of zero occurs when within group heterogeneity is greater than would be expected by chance (McCune and Grace 2002). The MRBP test statistic was the average pairwise distance between blocks (plots) within each group (sampling period). The p-value was generated by determining the proportion of all possible values of the test statistics that were less than or equal to the observed test statistic using a Pearson type III distribution (Mielke and Berry 2001).

Blocked indicator species analysis was used to identify species with strong affinities for specific sampling periods (Root et al. 2010; McCune and Mefford 2011). We used sampling period as groups, plots were blocks. This method pre-relativizes by



species within blocks and focuses on within block differences (McCune and Mefford 2011). Indicator species analysis produces indicator values (IV) that represent the tendencies for species to occur within specific a priori groups based on relative frequency and abundance information. Significance of IV's were determined by comparing observed values to results from 10,000 randomizations.

Non-parametric multiplicative regression (NPMR; McCune 2006) was used to evaluate indicator species responses to the strongest NMS community gradients. NPMR is a multiplicative kernel smoother, which automatically models interactions among predictors, and has built in over-fitting protection (McCune 2006). We used a local mean estimator, Gaussian kernel, “aggressive” model selection, and automatic average neighborhood size in HyperNiche 2.0 (McCune and Mefford 2009). Two predictor response surfaces for target indicator species abundance were overlaid as contours on the ordination. In order to overlay multiple indicator species response surfaces on to the ordination, we traced the third highest contour for each species and superimposed them onto the same plot. Resulting plots represented peak abundance of each target species within species space for the sampling period of interest (Nelson et al. 2014).

NPMR was performed using Hyperniche 2.0 (McCune and Mefford 2009) to identify important environmental and biotic predictors of species relative abundance turnover between sampling periods. Models were generated in a stepwise procedure. We evaluated the best models by balancing the number of predictors and each predictor's contribution to an overall cross-validated  $R^2$  ( $xR^2$ ) value. A predictor was added to the model if it increased the  $xR^2$  by at least 0.03. Sensitivity of each predictor is used to

identify the importance of each predictor with regards to its influence on the response variable. Sensitivity is the ratio of the relative mean difference in the response variable to the relative mean difference in the predictor. Therefore, a sensitivity of 1.0, reveals that a 5% change in the predictor would on average result in 5% change in the response variable (McCune 2006).

The relative abundance turnover between pairs of sampling periods was defined as the magnitude of understory relative canopy cover change within a plot between two sampling periods. For example, in order to calculate relative abundance turnover between the July 2012 and July 2013 sampling periods: 1) The complete species matrix was first relativized by row totals to get plots on equal footing with respect to total species cover; 2) Each sampling period was subset from the complete species matrix (120 plots by 259 species after deletion of rare species) resulting in two separate matrices (30 plots by 259 species), one corresponding to the 2012 sample period and the other representing the replicate 2013 sample period; 3) The 2013 species matrix was subtracted from the 2012 species matrix resulting in a new matrix (30 plots by 259 species) with differences in relative cover contained within each cell; 4) row totals were calculated by summing the absolute values of all cells within each row of the new matrix; 5) the final (relative abundance turnover) matrix consisted of 30 rows corresponding to plots and one column containing the total relative abundance turnover within each plot over that time period. Relative abundance turnover was calculated using the same method for intra-annual sampling (June, July, and August, 2013). However, because there were three different pairs of sampling periods, the resulting matrix dimensions were 30 plots by 3

columns, with each column containing the relative abundance turnover corresponding to one of three different pairs of sample periods [one (July-June); two (August – June); and three (August – July)].

## RESULTS

A total of 326 vascular plant species were observed within 150 subplots (2 m x 10 m) across all sampling periods. The species pool consisted of 254 native species including: eight conifers, 36 shrubs and deciduous trees, 29 graminoids, and 181 forbs. Approximately 22% (72 out of 326) of the total species pool was composed of non-native taxa including: 49 forbs, 21 graminoids, one deciduous tree, and one shrub species. The average species turnover between sampling periods was 27% and ranged from 20% between July 2013 and August 2013 to 32% between July 2012 and August 2013. Species richness ranged from 238 (73% of total pool) in August, 2013 to 264 (81% of total pool) in June 2013. Non-native species richness was highest (64) in July 2012, and ranged from 56 (August 2013) to 62 (June 2013) within one growing season (Figure 3.1). Native species richness was lowest (182) in August 2013 and highest (202) within the June 2013 sampling period (Figure 3.1). A total of 138 native taxa (54% of native pool) and 50 non-native taxa (67% of non-native pool) were persistent throughout all sampling periods (Figures 3.1). Approximately 9% (7 out of 75) of non-native species were unique to a specific sampling period compared to 17% (44 out of 254) of native species (Figure 3.1). The highest occurrence of unique species occurred during the early season (June 2013) sampling period (Figure 3.1).

Most common species (occurring in > 5% of subplots within any sampling period) were persistent throughout all sampling periods (Tables 3.2 and 3.3). Only six out of 89 (7%) common native species were absent in one or more sampling periods including an early season, lowland annual (*Clarkia pulchella*), and four mid to late summer montane/subalpine perennials (*Galium triflorum*, *Symphyotrichum cusickii*, *Symphyotrichum foliaceum*, *Agrostis scabra*; Table 3.3). Two common non-native species (*Bromus hordeaceus* and *Sanguisorba minor*) were not persistent (Table 3.2). *Bromus hordeaceus* was commonly observed throughout the 2013 season within lowland sites, but was not found during the July 2012 sampling period (Table 3.2). *Sanguisorba minor*, was common in August 2013 and was not found during the July 2012 or the June 2013 sampling periods (Table 3.2). Field observations indicated that *Sanguisorba minor* began to germinate in July 2013 along lowland roadsides and germinated later into August along montane roadside plots. Most native and non-native species unique to a particular sampling period were rare throughout the study area (Tables 3.2 and 3.3). Approximately 93% (41 out of 44) of unique native species and 86% (6 out of 7) of unique non-native species were found in three or less subplots (Tables 3.2 and 3.3). Two common species (*Lomatium triternatum*, *Asperugo procumbens*) were unique to the early season (June 2013) sampling period in 2013 (Tables 3.2 and 3.3).

### Community gradients

The two dimensional ordination of sample units in species space represented 85.5% of the variation in the distance matrix with 66.6%, and 18.9% represented by Axes 1 and 2 respectively (final stress = 11.5, final instability <  $10^{-5}$ , iterations = 83; Figure

2A). The randomization test indicated that the two dimensional NMS ordination was extracting stronger axes than would be expected by chance ( $p = 0.004$ ). The strongest correlations between environmental variables and species composition were found along axis 1. Percent silt ( $r = 0.938$ ), available water capacity (AWC) ( $r = 0.870$ ), and elevation ( $r = 0.755$ ) exhibited strong positive correlations with axis 1 (Table 3.4). Percent clay ( $r = -0.887$ ) had a strong negative correlation with axis 1 (Table 3.4). Average minimum annual temperature ( $-0.648$ ), temperature difference between the mean warmest month and the mean coldest month ( $r = -0.529$ ), and mean spring precipitation ( $r = 0.547$ ) were the environmental variables most highly correlated with axis 2 (Table 3.4). Two gradients are evident in Figure 3.2A: 1) there is a gradient most likely associated with plant water availability where plots with less available water are located low (left-side) along axis 1 and plots with high water availability are located high (right-side) along axis 1. Interactions between soil texture and climatic factors including increased silt content, increasing precipitation with elevation gain, and reduced evaporation with decreasing temperature all increase plant available water; and 2) there is a climate gradient along axis 2 where plots with higher temperatures, more extreme temperature variability, and lower spring precipitation occurred low along axis two, while plots with cooler temperatures, reduced temperature variability, and increased spring precipitation were located high along axis 2. The separation of the cooler and wetter subalpine forests and the warmer and drier montane forests is evident mid-way along axis 2 (Figure 3.2A).

Non-native species richness ( $r = -0.854$ ) and all non-native species trait categories had moderate to strong negative correlations with axis 1 and weak negative correlations

with axis 2, indicating a tendency for non-native species to be positively associated with clayey soils, decreased water availability, and increased seasonal temperature variation (Figure 3.2B). In contrast, native species richness ( $r = 0.772$ ), native perennial forb abundance ( $r = 0.880$ ) and native shrub abundance ( $r = 0.764$ ) had moderate to strong positive correlations with axis 1 and weak negative correlations with axis 2 (Figure 3.2B). Native perennial grass abundance showed a weak positive relationship ( $r = 0.317$ ) with axis 1 and a moderate negative association with axis 2 ( $r = -0.545$ ), revealing a tendency for high native perennial grass abundance within warmer and moderately wet montane forests (Figure 3.2B). Similar to non-native species, native annual forbs were associated with lowland communities (Figure 3.2B) as evident from a moderate negative correlation ( $r = -0.612$ ) with axis 1 and a weak negative relationship with axis 2 ( $r = -0.142$ ).

### Intra-annual community change

There was strong evidence that understory plant species composition changed as a function of sampling period within one growing season ( $A = 0.03$ ,  $p < 0.001$ , MRBP; Table 3.5). Pairwise comparisons revealed significant differences in species composition between each sampling period (Table 3.5). Within group homogeneity ( $A$ ) was low for all sampling periods and ranged from 0.025 for the June to July transition to 0.034 for the July to August transition (Table 3.5).

Intra-annual differences in species composition were identified for all trait categories except native shrubs within the lowland zone (Table 3.6). The strongest compositional shifts in the lowland community were associated with non-native annual

forbs ( $A = 0.15$ ; Table 3.6) and non-native annual grasses ( $A = 0.09$ ; Table 3.6). Within the montane zone, all native trait categories, non-native perennial forb and non-native perennial grass composition changed over the growing season where native annual forbs showed the largest effect size ( $A = 0.11$ ; Table 3.6). In the subalpine zone, native annual forb, native perennial grass, and native perennial forb composition differed among sampling periods (Table 3.6). Within-group homogeneity was low for all categories in the subalpine zone where significant effect sizes ( $A$ ) ranged from 0.03 for native perennial forbs to 0.08 for native perennial grasses (Table 3.6).

June had more ( $n=21$ ) indicator species than July and August (Table 3.7). Indicator species for the June sampling period consisted of a relatively equal mix of perennial ( $n = 9$ ) and annual ( $n = 12$ ) species (Table 3.7). All native indicator species in June were forbs where annuals were primarily found in the lowest elevation lowland and montane sites and perennial indicators were most abundant in the wetter montane and subalpine communities (Table 3.7; Figure 3.3). Approximately 40% (8 out of 21) of June indicators were non-natives consisting of four annual forbs, two annual grasses, and two perennial forbs (Table 3.7). Annual non-native June indicators were concentrated in the lowest elevation sites associated with lowland, grass/shrub communities and within dry montane forested sites (Figure 3.4). Perennial non-native June indicators were found primarily in the montane and subalpine zones. *Taraxacum officinale* was the most widespread non-native early season indicator species, as it occurred in all three mountain zones with maximum abundances within dry montane sites and in wet forested plots spanning from warmer montane sites to the cooler subalpine transition zone (Table 3.2;

Figure 3.4). *Veronica serpyllifolia* was the only non-native June indicator species found primarily in the subalpine zone (Figure 3.4). Twelve indicator species were identified in July (Table 3.7). Most native indicators for this period were perennial species and occurred in each of the three mountain zones (Figure 3.3). In contrast to the June sampling period, native perennial grass species (*Festuca idahoensis* and *Bromus marginatus*) were among the July indicators. Consistent with field observations, *Gayophytum diffusum*, which expressed an outbreak along lower subalpine roadsides in July was the only native annual indicator for this time period (Table 3.7; Figure 3.3). Three non-native annuals (*Bromus arvensis*, *Lactuca serriola*, and *Stellaria media*) were located primarily in lowland sites, and two perennial non-natives (*Cirsium arvense* and *Trifolium repens*) were most abundant in the montane zone during July (Table 3.7; Figure 3.4). August had the fewest indicator species (n=7; Table 3.7). The strongest indicators included two montane understory perennial grasses (*Bromus vulgaris*, *Agrostis scabra*), and *Galium triflorum*, a mid- to high-elevation, open forest, perennial forb (Table 3.7; Figure 3.3). Three non-native species were August indicators including: *Bromus racemosus*, an annual grass found primarily in lowland sites; *Sanguisorba minor*, a late season perennial forb that was primarily found along roadsides in lowland and dry montane areas; and *Plantago major*, a perennial forb that occurred along montane roadsides (Table 3.7; Figure 3.4).

Temporal trajectories varied widely across mountain zones (Figures 3.2C-D; Figure 3.5). Many lowland plots reverted towards early season (June) community space as the season progressed (Figure 3.2C –D; Figure 3.5). In contrast, montane and



subalpine plots shifted in a consistent direction throughout the growing season, though montane and subalpine plots shifted in different directions from each other (Figure 3.5). Visual comparisons of early and late season convex hull overlays showed contraction of plots in ordination space along both axes, revealing a potential decrease in species composition variability over the entire study area as the season progressed (Figure 3.2D). According to one-way ANOVA, vector lengths did not differ between mountain zones over the measured growing season (June to August;  $p = 0.26$ ), or the late season period ( $p = 0.28$ ), while the early season showed a weak difference ( $p=0.06$ ). Vector lengths differed across sampling periods within each zone. Vectors were longer during the early season for both lowland ( $p=0.02$ ) and montane ( $p=0.01$ ) zones indicating greater shifts in community composition from June to July than July to August. July to August vectors were longer than June to July vectors ( $p=0.01$ ) for the subalpine zone.

Total species richness, the Julian date on which the frost free period ended (eFFP), and whether or not a plot was considered a roadside plot (road) were the strongest predictors of early season turnover in relative abundance, explaining 85% of the variation in turnover between June and July. Total species richness was the most important predictor (sensitivity = 0.292) followed by eFFP (0.110), and road (0.008). Early season turnover was positively related to total species richness and increased with decreasing eFFP where species richness was highest (Figure 3.6). Early season turnover was greatest within roadside plots when species richness was high and low, however, proximity to road appeared to have less influence on vegetation turnover in plots with moderate species richness (Figure 3.6). Total species richness and percent sand were the

best predictors of late season relative abundance turnover, explaining 85% of the variation in relative species abundance difference between the July and August sampling periods). Total species richness was the strongest predictor (sensitivity = 0.465) followed by percent sand (0.149). Similar to early season observations, species relative abundance change was greatest at sites with high total species richness (Figure 3.6). The importance of sand suggests complex interactions between relative abundance change and soil characteristics along the species richness gradient (Figure 3.6). It is important to note that the addition of percent sand as a predictor had a small effect on the model fit and only increased the  $xR^2$  value from 0.82 to 0.85. Total species richness and canopy openness were the most important predictors of relative abundance change over the entire growing season, explaining 71% of the variation in relative species abundance turnover from June to August. Total species richness was the most important predictor (sensitivity = 0.423) followed by canopy openness (0.053). Consistent with both the early and late season patterns, relative abundance change over the entire growing season was associated with high total species richness (Figure 3.6). More open canopies had greater relative abundance change over the growing season where species richness was low to moderate and had little effect on relative abundance change at sites with high total species richness (Figure 3.6).

For each sample period transition, total species richness was the most important predictor of species relative abundance change between sampling periods. Three dimensional contour plots revealed that total species richness was highest in the drier, low elevation montane forests corresponding to an overlap between moderate levels of

non-native and native species richness and in wet montane forests where native species richness was the highest (Figure 3.7A-C). Turnover in species relative abundance patterns were similar to total species richness particularly later in the season (Figure 3.7). Early season relative abundance turnover occurred primarily within warmer montane forested sites with high species richness (Figure 3.7D). Relative abundance turnover increased at the highest subalpine sites during the late season transition (Figure 3.7E). Throughout all sampling period transitions, relative abundance change was lowest at the upper montane to subalpine transition located at the center of the ordination space (Figure 3.7E-F). These sites supported the lowest diversity in our study area (Figure 3.7A), and consisted of closed canopy, *Abies grandis* dominated over-story with a thick duff layer and few native forb species (*Linnaea borealis*, *Chimaphila umbellata*, *Goodyera oblongifolia*, and *Carex geyeri*) with frequent unoccupied space between individual plants.

### Inter-annual community change

Understory plant species composition differed between years (MRBP:  $A = 0.04$ ,  $p < 0.001$ ; Table 3.5). Pairwise comparisons revealed significant differences in species composition between year 1 (July 2012) and each sampling period during year 2 (June, July, and August 2013; Table 3.5). Within group homogeneity ( $A$ ) ranged from 0.03 for the July 2012 to June 2013 transition to 0.05 for the July 2012 to August 2013 transition. Sampling during year 1 occurred during a two week period (July 2 – 16) that fell between the early (June 18 – July 8) and mid-summer (July 18 -31) sampling periods during year 2. Therefore, inter-annual comparisons were only made between year 1 and the early and

mid-summer sampling periods and the late season (August 2013) sampling period was excluded from further analysis. Lower within-group homogeneity for the July 2012 to June 2013 (0.03) transition compared to the July 2012 to July 2013 (0.05) transition indicated that overall study area composition in year 1 was more similar to the early (June) sampling period compared to the mid-summer (July) sampling period in year 2 (Table 3.5).

Inter-annual changes in species composition were identified for all trait categories in the lowland zone (Table 3.8). However, the specific trait categories that differed between year 1 (July 2012) and year 2 (June or July 2013) depended on whether the year 1 sampling period was being compared to the June or July sampling period of year 2. Three trait categories (non-native annual forbs, non-native annual grasses, and native annual forbs) showed relatively consistent changes in species composition when comparisons were made between year 1 and both the June and July sampling periods of year 2 respectively. The strongest compositional differences were associated with non-native annual grasses ( $A = 0.24$ ) and native annual forbs ( $A = 0.13$ ; Table 3.8) in the lowland zone. Native perennial forb, native shrub, and non-native perennial grass communities did not differ when year 1 was compared to June of year 2, but did differ when year 1 was compared to the July sampling period of year 2 (Table 3.8). In contrast, the non-native perennial forb community did differ between the year 1 and June sampling period of year 2, but was not different when year 1 was compared to the July sampling period of year 2 (Table 3.8).

Inter-annual compositional shifts were detected for all native trait categories in the montane zone (Table 3.8). Native perennial grass, native perennial forb, and native shrub communities differed when the year 1 sampling period was compared to both the June and July sampling periods of year 2. Native annual forbs only differed between year 1 and the July sampling period of year 2 in the montane zone. Native perennial grasses ( $A = 0.13$ ) and native perennial forbs ( $A = 0.11$ ) showed the strongest shifts over both time periods and changed the most when year 1 was compared to the July sampling period of year 2 (Table 3.8). All native trait categories showed significant inter-annual composition change in the subalpine zone (Table 3.8). The strongest compositional shifts were associated with native perennial forbs ( $A = 0.15$ ) and native perennial grasses ( $A = 0.09$ ) which both showed the greatest change when year 1 was compared to the July sampling period of year 2 (Table 3.8). Native shrub composition differed when year 1 was compared to June but not when compared to July of year 2 in the subalpine zone (Table 3.8).

Mean log abundance for non-native perennial grasses within the lowland zone was greater in July, 2013 than in July 2012 but not different from the June or August, 2013 sampling periods (Figure 3.8). Non-native annual grass richness in the lowland zone was lower in July, 2012 when compared to both the July and August 2013 sampling periods and non-native annual forb and native perennial grass richness in lowland plots were greater during the July 2012 sampling period when compared to the August 2013 sampling period (Figure 3.8).

When year 1 was compared to the early (June) sampling period in year 2, indicator species analysis revealed 11 indicator species for year 1 compared to 20 for year 2 (Table 3.9). Indicator species for both years were found in all three mountain zones and consisted of mostly perennial species (Table 3.9, Figure 3.9). The three strongest indicators for year 1 were native perennial grasses including: *Bromus marginatus*, a widely distributed species in our area, primarily found in montane and subalpine sites (Figure 3.9); *Elymus glaucus*, a lowland and montane species that showed a substantial reduction in frequency of occurrence between year 1 and year 2 (Table 3.3; Figure 3.9); and *Poa secunda*, a bunchgrass that was common in lowland and montane sites during year 1, but rare throughout the study area during year 2 (Table 3.3; Figure 3.9). Three non-native species primarily found in montane sites (*Cynoglossum officinale*, *Plantago lanceolata*, and *Trifolium repens*) were identified as indicator species for year 1 (Table 3.9; Figure 3.9). The strongest indicators for year 2 (*Viola glabella*, *Hieracium albiflorum*, *Taraxacum officinale*, and *Arnica cordifolia*) were dominant in montane forests with high plant water availability (Table 3.9; Figure 3.9). Non-native indicators for year 2 included two annual lowland species (*Asperugo procumbens*, and *Bromus hordeaceus*), one biennial lowland forb (*Cichorium intybus*), and two perennial early season species (*Taraxacum officinale* and *Festuca rubra*) (Table 3.9; Figure 3.9).

