AN ABSTRACT OF THE THESIS OF

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As species of ash trees become increasingly threatened worldwide by exotic pests and pathogens, it is important to develop descriptions of their ecologies that help guide the conservation and restoration of forests in which they are a major component. Oregon ash (*Fraxinus latifolia*) is a dominant tree species in wetland forests of the Willamette Valley, Oregon. It is potentially threatened by the emerald ash borer, an exotic forest insect that is expanding in range in North America. The arrival of the emerald ash borer in the western United States is expected to cause high rates of Oregon ash mortality, which will likely highly alter structural and compositional characteristics of regional riparian and wetland forests. To investigate the structural development and plant community dynamics of Willamette Valley Oregon ash forests, I quantified species structure and composition for both overstory and understory communities along gradients of stand age and soil moisture. Community Type Wetland Index (CTWI) scores were calculated for each plot by multiplying plot-level species abundances by the national wetland indicator value for each species, and were used as an approximation of local soil moisture regimes. Ash forests and early seral savannas were sampled in 102 plots within 11 wetlands between Lane and Washington Counties, Oregon.

Early seral wetland savannas were dominated by herbaceous vegetation and had highly variable ash and other tree species recruitment. Young ash forests initiated on wetland sites that were formally maintained as savannas via anthropogenic disturbance. Structural development in these forests generally followed previously described post-disturbance stages: stem exclusion,

understory initiation, young multi-strata, and old growth. As stands aged, tree densities decreased and mean tree diameter increased. Mean stand densities (for trees >5 cm at 1.3 m height) ranged from 1727 trees per hectare in stem exclusion stands to 348 in old growth stands, while mean tree diameter increased from 12 to 32 cm between those same stages. Furthermore, understory vegetation shifted from herbaceous to shrub and understory tree species. Oregon ash had the greatest relative dominance of all tree species at all stages of structural development. Oregon white oak (*Quercus garryana*) was the only other tree species commonly found in forest canopies, though it was typically far less abundant than Oregon ash. Plots in which oak was present had a greater depth to soil mottling, indicating a lower depth to the annual high water table. Oregon ash was also the most commonly regenerating tree species in all stages of structural development, and nearly 70% of ash regeneration was vegetative. Other tree regeneration was typically restricted to understory species, especially cascara (*Rhamnus purshiana*) in forests and hawthorn (*Crataegus spp.*) in savannas. Forest structural diversity increased between each stage of development.

In total, 216 plant species were identified. Of these, 147 were found in forest plots. Community composition differed significantly between forests and savannas, and between "young" (stem exclusion and understory initiation) plots and "old" (young multi-strata and old growth) plots. Nonmetric multidimensional scaling (NMS) indicated that, for all wetland plots, the environmental variables most highly correlated with community composition were CTWI scores and canopy cover. For forest plots only, NMS indicated that CTWI scores and stand density were the environmental variables most related to patterns in community composition. Species richness was not correlated with canopy cover, but was negatively correlated with CTWI scores. Exotic species cover was negatively correlated with canopy cover, but was not correlated with CTWI scores. Exotic species composition was dependent on both canopy cover and CTWI scores. On wet sites, reed canary grass (*Phalaris arundinacea*) was particularly abundant, and was associated with low species richness. On drier sites, common exotic species included trees and shrubs such as blackberries (*Rubus spp.*), exotic roses (*Rosa spp.*), single-seeded hawthorn (*Crataegus monogyna*), and common pear (*Pyrus communis*) as well as several grass and forb species.

The results of this study suggest that, although overstory tree communities are characterized by low diversity, Oregon ash forests are important for landscape-scale structural

and plant community diversity in Willamette Valley wetlands. However, overstory tree communities lack diversity; Oregon ash appears to be both an early seral, colonizing species in open wetlands and a climax species that is capable of regenerating under a closed canopy. Few other trees are present regionally that are capable of maintaining a forested state in wetlands. Furthermore, closed canopy Oregon ash forests may suppress exotic species spread, and in the absence of management, overstory ash mortality may lead to increased exotic plant cover. Regardless of future forest health threats, intact Oregon ash forests, like other regional wetland-types, are currently few and limited in extent and should be considered a conservation priority.

Overstory Structure and Community Characteristics of Oregon Ash (*Fraxinus latifolia*) Forests
of the Willamette Valley, Oregon

by
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Sean Prive, Author

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CHAPTER 1: INTRODUCTION

BACKGROUND

In the Willamette Valley of western Oregon, Oregon ash (*Fraxinus latifolia*) is often the dominant tree species in valley bottom forested wetlands associated with deep, poorly draining soils (Owston 1990). These conditions occur intermittently in much of the Valley where lowland floodplains or alluvial fans are situated on fine textured soils, typically of the Bashaw, Natroy, and Waldo series (Wilson 1998). Historically, riparian forests covered kilometers-wide floodplains of the Willamette River and its tributaries (Towle 1982; Christy and Alverson 2011). However, Willamette Valley riparian corridors and associated wetlands have been highly altered since the 1840's. This is the result of extensive draining, stream channelization, flood control efforts, and land-use conversion (Taft and Haig 2003). Furthermore, Willamette Valley ash forests have a complex history of exclusion via Native American burning, followed by periods of expansion (due to Euro-American fire suppression) and, ultimately, widespread clearing for grass seed production and grain crops (Towle 1982).

Today, remnant valley bottom forests, including those dominated by Oregon ash, typically occupy narrow bands along creeks and rivers. In addition to Oregon ash, several tree species are associated with these forests, including black cottonwood (*Populus trichocarpa*), and white alder (*Alnus rhombifolia*) in seasonally flooded areas, and Oregon white oak (*Quercus garryana*), big-leaf maple (*Acer macrophyllum*), and Douglas-fir (*Pseudotsuga menziesii*) on drier sites (Owston 1990). Oregon ash becomes the dominant species on only the most poorly drained sites (Heinitz 1982). Among these sites, ash-dominated forested wetlands have developed over the past century in broad, flat floodplains where anthropogenic disturbance has been suppressed. In a highly developed region with few sites that retain intact native plant assemblages, ash forests represent unique, relatively undisturbed refuges for many marginalized species (Titus et. al., 2006; McCune, nd). However, despite the potential ecological importance of ash swamps in the Willamette Valley, the structure and composition, overall ecology, patterns of succession, associated plant communities, and functional and habitat characteristics of these systems are all poorly documented.

OREGON ASH ECOLOGY

The natural range of Oregon ash extends from southern California to northern Washington where it typically occupies riparian habitats below 910 m in elevation (Owston 1990). It grows on a wide range of soil types, but becomes particularly common on seasonally flooded clays and silty clays in the Willamette Valley (Frenkel and Heinitz 1987). Oregon ash is a dioecious tree species that can annually produce abundant seed. Fruits are wind-dispersed, single-winged samaras that mature in late summer (Arno and Hammerly 1977). Seed germination is suppressed on sandy or gravelly soils associated with scoured riverine systems. However, on soils rich in organic matter, germination can be quite high (Sudworth 1908). Young trees tend to grow quickly and are moderately shade tolerant (Owston 1990). Oregon ash commonly sprouts vegetatively from stumps and downed wood (Owston 1990). Where it is found encroaching into open wetlands, Oregon ash is often reduced to a shrubby form by frequent fires and other anthropogenic disturbances, though seeding and vegetative regeneration can be persistent and aggressive (pers. obs. 2015).

The combination of reduced germination on scoured, sandy soils and moderate shade tolerance causes Oregon ash to be a late-seral species in many riparian forests, such as those dominated by black cottonwood (Fierke and Kauffman 2005). However, in wetlands that do not experience high-intensity flood events, successional dynamics among tree species is less clear. On these sites, Oregon ash is often a colonizing tree species, and is one of few tree species that is capable of developing into a closed canopy forest. Other tree species, such as Oregon white oak, black cottonwood, and alder are very shade intolerant, and thus unlikely to persist in later seral stages. Therefore, Oregon ash is likely an important tree species over a broad range of developmental stages in Willamette Valley wetlands.

ASH FOREST STRUCTURE AND COMMUNITY DYNAMICS

The range of structural characteristics of Oregon ash forests currently present in the Willamette Valley, such as stand densities, canopy closure, basal area, and crown mortality, have not been previously described. In many cases, streamside portions of ash forests appear to have

preceded the broader adjacent forests that initiated upon the cessation of burning and/or grazing in the past century (Towle, 1982; pers. obs. 2015). Therefore, variation in canopy conditions and stand densities may be largely explained by site history and stand age. Additionally, variability in microtopography and soil texture often leads to heterogeneous distribution of soil inundation and pooling in Oregon ash swamps, and may explain some patterns in overstory tree community composition.

As in other freshwater wetland systems (Vivian-Smith 1997), topographical heterogeneity and the resulting differences in hydrologic regimes likely also explains patterns of understory plant community composition in Oregon ash forests. However, ash swamp community composition is poorly documented, records of which are largely limited to the work of Frenkel and Heinitz (1987). Those authors identified two common plant communities in the ash swamps at William L. Finley National Wildlife Refuge (WLFNWR): *Fraxinus latifolia/Carex obnupta* and *Fraxinus latifolia/Symphoricarpos albus*. They found that differences in community composition were largely associated with fine-scale microtopographical features such as natural levees, as well as stand age and density. Community similarity, both within and between stands, was found to be low. Environmental conditions found in ash stands outside of WLFNWR likely include differences in hydrologic regimes, age classes, severity of exotic species invasion, overstory composition, and structural complexity. Several additional plant associations have been developed for ash-dominated forests in the Willamette Valley. Titus et. al. (2006) established several Oregon ash plant associations based on surveys conducted throughout the Willamette Valley. They identified 20 plant community types in which Oregon ash is associated with a native understory (composed of various shrubs, grasses and forbs). Additionally, they identified two with an exotic understory, and several in which Oregon ash is present with other tree species.

EXOTIC PLANT SPECIES

Willamette Valley wetlands have been highly influenced by the arrival and spread of exotic plant species over the past 150 years (Pendergrass 1998; Magee and Kentula 2005; Titus et. al. 2006). Wetland grasslands are often dominated by exotic grasses, such as reed canary grass (*Phalaris arundinacea*) on wetter sites, and sweet vernal grass (*Anthoxanthum odoratum*)

and colonial bentgrass (*Agrostis capillaris*) on drier sites, and require extensive management to maintain remnant populations of native plants (Pendergrass 1998; Wilson 1998; Magee and Kentula 2005). Furthermore, exotic shrubs, including Armenian blackberry (*Rubus armeniacus*) and single-seeded hawthorn (*Crataegus monogyna*), often encroach on open wetlands (Wilson 1998). The extent to which wetland forests with an ash-dominated canopy have been impacted by exotic plant species has not been previously documented. Exotic plants that often persist in more open wetland systems may be at least somewhat limited by their tolerances for shade and/or extensive soil inundation. Therefore, patterns of exotic plant invasion in ash forests may be related to a combination of overstory cover and local soil moisture regime. Ash forests may represent a less hospitable habitat for certain exotic plant species when compared to other wetlands, and thus might be well-suited for the maintenance of unique plant assemblages with relatively high levels of native cover when compared to more open wetlands.

WETLAND SAVANNAS OF THE WILLAMETTE VALLEY

Non-forested plant communities are also associated with Willamette Valley sites with poorly drained soils (Wilson 1998). These include bunchgrass, forb, or shrub dominated wetland prairies, which typically include patchy tree communities. These sites are often successional to ash forest and must be maintained via regular disturbance (Clark and Wilson 2001). Both forested and non-forested native wetland habitats are quite rare in the Willamette Valley (Hulse and Gregory 2002), and serve as refugia for native organisms on a landscape that has been otherwise largely developed for agricultural or urban use. While wetland prairie plant communities and their ecology are well documented, ash-dominated plant communities are more poorly understood. Furthermore, dissimilarity of community composition between these two related habitat types may provide some insight into the role of ash trees in wetland ecology.

POTENTIAL FUTURE THREATS TO OREGON ASH

Globally, ash species are threatened by the movement of exotic forest pests and pathogens. Specifically, ash dieback (caused by the fungus *Hymenoscyphus pseudoalbidus*) and the emerald ash borer (*Agrilus planipennis*) (Coleoptera: Buprestidae) have caused the mortality

of tens of millions of ash trees worldwide, and their distributions are continuing to grow. Ash dieback is a fungal pathogen that has impacted urban and wild populations of ash in Europe (Pautasso et. al. 2013). It causes necrotic lesions and leaf wilting that typically lead to tree mortality (Kowalski and Holdenrieder 2009). While ash dieback has not yet been reported in North America, the pace of spread and high rate of mortality in European ash trees is a cause for concern should it arrive. The emerald ash borer (EAB) is an exotic insect that has devastated North American ash forests over the past decade and a half, and has caused billions of dollars in damage to wild and urban trees (Anulewicz et. al. 2009). Like all North American *Fraxinus* species, Oregon ash is highly susceptible to colonization by EAB (Anulewicz and McCullough 2012). Following its arrival in several Midwestern states, EAB has progressively spread across much of the continent. Populations have been located as far west as Colorado (Colorado Department of Agriculture 2013). Despite widespread efforts at eradication, it is now threatening all native North American ash species with functional extirpation (Herms and McCullough 2014). In response, efforts are being made to better understand the roles of ash species in ecosystem processes and track changes brought about by ash mortality.

In areas where EAB has already become established, canopy gaps resulting from ash mortality have been predicted to have dramatic effects on local plant communities. These effects include increased pressure from invasive plant species, and changes in successional trajectories, nutrient cycling, disturbance regimes, and habitat characteristics (Gandhi and Herms 2010). As the range of ash dieback and EAB expand, western ash forests and mixed woodlands may also be impacted. An initial assessment of current conditions is needed to be able to anticipate ecological changes brought about by potential ash mortality. Furthermore, a comparison of plant communities in ash swamps and more open wetlands that are successional to Oregon ash may give some indication of potential shifts in community composition in the event of extensive loss of overstory ash.

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CHAPTER 2: STRUCTURAL DEVELOPMENT AND SUCCESSIONAL DYNAMICS OF OREGON ASH *(FRAXINUS LATIFOLIA)* FORESTS OF THE WILLAMETTE VALLEY, OREGON

ABSTRACT

Oregon ash (*Fraxinus latifolia*) forests are a relatively rare feature in wetlands of the Willamette Valley, Oregon. Furthermore, they are potentially threatened by pests and pathogens affecting *Fraxinus* species worldwide, particularly the emerald ash borer. Documenting structural and compositional development of this forest type will help inform future conservation and restoration efforts, and may help land managers anticipate changes in regional wetlands in the event of widespread Oregon ash mortality. This exploratory study used an adapted chronosequence design to describe changes over time in structural and compositional characteristics of 17 Oregon ash stands within 11 management areas in the Willamette Valley, Oregon. Stands initiated in wetland savannas where anthropogenic disturbance was abandoned, then progressed through four stages of structural development: stem exclusion, understory initiation, young multi-strata, and old growth. Closed canopy forests expressed increased structural diversity when compared to early seral wetland savannas, and stands became more structurally diverse over time. Stand density, tree size, and understory vegetation structure all varied significantly within stands at different stages of development. Younger stands tended to have several hundred (up to several thousand) stems per ha, and these trees tended to be smaller than 20 cm in diameter. Younger stands also had an abundance of dead and dying suppressed trees. As stands aged, they became less dense and were dominated by increasingly large trees. However, vegetative sprouting from suppressed and downed ash trees as well as recruitment of minor tree species formed additional understory cohorts as stands aged. This process led to multi-strata and old growth forests with a diverse set of size classes that were often dominated by large (50+ cm DBH) trees. Oregon ash was the dominant species at all stages of development, and appeared to be the climax species on all sites sampled. Tree communities in these systems were compositionally very homogenous. Overstory composition was typically limited to just two species: Oregon white oak (*Quercus garryana*) and Oregon ash. Mean depth to soil mottling was lower in plots with an overstory oak component, suggesting that tree species composition was

associated with local levels of seasonal soil saturation. Oregon ash was often the sole overstory tree species on particularly wet sites, and even where oak was currently dominant, evidence indicated that stands were succeeding to ash.

INTRODUCTION

Oregon ash- (*Fraxinus latifolia*) dominated wetland forests are unique environmental features that contribute to landscape level structural and compositional complexity, buffer riparian corridors, and provide aesthetic value in the agricultural and urbanized Willamette Valley. This forest type has been widely cleared and/or excluded from the region for the purposes of grain production and livestock grazing (Towle 1982). Furthermore, Oregon ash, like other North American ash species, is threatened with functional extirpation by the emerald ash borer, to which it is highly vulnerable. Few studies have been conducted on the development of structural features and succession in Willamette Valley ash forests. These processes have been described in related riverine gallery forests in which Oregon ash is considered a climax species (Fierke and Kauffman 2005). However, those forests have a distinct disturbance regime of frequent, stand-replacing flood events and have an important early-seral cottonwood (*Populus trichocarpa*) component. Another study described the structure and composition of ash forests in William L. Finley National Wildlife refuge, though the range of successional stages expressed there was limited (Heinitz and Frenkel 1987). Overall, little has been published on Oregon ash or the forests in which it is a dominant species.

In general, Willamette Valley wetlands have been highly fragmented and diminished by urbanization and agricultural development (Taft and Haig 2003). Those that remain have undergone a series of disturbance regime changes, which have altered their structure and composition (Towle 1982; Benner and Sedell 1997). Historically, indigenous burning helped maintain Willamette Valley wetlands as a mosaic of relatively open prairies and savannas that supported populations of culturally important plant species (Johannessen et.al. 1971). Beginning in the mid-1800's, Euro-American settlers increasingly excluded fire from the landscape and converted wetlands to agricultural production throughout the region. Soon after, livestock

grazing and wheat cultivation, followed by grass seed production, largely replaced fire as the dominant disturbance mechanisms.

This long history of anthropogenic disturbance has arrested succession in most Willamette Valley wetlands. Consequently, forested wetlands are a particularly rare regional habitat type (Bernert et. al. 1999; Christy 2004; Christy and Alverson 2011), and are mostly restricted to narrow riparian corridors that bisect tracts of farmland (Benner and Sedell 1997; Christy 2004; Titus et. al. 2006). However, while historical land-use changes and disturbance regime interruptions have reduced the overall extent of naturally occurring wetlands and bottomland forests in the Willamette Valley, they have also provided several opportunities for forest establishment in areas formally maintained as wet prairie or savanna. As a result, forests have developed in several relatively small, isolated wetlands that are managed by public agencies and private conservation organization (Frenkel and Heinitz 1987; Titus et. al. 2006). Spatially and temporally heterogeneous disturbance histories on these sites have resulted in disjointed forested wetlands of varying ages and stages of structural development on a landscape scale (Towle 1982; Clark and Wilson 2001). Though the current condition and developmental trajectories of these forests have not been previously described, they likely possess a range of structural characteristics that serve as important wildlife habitat features and native plant refugia on an otherwise highly developed landscape.

Similar structural developments since Euro-American settlement have been well documented in upland forests of the Willamette Valley (Thilenius 1968, Cole 1977, Devine and Harrington 2006). Many sites that were formerly maintained as grasslands or open woodlands via indigenous burning have experienced increased Oregon white oak (*Quercus garryana*), grand fir (*Abies grandis*), and Douglas-fir (*Pseudotsuga menziesii*) recruitment. Drastically decreased fire frequency in these systems has resulted in increased stand densities and, as shade-intolerant oak trees have been over-topped, a gradual shift toward Douglas-fir dominance. As a result, upland grasslands, remnant large oak trees, and oak-dominated ecosystems characterized by frequent disturbance events have become a regional conservation priority (Hulse and Gregory 2002). As both upland and wetland ecosystems have been impacted by decades of fire exclusion, it is likely that a similar process has taken place in undeveloped Willamette Valley wetlands. However, successional dynamics among various tree species are more poorly understood in wetland ecosystems. As fire continues to be excluded in these systems, it is important to

understand the nature of their development in order to predict future structural and compositional states and to identify potential conservation concerns.

Willamette Valley forested wetlands tend to occur on broad, flat floodplains and alluvial fans associated with slow moving creeks and/or a perched water table (Wilson et. al. 1995). Seasonally anaerobic soil conditions exclude most native tree species on these sites. Oregon ash and Oregon white oak are the tree species most likely to dominate in overstory canopies where pulse disturbance events such as high severity flooding are rare or absent (Owston 1990; Titus et. al. 2006; Christy 2011). Of the two, Oregon ash is more tolerant of seasonally inundated soils, while Oregon white oak is present on more mesic sites or elevated levees (Frenkel and Heinitz 1987; Owston 1990). Additionally, Oregon ash is more shade tolerant than Oregon white oak. Therefore, successional dynamics in Willamette Valley forested wetlands are likely dependent on the local soil moisture regime, and on drier sites a shift in dominance from oak to ash may be occurring. The ability of Oregon ash to regenerate under a forest canopy has been documented, and likely allows that species to be a dominant component of climax forests in Willamette Valley wetlands and riparian forests (Niemiec et. al. 1995). However, rates of understory regeneration for any tree species, and the resulting implications for stand succession in Willamette Valley wetland ecosystems have not been previously quantified.

While changes in historical disturbance regimes over the past century and a half have already altered the extent and structure of forested wetlands in the Willamette Valley, these systems may be further impacted by future forest health threats. Most notably, Oregon ash is highly susceptible to infestation by the emerald ash borer (EAB) (*Agrilus planipennis*) (Coleptera: Buprestidae) (Anulwicz et. al. 2009), an introduced forest insect that has caused widespread mortality in other species of ash in North America (Poland and McCullough 2006). Although EAB has not yet been documented in Oregon, it has been observed as far west as Colorado (Colorado Department of Agriculture 2016, www.emeraldashborer.info), and could potentially invade Oregon ash forests in the coming years or decades.

In regions of North America where EAB has invaded, ash mortality has been high (Smith 2006, Herms and McCullough 2014). Furthermore, management prescriptions have called for the removal of ash trees in specified quarantine zones (Hausman et. al. 2010). Consequently, shifts in stand structure and composition have occurred as other tree and shrub species have grown into canopy gaps left by infested or culled ash trees (Gandhi and Herms 2010, Klooster 2012).

Similar rates of Oregon ash mortality would cause structural and compositional changes in forested wetlands of Oregon, Washington, and California. Future conditions of wetland forests in these areas are potentially dependent on the ability of other tree species to replace Oregon ash, which is in turn likely dependent on local soil moisture regimes and the current distribution of woody plant species. A description of the current state of Willamette Valley forested wetlands, as well as their successional dynamics, will aid in predicting a range of potential responses to future Oregon ash mortality in the event of an EAB invasion.

Only one study to date has described overstory structure and composition in Oregon ash dominated forests (Fenkel and Heinitz 1987), and that study was limited to the central portion of the Valley. Therefore, a more broad exploration of structural and compositional development in these forests would help to understand potential changes that may occur in regional wetlands if EAB invades the Willamette Valley. The objectives of this paper are to: 1) describe the range of structural and compositional characteristics of overstory tree communities that are currently present in ash and ash/oak dominated Willamette Valley forested wetlands, 2) characterize stages of stand development in ash and ash/oak dominated Willamette Valley forested wetlands, 3) describe tree community succession in these forests in the absence of anthropogenic disturbance, and how this process varies according to gradients in soil moisture, and 4) generate hypotheses regarding how the structure and overstory composition of Willamette Valley forested wetlands might be impacted by EAB-induced ash mortality.

METHODS

STUDY DESIGN

I adapted a chronosequence study design to quantify changes over time in structural characteristics, structural diversity, and tree species composition in Oregon ash-dominated forested wetlands in the Willamette Valley. Typically, a chronosequence study design relies on tree ring data to determine dates of stand initiation. Stands of known ages are then sampled along an age gradient, which serves as a substitute for repeat sampling of permanent plots (Foster and Tilman 2000). However, Oregon ash is excessively difficult to age using tree rings as it is prone to internal rot and indistinct, spongy rings (Heinitz and Frenkel 1987). Therefore, I utilized a combination of historical aerial photography and cluster analysis (see below) to assign each

stand to a stage of structural development. This approach assumes the predictable development of certain structural characteristics over time, and does not allow for the precise aging of forests beyond those that initiated since aerial photography has been available. However, I did corroborate the general pattern of development over time using rough age classes established by multi-temporal aerial photography. The youngest sampled forests were approximately 30 years old, while the oldest were well-established in 1936, making them over 80 years old at the time of this study. I also sampled wetland ash savannas that are maintained in an early-seral state via anthropogenic disturbance. These savannas have some overstory ash cover and extensive ash recruitment. I then compared structural characteristics across successive stages of forest development, beginning with the early-seral savanna stage, as an approximation of how structure and composition in this forest type change over time. Furthermore, I used soil morphological characteristics to estimate the annual average high water table for each plot, then described how tree community succession differs according to the resulting soil moisture conditions. Finally, I described ash forest expansion over the past several decades at Fern Ridge Wildlife Area's Coyote Management Unit, which served as a representative case study of Willamette Valley wetland forest initiation and expansion.

STUDY AREA

This study was conducted in the Willamette Valley of western Oregon. The Willamette Valley is a 13,355 km^2 area of low relief situated between the Coast Range and Cascade Mountains. The climate is characterized by mild temperatures, with mean high temperatures ranging from approximately 27 degrees C during summer months to 5 in the winter. Precipitation is highly variable by season; 50% of the roughly 1020 mm of annual precipitation falls between December and February, while summers tend to be very dry (Taylor and Bartlett 1993). The Willamette River bisects the valley from south to north with numerous tributaries draining the adjacent mountain ranges. All but one of the management units sampled are associated with small, sluggish tributaries of the Willamette River.

I sampled forested wetlands and adjacent wetland savannas within 11 management units in the Willamette Valley (Figure 2.1). I defined management units as areas of contiguous land ownership that are managed for conservation and that are within a common watershed. Forests

had greater than 50% tree cover, while savannas had 5-20% tree cover, as estimated by aerial photography. Areas of intermediate tree cover were not available for sampling.

SITE SELECTION

The primary site selection criterion for this study was the dominance or co-dominance of Oregon ash in forest canopies, which I defined as forests in which ash represented 50% or greater of the overall canopy cover. Savannas were selected that were located within 1 km of a sampled forest and that were successional to ash forest as evidenced by abundant ash regeneration.

I used aerial photography and communication with land managers to identify hardwood forests throughout the Willamette Valley that might contain a high percentage of overstory Oregon ash, then made site visits to determine suitability. While ash was present in the canopies of nearly every forest visited, it was often only a minor or understory species. This tended to be the case in riparian gallery forests associated with the Willamette River and its larger tributaries. These forests were typically dominated by black cottonwood (*Populus trichocarpa*) and/or bigleaf maple (*Acer macrophyllum*), and therefore were not sampled.

The second criterion used for site selection was stand size. Sampled forest stands and savannas were larger than five ha, and greater than 100 meters in width. Many ash and ash/oak forests in the Willamette Valley are currently present that are much smaller or narrower than this. Forests and savannas that met both of these criteria were limited to just a few conservation areas scattered throughout the Valley, and I believe the 11 sites included in this study represent the majority that are currently present.

FIELD MEASUREMENTS

I delineated individual stands of forested wetlands and savannas within each management unit using aerial photography. Stands were defined as contiguous forested areas that are uninterrupted by bodies of water or areas of disturbance. Plots were randomly arranged within stands to capture the naturally occurring range of soil moisture conditions and overstory structural characteristics. For each five ha of stand area, I established one $1/20^{th}$ ha (12.6 m

radius) plot from centerpoints randomly generated using KML Tools Project (University of New Hampshire Cooperative Extension). Stand area was rounded to the nearest 5 ha for the purposes of plot establishment. In total, 59 plots were established in 17 forest stands and 43 plots were established within 10 savannas. Initially, measurements were to be averaged at the stand level for the purposes of analysis. However, site visits revealed a high level of heterogeneity among structural characteristics, even within contiguous forested areas of just 5-20 ha. This made consideration of similar age and structural class exceedingly difficult when delineating stands. Therefore, I used plot level data to quantify stages of structural development. Furthermore, several plots were adjusted to $1/40^{th}$ ha due to very high tree densities.

On each plot, diameter at breast height (DBH), species, canopy position, and estimated percent live crown were recorded for each tree over 1.3 m tall and 5 cm DBH. Tree diameters were used to calculate total and per species basal area (m^2/ha). Canopy position was recorded as overstory (crowns at least partially exposed above the surrounding canopy) or understory (all of the crown shaded by the primary canopy). I estimated cover of understory vegetation by form: herbaceous, short shrub (<2 m height), and tall shrub/short tree (>2 m height, <5 cm DBH). I also recorded tree regeneration per species by counting the number of stems below 5 cm DBH. I distinguished between vegetative and sexual regeneration. Vegetative regeneration included all saplings growing within one meter of an established tree, or those visibly growing from downed dead or dying wood. First year seedlings were not quantified.

STAND AGING

For each management unit, one aerial photograph per decade (dating back to 1936) was available for review at the University of Oregon Map and Aerial Photography Library. I used these photographs to approximate a window of stand establishment for each plot by recording the first decade in which a forest canopy is visible. However, most plots were located under a canopy that established prior to 1936. Therefore, I assigned plots to three broad age classes ("savanna" = early seral/post-disturbance, n = 43; "post1936" = stands that have initiated since 1936 and represent an intermediate developmental stage, n = 20; "pre1936" = stands that initiated prior to 1936 and represent an older, later developmental stage, n = 39). I used cluster analysis of structural traits to further refine stages of structural development. This method

developmental stage identification somewhat follows that developed by Fierke and Kauffman (2005). Developmental stages were visually compared with the rough stand age classes developed from aerial photography using convex hull overlays in NMS ordinations (see below). Decade of initiation based on aerial photography was also used to broadly assign age classes to developmental stages.

I also used historical aerial photography of Coyote Management Unit at Fern Ridge Wildlife Area in Lane County, OR to present a case study of wetland forest expansion and development over the past 80 years. Using the ArcGIS online platform, I created polygons representing forested areas within the management unit during three different years (1936, 1975, and 2014). I calculated the area of each polygon to estimate change in forest size over the intervening time intervals. I also reported the stage of structural development associated with each sampled stand. While I did not repeat this process for all management units, Coyote Management Unit provides an instructive example of the rate at which Willamette Valley wetland forests develop and expand when anthropogenic disturbances are abandoned. It also serves as a useful visualization of the changes that have occurred in remnant Willamette Valley wetlands during the past century.

SOILS

At the center of each plot, soil cores were extracted to a depth of 25 cm using a 4-inch soil auger. Depth to mottling was measured as an indication of the average annual high water table, with greater depths indicating a lower average annual high water table (Fletcher and Veneman 2012). Depth to mottling was defined as the depth in the soil profile to the uppermost horizon with significant iron reduction, as indicated by low chroma coloration (less than or equal to 2) over at least 5% of the surface area with areas of higher chroma mottling.

Additionally, the soil series was obtained for each plot using the NRCS Web Soil Survey (http://websoilsurvey.nrcs.usda.gov/). Soil characteristics associated with each series is reported along with the extent of their distribution. This was used to estimate the extent of soils in the Willamette Valley that are conducive to the development of forested wetlands.