Comparisons of occurrence frequency within subplots for indicator species that separated year 1 and June of year 2 sampling periods revealed two patterns that helped to explain differences in species composition between years. The first pattern was that several indicator species suggested compositional differences that reflected clear

differences in species phenology between years. For example, year 2 indicators included late spring and early summer species (*Taraxacum officinale*, *Arnica cordifolia*, *Galium aparine*, *Potentilla gracilis*, and *Asperugo procumbens*) and mid to late summer species (*Trifolium repens*, *Madia sativa*, *Bromus marginatus*, and *Microseris nutans*) were more common during year 1 (Tables 3.2 and 3.3). The second pattern was that many indicator species showed substantial changes in occurrence frequency between years that did not appear to be related to seasonality. For example, five species (*Elymus glaucus*, *Poa secunda*, *Cynoglossum officinale*, *Plantago lanceolata* and *Luzula multiflora*) showed greater than 40% reductions in occurrence frequency between year 1 and all sampling periods during year 2 (Tables 3.2 and 3.3). Similarly, *Viola glabella*, *Hieracium albiflorum*, *Madia gracilis*, *Sorbus scopulina*, *Festuca rubra*, and *Trisetum canescense* occurrence frequencies increased by more than 40% from year 1 to all sampling periods during year 2 (Tables 3.2 and 3.3). Two year 2 indicator species including a non-native annual grass (*Bromus hordeaceus*) and a montane to subalpine perennial native forb (*Symphotrichum foliaceum*) were both common during year 2 but not found during year 1.

Indicator species analysis revealed 16 indicator species for year 1 compared to 24 for the July sampling period for year 2 (Table 3.10). Year 1 native indicators were distributed throughout all three mountain zones whereas the strongest native indicators for year 2 were concentrated in wet montane and subalpine sites (Figure 3.10). Only one early season non-native annual grass (*Bromus tectorum*) was an indicator of year 1 and six non-native species including annual and perennial species in both lowland and

montane sites were indicators for year 2 (Table 3.10; Figure 3.10). Similar to comparisons between year 1 and June of year 2 sampling periods, both species seasonality and inter-annual shifts in species occurrence appeared to explain most of the separation between indicator species between year 1 and July of year 2 sampling periods. Early season species (*Ranunculus uncinatus*, *Galium boreale*, *Clarkia pulchella*, *Collinsia parviflora*, *Melica subulata*, and *Bromus tectorum*) were indicator species for year 1 where mid to late season species (*Galium triflorum*, *Bromus vulgaris*, *Polygonum douglasii*, *Cirsium arvense*, and *Solidago canadensis*) were indicators of year 2 and suggested earlier season community characteristics during July of year 1 compared to July of year 2 (Table 3.10). Comparisons of subplot occurrence frequencies for strong indicator species revealed that many species (*Hieracium albiflorum*, *Viola glabella*, *Orthilia secunda*, *Trisetum canescens*, *Sympyotrichum ascendens*) were found in > 30% more subplots during all sampling periods in year 2 compared to year 1, and other species (*Elymus glaucus*, *Poa secunda*, and *Luzula multiflora*) were found in > 45% more subplots in year 1 compared to year 2 (Tables 3.2 and 3.3).

Inter-annual temporal trajectories varied between mountain zones and were relatively consistent when comparing year 1 to both the early (June) and mid-summer (July) sampling periods during year 2 (Figure 3.5). Contrasting lowland and subalpine trajectories revealed a potential divergence in understory community composition along axis 1 between years (Figure 3.5). Inter-annual lowland and montane trajectories were similar to early season lowland trajectories during year 2, and most subalpine trajectories were moving opposite to both early and late season trajectories in year 2 (Figure 3.5).



Vector lengths did not differ across mountain zones between years for either comparisons between year 1 and the early summer period of year 2 ( $p=0.22$ ; one-way ANOVA), or between year 1 and the mid-summer period of year 2 ( $p = 0.39$ ; one-way ANOVA) indicating similar variation in understory species composition within each zone over time. Vector lengths also did not differ within mountain zones when compared between different inter-annual periods ( $p > 0.05$ ; one-way ANOVA) indicating that similar shifts in species composition occurred within each mountain zone for both the year 1 to June of year 2 transition and the year 1 to July of year 2 transition.

Total species richness and aspect index were the strongest predictors of inter-annual species relative abundance change, explaining approximately 41% of the variation in relative abundance turnover between July 2012 and June 2013. Total species richness was the most sensitive predictor (sensitivity = 0.48) followed by aspect index (0.09). Relative abundance turnover was positively associated with total species richness and increased with lower aspect index (Figure 3.11). Aspect index ranged from 0 to 1 where 0 indicated SSW exposure and 1 indicated NNE exposure. Higher turnover with lower aspect index indicated that sites that warm up and dry out faster had higher turnover between years. A three dimensional plot of relative abundance turnover in ordination space revealed that most vegetation change occurred within warm montane plots (Figure 3.11). Total species richness, distance from the road, and mean annual minimum temperature were the strongest predictors of inter-annual species relative abundance turnover between July 2012 and July 2013, explaining 48% of the variation in relative species abundance change between years. Total species richness was the most important

predictor (sensitivity = 0.179), followed by mean annual minimum temperature (0.120), and distance from the road ( $< 0.0001$ ). Inter-annual relative abundance change was greatest within roadside plots and increased with higher total species richness (Figure 3.11). The greatest change in relative abundance corresponded to sites with high mean annual minimum temperatures and high species richness (Figure 3.11). Similar to comparisons between the year 1 and June of year 2, most relative abundance turnover occurred within the warm montane forests, however, turnover within the higher elevation, wetter montane forests occurred when year 1 was compared to the mid-summer period in year 2 (Figure 3.11).

## DISCUSSION

Understory vascular plant species changed in composition both between years (July 2012 to June 2013 and July 2012 to July 2013), and between sampling periods (June, July, and August 2013) within one growing season. Consistent with other studies, total species richness increased with the number of sampling efforts (Kirby et al. 1986; Ristau et al. 2001; Pokorny et al. 2004; Archaux et al. 2006), widely distributed species were consistently recorded throughout all sampling periods, and rare species were more likely to occur in a specific sampling period (Klimes et al. 2001; Ristau et al. 2001; Kercher et al. 2003). These differences are likely due to a combination of both sampling error and real community changes. At least some of the real changes appear to be phenological responses to inter- and intra-annual climatic variation.

Pseudo-turnover of species during repeat vegetation sampling is a product of overlooking species, species misidentification, and inconsistencies of plot relocation. We

observed turnover rates of 20% to 32% between sampling periods that were consistent with pseudo-turnover rates reported for single observer comparisons in similar systems (Leps and Hadincova 1992; Scott and Hallam 2002; Gray and Azuma 2005; Vittoz and Guisan 2007). Researchers that used teams of two or more observers for plot estimates like our study, often report lower pseudo-turnover rates between 10% and 20% (Nilsson and Nilsson 1983; Kercher et al. 2003; Vittoz et al. 2010). While we could not separate sampling error from true species turnover, we expect that sampling error for our study was no less than that reported by other researchers and contributed to at least 10% of the observed species turnover. Given the large environmental gradient covered in our study area, higher sampling error values closer to 20%, similar to those observed by Gray and Azuma (2005), may be more realistic.

Our finding that rare species showed the greatest turnover between sampling periods is consistent with other research and suggestive that overlooking species likely contributed to the increased rate of rare species turnover in our study area. Rare species are often the primary source of pseudo-turnover when sampling vegetation plots because species with low cover are easily missed during some sampling efforts and the chance of capturing rare species increases with multiple samples (Gray and Azuma 2005, Archaux et al. 2006). Kercher et al. (2003) found that species in the lowest cover class ( $< 0.5\%$ ) accounted for 16 times greater pseudo-turnover than species with cover  $> 8\%$  in wetland communities. Similarly, Fischer and Stocklin (1997) discovered that the removal of rare species ( $< 0.5\%$  cover) from their dataset resulted in almost a 70% reduction of pseudo-turnover for vascular plant species over a 35 year period in a European grassland

community. It is likely that the disappearance and reappearance of *Geum triflorum*, *Agoseris grandiflora*, and *Triteleia grandiflora* was a result of overlooking these rare species during the July sampling period. Seasonal occurrences of rare perennial species that develop over a long growing season period in our area like *Senecio fremontii*, *Crepis atribarba*, and *Heuchera micrantha* during the 2013 growing season may also have resulted from overlooking these species during most sampling periods rather than actual species turnover.

Changes in morphological characteristics that result in identification disagreement between sampling periods and inconsistencies in plot relocation are other potential sources of error. For example, the isolated occurrences of *Juncus parryi*, *Lupinus argenteus*, *Eriogonum marifolium*, and *Luzula arcuata* may reflect differences in phenological development that influenced the difficulty of species identification during particular sampling periods. These species can be difficult to separate from other more common species sharing the same genus in the Wallowa Mountains, and were likely overlooked or lumped with other species when not at the full reproductive stage. Additionally, inconsistency of plot relocation changes plot boundaries and often leads to the complete exclusion of rare species (Kercher et al. 2003). Because permanent markers were only placed at the ends of each plot (spaced 50 meters apart), exact placement of plots through time was improbable particularly in species rich sites with dense understory vegetation. Therefore, it is possible that plot relocation errors coupled with high habitat heterogeneity within species rich forested plots contributed to the turnover that we observed within these plots. The placement of road plots (parallel to and  $\leq 2$  meters from

road) was more repeatable because the transition to road-side vegetation marked one side of the plot boundary. Although plot relocation errors were probably higher within species rich plots, we believe that similar patterns of increased relative abundance turnover for both road and off-road plots with increasing species richness were evidence of a direct relationship between species richness and true species turnover in our study area.

Despite potential sampling error effects, clear patterns of seasonality between species abundances were evident. Vernal and early summer species (*Collinsia parviflora*, *Galium boreale*, *Ranunculus uncinatus*, and *Clarkia pulchella*) were among the strongest indicators for the early summer (June) sampling period for Year 2, and species that maximize growth during the mid to late growing season (*Galium triflorum*, *Bromus vulgaris*, *Cirsium arvense*, and *Viola orbiculata*) in our area were most abundant during July and August during Year 2. Previous research in temperate ecosystems suggests that vegetation sampling that coincides with peak biomass production often underestimate species richness and the distributions of early season vascular plant species (Holland 1971; Ristau et al. 2001; Tremblay and Larocque 2001; Pokorny et al. 2004). We detected a similar pattern, as greater species richness and higher numbers of indicator species were associated with the early (June) summer sampling period. Higher species richness in June was likely a result of an overlap between early season species and species that maximized growth in the mid to late summer period. Continuous declines in species richness and number of indicator species with increasing calendar date were

observed and indicate that late season sampling may fail to capture or underestimate the distribution of early season species in the Wallowa Mountains.

Some differences in indicator species between years could be explained by seasonal differences in peak abundances. Early season species (*Taraxacum officinale*, *Arnica cordifolia*, *Galium aparine*, and *Asperugo procumbens*) were indicators of June 2013 and mid to late summer species (*Bromus marginatus*, *Trifolium repens*, *Microseris nutans*, and *Cynoglossum officinale*) were indicators of Year 1. In contrast, when the year 1 sampling period was compared to the mid-summer (July) sampling period of Year 2, Year 1 had higher abundances of early season species (*Ranunculus uncinatus*, *Galium boreale*, *Clarkia pulchella*, *Collinsia parviflora*, and *Bromus tectorum*), and mid to late season species (*Galium triflorum*, *Solidago canadensis*, *Cirsium arvense*, *Polygonum douglasii*) were more abundant during Year 2. These results suggest that community phenology in most of our study area was likely in the earliest stages during June of year 2, followed by July of Year 1, and then July of Year 2, and are consistent with the calendar date order for each of the sampling periods.

Another consistent inter-annual pattern regardless of whether the Year 1 community was being compared to the June or July sampling period during Year 2 was that many species (*Hieracium albiflorum*, *Viola glabella*, *Anemone piperi*, *Bromus vulgaris*, *Orthilia secunda*, *Sorbus scopulina*, and *Goodyera oblongifolia*) found within wet montane and subalpine sites were more abundant during Year 2. Apparent increases of upper montane and subalpine species in year two could have resulted from differences in species phenology between years, true species turnover, or sampling error.

One potential explanation is that Year 1 had a later start to the growing season than in Year 2. This is consistent with cooler and wetter conditions during the spring and early summer period during Year 1 (See Appendix A, Figure 3.A1). A later start to the growing season in Year 1 compared to Year 2 is contradictory to other seasonal patterns for species primarily in the lowland and montane zones. However, inter-annual differences in snowpack and timing of snowmelt at higher elevation and closed canopy montane sites could explain the contrasting direction of shift in species phenology between different mountain zones.

Increased observer experience related to the identification of mid-to high elevation species may also explain greater abundance of some high montane species during Year 2. For example, *Abies lasiocarpa* and *Abies grandis* were indicator species that contributed to community differences between Year 1 and June of Year 2. Because our sampling protocols only estimated abundance of the understory vegetation, it is plausible that seedling turnover was responsible for inter-annual abundance differences between these two species. However, investigation of relative abundance change and frequency of occurrence for these two species indicated that decreased abundance of *Abies grandis* from Year 1 to Year 2 was coincident with increased abundance of *Abies lasiocarpa* primarily within the montane to subalpine transition zone (See Appendix A, Figure 3.A2). The low occurrence of *A. lasiocarpa* during Year 1 coupled with relatively consistent occurrence for this species throughout Year 2 suggest that observer ability to distinguish between *A. grandis* and *A. lasiocarpa* within the montane to subalpine transition zone improved between years. Our finding that these two common species we

considered easy to identify were often confused during Year 1 was surprising but consistent with Scott and Hallam's (2002) research that found the highest misidentification rates for trees and shrubs when looking at sampling error for vascular plant abundance measurements across a wide range of terrestrial habitats in the United Kingdom. These results reveal a potential lack of focus on species considered to be easily identified in our region during pre-sample training. It is likely that training over-emphasized the identification of challenging species and resulted in observer confusion and a reluctance to seek help when species considered less challenging to identify were encountered. It is also possible that a greater abundance of younger age class tree seedlings and saplings within the montane to subalpine transition due to recent wind-throw increased misidentification rates of these species.

Approximately 25% of non-native species showed tendencies towards specific sampling periods within one growing season. Most non-native indicator species were found in June and were primarily annual species located in lowland, grass/shrub habitats. Consistent with previous studies, most non-native species including all non-native trait categories identified were concentrated in the lowest elevation sites (Alexander et al. 2009; Barni et al. 2012). Therefore, it was not surprising that most non-native indicators were also found in lowland plant communities. Historically, lowland sites in our study area would have likely been dominated by native perennial bunchgrasses including *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Poa secunda*. These sites are currently dominated by introduced annual grasses including *Ventenata dubia* and *Taeniatherum caput-medusae* and are located within fenced cattle pastures. The apparent



low resistance of Pacific Northwest bunchgrass communities to annual grass invasions has been attributed to early overgrazing practices coupled with the introduction of pre-adapted species (Mack 1981; Johnson 1994; Wisdom and Chambers 2009). Continued disturbance, proximity to adjacent croplands and roads, and high propagule pressure are also thought to increase the persistence of high non-native species pools within bunchgrass communities (Corbin and D'Antonio 2004; Thomsen et al. 2006; Davies et al. 2013).

The tendency for early season non-native annuals to occupy lowland bunchgrass communities is related to the timing of water availability and life history traits. Plant available water is abundant shallow in the soil profile early in the growing season and becomes limiting in a typical year between mid to late summer (Johnson and Swanson 2005; Vavra et al. 2005). Introduced ruderal species are able to rapidly develop and capture resources prior to the development of native perennial species in these communities. Inter- and intra-annual precipitation and temperature can be highly variable in the Wallowa Mountains and result in shifts in the timing of available water resources and annual plant growth in the region. Our results indicated that non-native annual forb and non-native annual grass composition within the lowland zone had the highest intra-annual variation compared to all other trait categories and non-native annual grasses in lowland sites showed the greatest inter-annual composition change. Despite higher intra-annual variability for non-native annual forbs compared to native annual forbs in the lowland zone, native annual forbs had higher variation between years. The observed increase in native forb variability compared to the non-native forb community

appeared to be a result of large shifts in population density for a couple of species including *Clarkia pulchella* and *Madia gracilis*, and isolated occurrences of a few rare species including *Blepharipappus scaber*, *Cryptantha simulans*, and *Mimulus guttatus*. In contrast, non-native annual species appeared to be more stable between years, although frequency of occurrence and abundances of early season annual non-native forbs were higher during year 1 and likely reflected a later spring onset that year. It is important to note that disturbance factors like grazing have strong influences on species composition in grassland communities. Interactions between grazing and weather patterns are important in the Wallowa Mountain system, and may help to explain some of the variability in species distributions that we observed in lowland sites.

Kimball and Schiffman (2003) found that timing and intensity of grazing was important for determining competitive abilities between native and non-native forbs and grasses in California grasslands. Recovery from grazing was higher for low statured non-native annual forbs with indeterminate growth like *Erodium cicutarium* when compared to upright, determinate, native annual forbs (Kimball and Schiffman 2003). We observed greater cover of non-native perennial grasses during year 2 which was consistent with field observations where lower intensity grazing was noted for that year. A delayed growing season in year 1 may have resulted in grazing the lowland plant communities at an earlier phenological state, and could have suppressed recovery of sensitive, upright native annual forbs like *Clarkia pulchella*, resulting in lower populations the following year. This may also explain why *Poa secunda* was common in year 1 and rarely encountered during year 2. *Poa secunda* is generally thought to increase with grazing

pressure in native bunchgrass communities (Majerus et al. 2009). However, at least one study suggests that early season grazing can substantially reduce *Poa secunda* cover the following season (Kimball and Schiffman 2003). Future research may consider investigating the responses of *Poa secunda* to timing of grazing in annual grass invaded bunchgrass communities in the Wallowa Mountains. Other factors related to variations in population dynamics, reproductive success, competitive interactions, and temporal niche partitioning may be related to observed inter-annual patterns of native and non-native annual forb community changes in lowland sites. Regardless of specific drivers, contrasting variability of non-native annual forbs and native annual forbs suggests that direct or indirect influences of inter-annual climatic variation may differentially affect the phenology and abundances of these trait categories. These observations are consistent with other studies that reported differential phenological and functional trait responses between native and non-native forbs as a function of changing environmental and disturbance factors (Milberg et al. 1999; Wolkovich and Cleland 2011; Scharfy et al. 2011; Pearson et al. 2012).

Non-native indicator species were also identified in montane and subalpine communities and included widespread species including *Taraxacum officinale* and *Cirsium arvense*. Consistent with most montane and subalpine native indicators, non-native indicators in these communities were all perennial species. High elevation invaders particularly within subalpine and alpine communities are rare in mountain ecosystems (McDougall et al. 2009). Early season growth of many high elevation species differ from lowland species where timing of snow-melt and rate of temperature

change are often more important than average air temperature or photoperiod for initiating vegetative development (Inouye and McGuire 1991; Sparks and Menzel 2002; Lambert et al. 2010). Therefore, phenology of high elevation adapted non-native species may differ substantially from species found at lower elevation sites. *Veronica serpyllifolia* was the only non-native indicator species found primarily within the subalpine community. Despite a later start to the growing season for most vegetation in the subalpine zone, this species was most abundant during the early season (June 2013) sample period. Field observations indicate that *Veronica serpyllifolia* was producing seed during mid-June in our study area and therefore, almost at the end of its lifecycle. *Veronica serpyllifolia* is commonly associated with wet montane habitats fed by snow-melt in its native range (Birks 2007). Rapidly increasing temperature during early spring and timing of snowmelt are important triggers for high elevation adapted species like *Erythronium grandiflorum* in mountain ecosystems (Lambert et al. 2010), and may be important for initiating the development for high elevation adapted non-natives like *Veronica serpyllifolia* in the Wallowa Mountains.