ANALYSIS

To describe the current state of ash and ash/oak dominated forested wetlands of the Willamette Valley, I summarized structural and compositional characteristics for all forest plots with raw value means±SE and ranges. Structural variables were also used in diversity, cluster, and NMS analyses. These included six tree size classes (in trees/ha), total tree density (in trees/ha), average tree DBH, and the relative abundance of the following vegetation layers: overstory trees, understory trees, tall shrubs/regenerating trees, short shrubs, and herbaceous. Tree vegetation layers are reported as % of total stems/ha, while other vegetation layers are reported as relative % cover. I assigned trees to size classes based on rounded DBH values as follows (in cm): 5-10, 11-20, 21-30, 31-40, 41-50, and 50+ (Table 2.1). Other variables reported include snags/ha (defined as standing dead trees > five cm DBH), canopy cover, ash regeneration, other species regeneration, ash basal area, other species basal area, trailing shrub cover, and estimated age (Table 2.1).

I used hierarchical, agglomerative cluster analysis with Sørensen distance measure and a flexible beta (0.25) group linkage method to classify stages of stand development. Cluster analysis was performed on a matrix of 59 forest plots X 13 structural variables. Because variables were recorded using different units of measurement, this matrix was relativized by column maximums. Savanna plots were not included in cluster analysis, and were added to the dataset as an a priori developmental stage to create a 102 plot X 13 structural variable matrix.

I estimated structural diversity for each plot each plot using Shannon's H' (Shannon and Weaver 1949):

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

where p_i represents the within-plot abundance of each structural component in the relativized structural variable matrix that included both forest and savanna plots. Antilog of H' was reported and compared across structural stages.

I calculated the relative dominance of tree species in each plot as:

$$\text{Relative Dominance} = \text{Basal Area per species} / \text{Total Basal Area}$$

To include tree regeneration in relative dominance calculations, I assumed a DBH of 2.5 cm, which was the midpoint of the regeneration size class (0-5 cm). Relative dominance is reported for the eight most common tree species and is compared across developmental stages. I also combined the basal areas of all non-ash species in order to compare ash basal area to all other species among developmental stages.

Tukey's Honest Significant Difference Test, which is a post-hoc/post-ANOVA test of differences in mean values, was used to determine which structural characteristics differed among developmental stages. A two-sample *t*-test was used to test whether the depth to soil mottling was significantly higher in ash stands than in ash/oak stands.

Nonmetric Multidimensional Scaling (NMS) was used to visualize differences among plots in structural characteristic space. NMS was performed both with and without savanna plots to visualize relationships among forest plots and between forests and savannas. In both cases, NMS was run 200 times with random initial configurations. Sørenson distance was used, and distance measure ties were not penalized. Monte Carlo randomizations were used to test the significance of final ordinations, and the runs with the lowest stress are presented. Pearson's correlation coefficient (*r*) was used to report correlations between structural variables and ordination axes. I used joint plot overlays to represent direction and strength of structural variable correlations. Convex hull were overlaid on ordinations to group plots by structural stage. For the ordination with savanna plots included, I produced two NMS plots to visually compare developmental stages derived from cluster analysis with rough age classes derived from aerial photography (savanna, post1936, and pre1936). I also tested the significance of similarity in structural attributes between a priori age classes using multiple response permutation procedure (MRPP). Multivariate analyses, including cluster analysis, NMS, and MRPP, were performed using PC-ORD (McCune and Mefford 2011). All other analyses were performed using R statistical software version 3.0.2 (R Core Team 2013).

RESULTS

SUMMARY OF FOREST CHARACTERISTICS

For all tree species on all forest plots sampled, total basal area averaged 28.6±12.4 m^2/ha (range 6.2-58.2). Stand density averaged 854±734 trees/ha (range 60-4320). Canopy cover averaged 75±10.8% (range 27-93%). Crown mortality was highly variable (83±9.4%; range 52.9-96.9%). The percentage of trees that were suppressed under the primary canopy was also highly variable (35±19.2%; range 7-77%). Oregon ash was the dominant tree in all but one plot. On average, ash accounted for 93.8±11% (range 44-100%) of total stand basal area. Mean ash basal area was 26.8±12.2 m^2/ha (range 6.2-55.1). Oregon white oak was the second most abundant tree species in terms of basal area. Oak occurred in 23.7% of plots (n=14). Oak basal area averaged 5.6±5.9 m^2/ha (range 0.4-22.9) for plots in which it occurred. Other tree species were regularly observed, but were rarely present in the primary canopy. These include cascara (*Rhamnus purshiana*), Suksdorf's hawthorn species (*Crataegus suksdorfii*), common pear (*Pyrus communis*; exotic), Oregon crab apple (*Malus fusca*), and single-seeded hawthorn (*Crataegus monogyna*; exotic). Additionally, bigleaf maple (*Acer macrophyllum*) was observed on two plots and grand fir (*Abies grandis*) and sweet cherry (*Prunus avium*; exotic) were observed just once each.

STRUCTURAL DEVELOPMENT

Cluster analysis of structural attributes in forest plots revealed four distinct stages of stand development, when cut at approximately 35% information remaining. I interpreted these as the following structural classes (from youngest to oldest): stem exclusion, understory initiation, young multi-strata, and old growth. One plot was an outlier due to high overstory mortality. Values for that plot were separated from structural stage summaries, but were reported. Savanna plots represented an additional early-seral, post-disturbance stage. However, stands of an intermediate, early stem exclusion stage were not sampled, and few were observed at any of the study sites (though see figure 2.3). Developmental stages of Oregon ash-dominated forested wetlands are illustrated in a series of photos (Figures 2.2-2.7).

I expected earlier stages of structural development (stem exclusion and understory initiation) resulting from cluster analysis to be largely in agreement with the a priori post1936 age class. This was mostly, but not entirely, the case, primarily with understory initiation stands. 100% of stem exclusion stands initiated after to 1936, while just 39% of understory initiation

stands also did so. Inversely, I expected later stages of structural development (young multi-strata and old growth) to be in agreement with the pre1936 age class. Ninety percent of young-multi strata initiated prior to 1936, while 100% of old growth stands initiated prior to 1936. This suggests that cluster analysis identified age-dependent differences in structural characteristics and was useful in refining stages of stand development and succession, though some structural differences, especially in understory initiation stands, may be due to factors beyond stand age. Furthermore, structural characteristics did differ significantly among a priori age classes, with moderately high within-group agreement (MRPP, A=0.33, p<.00001).

For forest plots only, NMS of the structural variable matrix resulted in a three-dimensional ordination (though only the first two axes were interpreted) with final stress of 11.1 (Figure 2.8). This was lower than would be expected by chance (p<0.02). Final instability was ~0.0 after 73 iterations. Stand density and smaller tree size classes (5-10, 11-20, 21-30) were negatively correlated with axis one of the ordination, while larger size classes (31-40, 41-50, 50+) were positively correlated with axis one (Table 2.1). Therefore, I interpreted this axis as representing gradients in both tree size and stand density. Stem exclusion stands were associated with the left side of the ordination, old growth stands were associated with the right side, and understory initiation and young multi-strata were more or less intermediate (Table 2.1, Figure 2.8). The relative abundance of understory trees was the variable most highly positively correlated with axis two (Table 2.1, Figure 2.8). Overstory tree relative abundance was negatively correlated with axis two (Table 2.1, Figure 2.8). Therefore, I interpreted this axis as a gradient in the relative importance of understory trees in forest canopies. Plots were widely distributed along axis two. However, young multi-strata plots tended to be associated with the upper portion of the ordination, suggesting a greater association with understory tree abundance (Table 2.1, Figure 2.8). Small shrub abundance was most highly correlated with the first ordination axis, while tall shrubs and herbaceous cover were somewhat correlated with both axes (Table 2.1, Figure 2.8).

NMS of structural variables for all plots (including savannas) resulted in a two dimensional ordination with final stress of 10.2 (Figure 2.9). This was lower than would be expected by chance (p<0.02). Final instability was ~0.0 after 83 iterations. Visual comparison of an ordination plot with convex hulls around a priori age classes and an ordination plot with convex hulls around developmental stages derived from cluster analysis revealed that stem

exclusion and understory initiation stands tended to be positioned in the same region of structural variable space as post-1936 plots (Figure 2.9). Similarly, young multi-strata and old growth plots tended to be positioned in the same region of structural variable space as pre-1936 plots (Figure 2.9). All forest plots tended to group toward the right side of the ordination, while savanna plots were grouped toward the left. Herbaceous cover and stems/ha were both highly correlated with axis one, and likely explained most of the separation between savanna and forest plots (Table 2.1, Figure 2.9). A contour overlay helped to visualize patterns in structural diversity among developmental stages (Figure 2.10). The overlay explained most of the variation between the ordination of plots and structural diversity in structural variable space ($xR^2=0.892$). The contour lines increased along the left side of the first ordination axis where savanna plots grouped, then increased from the top to the bottom along the right side of the second ordination axis where forest plots grouped (Figure 2.10).

Many structural characteristics were significantly different among developmental stages (Tukey's HSD test, $\alpha=0.05$; Table 2.2). In general, tree sizes increased as stands progressed through developmental stages, though older stands had a more even distribution of tree sizes. Stem exclusion stands were characterized by trees in the 5-10 cm and 11-20 cm size classes, with virtually no trees larger than 30 cm (Table 2.2, Figure 2.11). Understory initiation stands had increased tree sizes, with few trees smaller than 11 cm, and nearly all trees between 30 and 40 cm (Table 2.2, Figure 2.11). Young multi-strata stands had a wide range of tree sizes, though trees up to and larger than 50 cm were common (Table 2.2, Figure 2.11). Old growth stands had the largest number of trees greater than 50 cm of all developmental stages (Table 2.2, Figure 2.11).

The relative abundance of understory trees increased sharply in the young multi-strata stage, then decreased somewhat in old growth stands (Table 2.2, Figure 2.12). Tall shrub cover increased somewhat between savanna, stem exclusion, and understory initiation stages, then increased dramatically in the young multi-strata stage (Table 2.2, Figure 2.12). Small shrub cover began to increase in the understory initiation stage and peaked in old growth stands (Table 2.2, Figure 2.12). Stand density increased drastically from the savanna stage to stem exclusion stage, then tended to decrease over time, though not all differences in stand density were significant (Tukey's HSD test $\alpha=0.05$; Table 2.2, Figure 2.13). Overall, average tree DBH increased over time (Table 2.2, Figure 2.13). Furthermore, structural diversity increased between

all stages of development. All increases in diversity were significant, except between young multi strata and old growth stands (Tukey's HSD test α = 0.05; Table 2.2, Figure 2.13).

OVERSTORY COMPOSITION, REGENERATION, AND SUCCESSION

Ash basal area accounted for the vast majority of total stand basal area in all stages (Table 2.2, Figure 2.14). Furthermore, Oregon ash was the dominant tree species in all stages of succession (Table 2.2, Figure 2.15). This was partially due to the sampling protocol, but it is important to note that this trend was consistent through all stages of development. Tree diversity was greatest in savanna plots, but declined sharply with the development of a closed canopy forest (Figure 2.15). Basal area of both oak and cascara peaked in the young multi-strata stage, but those species were still far less dominant than ash (Table 2.2, Figure 2.15). Oak was the only other tree that became dominant or co-dominant in sampled wetland forests. This tended to occur on sites with a relatively low annual average water table, as evidenced by the depth to soil mottling. Plots in which oak was present had a greater mean depth to soil mottling than plots with only ash in the canopy (two-sample t-test at $α=0.05$, p=0.03), indicating a more mesic soil moisture regime (Figure 2.16).

Oregon ash was also the most commonly regenerating tree species, averaging 594.8±676 st/ha (Table 2.3). Ash regeneration was greatest in savanna plots, and decreased steadily in successive developmental stages, though differences were not significant due to high variability (Table 2.2, Figure 2.14.1). Largely because of extensive cascara regeneration in several plots, tree regeneration for all species was greatest for forest plots in the young multi-strata stage (Table 2.2, Figure 2.14.1). Roughly 68% of ash regeneration was vegetative, mostly in the form of sprouting from root crowns and/or stems of downed and dying trees. First year seedlings were often abundant, but very few appeared to survive - though survival was not recorded. In stands where oak occurred, oak saplings were sparse, averaging just 54±50 trees/ha. Other tree species commonly regenerating included Pacific crab apple, common pear, native Suksdorf's hawthorn, and exotic single-seeded hawthorn (Table 2.3). Tree species found regenerating on two or fewer plots included domesticated apple (*Malus sp.*; exotic), sweet cherry, grand fir, bigleaf maple, and white alder.

SOILS

All plots had soils displaying coloration and mottling evident of a high annual average water table. Depth to mottling averaged 8.5±7.1 cm. Furthermore, seven soil series were associated with sampled forests (Table 2.4) that ranged in texture from fine clays to silty clay loams. All but one of these series are poorly or very poorly drained with features indicative of hydric, seasonally anaerobic conditions (NRCS Soil Survey). Though the forests sampled in this study only cover several hundred hectares, these hydric soil series are extensive in the Willamette Valley and cover an estimated 153,000 hectares (NRCS Soil Survey). Currently, most sites where these soils occur are artificially drained and/or tilled for grass seed and grain production (NRCS Soil Survey). This suggests that Oregon ash- dominated forested wetlands currently only occupy a very small portion of their potential range within the Willamette Valley.

FORESTED WETLAND EXPANSION AT COYOTE PRAIRIE MANAGEMENT UNIT

Coyote Management Unit (CMU) in Lane County, Oregon is a wetland area administered by US Fish and Wildlife and owned by the US Army Corps of Engineers. A review of historical aerial photography of CMU served as a case study for the expansion and development of forested wetlands under changing disturbance regimes. In 1936, forested areas at CMU were mostly restricted to immediate riparian zones along Coyote Creek, with scattered clusters of trees present in the surrounding grasslands (Figure 2.17). At that time the land was privately owned. Some tilling and road construction is evident on the 1936 aerial photo, but most of the area appears to be in an otherwise "natural" condition with intact hydrologic function and an anthropogenic disturbance regime that maintained an open vegetation community.

Fern Ridge reservoir was constructed in 1940 to provide flood control and irrigation for the southwestern portion of the Valley (Army Corps of Engineers, personal communication 2015). Around this time, the Army Corps of Engineers purchased the land around the reservoir, including CMU. Extensive dike construction, flooding of historical creek channels, and tilling

occurred at CMU between 1940 and 2014, which is evident on the 2014 aerial photograph (Figure 2.18). Ostensibly, on some marginal land at CMU, historical disturbance agents such as burning and sheep grazing were excluded. This appears to have resulted in an expansion of forested areas at the site. As of 2014, forested areas at CMU had expanded by 180%, from 23.4 to 65.2 ha (Figure 2.18). Four of the plots sampled at CMU were within areas forested in 1936, three of which were classified in this study as old growth, and one of which was classified as young multi-strata. Six plots were in forests that established between 1936 and 1975, with one additional plot that established around 1980 (Figure 2.18). All of these stands were classified as stem exclusion. While stand expansion was not quantified in other forests, six of the eleven sampled management units showed visible expansion over the past 80 years. Additionally, each of these six management units had stands in more than one stage of structural development.

DISCUSSION

FOREST STRUCTURAL DEVELOPMENT AND SUCCESSION

The results of this study showed that Oregon ash-dominated forests initiate on wetlands where the cessation of anthropogenic disturbance, such as burning, grazing, and tilling has occurred. On sites where previously open wetlands have been encroached upon by ash trees, the initial response has been the development of dense ash stands that increase in structural complexity over time and eventually develop important habitat features such as large trees and snags. Many models of structural development in other forested systems have been previously developed (Oliver 1980, Franklin, et. al. 2002). Most describe a similar generalized set of developmental stages that follow a discrete, high-severity disturbance event: the establishment of an initial tree cohort followed by canopy closure, competitive exclusion, and varying stages of increasing structural complexity as the initial cohort matures and is slowly replaced by understory regeneration. Often, structural development and species succession is guided by tree species' functional responses to disturbances and varying light intensities (i.e., shade tolerances), with different species characterizing each sere (Franklin and Hemstrom 1981, Finegan 1984).

This study provides evidence that the development of forested wetlands of the Willamette Valley follows this general pattern, though with two notable differences: 1) Historically, nearly all high-intensity disturbances in these systems were anthropogenic in nature. Furthermore, these disturbances were great enough in frequency and intensity to maintain most wetlands in a non-forested state (Christy and Alverson 2011). Consequently, recent stand establishment represents a changing of ecological states, rather than forest resilience following discrete disturbance events. 2) Seasonally anaerobic soil conditions limit initial and later cohort establishment to just one or two dominant species. On wetter sites, Oregon ash is dominant during all stages of stand development. On more mesic sites, Oregon white oak is often prevalent in forest overstories, but is likely being replaced by ash under current disturbance regimes. This suggests that compositional development is divergent according to local soil moisture characteristics, but that little overstory diversity is present in either case. Both of these developmental characteristics have implications for forested wetland management as well as potential structural changes resulting from future forest health threats.

Forested wetlands currently present in the Willamette Valley, while very limited in extent, express a diversity of structural forms. This is likely attributable to a highly complex and variable landscape-scale disturbance history. Christy and Alverson (2011) estimated that 0.63% of the Willamette Valley was composed of some form of "ash swamp" in 1850. While not precisely aged, the oldest stands included in this study may offer a description of pre-settlement ash forest structure. Currently, most forested wetlands in the Willamette Valley are in later stages of development. Sixty-four percent of plots sampled were located in stands that initiated prior to 1936. However, at most sites, younger stands were also located within several hundred meters of old-growth or young multi-strata stands. This has led to a high level of fine-scale structural heterogeneity, even though forests tend to be smaller than 20 ha in area.

In the Willamette Valley, Oregon ash plays an important role in each stage of wetland forest structural development; the suppression or development of an ash canopy largely determines the structural and compositional state of regional wetlands. Other regional forest types consist of multiple tree species that each enter understory and overstory canopies at different successional stages. For example, Fierke and Kauffman (2005) described succession in black cottonwood forests along the Willamette River. In those systems, forests initiate on newly deposited coarse alluvium, and early seral stages are characterized by black cottonwood and

various willow species. Over the course of several decades, barring additional flood events, forests succeed to relatively shade tolerant ash and maple trees. Similar dynamics have been observed in upland hardwood forests where Oregon white oak is succeeded by Douglas-fir and/or grand fir (Thilenius 1968). In contrast, except on the driest sites, Oregon ash is the dominant tree in all stages of succession in wetland forests.

FORESTED WETLAND EXPANSION

According to Christy and Alverson (2011), as of 1850, "White oak and Oregon ash were important along many of the smaller streams [of the Willamette Valley] where a narrow wooded riparian corridor was bounded by open prairie, but woody species were sometimes reduced to brush or sprouts because of fire." However, pollen analysis in the northern Willamette Valley has shown that, in certain areas, Oregon ash abundance has increased over the past 150 years as a response to fire suppression (Walsh et. al. 2010). This appears to be corroborated by aerial photography reviewed for this study, as exemplified by the drastic expansion of Oregon ash forests at Coyote Management Unit. While this regional regeneration of ash trees may somewhat off-set function and habitat loss of other valley-bottom forest types that has taken place over the same timeframe (Towle 1982, Sedell and Froggatt 1984), it also represents conservation challenges.

Woody plant encroachment has been reported in many systems worldwide, and is considered to be a threat to early-seral habitats that contribute to landscape ecological and biological diversity (Van Auken 2009). Regionally, the most well-documented example of this phenomenon may be the increasing density of conifers and oaks in low elevation, upland forests where fire has been excluded for decades (Devine and Harrington 2006). The conversion of open, oak-dominated woodlands and savannas to conifer forest has corresponded with altered light regimes, wildlife habitat features, and understory community composition (Hagar and Stern 2001, Thysell and Carey 2001). This has prompted widespread restorative forestry treatments that "release" legacy oak trees and their associated communities (Devine and Harrington 2006). Oregon ash encroachment has been recognized as a similar conservation issue in wetland prairies where prescribed fire, herbicide application, and mowing have all been used to limit ash

regeneration (Pendergrass et. al. 1998). However, the long term implications are unclear for wildlife habitat, understory community composition, and nutrient cycling characteristics as open wetlands and valley-bottom oak/ash savannas are converted to closed ash forests. This results of this study indicate that ash forest development increases structural diversity and that both wetland states are likely important landscape features. Furthermore, given the widespread distribution of hydric soils in the Willamette Valley, Oregon ash forests are currently highly underrepresented in their potential extent.

POTENTIAL IMPACTS OF THE EMERALD ASH BORER

As the North American EAB invasion radiates from its infestation epicenter in the midwestern United States, it is important to better understand how and where forests will be impacted. In the northwestern US, Oregon ash is the only native species of ash, and is the only species found in natural ecosystems. Whitehill et. al. (2009) found that Oregon ash, like other North American species of ash, is very susceptible to EAB. It is currently unclear how EAB will impact forest ecosystems containing Oregon ash, or how those impacts will vary according to species composition or forest structure. However, Smith (2006) found that neither stand structure nor composition were related to ash susceptibility in mixed-species forests of southeast Michigan, and that the only variable correlated with a decrease in ash mortality was distance from the invasion epicenter. This suggests that, eventually, all North American forests in which ash is a major component will experience dramatic overstory mortality in the event that EAB continues to spread. To date, EAB containment has been unsuccessful (Hausman et. al. 2010), and land managers in the western US should begin to consider how EAB will impact western ash forests.

Generally, overstory tree mortality due to exotic pests and pathogens produce both short- and long-term consequences. These include changes in nutrient cycling regimes, increased understory light availability, loss of ecosystem productivity, altered microclimatic conditions, and, over time, dramatic shifts in species dominance and forest structure (Lovett et. al. 2006). While more studies are needed to explore how each of these ecosystems characteristics may be affected in forested wetlands of the Willamette Valley, this study provides initial insight into pre-invasion conditions that will influence ecosystem responses. Furthermore, patterns observed in

other forest ecosystems that have experienced exotic pest and pathogen invasions can help to predict impacts to western forests.

Tree mortality on the scale of that caused by EAB has already been observed as a result of exotic pests and pathogens in forests of eastern North America. Jenkins et. al. (2002) used present tree species composition and species' life history characteristics to simulate successional changes in Northeastern forests in response to the hemlock woolly adelgid (*Adelges tsugae*). They found that compositional changes in forest overstories is dependent on both initial species composition and tree mortality rates, with stands that experience high rates of mortality rapidly transitioning to previously present late-successional species. Observational studies in forests impacted by chestnut blight (*Cryphonectria parasitica*) report similar findings. Woods and Shanks (1959) found that, in the Great Smoky Mountains National Park, gaps in forest canopies resulting from American chestnut (*Castanea dentata*) are typically filled by species already present in forest understories or those which were previously co-dominant. Good (1968) reported that co-dominant and suppressed trees in the Highlands of New Jersey filled gaps created by chestnut mortality via crown expansion. Similarly, multiple studies have reported that, following mortality caused by Dutch elm disease (*Ophiostoma spp.*), American elm trees tend to be replaced by previously present co-dominant overstory and/or shade tolerant late-successional species (Barnes 1976, Grittinger 1978, Parker and Leopold 1983). However, Huenneke (1983) found that, under certain conditions, large canopy gaps resulted in increased shrub cover that potentially suppressed tree recruitment. Dunn (1986) also found that shrub cover increased in Wisconsin forests when overstory elm mortality was greater than five stems/ha.

In each of these cases, previously present tree and shrub species determined the structural and compositional state of post-invasion forests. One major difference between the successional dynamics of forested wetlands in the Willamette Valley and those of most eastern forests is the lack of tree species diversity. In the absence of anthropogenic disturbance, Oregon ash appears to be the most important early-seral and climax species in these systems. The degree to which other species are present that could replace ash trees or fill canopy gaps caused by ash mortality is highly dependent on site-specific hydrology and soil moisture regimes. For forests included in this study, these soil characteristics were highly variable both within and between sites. Some forests apparently experience high levels of seasonal inundation, effectively excluding oak trees. For example, stands sampled in Jackson Frazier Wetland, Ankeny National Wildlife Refuge, and

Willamette Mission State Park were entirely lacking oaks, and virtually no other tree species were present in forest overstories. Other forests have a more patchy distribution of overstory trees, with oak and ash cover varying markedly on a scale of tens to hundreds of meters.

On wetter sites where Oregon ash is the primary - or only - overstory tree species, mortality resulting from an EAB invasion will likely cause drastic structural changes. There does not appear to be another tree species capable of forming closed canopy forests on these sites. The result might be a gradual shift to wetland shrubs and smaller tree species. Tree species already present on many sites include cascara, Suksdorf's hawthorn, single-seeded hawthorn, common pear, and Pacific crab apple, though its unclear what the developmental dynamics would be among these species in the absence of an ash overstory. It is important to note that both single-seeded hawthorn and common pear are exotic species that attained high abundance in several stands sampled in the southern Willamette Valley. These species are known to be particularly aggressive (Pendergrass et. al. 1998), and may be competitive with native small trees and shrubs following increased understory light exposure.

On more mesic sites, Oregon white oak does provide some overstory tree species redundancy. The importance of Oregon white oak in forested wetlands of the Willamette Valley is likely under-reported here, as ash dominance was used as the primary criterion for site selection. Regardless, whether oak trees will regenerate and maintain closed-canopy forests following a reduction in ash cover is unknown. Oregon white oak is a shade-intolerant species that relies on frequent disturbance for recruitment and maintained dominance (Devine and Harrington 2006). Because of this, Oregon ash appears to be the climax tree species even in Willamette Valley wetlands with a lower annual high water table, and forest structure during late stages of development will be highly altered by ash mortality even where oak is currently present in the overstory. For both relatively wet and mesic stands, future studies may be necessary in order to better predict how these species will respond to ash mortality and to provide specific guidelines regarding forest management strategies in these divergent wetland forest types.

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TABLES

Table 2.1 Willamette Valley Oregon ash forest structural variables used in cluster analysis and NMS Ordination; their mean, standard error and range of values; and correlation with ordination axes. Correlations with ordination axes are reported for two ordinations: one of forest only plots (Forest) and one of all plots (All).

Variable	Mean±SE (Range)	Axis 1 (Forest)	Axis 2 (Forest)	Axis 1 (All)	Axis 2 (All)
Trees/Size Class (st/ha)					
5-10	238±445 (0-2840)	-0.67	0.03	0.23	0.56
11-20	376±387 (0-1480)	-0.80	-0.17	0.44	0.73
21-20	127±136 (0-680)	-0.06	-0.31	0.51	0.26
31-40	51±46 (0-160)	0.71	0.01	0.64	-0.32
41-50	21±32 (0-120)	0.63	0.14	0.49	-0.39
50+	17±27 (0-100)	0.62	0.38	0.43	-0.52
Stems/ha total	854±735 (60-4320)	-0.78	-0.13	0.51	0.66
% Trees in Understory	35±19 (5-77)	0.27	0.90	0.80	-0.13
% Trees in Overstory	68±25 (23-95)	-0.33	-0.85	0.66	0.36
% Cover Tall Shrubs	26±20 (0-85)	0.43	0.60	0.58	-0.39
% Cover Small Shrubs	41±28 (1-120)	0.70	0.30	0.64	-0.42
% Cover Herbaceous	70±26 (25-117)	-0.37	-0.53	-0.66	0.25
Plot Average Tree DBH	22±8 (9-42)	0.91	0.17	0.87	-0.26

Table 2.2 Willamette Valley Oregon ash forest structural variable means±sd by structural stage). **Bold**=variables used in cluster analysis and NMS ordination. Values with corresponding capital letters were significantly different (Tukey's HSD test, α=0.05).

Variable	Savanna	Stem Exclusion	Understory Initiation	Young Multi-Strata	Old Growth
Number of plots	43	14	18	10	16
Trees/size class (st/ha)					
** 5-10**	0.3±1 D	764±684 ABCD	74±100 A	134±72 B B	38±46 C
** 11-20**	0.6±2 A	870±339 AB	433±271 AB	126±61 B	56±43 A
** 21-30**	0.1±0.5 ABC	64±93 A	289±148 ABC	86±48 C	56±44 B
** 31-40**	0.1±0.2 AC	3±11 AB	51±30 A	58±39 BC	91±45 A
** 41-50**	0	1±5 AB	9±21 B	30±30	48±38 AB
** 50+**	0	0 A	6±11 B	14±21 C	44±34 ABC
Stems/ha total	22±61 BC	1727±922 AB	862±430 AC	504±205 B	348±93 A
% Trees in understory	0.0±0 AEF	27±1 AD	29±2 BE	59±1 ABC	34±2 CF
% Trees in overstory	19±39 ABC	73±28 A	71±20 B	41±13 ABC	66±17 C
% Cover tall shrubs	8±12 CD	13±14 AB	20±14 C	50±19 BC	33±18 AD
% Cover small shrubs	14±13 BCD	17±16 A	40±24 B	44±27 C	62±28 AD
% Cover herbaceous	91±15 AB	76±26	77±26	55±22 A	62±23 B
Plot average tree DBH	2.5±6 ABC	12±2 AB	20±2 A	21±3 BC	32±5 AC
Estimated age (years)	0	30-50	50-80	80+	80+
Canopy Cover (mean%)	2±1 ABCD	77±5 A	75±8 B	79±14 C	75±8 D
Fraxinus BA (m^2)	0.3±1 ABCD	23±14 A	27±11 B	23±12 C	33±10 D
Quercus BA (m^2)	0.1±0.8	0.3±1	1.7±5	2.2±4	1.4±2.5
Other tree spp. BA (m^2)	0.1±0.3	0.7±2	0.2±5	1.0±4	0.2±3
Fraxinus relative dominance	0.47±0.43 ABCD	0.96±0.07 A	0.95±0.13 B	0.86±0.16 C	0.96±0.07 D
% Cover Trailing shrubs	0	1±3 A	10±10 B	1±21 8	32±27 AB
Diversity (antilog(H'))	2.5±1 AB	3.5±0.3 AB	4.6±0.6 AB	6.0±0.8 B	6.7±0.7 A
Ash regeneration	537±984	217±344	57±52	100±230	44±54
Regeneration for all *spp.*	846±523	327±169	301±335	550±668	195±215
Snags (st/ha)	1±6 AC	231±267 ABC	113±72 A	54±70 C	31±39 B

Table 2.3 Mean density (stems/ha), range of density, and frequency of occurrence for the seven most frequently recorded regenerating tree species on all Willamette Valley Oregon ash forest plots. * indicates exotic species.