Community composition change was greatest within the lowland and montane zones early in the season (between June and July), and later in the season (between July and August) within the subalpine zone. Delayed vegetation change at higher elevation sites was expected because of cooler and wetter conditions with increasing elevation. Despite an overall effect of increased vegetation change later in the season in the subalpine community, several native species including *Trautvetteria caroliniensis*, *Valeriana sitchensis*, and *Corallorhiza maculata* and two non-natives, *Veronica*

*serpyllifolia* and *Taraxacum officinale* were more abundant during the early season (June, 2013) sampling period. These observations indicate that some species in the subalpine zone show specialization to short and early growing seasons and that monitoring efforts focused on capturing peak biomass in this zone may underestimate the distributions of some species of interest.

Multivariate and indicator species analyses were more sensitive at detecting intra and inter-annual changes in species composition when compared to univariate comparisons of trait category abundances and richness. This was expected as univariate comparisons of trait categories relied on changes in aggregate community metrics (richness and total cover) which resulted in the loss of biological information.

Multivariate techniques (NMS and MRBP) as well as indicator species analysis were able to identify changes associated with individual species abundances despite smaller changes in overall community characteristics. Several trait categories showed compositional shifts over the growing season within each mountain zone. The largest composition shifts included non-native annual forbs and non-native annual grasses in the lowland zone and native annual forbs within the montane community and are consistent with other studies that show greater temporal variability among annual populations compared to species with multi-year life strategies (Legget et al. 2003; Wilson and Tilman 2003).

Perennial trait categories showed higher inter-annual variability compared to variation within one growing season. In general, annual trait categories that showed high inter-annual variability also had high variability throughout the 2013 growing season for

each mountain zone. MRBP revealed that some trait categories were more variable within the 2013 growing season compared to the year to year variation experienced during our study. For example the non-native annual forb community in the lowland zone and native annual forb composition within the montane zone changed more over the growing season when compared to inter-annual change. These observations are probably related to the stark contrast between abundant plant available water and low competition from perennial species early in the growing season and drought conditions with increased competition later in the summer compared to inter-annual variations between mid-summer (July) sampling efforts when water resources are typically just starting to become scarce.

Consistent with other research, temporal changes in species composition were greatest in plots with the highest total species richness (Cottingham et al. 2001; Bakker et al. 2003; Allan et al. 2011). These results supported indicator species analyses which identified montane species as the strongest indicators for each sampling period. Species richness was highest in the warmer montane forested sites where high species richness was a result of overlap between moderate numbers of non-native and native taxa at drier sites and high native richness at wetter sites. These sites were located between 1,260 and 1,350 meters and were characterized by high habitat heterogeneity due to mixed open and closed canopy forests, and high variability in slope, topographical shading, and soil moisture over short geographic distances. Dominant vegetation within these forests was highly variable and consisted of mixed open and closed canopy forests including *Pseudotsuga menziesii*, *Abies grandis*, *Pinus ponderosa*, and *Larix occidentalis* in the

over-story. In contrast to higher elevation sites, the mid canopy layer consisted of abundant tree and shrub species including *Acer glabrum*, *Holodiscus discolor*, *Amelanchier alnifolia*, *Ribes viscosissimum*, and *Sorbus scopulina*. The understory community was particularly diverse where lowland, montane, and high elevation grasses, sedges, and forbs overlapped including *Elymus glaucus*, *Bromus vulgaris*, *Carex geyeri*, *Luzula multiflora*, *Chimaphila umbellata*, *Anemone piperi*, *Epilobium brachycarpum*, and *Pedicularis racemosa*.

According to MRBP results, all native trait categories, non-native perennial forbs, and non-native perennial grasses showed changes in species composition within the montane zone. One way ANOVA did not reveal significant changes to trait category richness or log mean abundance in the montane zone despite heightened relative species abundance turnover in this zone. These results suggest that high species turnover and abundance changes of individual species may have been compensated for by increased abundance and entrance of other functionally similar species. For example early season montane annual species like *Collinsia parviflora* and *Claytonia perfoliata* were replaced by species like *Gayophytum diffusum* and *Gentianella amarella* later in the season. Similarly, declines in perennial forbs like *Galium boreale*, *Arnica cordifolia*, and *Ranunculus uncinatus* were synchronous with increased abundance of *Galium triflorum*, *Viola nutallii*, and *Plantago major*, and decreased mid-summer abundance of perennial grasses like *Bromus marginatus*, *Danthonia californica*, and *Festuca rubra*, were buffered by increases in *Agrostis scabra* and *Bromus vulgaris* in August in montane plots. In contrast, low elevation indicator species shifted from primarily annual species in the

early season to perennials in mid to late summer. High elevation sites also showed some replacement of functionally similar species including reduced abundance of perennial forbs including *Valeriana sitchensis*, *Trautvetteria caroliniensis* and *Corallorhiza maculata* early in the summer followed by increased abundance of *Potentilla glandulosa*, *Solidago canadensis*, and *Arnica parryi* late in the growing season. Similar, to the montane zone, most relative abundance turnover and functional replacement in the subalpine zone occurred where species richness was greatest. Our findings are consistent with research that shows increased species turnover and increased functional stability with higher species richness due to efficient temporal replacement of species with complementary traits (Cottingham et al. 2001; Allan et al. 2011). It is important to note that non-native perennial species such as *Taraxacum officinale*, *Plantago major*, and *Festuca rubra* expressed peaks of abundance in highly diverse plots that coincided with decreases in abundance of native species within the same trait categories. It is unclear if non-natives provide complementary traits that help stabilize community functioning when functionally similar native species abundance decreases. Further studies in the Wallowa Mountains may consider investigating the roles of temporal niche partitioning of functionally similar non-native and native species within high diversity montane communities.

### Management implications

We recommend that researchers and land managers should incorporate periodic sampling of vegetation communities during the growing season in mountain ecosystems to better estimate distributions of non-native vascular plants and their impacts on native



species composition over time. Specific goals of monitoring should be used to determine optimal sampling times. Monitoring efforts that target specific species or communities may require less sampling effort when compared to studies that cover large environmental gradients and aim to describe complete community change over time. For example, we found that abundance estimates of some non-natives such as *Ventenata dubia* and *Taeniatherum caput-medusae* were rather consistent throughout the growing season due to the retention of unpalatable and slow to decompose biomass after senescence. Other non-native species including *Erodium cicutarium*, *Sisymbrium altissimum*, and *Taraxacum officinale* showed substantial changes in abundance within one growing season, where frequency of occurrence decreased as the growing season progressed by 97%, 91%, and 31%, for *Erodium cicutarium*, *Sisymbrium altissimum*, and *Taraxacum officinale* respectively. Therefore, the timing of vegetation sampling during the summer may have little effect on estimation of abundance and distribution for some non-native species and be absolutely critical for capturing an accurate estimate of the presence and function for other invaders in this system.

We also recommend that studies that focus on the impact of non-native species on native plant populations should incorporate periodic sampling efforts even if the non-natives of interest maintain relatively consistent abundance throughout the growing season. For example, *Ventenata dubia* is a winter annual that uses shallow soil water resources early in the spring. Even though *Ventenata dubia* abundances are easy to capture at multiple times during the growing season, vernal native species with short growing seasons such as *Clarkia pulchella* are only detectable for a short window of

time, and are highly dependent on the same early season shallow soil water resources that *Ventenata dubia* uses. In order to truly assess impacts of plant invasions on native communities, efforts must be coordinated with intent to capture impacts on all life strategies.

Based on our results, we suggest that monitoring of vegetation composition along an elevation gradient in the Wallowa Mountains should be conducted at least twice during the growing season. Sampling in late spring to early summer should increase the chances of accurately estimating the presence and abundance of early season vernal species and sampling at peak biomass production in the mid- to late summer should increase the chances of accurately estimating the abundance and distribution of late season specialists and seasonally persistent species in this system. Climatic variability can delay or advance the growing season by as much as a couple weeks or more in the Wallowa Mountains as shown by the similarity of early season indicators between the July 2012 and June 2013 sampling periods in our study. Therefore, repeat sampling should rely more on plant phenology cues as opposed to specific calendar dates. When using plant phenology to initiate sampling, observers should consider each mountain zone separately because high elevation and low elevation plant growth may respond to different environmental cues (mean temperature, timing of snow-melt, rate of temperature change, photoperiod). This approach may be critical for capturing peak abundances of sub-alpine adapted non-native species like *Taraxacum officinale* and *Veronica serpyllifolia*, two non-natives that showed highest abundance during early season sampling periods within the subalpine mountain zone.

Univariate comparisons of aggregate community metrics such as trait category richness and abundance were not as informative as multivariate comparisons of inter- and intra-annual species composition change and indicator species analysis. Analyses of changes in non-native and native species distributions and impacts of non-native species on native species composition should use a combination of univariate and multivariate techniques in order to assess both variability of individual populations and variability of aggregate community properties. Replacement and asynchronous variations in abundance of functionally similar but temporally partitioned species (native and non-native) contributed to the stability of aggregate community metrics despite clear changes in individual species abundances over time in plots with high diversity. The establishment of long-term monitoring programs that capture both pre- and post-invasion processes may allow for an investigation of how functionally similar native and non-native species may influence the temporal stability of ecosystem processes.

## ACKNOWLEDGEMENTS

We thank the U.S.D.A. Forest Service Pacific Northwest Research Station for funding this work. We thank the following people for their outstanding work in the field: Kent Coe, Rachel Burton, Regina Thompson, Ryan Limb, and Samantha Pack.

## Figures

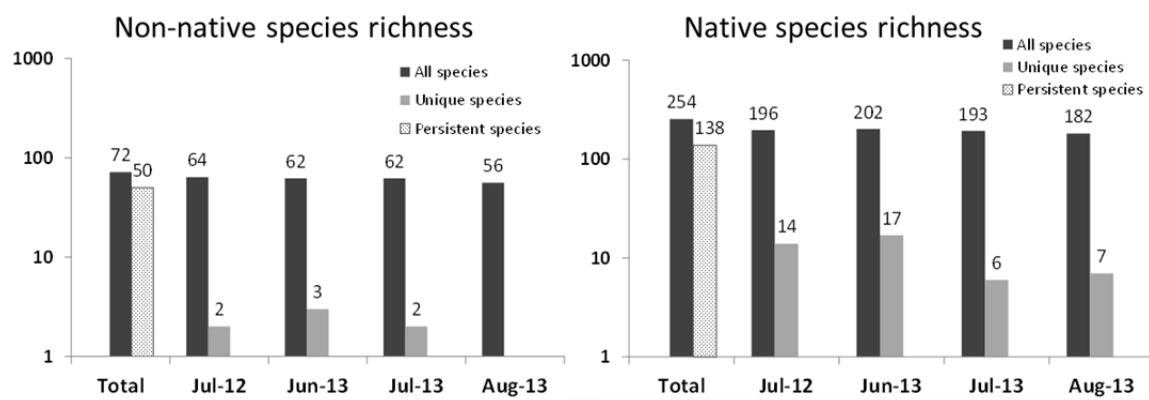


Figure 3.1: Non-native and native species richness measured within 150 (10m x 2m) subplots along an elevation gradient in the Wallowa Mountains, Oregon. Total (combined) species richness is depicted for each of four different sampling periods (July 2012 and June, July, and August 2013). Persistent species were those that were observed throughout all sample periods, and unique species were those only found within only one sampling period.

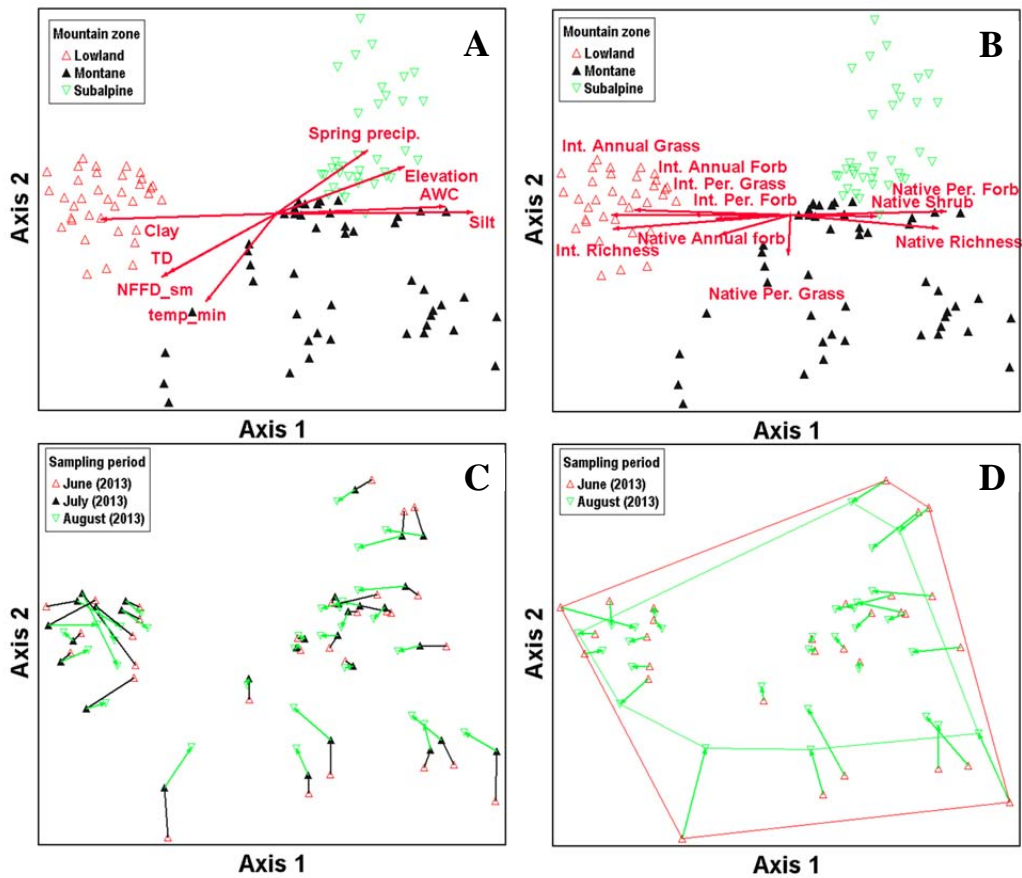


Figure 3.2: Two-dimensional NMS ordinations of sample units in species space (rotated by orthogonal principal axes). The total combined distance matrix variation combined is 85.5% with 66.6% and 18.9% being explained by axis 1 and axis 2 respectively. Symbol color represents mountain zone (lowland, montane, and subalpine) A) Relationships between environmental variables and ordination axes. B) Relationships between species trait categories and species richness with ordination axes. C) Temporal vectors connect the same plot over three sampling periods within one growing season. D) Temporal vectors depict the direction of change for plots in species space between June and August, 2013 sampling periods. Convex hulls represent the area of species space occupied by plots for these two sample periods. TD (temperature difference between the mean warmest month and the mean coldest month), temp\_min (average minimum annual temperature), NFFD\_sm (number of frost free days in the summer), AWC (fraction of soil water available), Int. Annual Grass (non-native annual grasses), Int. Annual Forb (non-native annual forbs), Int. Per. Forb (non-native perennial forbs), Int. Per Grass (non-native perennial grasses), Int. Richness (non-native richness).

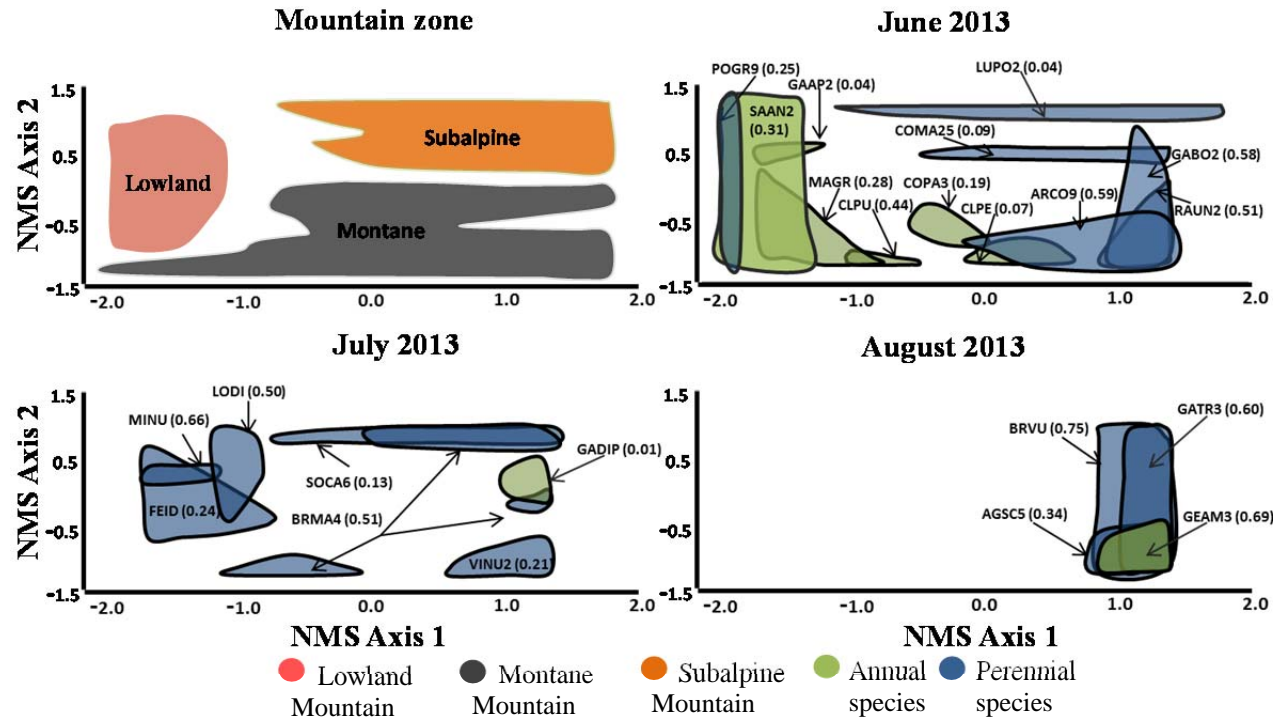


Figure 3.3: NPMR generated response surfaces for A) mountain zone sampling density (polygons show mountain zone sampling density in species space), and native indicator species abundance for B) June, C) July, and D) August as a function of NMS axes. Species shaded areas represent maximum density in ordination space for that species during the specified sampling period. Plant codes are depicted with corresponding  $xR^2$  values. AGSC5 (*Agrostis scabra*), ARCO9 (*Arnica cordifolia*), BRMA4 (*Bromus marginatus*), BRVU (*Bromus vulgaris*), CLPE (*Claytonia perfoliata*), CLPU (*Clarkia pulchella*), COMA25 (*Corallorrhiza maculata*), COPA3 (*Collinsia parviflora*), FEID (*Festuca idahoensis*), GAAP2 (*Galium aparine*), GABO2 (*Galium boreale*), GADIP (*Gayophytum diffusum*), GATR3 (*Galium triflorum*), GEAM3 (*Gentianella amarella*), LOLA3 (*Lomatium dissectum*), LUPO2 (*Lupinus polyphyllus*), MAGR (*Madia gracilis*), MINU (*Microseris nutans*), POGR9 (*Potentilla gracilis*), RAUN (*Ranunculus uncinatus*), SAAN2 (*Sanguisorba annua*), SOCA6 (*Solidago canadensis*), VINU2 (*Viola nutallii*).

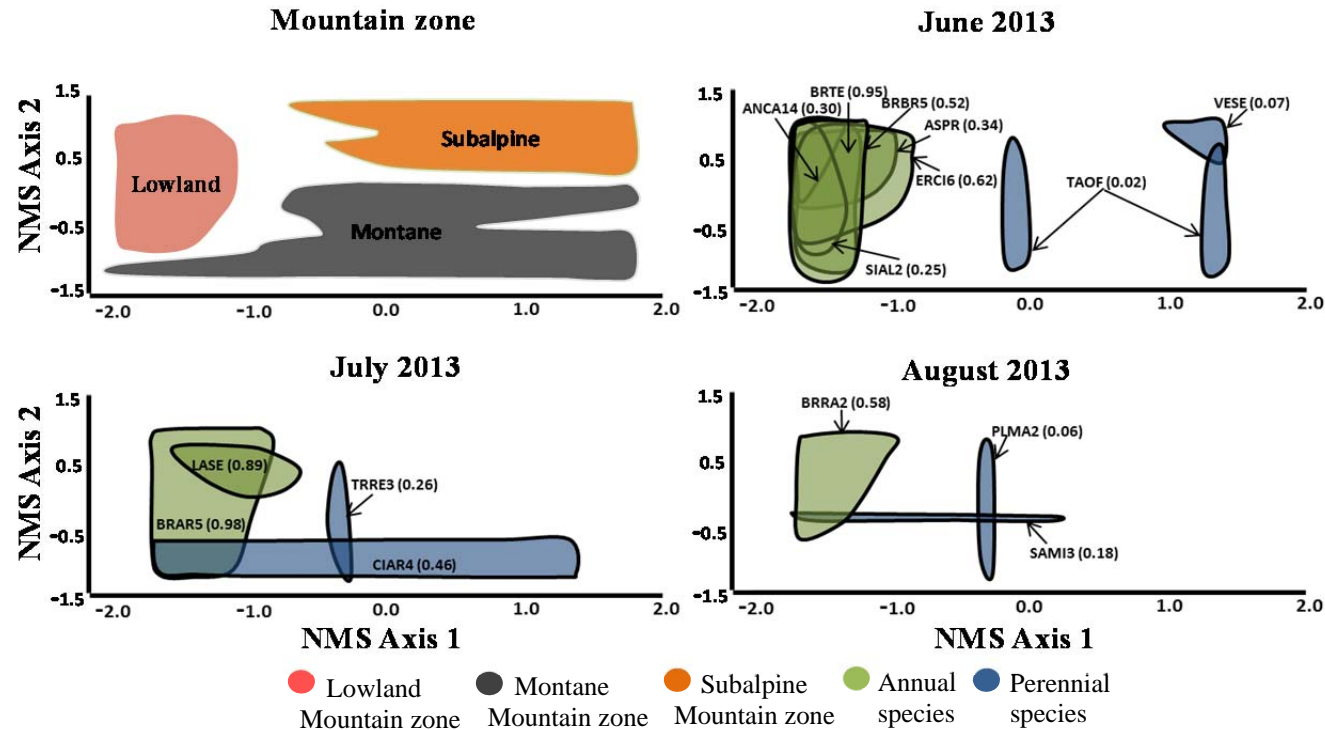


Figure 3.4: NPMR generated response surfaces for A) mountain zone sampling density, and non-native indicator species abundance for B) June, C) July, and D) August sampling periods as a function of NMS axes. Species shaded areas represent the maximum density in species space for that species during the specified sampling period. Plant codes are depicted with corresponding  $xR^2$  values. Multiple response surfaces were created by tracing the first three contours of each response from NPMR response surfaces with 15 contours and superimposing them into the ordination space. ANCA14 (*Anthriscus caucalis*), ASPR (*Asperugu procumbens*), BRAR5 (*Bromus arvensis*), BRBR5 (*Bromus brizaeformis*), BRRA2 (*Bromus racemosus*), BRTE (*Bromus tectorum*), CIAR4 (*Cirsium arvense*), ERC16 (*Erodium cicutarium*), LASE (*Lactuca serriola*), PLMA2 (*Plantago major*), SAMI3 (*Sanguisorba minor*), SIAL2 (*Sisymbrium altissimum*), TAOF (*Taraxacum officinale*), TRRE3 (*Trifolium repens*), VESE (*Veronica serpyllifolia*).

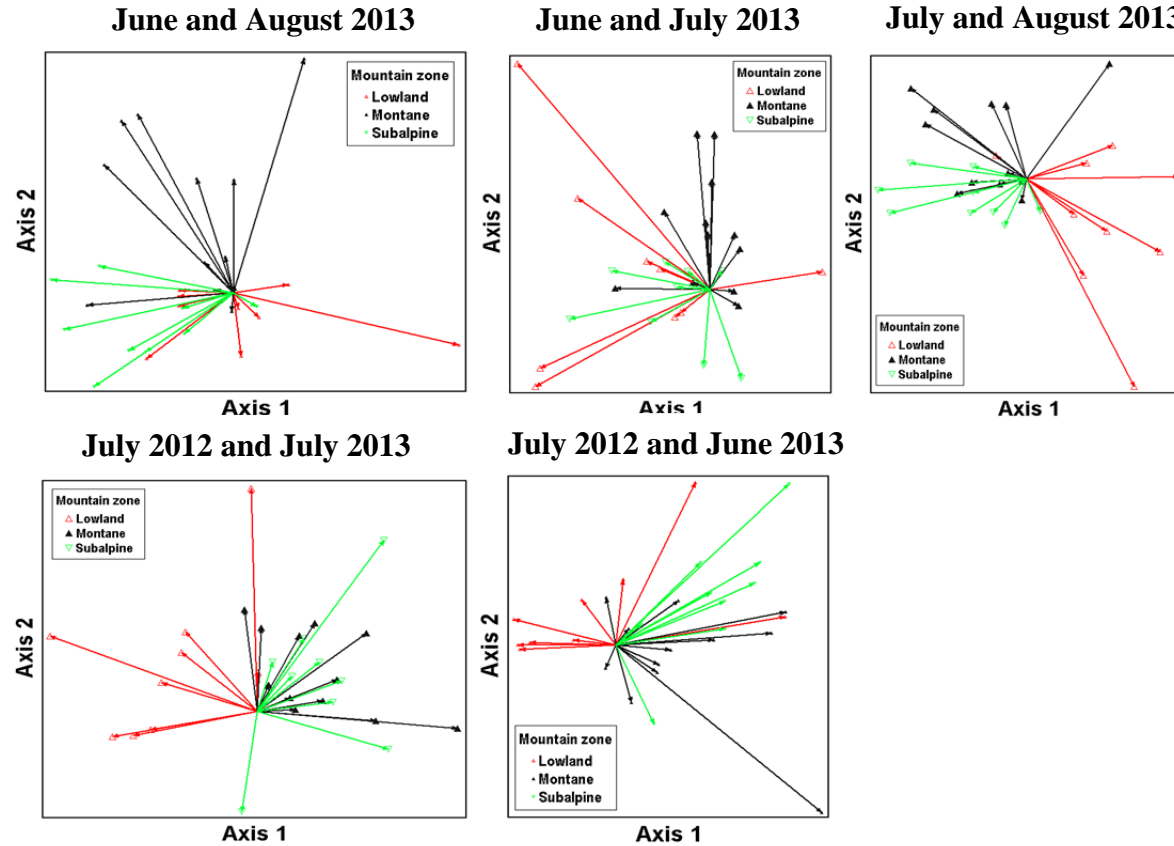


Figure 3.5: Temporal vectors from non-metric multidimensional scaling (NMS) ordination of understory vascular plant species composition between replicate vegetation samples of the same plots for both intra-annual (June, July and August 2013) and inter-annual (July 2012 to July 2013 and July 2012 to June 2013) sampling periods. Colors correspond to different mountain zones (red = lowland; black = montane; green = subalpine). Length and direction of vectors indicate magnitude and direction of community change within each plot respectively.



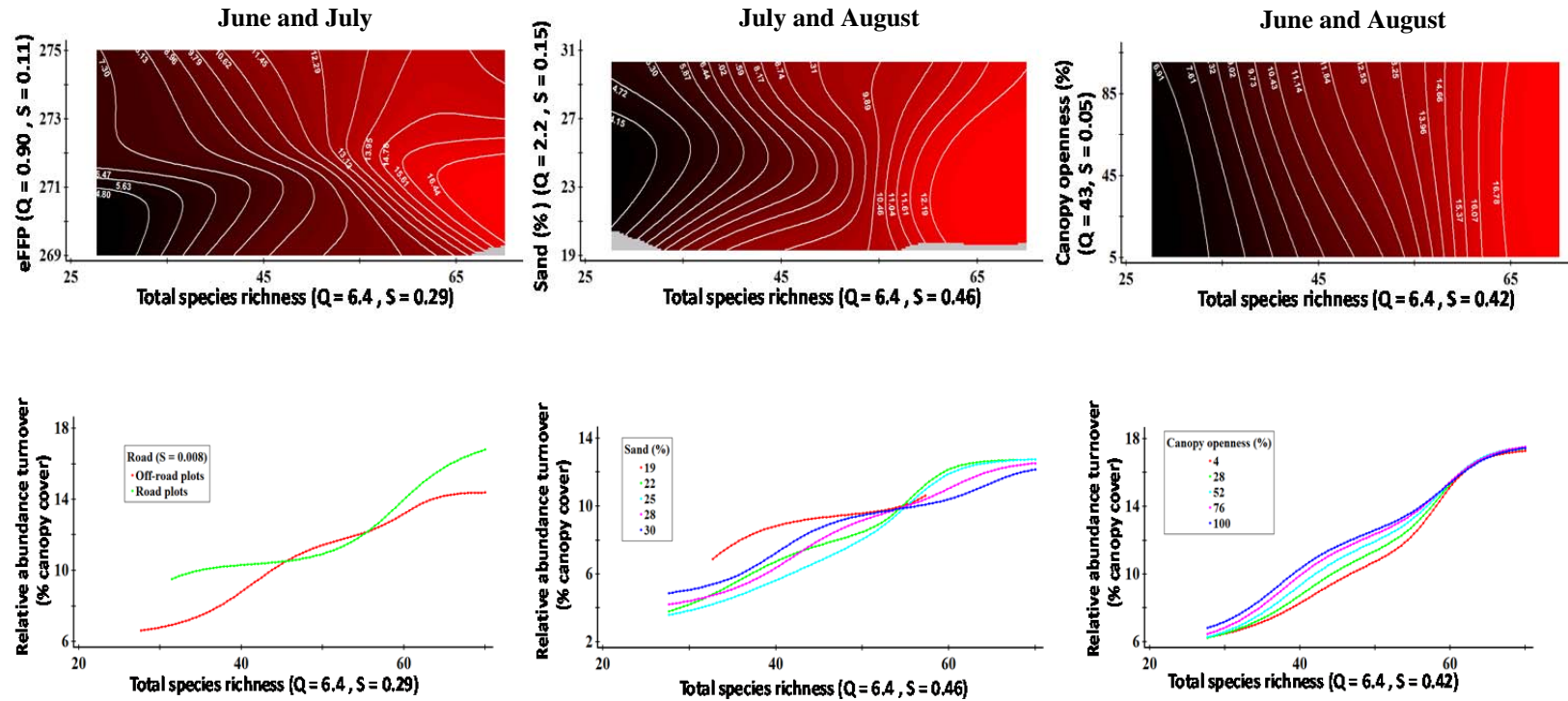


Figure 3.6: Estimated relative abundance turnover as a function of the most important predictors for each intra-annual sample period transition determined by non-parametric multiplicative regression (NPMR). Relative abundance turnover was measured as the total difference in relative canopy cover for all species within a plot between the two sampling periods being compared. Three dimensional contour plots depict estimated relative abundance turnover as a function of the most (x-axis) and second most (y-axis) important predictors. Red shading corresponds to higher turnover and dark shading indicates lower turnover. Two dimensional line graphs depict percent relative abundance turnover (y-axis) as a function of total species richness (the most important predictor of relative abundance turnover for each sampling period) with responses sliced by values of a second predictor variable. Shown next to each predictor is the tolerance (Q) and sensitivity (S). The road variable does not have an associated tolerance value because it was a categorical variable.

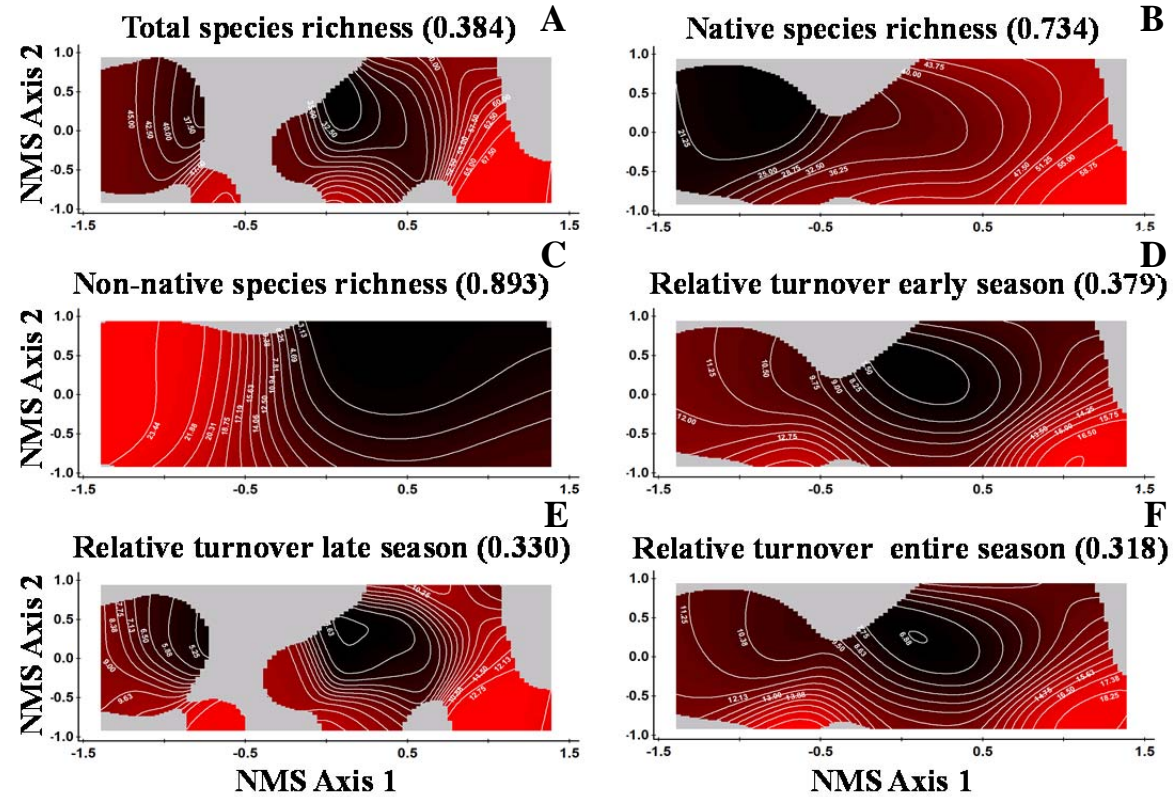


Figure 3.7: Estimated A) total species richness, B) native species richness, C) non-native species richness, D) early season (June and July 2013) relative abundance turnover, E) late season (July and August 2013) relative abundance turnover, and F) entire season (June and August 2013) relative abundance turnover as a function of NMS axes 1 and 2 determined by non-parametric multiplicative regression (NPMR). Three-dimensional contour plots depict estimated response surfaces where red shading corresponds to higher richness and turnover respectively, and dark shading indicates low richness and low vegetation turnover for corresponding response variables. Cross validated  $r$ -squared ( $xR^2$ ) values are indicated parenthetically along-side plot titles.

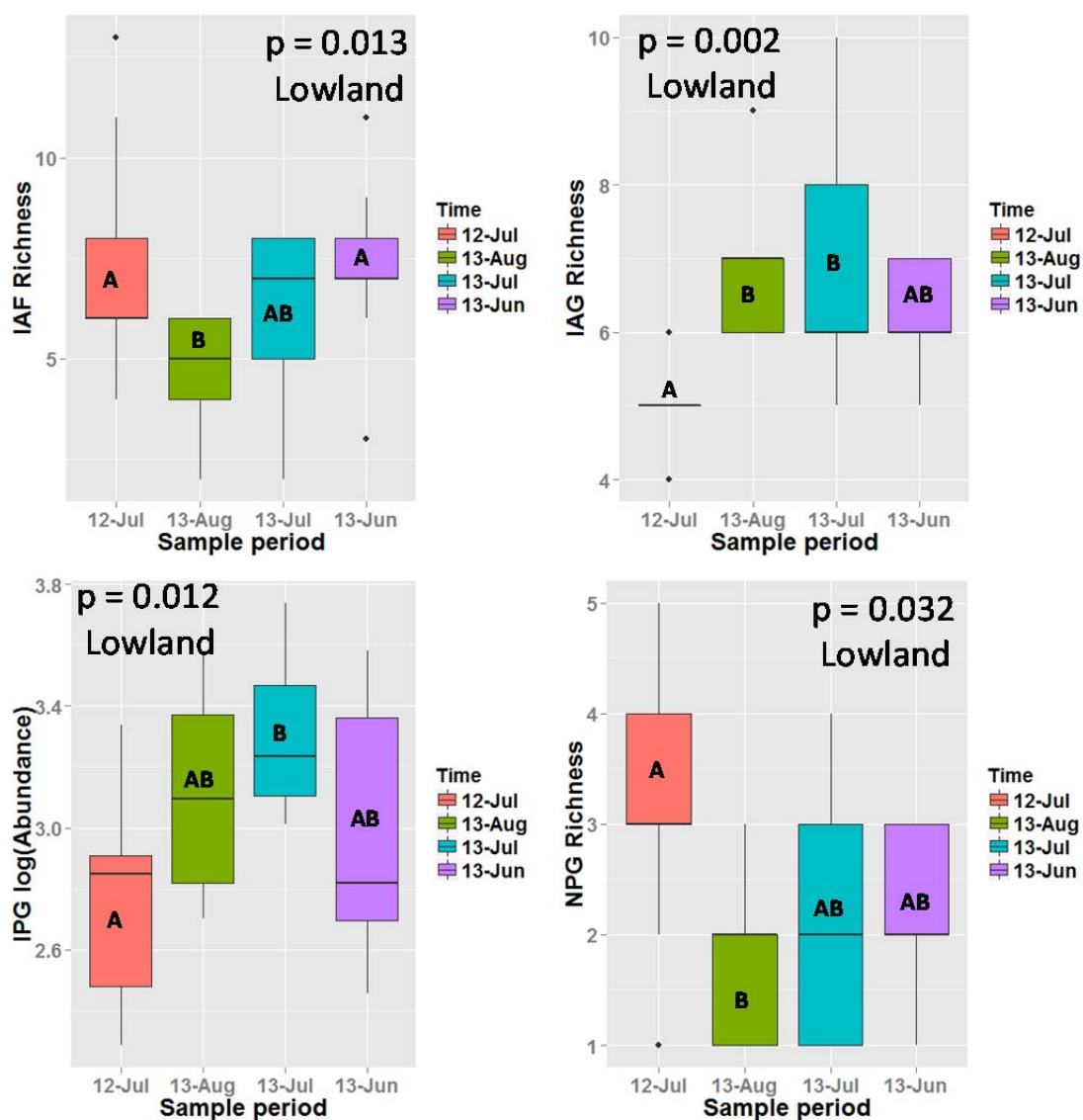


Figure 3.8: Boxplots of mean log abundance (canopy cover) and richness for trait categories within mountain zones that differed ( $p < 0.05$ ) between sampling periods. Boxes show the first and third interquartile ranges and whiskers extend to 1.5 times the interquartile ranges. Trait categories: IAF (non-native annual forb); IAG (non-native annual grass); IPG (non-native perennial grass); NPG (native perennial grass).