Species	Mean	Range	% of Plots
Oregon ash	594.8	0 - 2880	98.0
Cascara	134.2	0 - 1000	54.2
Suksdorf's hawthorn	34.0	0 - 220	42.3
Single-seeded hawthorn*	34.0	0 - 720	28.8
Pacific crab apple	8.0	0 - 80	20.3
Common pear*	20.0	0 - 260	20.3
Oregon white oak	8.1	0 - 180	15.0

Table 2.4 Soil series associated with sampled Oregon ash forests, their key characteristics, and extent in the Willamette Valley. Most series are poorly drained clays and silty clays. Oregon ash is an important native species on each series. Together, these soils cover approximately 150,000 hectares in the Valley, though most are currently used for grass seed and grain production and/or pasture. (NRCS Web Soil Survey)

Soil series	Characteristics	# of plots	Extent in Willamette Valley (Ha)
Natroy	Fine-clayey, deep, seasonally inundated	20	6541
Waldo	Very deep, very poorly drained, clayey	18	10121
Bashaw	Fine-clayey, deep, seasonally inundated	9	16556
Amity	Fine-silty, somewhat poorly drained	4	39507
Wapato	Very deep, poorly drained, silty clay loam	4	21448
McBee	Fine-silty, moderately well-drained	3	12676
Dayton	Silty or clayey, very deep, poorly drained	1	46151

FIGURES
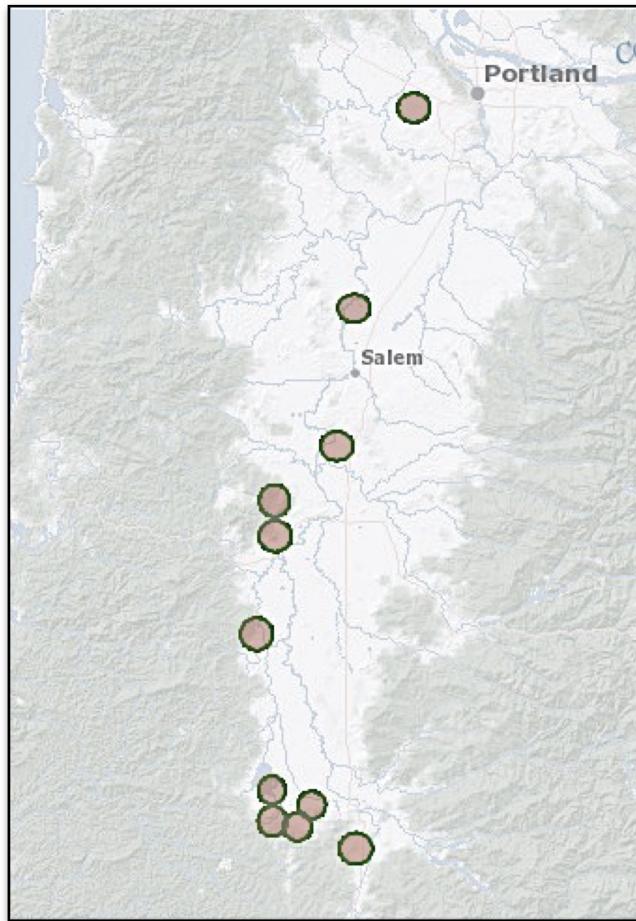
Figure 2.1 Map of Willamette Valley, OR with locations of sampled Oregon ash forests. Locations sampled were: Lane County Quamash Prairie Restoration Site (forest), Willow Creek Preserve (forest and savanna), Coyote-Spencer Wetlands (forest and savanna), Fern Ridge Wildlife Management Area (forest and savanna), William L. Finley National Wildlife Refuge (forest and savanna), Jackson Frazier Wetlands (forest and savanna), OSU Soap Creek Ranch (forest), Ankeny National Wildlife Refuge (forest), Willamette Mission State Park (forest), Tualatin Hills Nature Park (forest).

Figure 2.2 Ash trees resprouting in an ash savanna one year after a prescribed burn. Frequent disturbance is necessary to prevent ash forest establishment. These stands were all recently disturbed, and were generally less than three years old (though older trees were present in most cases). Fern Ridge Wildlife Area, Fisher Butte Unit. Summer 2015.

Figure 2.3 Young Oregon ash forest several years after establishment. Located on privately owned land. Few stands in this stage were observed at study sites, and none were sampled. Lane County, Oregon. Spring 2015.

Figure 2.4 Oregon ash stand in the "stem exclusion" stage of development. Note the crowded, single cohort of Oregon ash with understory cover primarily in the form of herbaceous plants. Sampled stem exclusion stands were typically 30-50 years old. Fern Ridge Wildlife Area, Coyote Management Unit; Lane County, OR.

Figure 2.5 Oregon ash stand in the "understory initiation stage" of development. These stands were typically greater than 50 years old. Coyote Spencer Wetlands; Lane County, OR.

Figure 2.6 Oregon ash stand in the "young multi-strata" stage of development. These stands had a diverse set of tree sizes and increased abundance of understory trees and shrubs. They were typically greater than 80 years old. W. L. Finley National Wildlife Refuge; Benton County, OR.

Figure 2.7 Oregon ash stand in the "old growth" stage of development. Large, widely spaced ash trees characterized these stands, though all size classes were typically represented. Small shrubs tended to be dense, particularly trailing blackberry (*Rubus ursinus*). Old growth stands all appeared to be mature forests in 1936, and are likely much older than 80 years. Ankeny National Wildlife Refuge; Marion County, OR.
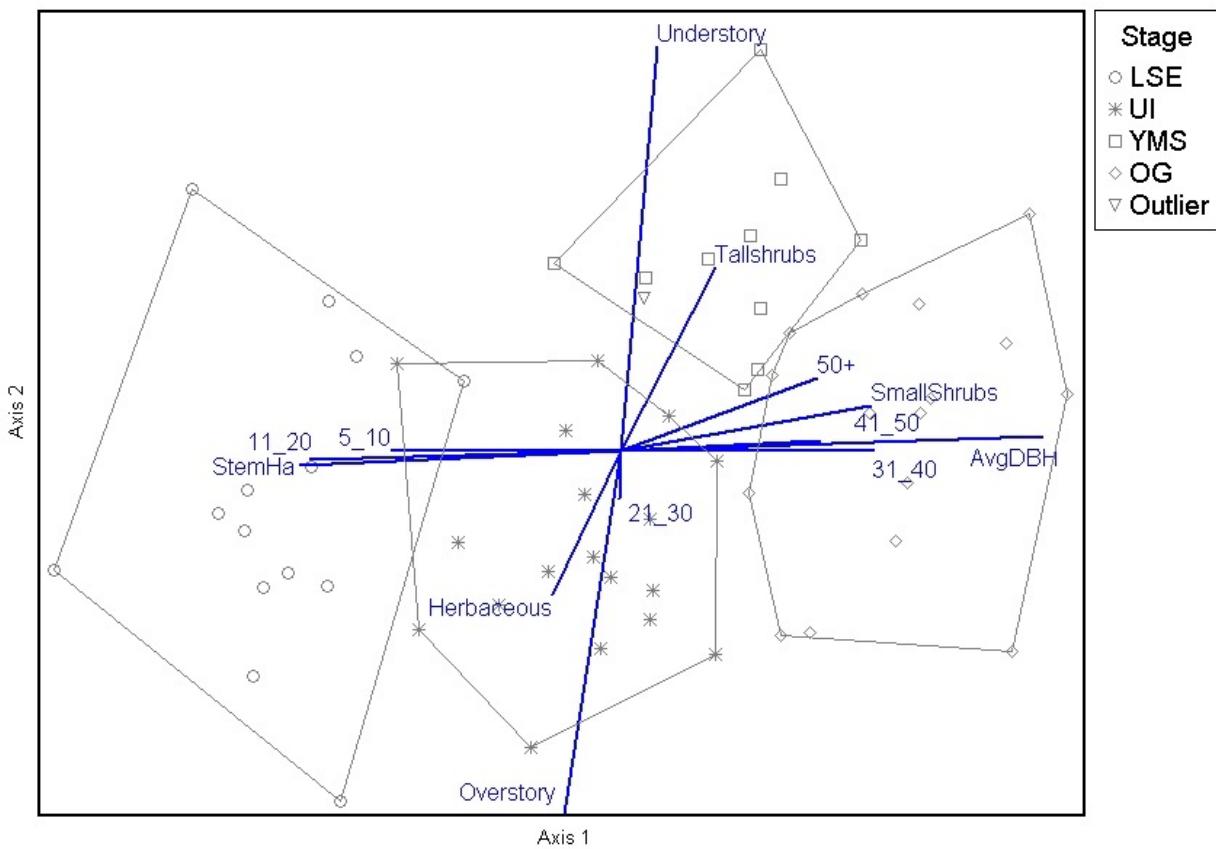
Figure 2.8 NMS ordination of Willamette Valley Oregon ash forest plots in structural characteristic space. Convex hulls represent developmental stage membership: LSE = stem exclusion, UI = understory initiation, YMS = young multi-strata, OG = old growth. One plot was considered to be an outlier due to extensive overstory mortality, but it grouped with YMS plots. Joint plot lines indicate direction and strength of correlations between structural variables and ordination axes. Understory = % relative abundance of understory trees, Overstory = % relative abundance of overstory trees, Herbaceous = % relative abundance of herbaceous vegetation, Tallshrubs = % relative abundance of tall shrubs, SmallShrubs = % relative abundance of small shrubs, AvgDBH = mean DBH for all trees in stand. Six size classes are also represented (measured in cm DBH).
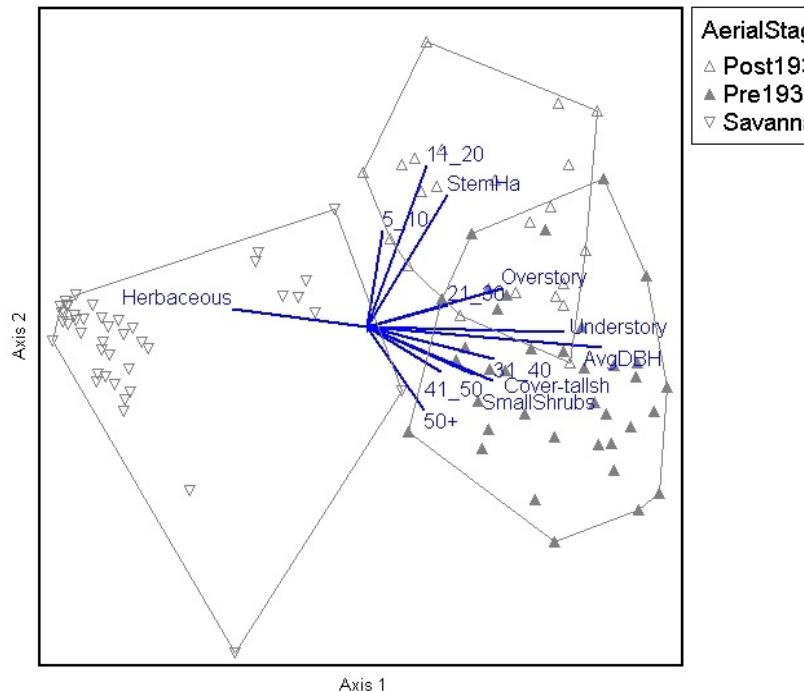
Figure 2.9.1
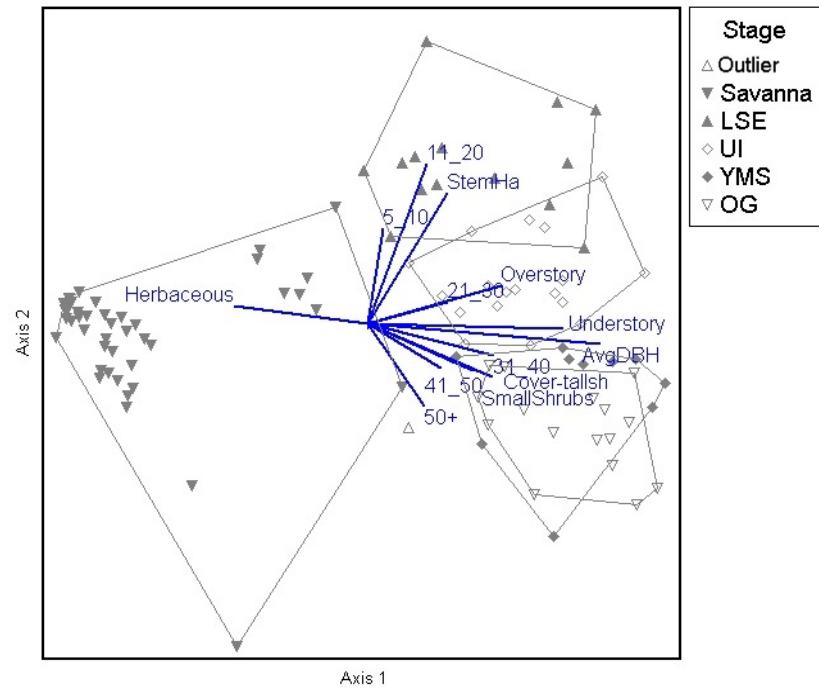
Figure 2.9.2