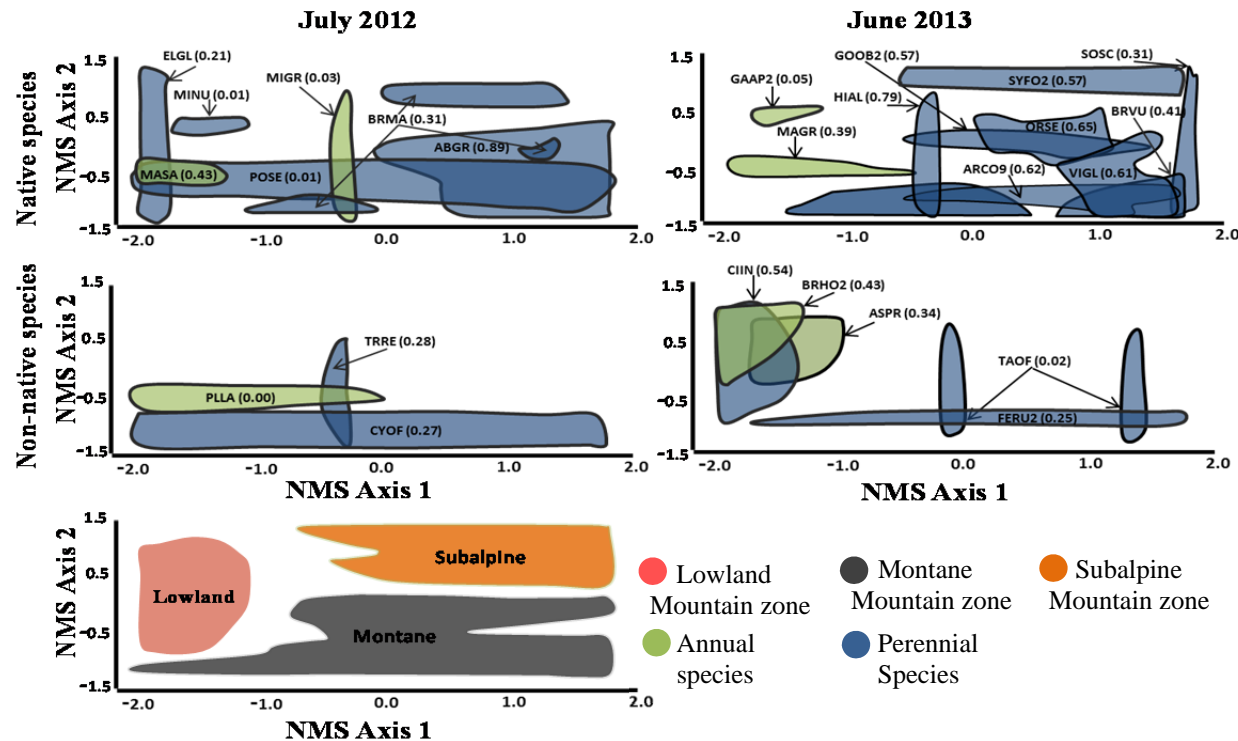


Figure 3.9: NPMR generated response surfaces of indicator species abundance as a function of NMS axes. Species shaded areas represent the maximum density in species space for identified species during the specified sampling period. Plant codes are depicted with corresponding  $xR^2$  values. ARCO9 (*Arnica cordifolia*), ABGR (*Abies grandis*), ASPR (*Asperugo procumbens*), BRMA (*Bromus marginatus*), BRHO2 (*Bromus hordeaceus*), BRVU (*Bromus vulgaris*), CIIN (*Cichorium intybus*), CYOF (*Cynoglossum officinale*), ELGL (*Elymus glaucus*), FERU2 (*Festuca rubra*), GAAP2 (*Galium aparine*), GOOB2 (*Goodyera oblongifolia*), HIAL (*Hieracium albiflorum*), MAGR (*Madia gracilis*), MASA (*Madia sativa*), MIGR (*Microsteris gracilis*), MINU (*Microseris nutans*), ORSE (*Orthilia secunda*), PLLA (*Plantago lanceolata*), POSE (*Poa secunda*), SOS2 (*Sorbus scopulina*), SYFO2 (*Symphotrichum foliaceum*), TAOF (*Taraxacum officinale*), TRRE3 (*Trifolium repens*), VIGL (*Viola glabella*).

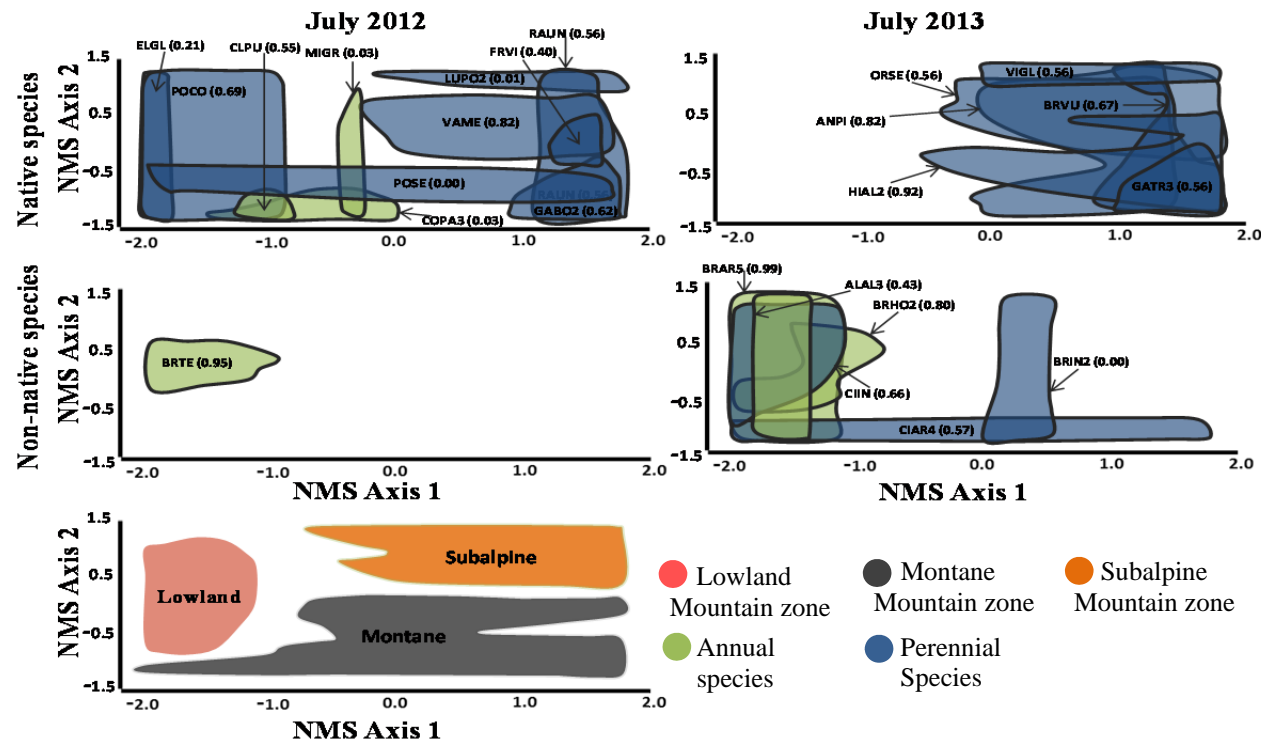


Figure 3.10: NPMR generated response surfaces of indicator species abundance as a function of NMS axes. Species shaded areas represent the maximum density in species space for that species during the specified sampling period. Plant codes are depicted with corresponding  $xR^2$  values. ALAL3 (*Alyssum alyssoides*), ANPI (*Anemone piperi*), BRAR5 (*Bromus arvensis*), BRHO2 (*Bromus hordeaceus*), BRIN2 (*Bromus inermis*), BRTE (*Bromus tectorum*), BRVU (*Bromus vulgaris*), CIAR (*Cirsium arvense*), CIIN (*Cichorium intybus*), CLPU (*Clarkia pulchella*), COPA3 (*Collinsia parviflora*), ELG (*Elymus glaucus*), FRVI (*Fragaria virginiana*), GABO2 (*Galium boreale*), GATR3 (*Galium triflorum*), HIAL2 (*Hieracium albiflorum*), MIGR (*Microsteris gracilis*), POCO (*Poa compressa*), POSE (*Poa secunda*), ORSE (*Orthilia secunda*), RAUN (*Ranunculus uncinatus*), VAME (*Vaccinium membranaceum*), VIGL (*Viola glabella*).

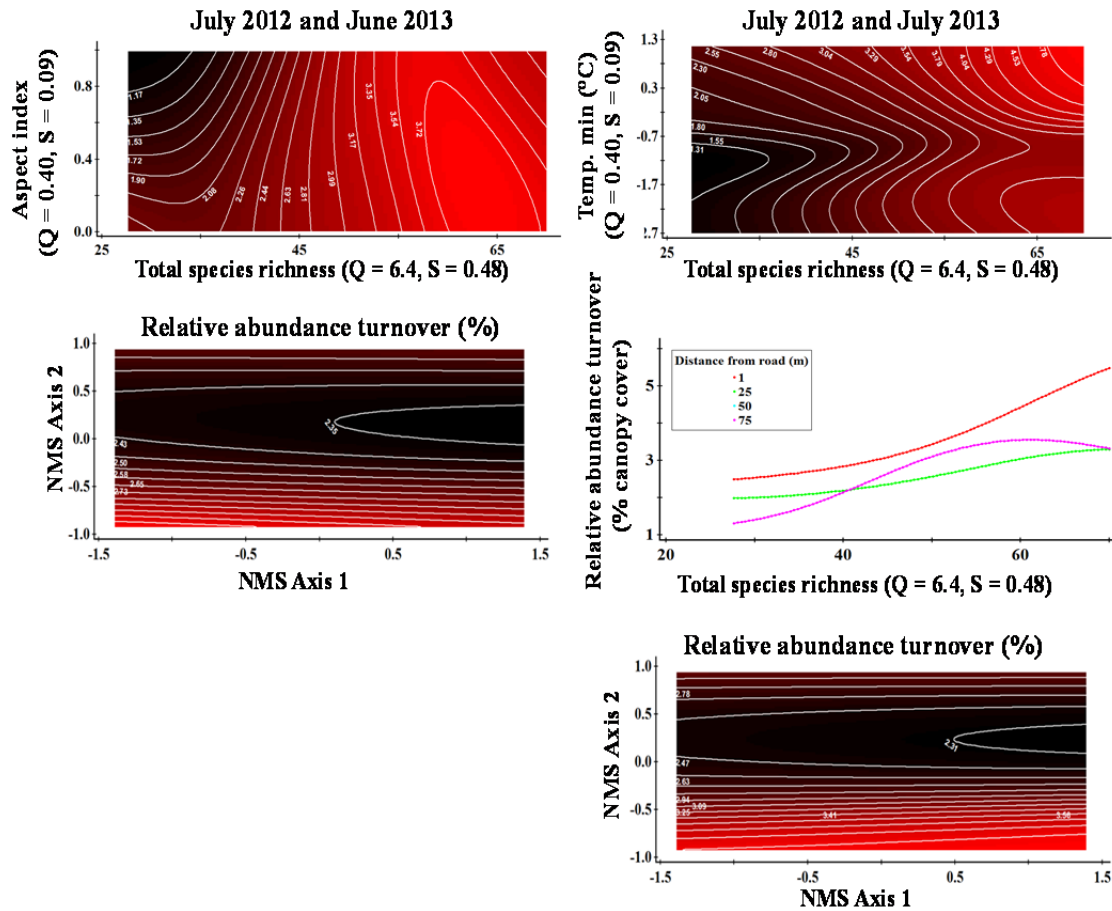


Figure 3.11: Estimated relative abundance turnover as a function of the most important predictors and NMS ordination axes for each inter-annual sample period transition (July 2012 to June 2013 and July 2012 to July 2013) determined by non-parametric multiplicative regression (NPMR). Relative abundance turnover was measured as the total difference in relative canopy cover for all species within a plot between the two sampling periods being compared. Three dimensional contour plots depict estimated relative abundance turnover as a function of the most (x-axis) and second most (y-axis) important predictors. The univariate graph depicts percent relative abundance turnover (y-axis) as a function of total species richness (the most important predictor of relative abundance turnover for each sampling period) with responses sliced by values of the third most important predictor variable (distance from road). Shown next to each predictor is the tolerance (Q) and sensitivity (S).

## Tables

Table 3.1: Transects and corresponding elevation, temperature, precipitation, and mountain zone. Transects were located along Mt. Harris road in Union County, OR. Mountain zone classification: lowland (plots below the tree-line where the vegetation community was dominated by grasses forbs or shrubs with sparse to no tree cover); montane (open and closed canopy forest with over-story dominated by *Abies grandis*, *Pseudotsuga menziesii*, or *Pinus ponderosa*); and subalpine (vegetation over-story dominated by *Abies lasiocarpa* in our study area)

Transect I.D.	Elevation (m)	Mean Winter Temperature (c)	Mean Summer Temperature (c)	Mean Precipitation (mm)	Mountain Zone
MH-01	902	0.3	18.5	608	Lowland
MH-02	961	0.1	18.2	623	Lowland
MH-03	1042	-0.1	17.9	643	Lowland
MH-07	1260	-1	16.4	700	Montane
MH-08	1317	-1.3	15.9	885	Montane
MH-10	1441	-1.7	15.2	975	Montane
MH-13	1619	-2.1	14.7	1099	Montane
MH-15	1743	-2.3	14.1	1199	Subalpine
MH-17	1865	-2.6	13.8	1282	Subalpine
MH-19	1981	-2.9	13.3	1356	Subalpine



Table 3.2: Non-native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Aegilops cylindrica</i>	5	2.5	11	10.6	11	6.1	9	5.6
<i>Alliaria petiolata</i> *U					1	0.6		
<i>Alopecurus pratensis</i> *	5	4.2	3	17.5	2	25.6	3	11.9
<i>Alyssum alyssoides</i>	5	0.3	12	0.6	16	0.4	14	0.5
<i>Anthriscus caucalis</i>	9	4.7	11	14.5	6	3.6	3	7.2
<i>Asperugo procumbens</i>			9	0.5				
<i>Bromus arvensis</i>	42	6.1	39	7.9	47	8.6	44	4.3
<i>Bromus brizaeformis</i>	9	1.1	20	1.9	11	1.6	9	1.5
<i>Bromus hordeaceus</i>			22	2.4	26	0.9	13	0.6
<i>Bromus inermis</i> *	2	0.4	7	0.9	8	0.9	4	1.9
<i>Bromus racemosus</i>	1	0.2	2	0.9	6	0.7	14	0.8
<i>Bromus tectorum</i>	44	4.1	39	5.2	37	2.0	33	3.2
<i>Capsella bursa-pastoris</i> *U	3	0.2						
<i>Centaurea solstitialis</i>	8	1.4	4	0.9	9	3.5	11	2.3
<i>Cichorium intybus</i>	8	1.1	12	1.4	17	4.8	14	5.9
<i>Cirsium arvense</i>	8	1.0	9	0.5	19	0.6	12	0.8
<i>Cirsium vulgare</i> *	6	0.6	4	0.6	1	1.2		
<i>Convolvulus arvensis</i>	28	9.3	27	7.4	26	12.9	27	7.9
<i>Cynoglossum officinale</i>	29	0.7	12	0.8	13	1.3	8	0.9
<i>Dactylis glomerata</i>	10	4.2	10	2.7	10	3.0	8	5.0
<i>Daucus carota</i>	32	4.6	29	3.4	19	2.8	28	11.7
<i>Dianthus armeria</i>	8	1.7	5	1.5	9	1.5	8	1.7
<i>Dipsacus fullonum</i>	20	2.2	17	2.6	14	2.7	14	3.2
<i>Draba verna</i> *	1	0.2	1	0.2				
<i>Erodium cicutarium</i>	25	1.7	30	1.2	13	0.8	2	0.5
<i>Fescuta rubra</i>	1	0.2	13	3.8	2	0.6	6	1.2
<i>Geranium pusillum</i> *	5	1.1	5	1.0	2	0.4		
<i>Hypericum perforatum</i>	11	2.5	9	1.1	12	1.6	9	1.6
<i>Lactuca serriola</i>	42	2.2	44	2.4	46	6.1	45	5.9
<i>Lepidium campestre</i> *	8	0.3			2	0.2		
<i>Lepidium perfoliatum</i> *	3	0.2	1	3.4			1	0.2
<i>Lepidium sativum</i> *U			2	0.3				
<i>Malus sp</i> *	1	71.0	2	28.8	2	46.6	2	41.7
<i>Marrubium vulgare</i> *	4	3.3	2	0.5	1	0.6	2	0.4
<i>Matricaria discoidea</i> *U			2	1.6				
<i>Medicago lupulina</i>	17	1.8	15	3.6	29	1.9	16	2.3

\* indicates rare species (occurring in  $\leq 5\%$  subplots for all sampling periods); U (unique species)



Table 3.2 continued: Non-native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species Name	July 2012		June 2013		July 2012		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Medicago sativa</i> *	2	0.6	2	2.4	4	1.8	3	6.5
<i>Melilotus officinalis</i>	7	1.6	10	0.7	6	1.2	10	1.2
<i>Myosotis stricta</i> *	1	0.4	2	0.4				
<i>Phleum pretense</i>	12	3.7	8	2.0	13	4.8	14	3.6
<i>Plantago lanceolata</i>	14	0.5	2	0.6	7	1.0	2	1.8
<i>Plantago major</i>	8	1.7	8	2.3	14	3.6	20	2.0
<i>Poa bulbosa</i>	29	2.0	35	1.4	34	1.0	22	0.4
<i>Poa compressa</i>	61	4.0	46	5.4	46	9.5	45	6.1
<i>Poa pratensis</i>	35	3.6	28	4.2	27	5.5	18	5.5
<i>Polygonum aviculare</i>	1	0.2			3	0.2	11	1.0
<i>Polypogon monspeliensis</i> *U					1	0.2		
<i>Potentilla recta</i>	10	2.0	14	2.8	12	4.8	12	1.5
<i>Prunus domestica</i> *	1	34.9	1	2.4	1	4.0	1	6.6
<i>Rumex acetosella</i>	11	0.7	12	0.8	11	0.8	9	0.5
<i>Rumex crispus</i> *	4	0.3	2	0.6	2	0.4	3	0.3
<i>Sanguisorba minor</i>					11	9.2	21	0.9
<i>Secale cereal</i> *			2	0.7	2	0.2	1	0.6
<i>Sisymbrium altissimum</i>	1	0.2	11	0.7	4	1.2	1	0.2
<i>Spergularia rubra</i>	5	0.4	3	0.4	7	0.4	14	0.3
<i>Stellaria media</i> *	2	6.8	1	3.2	6	1.7		
<i>Taeniatherum caput-medusae</i>	39	17.1	41	17.7	42	22.0	43	21.3
<i>Taraxacum laevigatum</i>	11	0.6	6	0.5	9	0.4	3	0.3
<i>Taraxacum officinale</i>	38	1.4	51	1.6	41	1.9	36	1.1
<i>Thinopyrum intermedium</i>	31	11.3	30	17.2	30	20.1	31	19.4
<i>Tragopogon dubius</i>	26	1.4	23	1.6	28	3.0	26	1.9
<i>Tragopogon porrifolius</i> *			1	3.0	1	0.2		
<i>Trifolium aureum</i> *					1	0.6	4	0.6
<i>Trifolium pretense</i> *	5	0.6	7	5.8				
<i>Trifolium repens</i>	30	5.5	18	9.9	28	7.8	21	7.3
<i>Ventenata dubia</i>	52	36.1	52	25.6	54	26.3	49	22.8
<i>Veronica persica</i> *U	3	1.5						
<i>Verbascum blattaria</i>	12	1.2	4	0.6	6	0.6	9	0.7
<i>Verbascum thapsus</i>	14	0.5	7	5.6	12	1.0	9	0.7
<i>Veronica serpyllifolia</i>	4	0.5	12	0.5	3	0.5	7	0.6
<i>Vulpia myuros</i> *					4	1.4	4	1.8

\* indicates rare species (occurring in  $\leq 5\%$  subplots for all sampling periods); U (unique species)

Table 3.3: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Abies grandis</i>	73	9.1	66	7.6	70	7.3	63	5.9
<i>Abies lasiocarpa</i>	29	14.2	40	13.0	40	9.0	36	11.5
<i>Acer glabrum</i>	18	9.7	16	10.2	19	8.1	19	6.4
<i>Achillea millefolium</i>	54	1.3	59	1.5	58	1.3	56	0.9
<i>Adenocaulon bicolor</i>	17	1.7	18	3.1	19	2.1	19	3.5
<i>Agoseris aurantiaca</i> *			2	0.4	3	0.3	1	0.2
<i>Agoseris grandiflora</i>	1	0.2	3	0.5			9	0.5
<i>Agoseris heterophylla</i>	6	1.0	10	0.7	20	1.0	5	0.2
<i>Agrostis scabra</i>			1	12.5	16	5.2	24	4.0
<i>Allium acuminatum</i> *	1	0.2						
<i>Alnus incana</i>	30	26.0	31	27.1	29	24.3	30	15.2
<i>Amelanchier alnifolia</i>	18	5.2	21	4.7	16	5.4	18	4.8
<i>Amsinckia intermedia</i>	8	0.7	16	1.6	14	2.8	13	1.0
<i>Amaranthus powellii</i> *	1	0.2						
<i>Anaphalis margaritacea</i>	37	3.6	38	3.3	38	3.7	39	2.9
<i>Anemone oregana</i>	4	0.2	13	2.4	1	0.6		
<i>Anemone piperi</i>	57	1.2	67	1.7	84	1.6	74	0.9
<i>Antennaria rosea</i>	16	2.1	13	1.6	15	0.8	16	1.0
<i>Antennaria stenophylla</i> *	1	3.0						
<i>Antennaria umbrinella</i>	6	5.5	8	9.9	9	7.6	9	7.3
<i>Apocynum androsaemifolium</i>	8	8.9	8	9.6	9	4.5	13	5.5
<i>Aquilegia flavescens</i>	8	1.8	10	1.7	9	0.7	10	0.6
<i>Aquilegia Formosa</i> *	4	0.5	5	0.2	6	0.5	2	0.4
<i>Arnica cordifolia</i>	59	5.6	72	10.1	60	8.1	49	4.4
<i>Arabis hirsute</i> *					1	0.6		
<i>Arctostaphylos nevadensis</i> *							1	0.2
<i>Arnica parryi</i> *	5	3.2	5	2.2	6	1.1	4	1.4
<i>Arctostaphylos uva-ursi</i> *	6	1.7	8	1.3			1	0.2
<i>Astragalus canadensis</i>	21	1.7	20	3.1	19	2.3	20	1.0
<i>Asclepias speciosa</i>	25	4.6	27	3.3	15	6.1	13	4.2
<i>Blepharipappus scaber</i> *			1	0.8	1	3.6	1	1.2
<i>Bromus marginatus</i>	68	1.4	28	1.8	56	1.4	5	1.0
<i>Bromus vulgaris</i>	18	1.3	50	2.7	51	1.8	74	2.0
<i>Calypso bulbosa</i> *	2	0.2	2	0.4				
<i>Calochortus elegans</i> *	1	0.2	1	1.4				
<i>Carex geyeri</i>	36	1.6	50	2.5	40	2.0	38	2.3

\* indicates rare species (occurring in  $\leq 5\%$  subplots for all sampling periods); U (unique species)

Table 3.3 continued: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Ave	Freq
<i>Carex spp.</i>	82	2.5	81	3.8	101	3.8	95	3.7
<i>Calamagrostis rubescens</i>	22	4.5	26	10.0	13	21.2	11	9.1
<i>Castilleja sp*</i>	2	0.5	4	1.0	4	0.8	3	0.2
<i>Castilleja tenuis</i>	16	1.7	2	0.7				
<i>Ceanothus sanguineus*</i>	2	1.8	2	6.6	1	0.6	1	0.6
<i>Ceanothus velutinus*</i>	4	6.3	3	17.3	4	7.4	5	5.9
<i>Chamerion angustifolium</i>	24	5.8	15	5.5	17	4.6	14	2.8
<i>Chlorocrambe hastata</i>					1	0.6		
<i>Chenopodium rubrum*</i>	2	0.2			1	0.2	1	0.2
<i>Chamaesyce serpyllifolia*</i>	2	0.3	1	0.2	3	0.9	2	0.6
<i>Chimaphila umbellata</i>	51	4.1	46	5.5	51	5.6	50	5.0
<i>Circaea alpine*</i>	5	0.3	4	2.2	6	0.9	1	0.4
<i>Cirsium brevifolium*</i>	7	0.4	5	0.4	5	0.6		
<i>Cirsium canovirens</i>					1	0.6	2	0.6
<i>Claytonia perfoliata</i>	12	1.3	9	0.6				
<i>Clarkia pulchella</i>	34	0.7	13	0.8				
<i>Clarkia rhomboidea*</i>	1	0.4						
<i>Clintonia uniflora</i>	18	4.7	17	6.8	16	8.0	20	6.3
<i>Conyza Canadensis*</i>					1	0.2	3	0.5
<i>Collomia grandiflora</i>	11	1.5	22	0.9	10	0.3	19	0.7
<i>Collomia linearis</i>	11	0.4	11	0.5	1	0.2		
<i>Corallorhiza maculate*</i>	2	0.5	7	0.7	1	0.6	1	0.8
<i>Collinsia parviflora</i>	27	0.7	29	0.6	8	0.4	2	0.2
<i>Cornus sericea*</i>	1	3.2	1	3.0	1	3.0	1	3.6
<i>Cryptantha affinis</i>	9	0.4	8	0.3	4	0.3		
<i>Crepis atribarba*</i>			1	0.6				
<i>Crataegus douglasii</i>	11	34.4	15	19.5	17	24.7	14	30.4
<i>Cryptantha simulans*</i>	4	1.5						
<i>Cypripedium montanum*</i>	1	0.2	3	0.3	1	0.2	3	0.3
<i>Danthonia californica</i>	4	1.4	6	6.1	21	13.0	4	2.8
<i>Danthonia unispicata*</i>	2	0.4	1	3.0	2	0.2		
<i>Deschampsia danthonioides*</i>	6	0.8	4	0.7	6	1.0		
<i>Delphinium depauperatum*</i>	1	0.6						
<i>Deschampsia elongata</i>	39	1.2	28	1.7	26	0.9	27	2.1
<i>Descurainia incana*</i>	1	0.2			1	0.6	1	1.2

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Table 3.3 continued: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		July 2013		July 2012		June 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Ave	Freq
<i>Elymus glaucus</i>	32	1.5	17	1.4	19	2.6	19	3.0
<i>Epilobium brachycarpum</i>	31	0.8	38	1.4	50	2.7	45	3.1
<i>Epilobium ciliatum</i>	16	0.8	17	0.5	15	0.8	17	0.5
<i>Epilobium densiflora</i> *	3	1.5	2	0.6	4	3.7	3	2.3
<i>Epilobium minutum</i> *			3	1.5	7	0.8		
<i>Equisetum arvense</i> *			2	1.5				
<i>Equisetum hyemale</i> *	5	4.7	4	1.3	5	1.1	5	1.2
<i>Erigeron coulteri</i> *					3	1.1	3	0.2
<i>Eriogonum flavum</i> *					1	0.6	1	3.6
<i>Erythronium grandiflorum</i> *	1	1.2	1	1.0	1	0.6		
<i>Eriogonum marifolium</i> *U			1	0.6				
<i>Eurybia integrifolia</i> *	2	3.3			4	4.8	4	5.4
<i>Festuca idahoensis</i>	24	7.2	33	6.0	38	8.4	33	6.7
<i>Festuca occidentalis</i> *			1	1.8	1	1.8	1	3.0
<i>Fragaria vesca</i>	52	3.3	60	4.9	64	2.9	57	2.4
<i>Fragaria virginiana</i>	36	1.4	33	2.6	28	2.0	35	2.2
<i>Galium aparine</i>	7	0.7	16	2.1			3	0.4
<i>Galium boreale</i>	55	1.8	45	2.6	29	1.0	32	0.6
<i>Gayophytum diffusum</i>			5	2.9	10	1.7	5	0.5
<i>Galium triflorum</i>			11	2.1	43	1.6	44	0.8
<i>Gentianella amarella</i>	4	0.5	3	0.8	7	0.5	13	0.9
<i>Geum macrophyllum</i> *	7	1.5	2	3.0	6	0.7	3	1.1
<i>Gentianella propinqua</i> *U					1	0.2		
<i>Geum triflorum</i> *			3	0.8			2	0.2
<i>Geranium viscosissimum</i> *	1	0.6	7	0.5				
<i>Gnaphalium sp</i> *	1	0.2						
<i>Goodyera oblongifolia</i>	31	0.7	37	1.1	38	0.9	40	0.9
<i>Grindelia squarrosa</i> *	1	0.6			3	2.8	1	0.6
<i>Hackelia micrantha</i> *	3	5.3	2	9.9	1	0.6		
<i>Hemizonella minima</i> *	6	1.7	6	3.4	2	0.2		
<i>Heuchera micrantha</i> *U			2	0.2				
<i>Helianthella uniflora</i>	13	2.4	13	3.1	13	1.9	13	1.0
<i>Hieracium albiflorum</i>	60	1.1	84	1.9	89	1.9	86	1.5
<i>Hieracium cynoglossoides</i> *U							1	0.6

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Table 3.3 continued: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Hieracium longiberbe</i> *	1	0.2					1	0.6
<i>Hieracium scouleri</i> *	4	5.6	3	6.4	3	6.8	2	0.4
<i>Hieracium scabrum</i> *U							3	1.7
<i>Holodiscus discolor</i>	17	17.8	16	17.5	15	12.9	16	14.0
<i>Hydrophyllum capitatum</i> *	1	0.4	1	0.2				
<i>Juncus bufonius</i>					2	0.5	2	0.7
<i>Juncus sp</i>	8	2.1	12	1.9	10	1.6	9	1.7
<i>Juncus parryi</i> *U					1	0.2		
<i>Koeleria macrantha</i>	5	0.3	11	0.4	7	1.3	3	1.5
<i>Lathyrus nevadensis</i> *	2	1.6	7	0.6	5	0.4	6	0.7
<i>Larix occidentalis</i>	11	2.7	12	2.9	7	2.6	10	1.2
<i>Leptosiphon harknessii</i>	16	1.0	18	1.3	18	1.7	15	1.5
<i>Linnaea borealis</i>	43	15.6	43	17.7	43	20.5	42	18.4
<i>Listera caurina</i>	1	0.2	9	0.6	9	0.4	7	0.3
<i>Lithospermum ruderales</i> *	1	3.0	1	0.6	2	2.2	2	0.4
<i>Lomatium dissectum</i>	8	1.0	4	1.8	13	2.0	11	0.9
<i>Lomatium spp.</i>	5	2.4	9	1.7	2	0.6		
<i>Lomatium triternatum</i> *U			8	6.0				
<i>Lotus purshianus</i>	24	4.5	38	5.0	32	10.8	30	5.4
<i>Lonicera utahensis</i>	12	5.4	29	6.9	38	3.8	32	2.4
<i>Lupinus argenteus</i> *	1	7.8			1	0.6		
<i>Luzula arcuata</i> *U					3	1.5		
<i>Lupinus caudatus</i> *U	2	3.6						
<i>Luzula multiflora</i>	11	0.9					4	0.4
<i>Lupinus sp</i>	16	1.4	40	2.2	33	1.8	29	1.3
<i>Lupinus polyphyllus</i>	25	3.6	19	2.4	17	1.6	16	1.6
<i>Madia glomerata</i>	20	2.1	19	2.2	24	1.9	24	1.1
<i>Madia gracilis</i>	1	0.2	19	1.1	17	3.2	12	2.9
<i>Maianthemum racemosum</i> *	4	5.6	1	0.6	1	0.2	1	0.6
<i>Mahonia repens</i>	5	3.1	6	0.9	8	2.4	8	1.3
<i>Madia sativa</i>	17	5.0	5	1.2	17	1.8	11	2.1
<i>Maianthemum stellatum</i>	18	2.6	17	7.1	19	5.8	16	5.0
<i>Melica Fugax</i> *U							2	0.6
<i>Melica subulata</i>	11	0.6	10	3.0	2	0.6	6	0.9
<i>Mertensia paniculata</i> *	7	10.2	6	12.2	7	5.3	7	5.7

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Table 3.3 continued: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Mimulus breweri</i> *			2	6.6	2	6.7		
<i>Microsteris gracilis</i>	29	0.9	19	0.9	12	0.5	2	0.2
<i>Mimulus guttatus</i> *	3	2.8	1	0.6				
<i>Mimulus lewisii</i> *	3	1.1	3	0.6	4	1.6	2	2.5
<i>Microseris nutans</i>	12	0.7			5	0.8	3	0.3
<i>Mitella stauropetala</i>	65	1.9	67	3.0	63	2.7	58	3.0
<i>Moehringia macrophylla</i>	50	0.8	51	1.7	62	1.2	54	1.0
<i>Muhlenbergia richardsonis</i> *			5	9.1	7	16.5	7	13.3
<i>Navarretia intertexta</i>	21	1.1	20	2.2	15	1.8	12	2.3
<i>Noccaea fendleri</i> *			2	0.5	1	1.0	1	0.6
<i>Orthilia secunda</i>	39	2.7	55	3.1	58	3.1	57	3.4
<i>Osmorhiza berteroi</i>	60	1.1	41	1.1	47	1.0	38	0.6
<i>Paeonia brownie</i> *U			1	0.2				
<i>Panicum capillare</i>	5	2.4			12	2.1	13	1.4
<i>Paxistima myrsinites</i>	19	2.1	21	2.9	24	2.7	23	2.5
<i>Penstemon deustus</i>	6	3.0	10	1.8	7	2.5	5	2.8
<i>Penstemon globosus</i> *U							1	0.6
<i>Penstemon sp</i> *	4	1.0	3	4.3	2	2.8		
<i>Pedicularis racemosa</i>	14	4.4	19	3.2	20	3.8	19	2.6
<i>Penstemon rydbergii</i> *U			1	6.6				
<i>Phacelia hastata</i>			2	0.4	10	0.5	9	0.3
<i>Phacelia heterophylla</i> *	2	0.9	2	0.8				
<i>Philadelphus lewisii</i> *U					1	0.6		
<i>Phlox longifolia</i> *U			4	0.4				
<i>Physocarpus malvaceus</i> *	2	1.2	1	0.2	2	0.7		
<i>Piperia candida</i> *U			1	0.6				
<i>Pinus contorta</i>	21	3.1	25	3.2	27	3.2	25	3.2
<i>Picea engelmannii</i>	44	4.5	49	4.1	46	4.6	46	2.7
<i>Pinus ponderosa</i> *	8	3.7	6	2.0	6	0.4	4	3.1
<i>Platanthera dilatata</i> *U	1	0.2						
<i>Plantago patagonica</i> *			1	3.0	3	0.5	2	0.4
<i>Populus balsamifera</i> *	6	25.6	6	10.1	7	13.4	6	15.8
<i>Polygonum douglasii</i>	3	0.3	5	0.5	25	0.5	24	0.6
<i>Potentilla glandulosa</i>	17	0.9	24	0.8	25	0.9	18	0.6

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Table 3.3 continued: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Potentilla gracilis</i>	4	0.4	10	0.4	4	1.4	3	0.7
<i>Polemonium micranthu</i> *U	1	0.2						
<i>Polygonum minimum</i> *	3	0.9			1	1.6	3	1.5
<i>Polygonum phytolaccifolium</i> *	6	9.9	4	18.7	6	14.9	3	22.9
<i>Polygonum polygaloides</i> *	5	0.3					1	0.2
<i>Polemonium pulcherrimum</i>	28	2.6	26	5.2	31	3.8	30	3.3
<i>Poa secunda</i>	23	4.8	1	0.2	5	1.1		
<i>Prunus virginiana</i> *	1	0.2			1	3.4	1	3.6
<i>Prunella vulgaris</i>	11	2.9	8	6.4	14	3.3	12	2.8
<i>Pseudotsuga menziesii</i>	70	3.9	54	4.2	60	4.9	60	4.5
<i>Pseudoroegneria spicata</i> *	5	6.1	7	1.6	5	7.2	3	1.6
<i>Pterospora andromedea</i> *			4	0.9	3	0.2		
<i>Pteridium aquilinum</i> *	1	14.1	2	2.1	2	2.1	2	5.6
<i>Pyrola picta</i>	10	0.8	1	0.2				
<i>Ranunculus occidentalis</i> *	5	2.4			1	0.2	3	0.3
<i>Ranunculus orthorhynchus</i> *							1	0.6
<i>Ranunculus uncinatus</i>	54	0.9	43	1.2	19	0.6	4	0.5
<i>Ribes aureum</i> *	1	0.6			1	0.2		
<i>Ribes hudsonianum</i> *	1	0.2	2	0.7	1	3.0	1	3.0
<i>Ribes lacustre</i>	10	7.5	12	7.5	19	6.5	12	5.2
<i>Ribes viscosissimum</i>	14	5.4	18	4.9	12	4.0	15	5.9
<i>Rosa gymnocarpa</i>	24	5.9	26	5.1	32	4.1	24	5.6
<i>Rosa woodsii</i>	17	2.7	11	2.0	9	0.7	14	1.6
<i>Rudbeckia occidentalis</i>	16	1.9	13	2.7	9	2.9	9	2.2
<i>Rubus parviflorus</i>	14	13.9	13	9.3	14	12.8	14	9.0
<i>Sanguisorba annua</i>	32	1.5	32	1.7	29	1.4	19	2.6
<i>Sanicula graveolens</i> *	3	0.3	4	2.2	2	0.5	1	0.2
<i>Salix lasiolepis</i> *	5	3.3	5	7.5	6	7.5		
<i>Salix lemmonii</i> *					2	15.6	4	12.9
<i>Salix sp</i>			7	4.8	5	1.2	10	6.1
<i>Sambucus nigra</i> *U							2	3.0
<i>Saxifraga oregano</i> *	3	0.5	1	0.2				
<i>Sambucus racemosa</i> *	3	6.8	3	11.7	3	5.5	4	7.0
<i>Sagina saginoides</i> *U	2	0.2						
<i>Salix scouleriana</i>	9	19.4	7	5.9	4	1.9	3	4.8

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Table 3.3 continued: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Senecio fremontii</i> *U					1	3.0		
<i>Senecio integerrimus</i> *	2	0.6	2	0.2				
<i>Sedum stenopetalum</i> *	4	0.4	6	0.6	5	0.4	1	0.2
<i>Senecio triangularis</i> *	1	0.6	5	0.4			3	0.3
<i>Shepherdia canadensis</i> *U	1	0.6						
<i>Silene menziesii</i> *	1	0.2						
<i>Sidalcea oregana</i>	9	1.6	11	0.5	15	1.2	10	0.4
<i>Sibbaldia procumbens</i> *			2	0.4				
<i>Solidago canadensis</i>	2	0.6	7	4.6	15	4.6	9	5.5
<i>Solidago missouriensis</i> *							5	1.6
<i>Sorbus scopulina</i>	9	2.7	16	3.5	13	3.1	15	2.8
<i>Spiraea betulifolia</i>	21	3.1	23	5.5	21	5.0	22	5.0
<i>Streptopus amplexifolius</i> *			2	0.4	2	0.4	1	0.6
<i>Stellaria longipes</i> *U			2	0.4				
<i>Stellaria nitens</i> *U			1	0.2				
<i>Symphoricarpos albus</i>	46	8.1	38	11.2	40	9.0	35	8.9
<i>Symphyotrichum ascendens</i>	6	12.8	14	4.4	29	4.3	26	5.1
<i>Symphyotrichum cusickii</i>	18	7.5	4	1.2	2	1.9		
<i>Symphyotrichum foliaceum</i>			25	7.7	27	5.2	30	3.4
<i>Thermopsis montana</i>			10	1.8	1	0.4		
<i>Thalictrum occidentale</i>	46	4.9	55	3.9	51	2.9	44	2.0
<i>Tiarella trifoliata</i> *			5	0.5	7	0.4	6	0.3
<i>Trautvetteria caroliniensis</i>	1	7.7	11	2.8	1	0.6	3	5.0
<i>Trisetum canescens</i>	4	0.3	15	0.9	33	1.2	25	0.9
<i>Triteleia grandiflora</i> *	5	0.8	2	0.3			1	0.2
<i>Trifolium microcephalum</i> *U			2	0.3				
<i>Trillium ovatum</i> *	1	0.2	7	0.5	8	0.6	1	0.6
<i>Triodanis perfoliata</i> *U			1	0.2				
<i>Trifolium plumosum</i> *	3	0.6	1	0.6	1	0.2	1	0.2
<i>Trisetum spicatum</i> *			3	1.0	4	0.7		
<i>Tsuga mertensiana</i>	9	5.4	18	11.4	10	5.5	10	6.0
<i>Typha latifolia</i> *U	1	0.6						
<i>Vaccinium membranaceum</i>	62	29.1	63	22.7	61	27.5	63	24.7
<i>Vaccinium scoparium</i>	26	13.9	28	11.7	26	16.3	26	11.8

\* indicates rare species (occurring in  $\leq 5\%$  subplots for all sampling periods); U (unique



Table 3.3 continued: Native species list encompassing four different sampling dates along an elevation gradient in the Wallowa Mountains, Oregon. Green cells indicate species that were absent during July 2012 sampling period; Blue cells correspond to species that only occurred during the July 2012 sampling season; Grey cells indicate sampling periods where species were absent during the 2013 sampling periods.