Figure 2.9 NMS ordination of all sampled Willamette Valley Oregon ash savanna and forest plots in structural characteristic space. The same ordination is presented twice with different convex hull overlays. Convex hulls in **Figure 2.9.1** represent plots grouped by age class as determined by aerial photography. Age classes are broadly defined as early seral, recently initiated (savanna), mid-seral closed canopy forests that initiated after 1936 (Post1936), and later seral stands that initiated prior to 1936 (Pre1936). Differences in a priori age classes were significant (MRPP, A=0.33, p<0.0001). Convex hulls in **Figure 2.9.2** represent forest developmental stages derived by cluster analysis. Earlier stages of development (SE and UI) tend to align with Post1936 plots, while later stages (YMS and OG) tend to align with Pre1936 plots. LSE = stem exclusion, UI = understory initiation, YMS = young multi-strata, OG = old growth. Joint plot lines indicate direction and strength of correlations between structural variables and ordination axes. Understory = % relative abundance of understory trees, Overstory = % relative abundance of overstory trees, Herbaceous = % relative abundance of herbaceous vegetation, Tallshrubs = % relative abundance of tall shrubs, SmallShrubs = % relative abundance of small shrubs, AvgDBH = mean DBH for all trees in stand. Six size classes are also represented (measured in cm DBH).
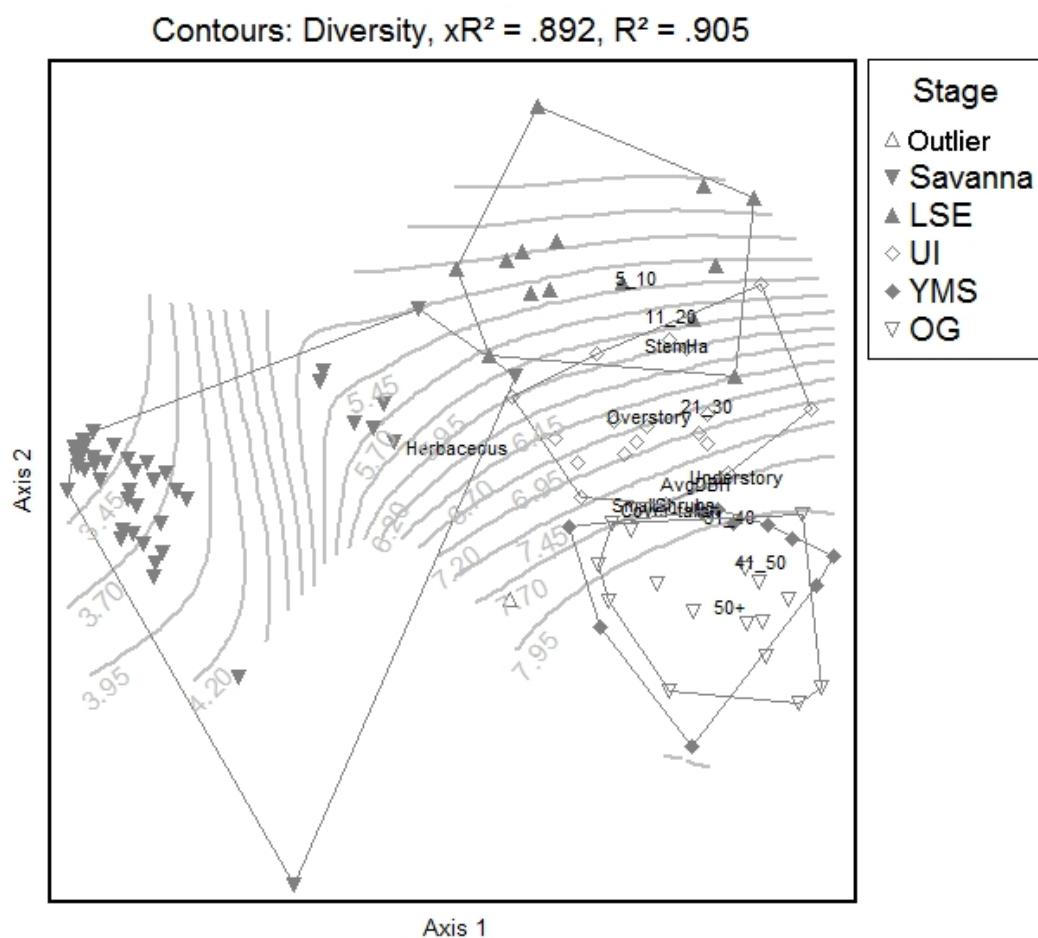
Figure 2.10 NMS ordination of all sampled Willamette Valley Oregon ash plots in structural characteristic space. Convex hulls represent developmental stages. Structural variables are labeled at their centroid. Contour lines represent a structural diversity gradient. The contour overlay explained most of the variation in structural diversity (xR^2=0.892). LSE = stem exclusion, UI = understory initiation, YMS = young multi-strata, OG = old growth.
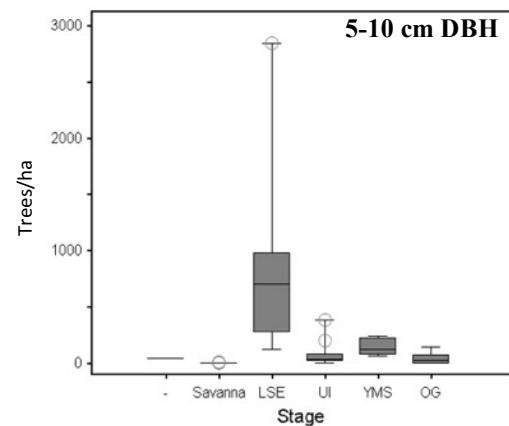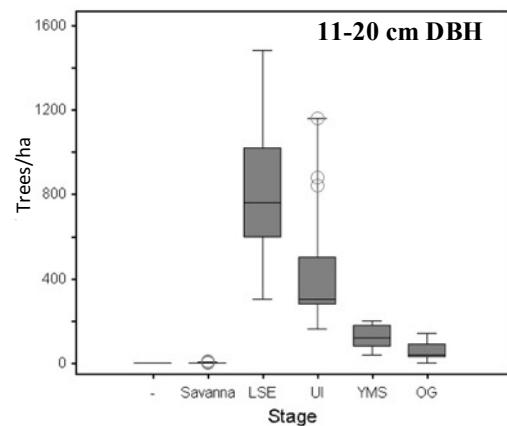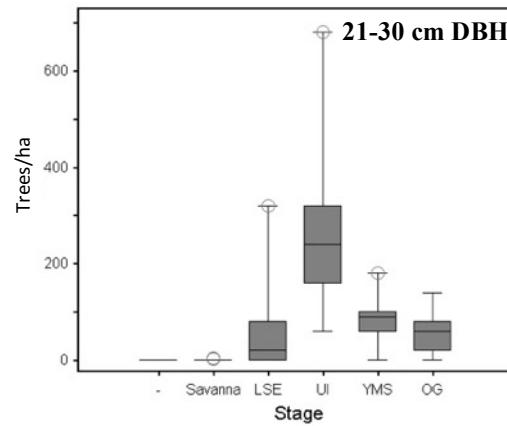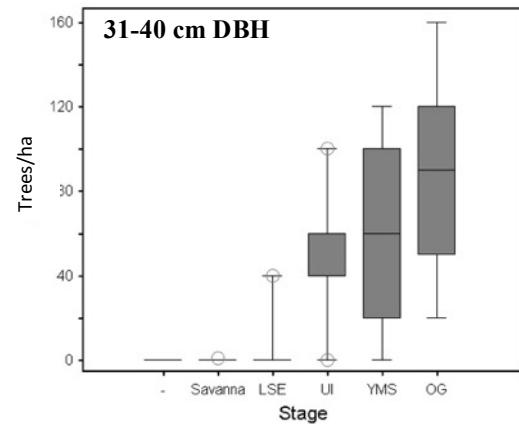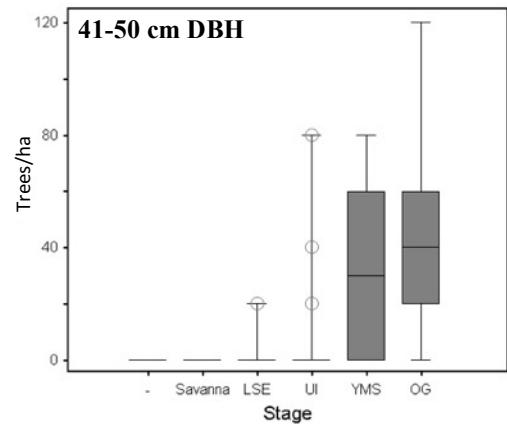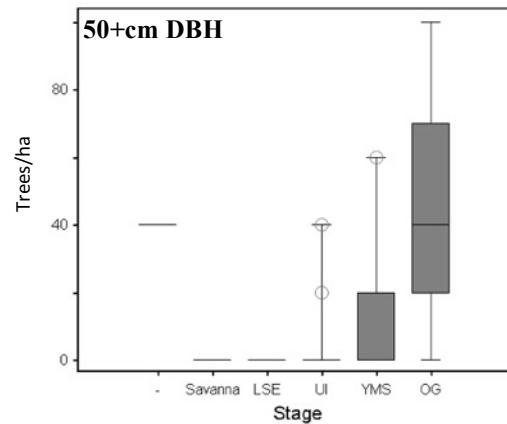
Figure 2.11.1

Figure 2.11.2

Figure 2.11.3

Figure 2.11.4

Figure 2.11.5

Figure 2.11.6

Figure 2.11 Box plots summarizing trees per hectare in each of six tree size classes by forest developmental stage for all sampled Willamette Valley Oregon ash forests and savannas. Larger size classes tended to be more common in later developmental stages, though later developmental stages also had a more even distribution of size classes. Size classes are sequentially ordered as 5-10, 11-20, 21-30, 31-40, 41-50, and 50+ cm DBH. LSE = stem exclusion, UI = understory initiation, YMS = young multi-strata, OG = old growth. Outlying plot labeled with -.
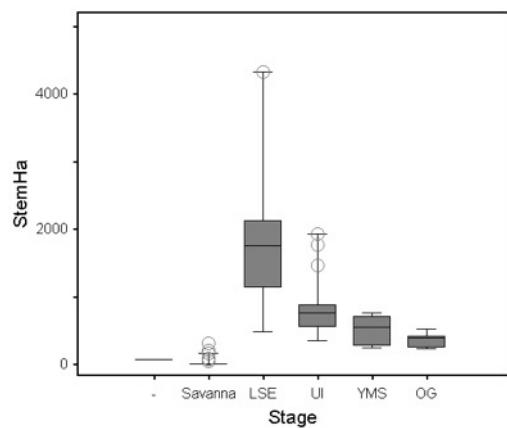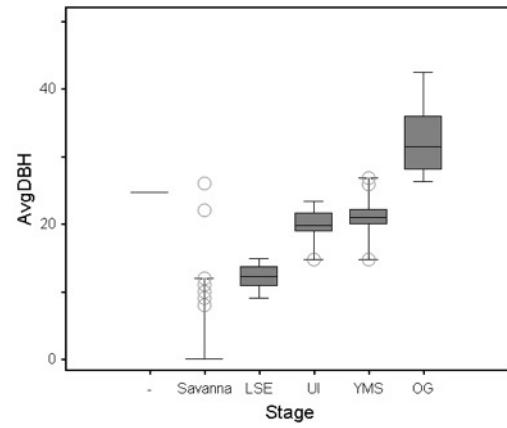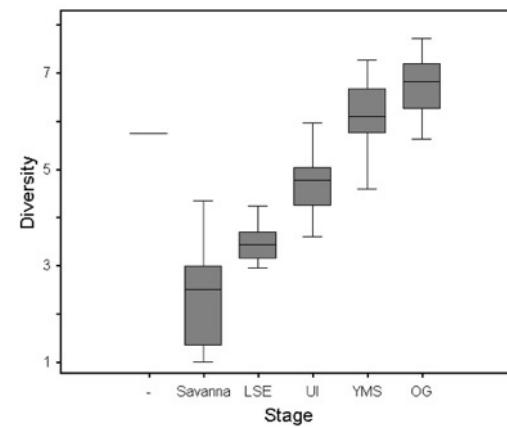
Figure 2.12.1

Figure 2.12.2

Figure 2.12.3

Figure 2.12 Boxplots summarizing overall Willamette Valley Oregon ash forest and savanna stand densities, average tree size, and structural diversity by developmental stage. Savannas were by far the least dense. Stem exclusion plots were the most dense, with tree densities declining in successive stages. In general, tree sizes increased as stands developed. While average tree size was similar for understory initiation and young multi-strata plots, this is likely due to the presence of both large and small trees in young multi-strata plots. Structural diversity increased with each successive developmental stage. StemHa = stems/ha; AvgDBH = average tree DBH; Diversity = structural diversity measured in the antilog of Shannon's H'. LSE = stem exclusion, UI = understory initiation, YMS = young multi-strata, OG = old growth. Outlying plot labeled with -.
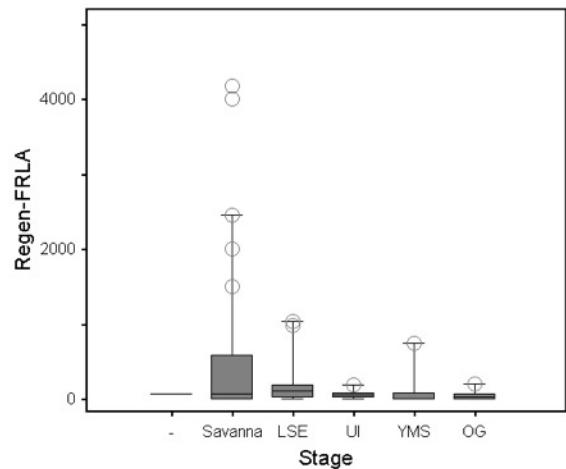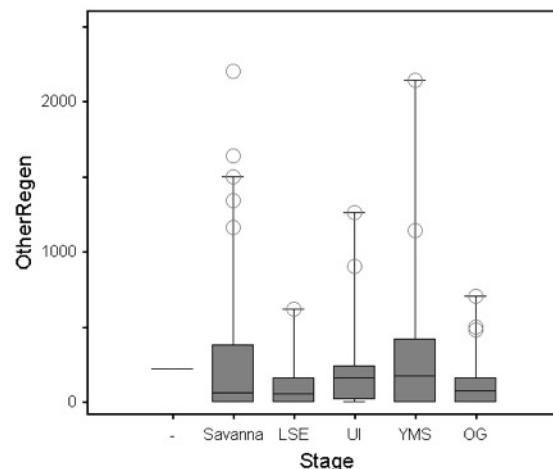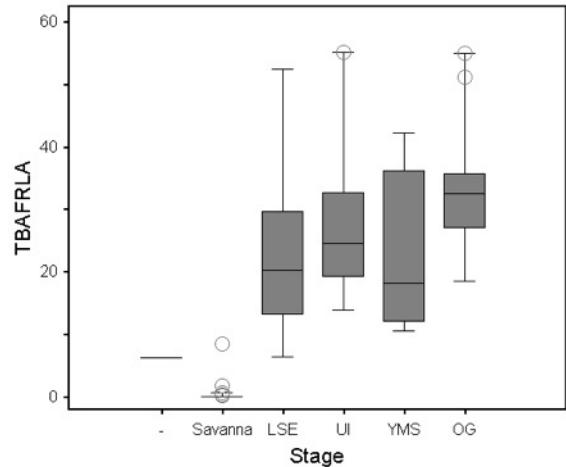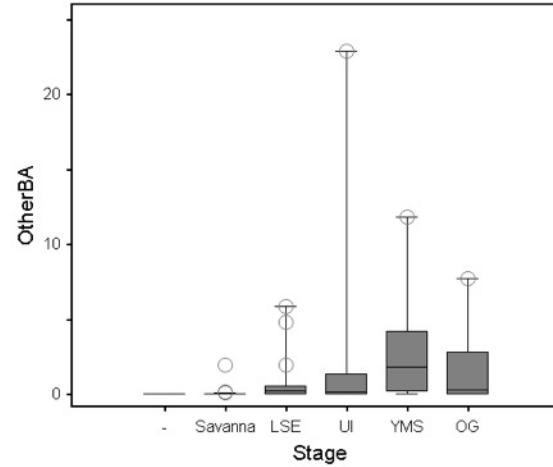
Figure 2.13.1