Species name	July 2012		June 2013		July 2013		August 2013	
	Freq	Ave	Freq	Ave	Freq	Ave	Freq	Ave
<i>Valeriana sitchensis</i>	16	17.7	15	11.6	15	5.0	14	4.7
<i>Veratrum californicum</i> *	1	0.6					1	0.2
<i>Veronica scutellata</i> *U	3	0.7						
<i>Veronica wormskjoldii</i> *U			3	3.7				
<i>Viola adunca</i>	55	1.0	51	2.1	56	2.2	35	1.4
<i>Vicia americana</i>	12	1.3	15	1.9	11	1.6	11	1.2
<i>Viola glabella</i>	10	0.9	44	1.2	56	1.4	37	1.2
<i>Viola nuttallii</i>	4	0.3	10	0.9	16	0.5	8	0.6
<i>Viola orbiculata</i>	26	2.3	36	1.6	59	1.8	56	1.7
<i>Viola purpurea</i> *U			1	0.2				
<i>Xanthium strumarium</i> *					1	0.6	1	3.0

\* indicates rare species (occurring in  $\leq 5\%$  subplots for all sampling periods); U (unique species)

Table 3.4: Correlations between environmental variables and NMS ordination axes

Variable	r	r
	Axis 1	Axis 2
Spring precipitation	0.642	0.547
Summer precipitation	0.593	0.507
Frost free days –spring	-0.587	-0.415
Frost free days - summer	-0.577	-0.397
Continentality (TD)	-0.693	-0.529
Mean annual precipitation	0.664	0.521
Mean summer precipitation	0.693	0.507
Frost free period start date	-0.582	0.452
Frost free period end date	-0.656	-0.452
Frost free period	-0.643	-0.421
Extreme minimum temp (30 years)	0.643	-0.489
Hargreaves climate moisture deficit	-0.541	-0.350
Canopy openness (%)	-0.641	0.197
<b>Elevation</b>	0.755	0.473
Slope	-0.010	-0.003
Aspect Index	0.466	0.-147
Bare-ground (%)	-0.056	0.021
<b>Maximum average temperature</b>	-0.791	-0.374
Minimum average temperature	-0.543	-0.648
Distance to road	0.029	-0.019
Disturbance intensity	0.029	0.200
<b>AWC (Available water capacity)</b>	0.870	0.169
<b>Available water supply (0-25 cm)</b>	0.860	0.178
<b>Clay (%)</b>	-0.887	-0.200
Depth to restrictive layer	0.570	-0.163
Organic Matter	0.561	0.365
Sand (%)	0.261	-0.427
<b>Silt (%)</b>	0.938	0.085
Variables with $r > 0.7$ or $r < -0.7$ are bolded		

Table 3.5: Blocked multi-response permutation procedure (MRBP) comparing understory plant communities (vegetation plots were blocks), between three sampling periods (June, July, and August 2013; intra-annual vegetation community change) within one growing season (sampling period was the grouping variable), and between year sampling periods (inter-annual vegetation community change). Pair-wise comparisons are shown for each combination of sampling periods (p-values have been corrected for multiple comparisons using Bonferroni adjustment).

Intra-annual vegetation community change							
Distance Measure	Observed $\delta$	$\delta$ Under null hypothesis			T	A	p
		Expected $\delta$	Variance	Skewness			
Euclidean	4.444	4.576	4.94E-05	-0.549	-18.793	0.029	1E-07
Multiple comparisons (Euclidean)		T	A	p			
June 2013 vs. July 2013		-8.785	0.025	3E-08			
June 2013 vs. August 2013		-9.593	0.031	6E-08			
July 2013 vs. August 2013		-11.032	0.034	<1E-08			
Inter-annual vegetation community change							
Distance Measure	Observed $\delta$	$\delta$ Under null hypothesis			T	A	p
		Expected $\delta$	Variance	Skewness			
Euclidean	4.826	5.024	5.02E-05	-0.502	-27.946	0.039	<1E-08
Multiple comparisons (Euclidean)		T	A	p			
July 2012 vs. June 2013		-10.516	0.034	<1E-08			
July 2012 vs. July 2013		-12.686	0.047	<1E-08			
July 2012 vs. August 2013		-13.233	0.054	2E-08			

Table 3.6: Blocked multi-response permutation procedure (MRBP) comparing understory plant composition by trait category within each of three mountain zones (lowland, montane, and subalpine) between three sampling periods (June, July, August 2013) within one growing season. Trait category abbreviations: IAF (non-native annual forb), IPF (non-native perennial forb), IAG (non-native annual graminoid), IPG (non-native perennial graminoid), NAF (native annual forb), NPG (native perennial graminoid), NPF (native perennial forb), NPS (native perennial shrub).

Trait Category	Lowland		Montane		Subalpine	
	A	P	A	P	A	P
IAF	<b>0.153</b>	<b>4 E-06</b>	0.023	0.087	-0.013	0.742
IPF	<b>0.048</b>	<b>0.022</b>	<b>0.079</b>	<b>2 E-05</b>	0.001	0.448
IAG	<b>0.090</b>	<b>0.001</b>	0.001	0.424	NA	NA
IPG	<b>0.067</b>	<b>0.011</b>	<b>0.063</b>	<b>0.004</b>	-0.008	0.59
NAF	<b>0.073</b>	<b>1 E-05</b>	<b>0.11</b>	<b>1 E-06</b>	<b>0.036</b>	<b>0.012</b>
NPG	<b>0.067</b>	<b>0.007</b>	<b>0.053</b>	<b>2 E-04</b>	<b>0.075</b>	<b>0.005</b>
NPF	<b>0.073</b>	<b>2 E-04</b>	<b>0.065</b>	<b>4 E-07</b>	<b>0.032</b>	<b>0.002</b>
NPS	0.020	0.090	<b>0.014</b>	<b>0.046</b>	0.012	0.170

Table 3.7: Indicator species for different understory vascular plant surveys taken at 3 different times (June, July, and August 2013) during one growing season (Intra-annual analysis). All indicator species had  $P < 0.05$ . Higher indicator values (IV) shows a stronger tendency for a species to a particular sampling period.

Indicator Species	IV	Trait Category	Indicator Species	IV	Trait Category
<b>June 2013 Sampling Period</b>			<b>July 2013 Sampling Period</b>		
<i>Collinsia parviflora</i>	37.5	NAF	<i>Bromus marginatus</i>	35.7	NPG
<i>Galium boreale</i>	33.4	NPF	<i>Festuca idahoensis</i>	21.3	NPG
<i>Taraxacum officinale</i>	32.8	IPF	<i>Viola nuttallii</i>	20.9	NPF
<i>Ranunculus uncinatus</i>	29.0	NPF	<i>Trifolium repens</i>	19.5	IPF
<i>Arnica cordifolia</i>	28.4	NPF	<i>Cirsium arvense</i>	17.7	IPF
<i>Clarkia pulchella</i>	26.7	NAF	<i>Solidago canadensis</i>	16.6	NPF
<i>Madia gracilis</i>	23.0	NAF	<i>Lactuca serriola</i>	15.6	IAF
<i>Asperugo procumbens</i>	20.0	IAF	<i>Microseris nutans</i>	13.2	NPF
<i>Galium aparine</i>	19.7	NAF	<i>Bromus arvensis</i>	12.1	IAG
<i>Bromus brizaeformis</i>	19.4	IAG	<i>Stellaria media</i>	11.7	IAF
<i>Veronica serpyllifolia</i>	19.1	IPF	<i>Gayophytum diffusum</i>	9.9	NAF
<i>Erodium cicutarium</i>	18.2	IAF	<i>Lomatium dissectum</i>	9.1	NPF
<i>Arctostaphylos uva-ursi</i>	17.1	NPF	<b>August 2013 Sampling Period</b>		
<i>Sanguisorba annua</i>	15.7	NAF	<i>Galium triflorum</i>	25.3	NPF
<i>Potentilla gracilis</i>	14.4	NPF	<i>Bromus vulgaris</i>	25.1	NPG
<i>Claytonia perfoliata</i>	13.3	NAF	<i>Agrostis scabra</i>	18.3	NPG
<i>Anthriscus caucalis</i>	13.3	IAF	<i>Bromus racemosus</i>	17.2	IAG
<i>Sisymbrium altissimum</i>	12.6	IAF	<i>Gentianella amarelle</i>	15.5	NAF
<i>Lupinus pollyphyllus</i>	11.8	NPF	<i>Sanguisorba minor</i>	15.5	IPF
<i>Corallorhiza maculata</i>	11.7	NPF	<i>Plantago major</i>	9.2	IPF
<i>Bromus tectorum</i>	11.3	IAG			

Table 3.8: Blocked multi-response permutation procedure (MRBP) comparing understory plant composition by trait category within each of three mountain zones (lowland, montane, and subalpine) between four sampling periods (July 2012; June 2013; July 2013; and August 2013). Inter-annual comparisons included July 2012 and July 2013 sampling periods. Intra-annual comparisons included June, July, and August 2013 sampling periods. Plots sampled were blocks and sampling periods were the grouping variables. IAF (non-native annual forbs), IPF (non-native perennial forbs), IAG (non-native annual grasses), IPG (non-native perennial grasses), NAF (native annual forbs), NPG (native perennial grasses), NPF (native perennial forbs), and NPS (native perennial shrubs).

Category	Lowland				Montane				Subalpine			
	July12/June13		July12/July13		July12/June13		July12/July13		July12/June13		July12/July13	
	A	P	A	P	A	P	A	P	A	P	A	P
IAF	<b>0.062</b>	<b>0.012</b>	<b>0.068</b>	<b>0.009</b>	0.019	0.141	-0.001	0.424	-0.051	0.841	-0.003	0.811
IPF	<b>0.052</b>	<b>0.045</b>	0.034	0.103	0.012	0.259	0.029	0.068	-0.004	0.446	-0.024	0.884
IAG	<b>0.241</b>	<b>0.004</b>	<b>0.239</b>	<b>0.002</b>	-0.012	0.821	-0.009	0.811	NA	NA	NA	NA
IPG	0.024	0.181	<b>0.062</b>	<b>0.043</b>	0.047	0.055	-0.004	0.556	0.019	0.159	0.035	0.079
NAF	<b>0.116</b>	<b>0.003</b>	<b>0.129</b>	<b>0.001</b>	-0.027	0.943	<b>0.046</b>	<b>0.042</b>	0.023	0.092	<b>0.080</b>	<b>0.016</b>
NPG	<b>0.063</b>	<b>0.008</b>	0.047	0.081	<b>0.105</b>	<b>0.002</b>	<b>0.130</b>	<b>0.001</b>	<b>0.078</b>	<b>0.007</b>	<b>0.087</b>	<b>0.002</b>
NPF	0.039	0.079	<b>0.104</b>	<b>0.004</b>	<b>0.078</b>	<b>2 E-04</b>	<b>0.113</b>	<b>1 E-04</b>	<b>0.096</b>	<b>0.004</b>	<b>0.153</b>	<b>0.003</b>
NPS	0.089	0.063	<b>0.100</b>	<b>0.049</b>	<b>0.019</b>	<b>0.041</b>	<b>0.048</b>	<b>0.004</b>	<b>0.066</b>	<b>0.024</b>	0.021	0.220

Table 3.9: Indicator species for different understory vascular plant surveys taken during two different years (July 2012 and June 2013). All indicator species had  $p < 0.05$ . Higher indicator values (IV) shows a stronger tendency for a species to a particular sampling period.

Indicator Species	IV	Trait Category	Indicator Species	IV	Trait Category
<b>July 2012 Sampling Period</b>			<b>June 2013 Sampling Period</b>		
<i>Bromus marginatus</i>	47.1	NPG	<i>Viola glabella</i>	47.5	NPF
<i>Elymus glaucus</i>	38.7	NPG	<i>Hieracium albiflorum</i>	43.9	NPF
<i>Poa secunda</i>	36.8	NPG	<i>Taraxacum officinale</i>	41.0	IPF
<i>Microsteris gracilis</i>	32.9	NAF	<i>Arnica cordifolia</i>	39.0	NPF
<i>Trifolium repens</i>	31.7	NPF	<i>Madia gracilis</i>	36.0	NAF
<i>Abies grandis</i>	30.7	TREE	<i>Bromus vulgaris</i>	34.9	NPG
<i>Cynoglossum officinale</i>	29.1	IPF	<i>Orthilia secunda</i>	34.8	NPF
<i>Madia sativa</i>	21.4	NAF	<i>Sorbus scopulina</i>	27.3	NPS
<i>Plantago lanceolata</i>	20.4	IAF	<i>Bromus hordeaceus</i>	23.3	IAG
<i>Microseris nutans</i>	20.0	NPF	<i>Symphyotrichum foliaceum</i>	23.3	NPF
<i>Luzula multiflora</i>	20.0	NPG	<i>Goodyera oblongifolia</i>	22.5	NPF
			<i>Galium aparine</i>	22.2	NAF
			<i>Lupin sp</i>	22.0	NPF
			<i>Potentilla gracilis</i>	21.1	NPF
			<i>Asperugo procumbens</i>	20.0	IAF
			<i>Salix sp</i>	20.0	NPS
			<i>Chicorium intybus</i>	19.1	IPF
			<i>Festuca rubra</i>	18.8	NPG
			<i>Trisetum canescense</i>	18.3	NPG
			<i>Abies lasiocarpa</i>	17.4	TREE

Table 3.10: Indicator species for different understory vascular plant surveys taken during two different years (July 2012 and July 2013). All indicator species had  $p < 0.05$ . Higher indicator values (IV) shows a stronger tendency for a species to a particular sampling period.

Indicator Species	IV	Trait Category	Indicator Species	IV	Trait Category
July 2012 Sampling Period			July 2013 Sampling Period		
<i>Ranunculus uncinatus</i>	42.6	NPF	<i>Carex sp</i>	56.9	NPG
<i>Poa compressa</i>	39.8	NPG	<i>Hieracium albiflorum</i>	48.8	NPF
<i>Galium boreale</i>	38.0	NPF	<i>Viola glabella</i>	46.5	NPF
<i>Microsteris gracilis</i>	37.8	NAF	<i>Galium triflorum</i>	43.3	NPF
<i>Elymus glaucus</i>	37.0	NPG	<i>Bromus vulgaris</i>	38.9	NPG
<i>Clarkia pulchella</i>	36.7	NAF	<i>Anemone piperi</i>	38.7	NPF
<i>Poa secunda</i>	35.4	NPG	<i>Orthilia secunda</i>	32.2	NPF
<i>Fragaria virginiana</i>	34.9	NPF	<i>Trisetum canescens</i>	32.2	NPG
<i>Lupinus pollyphylus</i>	31.1	NPF	<i>Polygonum douglasii</i>	29.0	NAF
<i>Deschampsia elongata</i>	31.1	NPG	<i>Viola nuttallii</i>	28.2	NPF
<i>Collinsia parviflora</i>	27.9	NAF	<i>Symphyotrichum ascendens</i>	27.6	NPF
<i>Vaccinium membranaceum</i>	26.2	NPS	<i>Bromus hordeaceus</i>	26.7	IAG
<i>Ranunculus occidentalis</i>	25.0	NPF	<i>Phacelia hastate</i>	26.7	NPF
<i>Melica subulata</i>	23.1	NPG	<i>Symphyotrichum foliaceum</i>	26.7	NPF
<i>Bromus tectorum</i>	21.0	IAG	<i>Cirsium arvense</i>	26.6	IPF
<i>Luzula multiflora</i>	20.0	NPG	<i>Carex geyeri</i>	25.5	NPG
			<i>Madia gracilis</i>	25.4	NAF
			<i>Lupin sp</i>	25.0	NPF
			<i>Solidago canadensis</i>	23.4	NPF
			<i>Cichorium intybus</i>	20.4	IPF
			<i>Listera caurina</i>	19.5	NPF
			<i>Alyssum alyssoides</i>	19.1	IAF
			<i>Bromus arvensis</i>	17.8	IAG
			<i>Bromus inermis</i>	17.7	IPG



## Appendix A. Supporting figures

## Monthly Precipitation (mm)    Monthly Temperature (°C)

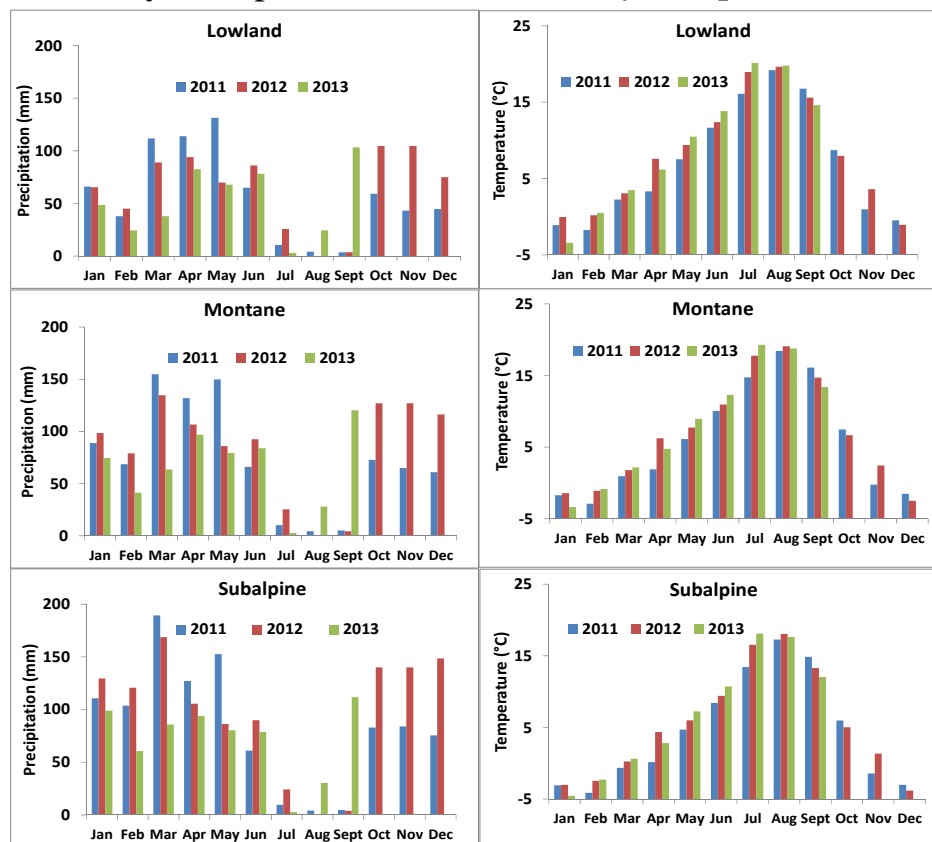


Figure 3.A1: Monthly total precipitation (mm) and average temperature (°C) for 2011, 2012, and 2013 for each mountain zone along Mt. Harris road in the Wallowa Mountains located in northeastern Oregon. Precipitation and temperature data were extracted from the Prism model (Daly et al. 2002) and values shown were averaged among all transects within each mountain zone.

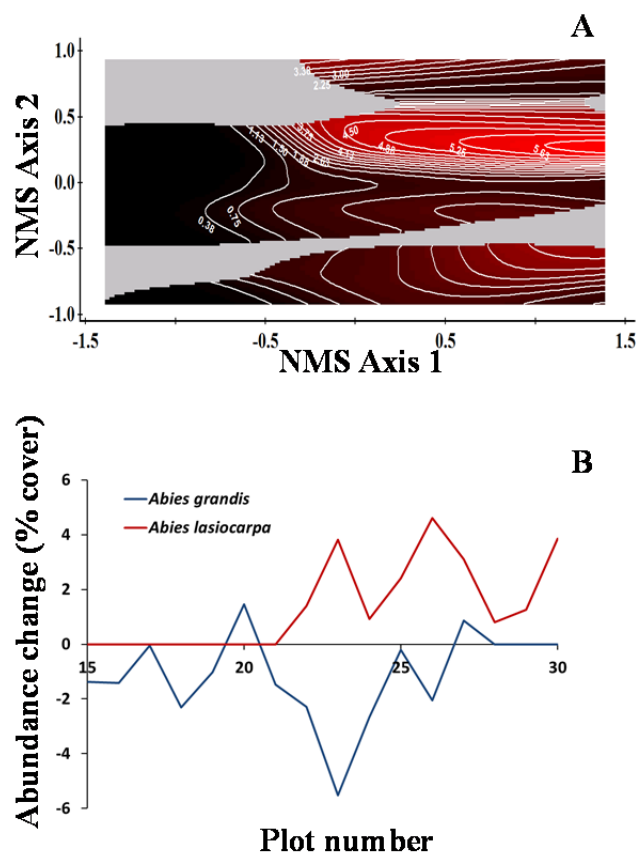


Figure 3.A2: Change in *Abies grandis* and *Abies lasiocarpa* canopy cover (%) between July 2012 and June 2013. A) Three dimensional contour plot depicts the combined density of *A. grandis* and *A. lasiocarpa* abundance change between sampling periods in species space. The response variable was the sum of canopy cover change for both species within each plot. The predictor variables were NMS Axes 1 and 2. Red shading indicates high density of abundance change between sampling periods and dark black shading depicts low abundance change. B) Two dimensional plots of *A. grandis* and *A. lasiocarpa* abundance change (% canopy cover) as a function of plot number.

## Chapter 4 Conclusions

This thesis contributes to the study of plant invasion ecology in temperate mountain environments through: 1) the identification of important correlates of non-native plant abundance and richness along an elevation gradient; 2) the detection of potential barriers to non-native vascular plant establishment across various plant communities in the Wallowa Mountains; 3) the provision of descriptive comparisons of native and non-native vascular plant species distributions in a mountain ecosystem; and 4) an evaluation of the effects of sampling time on inter- and intra-annual changes in plant community composition and individual species distributions across various communities in the Wallowa Mountains. Additionally, this study establishes a baseline for future comparisons of non-native and native understory vascular plant community patterns to other mountain systems within the MIREN research community, and plant species composition and individual species distribution changes over time in the Wallowa Mountains.