Figure 2.13.2

Figure 2.13.3

Figure 2.13.4

Figure 2.13 Boxplots summarizing the regeneration and basal area of Oregon ash vs. all other tree species by Willamette Valley Oregon ash forest developmental stage. Regeneration is in stems/ha. Basal area is in m^2. Regen FRLA = Oregon ash regeneration; OtherRegen = regeneration of all other species; TBAFRLA = per plot basal area of Oregon ash trees; OtherBA = per plot basal area of all other tree species. LSE = stem exclusion, UI = understory initiation, YMS = young multi-strata, OG = old growth. Outlying plot labeled with -.
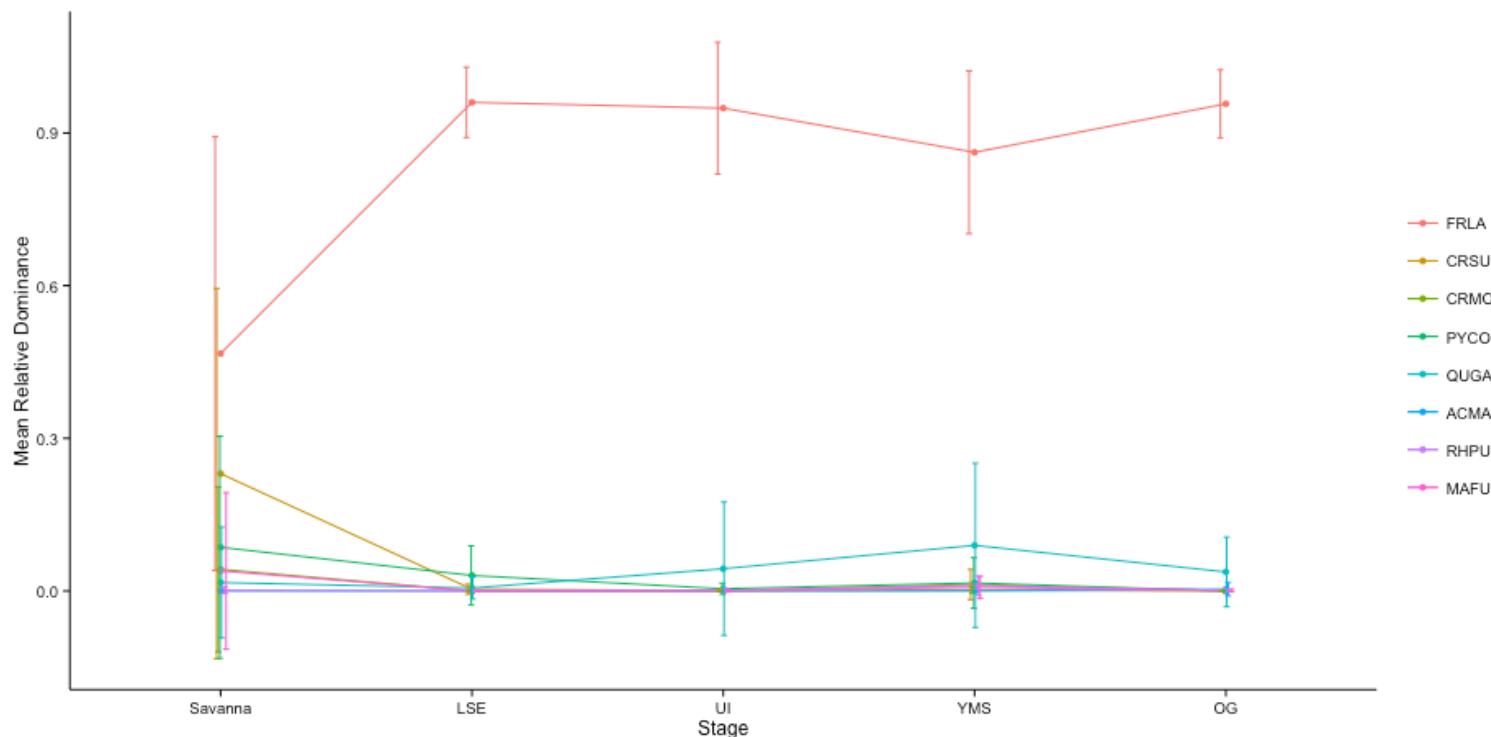
Figure 2.14 Relative dominance of eight most dominant tree species by Willamette Valley Oregon ash forest developmental stage. Error bars represent standard error by species. Oregon ash had the greatest relative dominance of all tree species in all developmental stages. Species are color coded and listed by four letter codes. FRLA = Oregon ash; CRSU = Suksdorf's hawthorn (*Crataegus suksdorfii*); CRMO = single-seeded hawthorn; PYCO = common pear; QUGA = Oregon white oak; ACMA = bigleaf maple; RHPU = cascara; MAFU = Pacific crab apple. LSE = stem exclusion, UI = understory initiation, YMS = young multi-strata, OG = old growth.
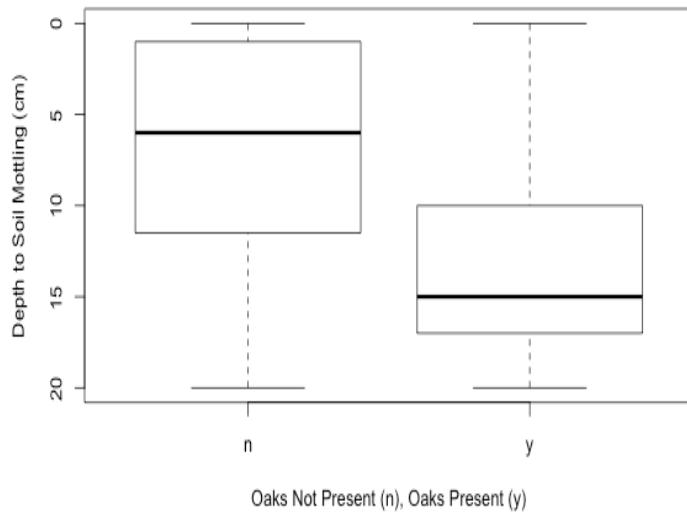
Figure 2.15 Depth to soil mottling was significantly greater in Willamette Valley Oregon ash forest stands that had overstory oak trees (two-sample t-test, p=0.031).
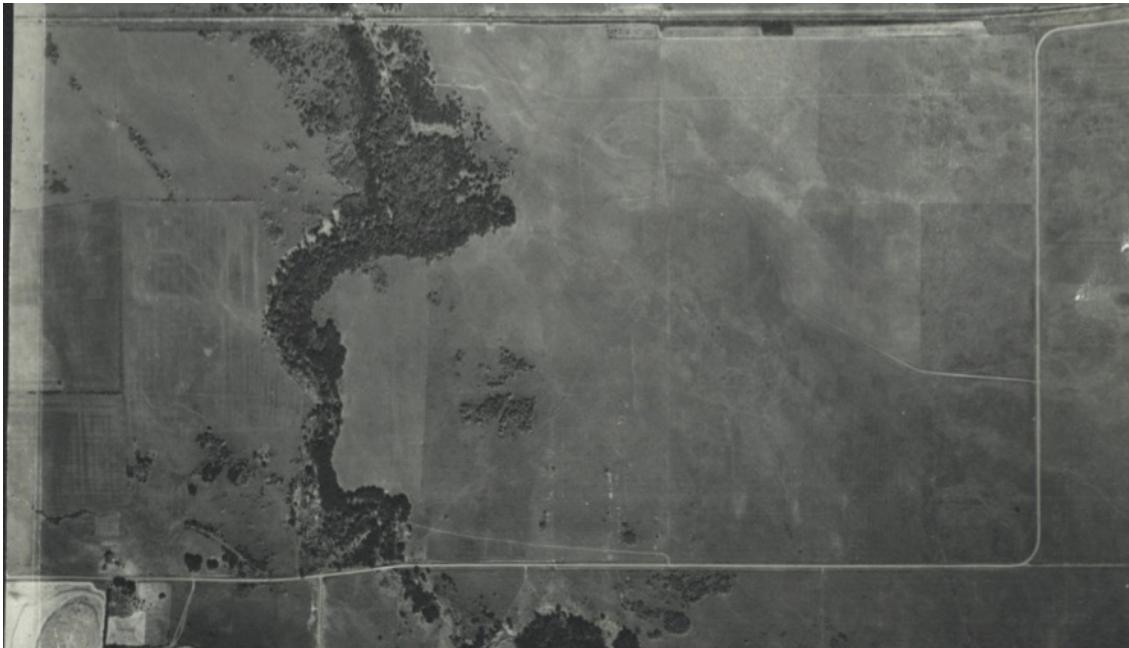
Figure 2.16 1936 aerial photograph of what is now Coyote Management Unit. Photograph depicts mature ash and oak/ash forests along Coyote Creek prior to extensive tillage, diking, and the establishment of Fern Ridge Reservoir.

Figure 2.17 2014 aerial photograph of Coyote Management Unit. Overall forested area is 180% greater than in 1936. Polygons represent forest stands in varying stages of structural development. Orange polygons represent stands that were present in 1936. Green polygons represent stands that developed between 1936 and 1975. Purple polygons represent stands that developed after 1975. Overlaid shapes represent sampled plots. Diamonds=old growth plots, squares=young multi-strata plots, circles=stem exclusion plots.

CHAPTER 3: OREGON ASH (*FRAXINUS LATIFOLIA*) PLANT COMMUNITIES OF THE
WILLAMETTE VALLEY, OREGON

ABSTRACT

I identified major environmental and successional gradients associated with vascular plant community composition in Oregon ash-dominated Willamette Valley wetlands. On sites where closed canopy ash and ash/oak forests have developed, community composition was significantly different than in nearby open wetland savannas. However, species richness was not lower in forested wetlands. Exotic species cover was, on average, greater in areas with reduced or no canopy cover. Within-forest compositional differences were also associated with stand age, as represented by stage of structural development. These differences were greatest between "young" (stem exclusion and understory initiation, which were typically less than 80 years old) and "old" (young multi-strata and old growth, which were typically greater than 80 years old) stands, and several species were identified as indicators of these developmental stages. In all sampled wetlands, soil moisture regime (as approximated by Community Type Wetland Index scores) was a driver of community composition. Exotic species cover was not correlated with soil moisture, but exotic species composition was largely a factor of both canopy cover and CTWI score. Furthermore, overall species richness was negatively correlated with CTWI scores. Willamette Valley wetlands dominated by Oregon ash contribute to landscape-scale species richness and native-dominated plant communities. A decline in Oregon ash cover resulting from looming forest health threats such as the emerald ash borer, could homogenize regional wetland communities and accelerate the spread of exotic plant species.

INTRODUCTION

Wetland forests dominated by Oregon ash (*Fraxinus latifolia*) are relatively rare, yet prominent ecological features in the Willamette Valley of western Oregon. For centuries, anthropogenic disturbance, primarily indigenous burning, followed by Euro-American livestock grazing, has prevented ecological succession and the formation of forests in Willamette Valley wetlands. (Towle 1982). More recently, Willamette Valley wetlands have been widely lost or altered due to agricultural and urban development, disruptions to naturally occurring hydrologic

processes, and the introduction of exotic species (Taft and Haig 2003). In remnant Willamette Valley wetlands, Oregon ash (*Fraxinus latifolia*) forest is the climax vegetation type on many sites (Heinitz and Frenkel 1987 ; Prive 2016). In the absence of anthropogenic disturbance, Oregon ash rapidly establishes in wetlands and forms a closed canopy. In areas where old growth ash forests have persisted, or where younger ash forests have initiated, understory communities and the environmental gradients that influence their composition, are poorly understood (Heinitz and Frenkel 1987).

Where ash forests have recently developed, local plant communities have likely been highly altered. Disturbance regime changes over the past century have allowed for woody plant encroachment in many of the region's remnant grasslands (Johannessen et. al 1971, Towle 1982). These relatively recent changes in Willamette Valley grassland ecology have caused shifts in vegetation composition and structure in both wetland and upland ecosystems, and have been implicated in the loss of habitat for species reliant on early seral conditions (Christy and Alverson 1994). Currently, less than 1% of the historical extent of Willamette Valley wetland grasslands (hereafter referred to as (ash) savannas) remains (Christy and Alverson 1994). The potential conversion of remnant Willamette Valley wetland savannas to Oregon ash forest, and the resulting loss of early seral habitat, has prompted land managers to use fire, mechanical treatments, and/or herbicides to limit woody plant encroachment in areas managed for wetland grassland conservation (Pendergrass 1995; Clark and Wilson 2001). However, differences in plant species composition between wetland savannas and Oregon ash forests in Willamette Valley wetlands has not been previously described. Consequently, the potential for the loss or recruitment of species as these systems shift between states is unclear.

While the drastic reduction in extent of wetland savannas in the Willamette Valley has caused their conservation to become increasingly prioritized among public and private land management organizations, similar attention has not been paid to regional forested wetlands. It is likely that these forests host unique plant assemblages that contribute to landscape-level biological diversity, though few descriptions of Willamette Valley forested wetland communities are available. In other forest types, overstory structure and composition are predictive of understory community characteristics (McKenzie, et al. 2000). The presence, density, and composition of a forest canopy can influence understory species composition by altering local light, hydrologic, and nutrient cycling regimes (Barbier, et al. 2008). In upland ecosystems of the

Pacific Northwest, this phenomenon has been described on sites that have transitioned from grassland to woodland to conifer-dominated forest (Thysell and Carey 2001); each state is largely determined by human management activities and is associated with a unique understory community. The maintenance of a landscape mosaic that incorporates each ecological state is important to retain heterogeneous habitat characteristics, ecosystem functionality, and biological diversity. However, those ecosystem attributes are poorly understood for forested wetlands in the Willamette Valley, and a description of their associated communities – as well as how they differ from those of other wetland communities – will help inform future management efforts.

In coming years or decades, ash-dominated forested wetlands may be threatened with invasion by the emerald ash borer (*Agrilus planipennis*; Coleoptera:Buprestidae), an exotic forest insect that has caused widespread ash mortality in other parts of North America (Herms and McCullough 2014). In portions of the mid-western United States where ash trees have been removed from overstory canopies, understory composition has been altered, often resulting in increased exotic plant cover (Hausman et al. 2010). It is currently unclear how Willamette Valley forested wetland communities would respond to such overstory mortality caused by an emerald ash borer infestation. However, increased potential for invasion by exotic species is of particular concern if overstory ash trees are lost due to exotic pest introduction. Exotic plant species are widely considered a threat to biological diversity and natural ecological succession (Levine et al. 2003).

Willamette Valley wetlands have already experienced an influx of exotic plant species, which has had widespread impacts on community composition (Clark and Wilson 2001). Reed canary grass (*Phalaris arundinacea*) is especially aggressive, and on many sites forms nearly monotypic patches that potentially alter successional trajectories of wetland communities (Apfelbaum and Sams 1987) and can lower native species richness (Perkins and Wilson 2005). Several exotic woody species also threaten Willamette Valley wetlands with high rates of invasion. These include Armenian blackberry (*Rubus armeniacus*), sweetbrier and multiflora rose (*Rosa eglanteria* and *R. multiflora*), common pear (*Pyrus communis*), and single-seeded hawthorn (*Crataegus monogyna*). Exotic species are often controlled in open wetland systems with regular mowing and/or burning (Pendergrass et al. 1995). However, in relatively unmanaged wetland forests, exotic species invasion is likely only controlled by local environmental conditions.

Forest canopies alter local light regimes, which can suppress the growth of certain exotic plants (Knapp and Canham 2000). Disturbance and/or increased forest edge can increase forest area that is susceptible to exotic plant invasion (Goldblum and Beatty 1999). In the Willamette Valley, closed canopy ash forests may limit the spread of exotic species in regional wetlands. Inversely, overstory ash mortality may provide an opportunity for increased site invasion. Understanding patterns of exotic species distribution between Willamette valley wetland grasslands and forests will aid in the anticipation of future invasion risks in the event that ash trees are lost to the emerald ash borer. Comparing plant communities of Willamette Valley wetlands along important environmental gradients may offer some insight into potential future states in these systems as well as the role of ash canopies in supporting unique native plant assemblages.

The objectives of this research are to: 1) Classify understory plant communities in ash-dominated Willamette Valley forested wetlands. 2) Compare plant community composition among stages of forest structural development. 3) Compare plant community composition between Willamette Valley wetlands in which a closed canopy forest has developed and those that are maintained in an early seral, open savanna state. 4) Identify important environmental gradients influencing wetland community composition, and relate these to differences in the composition and abundance of exotic species.

METHODS

STUDY AREA

This study was conducted within remnant wetlands in the Willamette Valley of western Oregon (Figure 3.1). The Willamette Valley covers approximately 13,355 km^2, and is composed of agricultural and urban areas interspersed with naturally occurring wetland and upland grasslands, Oregon white oak woodlands, riparian gallery forests, and conifer forests. The Valley's grasslands and hardwood forests contrast with the mostly conifer-dominated forests of the adjacent Coast Range and Cascade Mountains. The climate of the Willamette Valley is marked by mild temperatures and seasonally variable precipitation. Mean high temperatures range from 27° C in the summer to five in the winter. Wetlands in the Willamette Valley are

characterized by seasonally flooded valley bottom soils with a prominent, poorly draining clay horizon. Soils on these sites typically become inundated and anaerobic during the region's rainy season, which occurs between November and April, then become dry and cracked during hot, dry summer months.

PLOT ESTABLISHMENT

During the summer of 2015, I sampled plant communities of ash-dominated forested wetlands in 11 management units between Lane and Washington counties in the Willamette Valley (Figure 3.1). I defined management units as areas of contiguous land ownership that are managed for conservation and that are within a common watershed. All management units were more or less flat with poorly draining soils. Oregon ash (*Fraxinus latifolia*) and, to a lesser extent, Oregon white oak (*Quercus garryana*) dominated the sampled forests.

I also sampled plant communities in wetland savannas at five management units where savannas occurred adjacent to, or within 1 km of, sampled forests. All savannas have been maintained in an early seral, grassland state via prescribed burning and/or mowing. Additionally, all had extensive Oregon ash regeneration, suggesting that, in the absence of anthropogenic disturbance, these sites are successional to ash forest.

Within each management unit, I delineated forests and savannas using aerial photography. Forests were considered to have greater than 50% tree cover, while savannas had 5-20% tree cover (as estimated using aerial photography). I then randomly established one 0.2 ha circular plot for every five hectares of each wetland type. In total, 59 forest and 43 savanna plots were sampled.