I discuss the contributions of each chapter below including a summary of our major findings, management implications, and future research directions that emerged from each respective chapter. Lastly, an overall summary ties together both chapters and provides suggestions of how this study can further inform local and global research related to plant invasions in mountain environments.

Chapter 2 describes an exploratory analysis of non-native vascular plant distributions along an elevation gradient in the Wallowa Mountains of northeastern Oregon. We evaluated the main drivers of plant invasions in the Wallowa Mountains,

and explored the extent patterns of native species distributions and their causes differed from non-native species along an elevation gradient.

Consistent with most studies in temperate mountain systems, non-native species richness decreased continuously with increasing elevation (Alexander et al. 2011; Barni et al. 2012; Seipel et al. 2012) and native species richness displayed a unimodal distribution with maximum richness occurring at the mid-elevations (Nogués-Bravo et al. 2008). Complementary analyses including non-metric multidimensional scaling (NMS), non-parametric multiplicative regression (NPMR), and indicator species analysis (ISA) suggested that elevation, canopy openness and disturbance were the most important factors influencing non-native species distributions along an elevation gradient in our study area. The tendency for non-native species to dominate in low elevation grass and shrub habitats also indicated that bunchgrass communities were particularly susceptible to plant invasion in the Blue Mountain region. Non-native species were primarily concentrated in the low elevation sites with high canopy openness and moderate to high disturbance levels. In contrast, we found that closed canopy forests and subalpine communities were relatively free of non-native plants. Modeling of elevation and canopy openness niche widths for all common non-native species in our area showed no evidence of shade or high elevation specialization. These collective results contribute to the further development of theories that explain patterns of non-native species assembly in mountain ecosystems. Our findings are supportive of researchers who found that most mountain invaders tend to be ruderal species that depend on disturbance for spread in mountain environments (Peryna et al. 2002; Pickering and Hill 2007;

Kalwij et al. 2008) and are consistent with the directional ecological filtering hypothesis (Alexander et al. 2011) which assumes that non-native plants are preferentially introduced into low elevations, pre-adapted species establish, species are sequentially filtered out along the elevation gradient, and generalist species end up occupying the broadest elevation range.

We found that elevation and canopy openness were the dominate gradients associated with understory vascular plant community variability. Relationships between non-native species abundance and the strongest community gradients revealed that the transition into the lower subalpine community and over-story canopy closure exceeding 60 percent were potential barriers to non-native species establishment in our study area. A paucity of open canopy forest within the montane zone likely contributed to a decrease of non-native propagule pressure within subalpine communities. However, our findings that non-native species richness and abundance showed the same abrupt decline coincident with a transition into the subalpine community along all three roads despite differences in disturbance history, geographical distances between mountain zones, and traffic volume suggest that a common mechanism may be responsible for both triggering shifts in native vegetation from montane to subalpine communities and limiting non-native establishment in the subalpine community. NMS indicated that the continuous decline of non-native species richness and abundance from the lowland through the montane zone was largely due to greater canopy openness with increased elevation. After accounting for canopy openness non-native abundance and richness remained relatively constant

throughout the lowland and montane zones and decreased abruptly at the subalpine community transition.

Perhaps our most important contributions to both the field of plant invasion ecology and land managers in the Wallowa Mountains are our findings that over-story canopy closure is likely the dominant factor limiting non-native species abundance in the montane zone and that the low subalpine community transition is the most important barrier for non-native species establishment at high elevations. The apparent global phenomenon of decreasing non-native species abundance with increasing elevation is informative because it suggests that a common mechanism is responsible for filtering non-native species in mountains, but at the same time is unsatisfying because causal mechanisms have not been separated from an overall elevation effect due to the high correlation between elevation and other factors including propagule pressure, disturbance, temperature, precipitation, and soil characteristics (Barni et al. 2012). Our results suggest that climatic factors including temperature and precipitation are the primary barriers to non-native plant establishment into high elevations in the Wallowa Mountains. Additionally, our ability to identify a well-defined transition zone as the primary barrier to non-native species establishment into high elevations should allow for the design of future studies that can separate out the contributions of specific factors that limit non-native establishment in the low subalpine community.

Current land management goals in the Blue Mountains include the use of tools such as prescribed fire, and alterations to logging and grazing practices to more closely mimic natural disturbance regimes of forested communities in the Blue

Mountains (Quigley et al. 1997; U.S. U. S. Department of Agriculture 2014). Desired conditions include shifts in forest structure of low elevation and south facing forests (dry forests) from “unhealthy” stands characterized by closed canopies of fire intolerant fir (*Abies*) species back into open-park like stands of *Pinus ponderosa* (Johnson 1994; Quigley et al. 1997; U.S. Department of Agriculture 2014). It is unclear if increased canopy openness and frequent disturbance will increase the invasion potential of forests in the montane zone or if re-colonization of fire tolerant native species will be able to outcompete non-natives in these areas (U.S. Department of Agriculture 2014). Based on our results, we expect that the response potentials of montane forests in the Wallowas have been altered with the introduction of exotic species and recommend that invasive plant control and monitoring be a critical component of land management practices that create early successional conditions and are likely to increase the invasion potential of montane forests in the Wallowa Mountains.

The apparent resistance of subalpine communities to invasion by non-native plants in the Wallowa Mountains indicates that native subalpine communities may be able to recover from disturbances that increase canopy openness and bare-ground with little threat of plant invasion under current conditions. However, this does not necessarily mean that land managers should not be concerned about future invasion into subalpine communities. Direct introductions of high elevation adapted species are expected to increase with time (Pauchard et al. 2009), and increased residency time of non-natives increases the probability of invasion due to alleviation of

dispersal limitations and/or range expansion through local adaptation (Dietz and Edwards 2006).

Many subalpine communities in the Wallowa Mountains have shown substantial departure from natural conditions due to early overgrazing and fire suppression (Johnson 1994; Quigley et al. 1997) and therefore, may be more susceptible to invasion by high elevation adapted species (Hobbs and Huenneke 1992; Harrod 2001). Recently introduced species that have proven invasive in other subalpine habitats including *Hieracium aurantiacum* and *Hieracium caespitosum* (Williams et al. 2008) have been identified in the Wallowa Mountains (Parks et al. 2005), and may establish and spread in subalpine communities that have been altered from historical conditions by human activities (Harrod 2001). The apparent resistance of subalpine areas to invasion may allow managers a window to reinstate natural disturbance regimes and restore degraded areas in order to promote healthy native communities that are less susceptible to increased pressure by invasive plants.

Chapter 2 results pave the way for future research opportunities that focus on identifying the specific mechanisms responsible for filtering non-native plants along an elevation gradient. We identified two important barriers to non-native establishment in the Wallowa Mountains including over-story canopy closure within the montane zone and a transition into the subalpine community. Plant community and population studies that are intensively focused at the upper montane to subalpine transition zone should be able to separate out the contributions of different factors such as temperature, precipitation, propagule supply, disturbance, and soil characteristics that create barriers to non-native species spread into the Wallowa's



subalpine communities. Researchers may also consider the use of meteorological stations or sensors (temperature, precipitation, soil moisture, etc.) at each site to allow for separation of highly correlated climatic factors.

The effect of propagule pressure is often considered to be an understudied factor with regards to plant invasion processes (Eschtruth and Battles 2009; Rejmanek et al. 2013). The discovery of a potential non-native plant dispersal barrier consisting of closed canopy forests within the high elevation montane zone provides an excellent opportunity to study the influence of spatial patterns of over-story forest canopy structure on the dispersal of non-native plants in a mountain ecosystem. Additionally, because roads provide efficient transport of propagules and continuous disturbed habitat, propagule pressure studies that look at interactions between road corridors and adjacent habitat structure should provide important information regarding non-native plant dispersal into the Wallowa Mountains. The presence of the Eagle Cap Wilderness area within the Wallowa Mountain Range provides an ideal setting for comparisons of non-native seed dispersal and propagule pressure between roadless areas and areas with forest roads.

Chapter 3 investigated inter- and intra-annual changes in vascular plant species composition along an elevation gradient in the Wallowa Mountains. Our specific objectives were to determine how sampling period influenced changes in native and non-native species composition, identify species that showed the most variation on an inter- and intra-annual basis, and evaluate the most important abiotic and biotic factors associated with inter and intra-annual vegetation change.

Vascular plant species composition changed both between years and between each sampling period during one growing season. Our results indicated that species community changes were due to a combination of sampling error and real temporal shifts in species composition.

Consistent with other studies, species richness increased with sampling effort (Kirby et al. 1986; Archaux et al. 2006), dominant species were consistently found throughout all sampling periods, and rare species showed the highest rate of turnover between sampling periods (Klimes et al. 2001; Ristau et al. 2001; Kercher et al. 2003). Higher rates of rare species turnover and the disappearance and re-appearance of rare species during different sampling periods indicated that overlooking species contributed to observed changes in species composition between sampling periods. Species identification disagreement between sampling periods also contributed to apparent changes in species composition. Most errors associated with species disagreement appeared to involve confusing taxa from the same genus. Additionally, we were able to detect a negative correlation between the occurrence of *Abies grandis* and *Abies lasiocarpa* between year 1 and year 2 in a community where these species are known to overlap indicating that misidentification of species considered easy to identify contributed to sampling error in this study.

Despite sampling error effects, we were able to detect clear patterns of seasonal vegetation change between sampling periods. The highest species richness and greatest number of indicator species were associated with the early summer (June) sampling period. Both native and non-native species richness decreased from June to August during one growing season. Approximately one quarter of non-native

species showed tendencies to a specific sampling period with the vast majority of them favoring the early summer period. Most early summer non-native indicator species were annual species and were found in the lowland grass/shrub communities. However, two non-natives (*Taraxacum officinale* and *Veronica serpyllifolia*) that were found in subalpine communities were also indicator species of the early summer sampling period. Higher species richness and greater numbers of indicator species during the early summer sampling period are consistent with other research in temperate ecosystems and likely due to an overlap between vernal and early summer species and species that develop and continue to grow over a longer growing season (Ristau et al. 2001; Pokorny et al. 2004).

Non-native annual forbs and non-native annual grasses in the lowland zone (grass/shrub communities) and native annual forbs in the montane zone showed the highest intra-annual variation in species composition. Inter-annual variability in species composition was highest for non-native annual grass species in the lowland zone. These findings suggest that single vegetation monitoring events fail to capture the natural temporal variation of annual species distributions in our study area.

Most vegetation change in the lowland and montane zones occurred between the June and July sampling periods and vegetation change was greatest between July and August in the subalpine community. Although most species showed later development in the subalpine community, several native species (*Trautvetteria caroliniensis*, *Valeriana sitchensis*, and *Corallorhiza maculata*) and two non-natives (*Veronica serpyllifolia* and *Taraxacum officinale*) were most abundant during the early summer sampling period.

Total species richness was the most important predictor of vegetation turnover for each sampling period transition. Consistent with other studies, we observed increased turnover of species and increased community composition change with higher species richness (Cottingham et al. 2001; Allan et al. 2011). Stable trait category abundance and richness and asynchronous variations of functionally similar but temporally partitioned species were also observed in sites with high species richness.

Chapter 3 results contribute to the future advancement of long-term monitoring methodology for the purpose of detecting vegetation changes over time in mountain ecosystems. Our results suggest that monitoring efforts should include periodic sampling during the growing season. Sampling once during the late spring or early summer and then again coinciding with peak biomass should increase the chances of capturing both early season vernal species and later season species. Multiple sampling efforts may be critical for repeatable and accurate descriptions of non-native species distributions in the Wallowa Mountains because most non-native species occur in the low elevation grass/shrub communities where mid and late season drought tend to favor early growing season specialization. Our findings also suggest that sampling multiple times in high elevation communities will be necessary to capture the dynamics of non-native species spread and impacts on subalpine communities. The tendency for a few native and non-native high elevation adapted species to favor the early summer sampling period within the subalpine community indicates that mid and late summer sampling of high elevations in the Wallowas may

result in an underestimation of non-native species spread and invasion impact in these areas.

Our results indicated that both annual and perennial species can vary substantially from year to year. Long-term sampling of communities at the same phenological timing each year coupled with multiple sampling periods within each growing season should help researchers and managers separate out natural variability of plant species compositional changes from long-term trends in vegetation change.

Sampling error associated with overlooking species, species identification disagreement between sampling periods, and inconsistent plot relocation likely contributed to apparent changes in species capture and abundance between sampling periods for our study. Based on literature, we expect that our use of teams of two or more observers to sample vegetation plots helped to minimize sampling error (Nillson and Nillson 1983; Vittoz et al. 2010). Ideally, experienced professionals skilled in the identification and sampling of vegetation in the area of interest should be used to minimize sampling error. However, much of field sampling is carried out by technicians with varying levels of experience. Our field technicians varied in skill level from expert (Forest Service Botanist with over 25 years' experience in the Blue Mountains) to undergraduate Biology and Rangeland Ecology students with little field experience prior to the 2012 sampling period. Training prior to vegetation sampling has been shown to substantially decrease sampling error between observers (Gray and Azuma 2005). Our results indicate that pre-sampling season training likely focused on challenging species and may have glossed over some species considered easy to identify. Future training efforts should aim to build proficiency in

identification of a broad range of common species in the area of interest prior to sampling and instill confidence in field technicians to encourage continued communication about species identification and discourage apprehensive attitudes about seeking help when problems arise.

We recommend that additional effort be allocated to improve the marking of permanent plot boundaries in our study area. Currently the markers are located at 50 meter intervals at the plot ends. The wide spacing between plot markers can result in location errors of plot boundaries particularly in sites with thick understory vegetation. Placing permanent markers at finer increments along plot boundaries will cause a little more effort upfront, but should more than make up for the additional costs with greater repeatability of measurements over time.

Multivariate analysis of plant species composition is generally robust to sampling error that is typical for vegetation surveys due to statistical redundancy of multivariate species information (McCune et al. 1997). Therefore, given reasonable attempts to minimize sampling error, analysis of species composition change over time in permanent plots should provide useful information to gauge vegetation change over time in our study area. However, sampling error can be problematic when estimating species richness and attempting to capture rare species (McCune et al. 1997). Researchers may consider using complementary sampling techniques such as adaptive sampling methods (Maxwell et al. 2012) or modified-Whittaker plots (Stohlgren et al. 1995) to improve capture of species in a given area. Intensive sampling of larger areas using experienced observers at lower frequency intervals

than community monitoring may also be used to provide more thorough lists of non-native species present within a given area.

Chapter 3 results reveal a need for researchers to consider natural variability in species composition both on an inter- and intra-annual basis in order to truly describe non-native species dynamics, distributions, and impacts in the Wallowa Mountain system. We found that many non-native plants in bunchgrass communities were more abundant during the early summer period and declined as the growing season progressed. Selection of our sampling time window (mid-June through late August) was consistent with prior research (Ristau et al. 2001; Korb and Fule 2008), but the beginning of the field season was guided by the university calendar rather than based on ecological information. The tendency for most specialist species and greatest species richness to occur during the June time frame suggests that future research should investigate change in species composition and richness at earlier sampling periods during the spring. This may be particularly important for evaluating distributions and impacts of non-native species in the Wallowa Mountains as most non-native species were early seral species and tended to occur in the low elevation bunchgrass communities where mid- and late season water resources are limiting. For example, personal observations of low montane sites (elevation  $\simeq$  1,150 meters) between April 3<sup>rd</sup> – April 16<sup>th</sup>, 2014 in the Blue Mountains, revealed many early season species that were either absent or rare in our dataset. Common non-native species observed blooming in a qualitative mid-April sample that were absent or nearly so in our dataset include *Erythronium grandiflorum*, *Claytonia lanceolata*, *Lathyrus nevadensis*, *Olsynium douglasii*, *Orogenia linearifolia*, *Ranunculus*

*glaberrimus*, and *Lomatium cous*. Two non-native species that were dominant on many sites and were also flowering at this time included *Draba verna*, a species that was rarely encountered during our survey, and *Poa bulbosa*. Many of these species and other early season native and non-native forbs are extremely common in bunchgrass, prairie, and dry forest communities during early to mid-spring in the Blue Mountains and are likely missed or underrepresented with vegetation sampling schedules that begin as late as mid-June in the region. The inclusion of vernal species in species distribution studies may totally alter our concepts of species richness patterns and non-native species dynamics in this system particularly when low elevation areas where these species appear early in the growing season and disappear by early or mid-summer are the same communities that currently show the highest invasion potential and comparatively low biodiversity. Vegetation monitoring that captures vernal species distributions in the Blue Mountains should improve our understanding of non-native plant dynamics and patterns of diversity along elevation gradients in mountain ecosystems.

Our chapter 3 results also suggest that research focussed on species turnover as a function of richness should provide useful information in regards to the role that non-native species may play in either disrupting or contributing to ecosystem stability. We found that the highest species turnover and relative vegetation abundance turnover was highest in species rich areas. Increased species richness also appeared to be coincident with temporal niche partitioning between functionally similar native and non-native species. Long-term monitoring of biotic interactions in species rich montane sites within the Blue Mountains may provide information that



informs both non-native assembly processes and potential impacts on ecosystem stability in diverse mountain ecosystems.

## Synthesis

Non-native plant invasion into mountain environments threatens ecosystem integrity and socioeconomic welfare in many areas. Mountain ecosystems are still in the beginning stages of the invasion process. Examining non-native species distribution patterns in mountains can yield important insight into the invasion process as well as inform invasive plant control and management to stop the spread of non-native species into mountain ecosystems.

This thesis contributes to the understanding of the plant invasion process along an elevation gradient and informs the improvement of sampling methodology for long-term monitoring of permanent plots in mountain ecosystems. Chapter 2 results provide contributions to the study of plant invasion ecology in mountain ecosystems through the identification of important correlates (elevation, canopy openness, disturbance) of non-native species abundance and richness and the detection of major barriers (transition to subalpine community, canopy openness > 60%) to non-native species establishment in the Wallowa Mountains. Furthermore Chapter 2 results suggest that introduction pathways have played a major role in shaping the current patterns of non-native species in the Wallowa Mountain range. Therefore, altered introduction pathways are likely to change plant invasion dynamics and species distribution in the Wallowa Mountains. Chapter 2 results are limited because they are based on species abundance taken at one single snapshot in time.

Long-term monitoring of plots that were permanently located in this study is a priority for MIREN. Examining changes in species distribution patterns over time can provide additional information regarding changes in causal factors of plant invasion over time, impacts to native communities, and rate and magnitude of spread. Chapter 3 results contribute to the design of long-term monitoring methodology to improve repeat sampling of vegetation in a mountain ecosystem. Chapter 3 results indicate that periodic sampling is needed to more accurately capture native and non-native species distribution patterns in the Wallowa Mountains. Our results suggest that late spring and early summer sampling is particularly critical for accurate representation of species distributions in low elevation semi-arid bunchgrass communities. Chapter 3 results also suggest that overlooking species and misidentification of species were likely amplified by a combination of inconsistent plot relocation and pre-sample training limitations.

The results from this study can readily be extended to direct future research directions and inform invasive plant management in mountain ecosystems. Some future research questions that are natural extensions of this research include: what is the specific mechanism responsible for filtering non-native species at the subalpine transition zone; how does the interaction between canopy openness and different disturbances influence non-native establishment in the montane zone of the Wallowa Mountains; how does the interaction between road networks and over-story canopy structure affect dispersal of non-native plants into subalpine and alpine communities in the Wallowa Mountains; and does non-native plant establishment facilitate or disrupt ecosystem stability in species rich montane forests?

Our results also provide important information for land managers working in the Wallowa Mountain region including: 1) disturbances that increase canopy openness in the montane zone are likely to facilitate non-native species spread in those areas; 2) subalpine communities appear more resistant to plant invasions under current conditions and may require less intensive invasive plant control measures following disturbance; 3) control of non-native species in lowland and roadside habitats as well as disconnecting corridors of suitable (disturbed and open canopy) habitat should reduce the expansion of non-natives species into higher elevations; and 4) periodic sampling during the growing season will improve capture and distribution estimates of species along an elevation gradient.

Lastly, as a requirement of this project, all data collected during the 2012 field season was delivered to the MIREN team. Our data consisting of complete understory vascular plant species abundances along an elevation gradient in the Wallowa Mountains have been compiled with datasets collected using the same standard protocol from eight other mountain ranges around the world. The MIREN team is currently working on a global scale analysis of non-native and native understory vascular plant distribution patterns that will complement our work and should allow for multi-spatial scale interpretation of patterns of species distributions on local (mountain range), regional (mountain ranges on the same continent), and global (mountain ranges across different continents) scales.

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