I used an adapted chronosequence approach to quantify changes in plant community composition in plots at varying stages of forest structural development. I sampled stands at five stages of structural development: savanna/stand initiation, stem exclusion, understory initiation, young multi-strata, and old growth. These developmental stages were established using an average linkage cluster analysis of structural characteristics, and were verified with historical aerial photography.

DATA COLLECTION

In each plot, I censused all vascular plant species. Species abundance estimates were made within a 25 m² circular subplot established at the center point of each larger plot. I used octave-scale cover classes for abundance estimates as recommended by Gauch (1982). I recorded the DBH and species of each tree >5 cm DBH and >2 m tall. I used this to calculate stand density as stems per hectare as well as basal area in m²/ha for each tree species. Relative dominance per species was calculated as basal area per species divided by total plot basal area. I directly measured canopy cover at the center of each plot using a densiometer. For each plot, canopy cover values represent the mean cover recorded at four cardinal directions.

To quantify local soil moisture regimes, I adapted the methods used by Coles-Ritchie (2007) to calculate a community type wetland index (CTWI) score for each plot. This approach uses a previously derived wetland indicator status for each plant species to ascribe a community-level wetland score. A species' wetland indicator status is the estimated probability that species will occur in a wetland, and is assigned as a categorical variable from obligate upland (1% probability of occurring in a wetland) to obligate wetland (99% probability of occurring in a wetland). A wetland indicator value (WIV) was assigned to each species based on its wetland indicator status (WIS), as established in Lichvar, et al. (2013). WIV was assigned as follows: obligate upland = 0.0, facultative upland = 0.25, facultative = 0.5, facultative wetland = 0.75, obligate wetland = 1.0. CTWI was calculated by multiplying the estimated abundance of each species in a subplot by their WIV and summing the products. Because species abundance estimates did not total 100% for each plot, species abundances were relativized by plot totals prior to calculating CTWI scores.

DATA STRUCTURE, ADJUSTMENTS, AND OUTLIERS

My sampling protocol produced several matrices that described community composition and environmental variables. Community data for all plots were represented by two matrices with species as columns, and plots (sample units) as rows. The first community matrix (102 plots x 217 species) contained species presence/absence counts for each plot. The second community matrix (102 subplots x 177 species) contained species abundance estimates for each subplot. To describe only forest communities, I removed savanna plots from each matrix. This

resulted in a forest-only presence/absence matrix (59 plots x 147 species) and a forest-only species abundance matrix (59 subplots x 113 species). Environmental data were represented by a matrix with environmental variables as columns and sample units as rows. The environmental matrix (102 plots x 12 environmental variables) contained measurements of canopy cover, CTWI scores, percent cover of common exotic species, and a categorical variable assigned by wetland forest developmental stage (i.e. savanna, stem exclusion, understory initiation, young multi-strata, and old growth).

Plots with an average Sørensen distance from all others of more than two standard deviations from the grand mean were defined as outliers. Four plots were identified as outliers in the presence/absence matrix, though no subplot was more than 2.7 standard deviations from the grand mean. Interpretability of analyses was not affected by outliers, so all plots were retained in the dataset. Due to a higher cover of bare ground and bryophytes, forest plots tended to have lower abundance totals than prairie plots. Therefore, the abundance matrix was relativized by plot totals to emphasize the relative abundances of species present rather than overall vegetation coverage.

ANALYSIS

Multivariate community analyses were performed with PC-ORD version 7 (McCune and Mefford 2016). Other analyses were performed using R statistical software (R Core Team 2013). I used Sørenson distance measure for all ordinations and cluster analyses. I also report alpha (plot-level species richness), gamma (landscape-level species richness), and beta (gamma/alpha) diversity for each wetland type (Wittaker 1975).

I used multi-response permutation procedure (MRPP) to evaluate differences in vascular plant community composition among stages of structural development. MRPP is a non-parametric randomization test for multivariate differences among predetermined groups. It produces a test statistic (A), which summarizes within-group agreement on a scale of 0-1, with 1 indicating groups that are completely dissimilar. A p-value is also produced that indicates the likelihood the observed difference between groups is obtained by chance.

I tested species association with each stage of structural development using Indicator Species Analysis (ISA) (Dufréne and Legendre 1997). ISA uses a species' within-group relative

abundance and relative frequency to calculate an indicator value (IV). Because ISA relies on species abundance information, I used the species abundance community matrices to derive IV's. Randomization tests with 4999 iterations were used to test the significance of IV's. Because differences between some adjacent structural stages were not significant (see Results), plots are grouped into young (stem exclusion and understory initiation) and old (young multi-strata and old growth) for purposes of reporting ISA values. Additionally, on the full species abundance matrix (forest and savanna plots), I performed hierarchical agglomerative cluster analysis with Sørensen distance measure and a flexible beta of -0.25 to identify vegetation site types. I repeated ISA to determine indicator values for each site type.

Nonmetric multidimensional scaling (NMS; Kruskal 1964) was used to assess relationships among plots in species space. I overlaid convex hulls and joint plots onto NMS ordinations to analyze relationships between plots and environmental variables. Two ordinations were produced: one of forest plots only, and of forest and savanna plots. I selected NMS as an appropriate ordination technique because it tends to remain robust to datasets with large numbers of zero values and retains ecological relationships in non-linear, non-normal datasets (McCune and Grace 2002). NMS was run 200 times with a random initial configuration. In each case, the run with the lowest stress was used for analysis. Distance measure ties were not penalized. Monte Carlo randomizations were used to test the significance of final ordinations. Pearson's correlation coefficient (r) is reported for environmental variables and common species as a measure of correlation with ordination axes. Finally, I used regression analysis to summarize the correlation between environmental variables (canopy cover and CTWI) and both exotic cover and species richness.

RESULTS

OREGON ASH UNDERSTORY PLANT COMMUNITIES

Total understory species richness for sampled 0.2 ha forest plots was 147. Richness averaged 24 (range: 7-42) species per plot. Species turnover between plots was moderate (β_w = 6.12) (Table 3.1). Many species were infrequently found; only 64 (44%) were found on >10% of plots. Furthermore, nearly 84% of the elements in the forest presence/absence matrix were zero

values. The most frequently occurring forest species (those that occurred on >50% of plots) were *Amelanchier alnifolia, Carex leptopoda, Carex obnupta, Galium aparine,* native *Rosa spp., Poa pratensis, Polypodium glycyrrhiza, Rubus ursinus, Rumex spp.* and *Symphoricarpos albus.* Only one of the most frequently found species was exotic (*Poa pratensis*). Overall exotic richness was 47 and exotic cover averaged 28.5% (range: 0-94%).

Plant community composition differed among forest developmental stages (MRPP: *A*=0.26, *p*<0.0001). However, pairwise comparisons showed that not all developmental stages were significantly different (Table 3.2). Old growth and young multi-strata plots did not differ in community composition (MRPP: *A*=-0.001, *p*=0.45). Stem exclusion and understory initiation plots were also not significantly different (MRPP: *A*=0.02, *p*=0.15). Stem exclusion and old growth plots were the least similar (MRPP: *A*=0.05, *p*=0.003). After grouping forest plots to emphasize differences in composition between developmental stages ("young" and "old"), indicator species analysis revealed that many species were found in both young and old forests, but that several were indicators of forest age (Table 3.3). In particular, indicators of young forests included *Elymus glaucus, Juncus patens, Lysimachia nummularia, Myosotis laxa, Perideridia gairdneri, Poa pratensis, Rumex spp., Thelictrum fendleri* and various sedge species. Species that were indicators of old forests included *Cornus sericea, Geranium lucidum, Rubus ursinus, Symphoricarpos albus,* and *Tellima grandiflora*.

Cluster analysis of the entire species abundance matrix yielded 9 site types when cut at approximately 33% information remaining. Of these, six were associated with forest plots. ISA yielded significant indicator species for each site type (Table 3.3). Environmental characteristics were variable among site types, including ash and oak relative dominance (RD), CTWI, stand density, exotic cover, and species richness (Table 3.4).

Site type one included 27% of sampled plots (n = 16), and was characterized by low stand density, relatively low, yet highly variable CTWI scores, and a mostly ash overstory. Exotic species cover was relatively low, and species richness was moderate (Table 3.4). Indicator species included *Rubus ursinus, Claytonia siberica, Mimulus dentatus, Polystichum munitum, and Rhamnus purshiana* (Table 3.3).

Twenty-four percent (n = 14) of plots were included in site type two. This site type also had relatively low CTWI scores with a minor oak component in overstory canopies. Stand densities were highly variable in site type 2, though they tended to be relatively high. Both exotic

cover and species richness were high in this site type (Table 3.4). Understory communities were characterized by *Carex densa, Carex leporina, Carex pachystachya, Epilobium spp., Juncus patens, Poa pratensis, Ranunculus uncinatus, Rubus armeniacus, Schedonorus arundinaceus, Symphoricarpos albus, Tellima grandiflora, Thalictrum fendleri, Toxicodendron diversilobum,* and *Vicia sativa* (Table 3.3).

Site type three accounted for 15% (n = 9) of the sampled plots, was characterized by moderately low CTWI scores, and had the highest average oak RD. Species richness and exotic cover were both high (Table 4). Indicator species for site type three included *Camassia leichtlinii, Elymus glaucus, Geranium lucidum,* and *Oemlaria cerasiformis* (Table 3.3).

Site type four included 12% (n = 7) of plots. This site type had high CTWI scores with no overstory oak trees. Species richness was relatively low, and exotic species cover was moderate. Stand densities were relatively low (Table 3.4). While *Carex obnupta* was widespread in ash communities, it was overwhelmingly dominant on this site type. *Oenanthe sarmentosa* also attained high cover in some plots. *Solanum dulcamara* was a significant exotic indicator species (Table 3.3).

Just three plots occurred in site type five (5%), which was characterized by high CTWI scores, high stand density, and moderate oak RD. Both species richness and exotic cover were low (Table 3.4). Indicator species included *Carex leptopoda, Carex unilateralis, Eleocharis acicularis, Galium trifidum, Lysimachia nummularia, Myosotis laxa, Ranunculus alismifolius, and Spirea douglasii* (Table 3.3).

Site type six occurred in both forests and savannas, and had very high *Phalaris arundinacea* cover (Table 3.3). This site type included 17% (n = 10) of sampled forest plots. It was characterized by relatively high CTWI scores and low stand densities. Overstory tree communities were nearly entirely dominated by Oregon ash. Exotic cover was very high, and species richness was very low (Table 3.4).

NMS of forest plots in species space produced a three dimensional ordination with a final stress of 13.6 and a final instability <0.0001 after 49 iterations. Instability was less than would be expected by chance (*p* = 0.004). This ordination explained 84.5% of the total dataset variation. Axis one accounted for 35% of the community variation, while axis two and axis three accounted for 39% and 13%, respectively. NMS identified major gradients in community composition (*r* > |0.15|; Figure 3.2). Stand density was most highly correlated with axis one (*r* = (0.63); Table 3.5,

Figure 3.2). Furthermore, younger stands (stem exclusion and understory initiation) tended to group toward the right side of the ordination, while older stands (young multi-strata and old growth) tended to group toward left - though there was overlap between developmental stages. CTWI scores were most highly correlated with axis two ($r = (0.7)$; Table 3.5, Figure 3.2). Species richness was positively correlated with axis one ($r = (0.5)$; Table 3.2) , and negatively correlated with axis two ($r = (-0.61)$; Table 3.5, Figure 3.2). Axis three was not interpreted as it did not appear to represent an additional measured gradient.

For the forest plot ordination, convex hulls helped to visualize plot inclusion in six forested site types (Figure 3.3). *Rubus ursinus*, which was the species with the highest IV score for site type one, was highly negatively correlated with axis one (Table 3.6). *Carex spp.* and *Symphoricarpos albus*, which were indicators of site type two, tended to be weakly to strongly positively correlated with axis one and negatively correlated with axis 2. Exotic indicators of site type two, including *Rubus armeniacus* and *Schedonorus arundinaceus* were also positively correlated with axis 1 and negatively correlated with axis two (Table 3.6). Indicators of site type three, including *Camassia leichtlinii, Elymus glaucus,* and *Geranium lucidum* were positively correlated with axis 1 and negatively correlated with axis 2 (Table 3.6). *Carex obnupta*, which dominated site type four, was negatively correlated with axis 1 and positively correlated with axis 2 (Table 3.6). Indicator species of site type five, including *Carex leptopoda, Carex unilateralis* and *Ranunculus alismifolius* tended to be positively correlated with axis 1 and somewhat positively correlated with axis 2, though *Spirea douglasii* and *Myosotis laxa* were more highly positively correlated with axis 2 (Table 3.6). *Phalaris arundinacea* was negatively correlated with axis 1 and positively correlated with axis 2 (Table 3.6).

EFFECT OF FOREST CANOPY ON WETLAND COMMUNITY COMPOSITION

Community composition among all plots (forest and savanna) was highly heterogeneous, with a beta diversity of 9.18 (Table 3.1). Furthermore, nearly 93% of elements in the presence/absence community matrix consisted of zero values. Overall species richness was 216, with 142 species occurring in savannas. Of these, 49% (69) were not found in forest plots.

Community composition differed between early seral savanna plots and forest plots (MRPP, $p<0.0001$), though within-group agreement was low ($A=0.05$). ISA revealed that these

wetland types had significant indicators (Table 3.3). *Carex obnupta, Carex leptopoda, Gallium aparine, Geum macryphyllum, Poa pratensis, Symphoricarpos albus*, *Ranunculus uncinatus,* and *Rubus ursinus* were most characteristic of forest plots. Grass species such as *Agrostis capillaris, Anthoxanthum odoratum*, and *Deschampsia cespitosa* were indicators of prairie plots (Table 3.3). Several species were common in both prairie and forest plots, and so did not have significant indicator values or had significant indicator values for site types found in forests and savannas. These included *Phalaris arundinacea, Oenanthe sarmentosa,* both native and exotic *Rosa spp.*, and *Veronica scutellata*.

Of the nine site types yielded by cluster analysis, three were found only in savannas. Two others, site types four and six, were found in both forests and savannas. Drier savannas with lower CTWI scores included two site types: site type seven and site type eight (Tables 3.3, 3.4). Site type seven was dominated by *Agrostis capillaris*, but also supported other native and exotic herbaceous species. Site type eight was occupied by both native and exotic grasses, primarily *Deschampsia cespitosa and Anthoxanthum odoratum.* Site type nine had higher CTWI scores, and was characterized by high *Mentha pulegium* cover, as well as several native sedges and forbs (Tables 3.3, 3.4). Each of these, in addition to site type six, had high exotic cover (Table 3.4). Site type four, which was dominated by *Carex obnupta* and *Oenanthe sarmentosa*, was also found in both forests and savannas, but had relatively low exotic cover. Ash had low RD in site type seven (Table 3.4), primarily due to extensive *Crataegus* regeneration there (Table 3.3).

NMS of both wetland types produced a two-dimensional ordination (Figures 3.4, 3.5) with final stress of 17.9. This was less than would be expected by chance (p=0.004). Final instability was <0.0001 after 76 iterations. Cumulative variance explained by both axes was low (24.6%; 15.1% on axis 1, and 9.5% on axis 2). Canopy cover was the most highly correlated environmental variable, and was positively correlated with axis one (r=0.91; Table 3.5; Figure 3.4). Prairie and forest plots grouped toward the left and right of axis 1 respectively. CTWI was highly positively correlated with axis two (r=0.74; Table 3.5; Figure 3.4). Site types overlapped somewhat within species space, though convex hulls around site types helped to visualize the arrangement of site types along ordination axes (Figure 3.5).

Species richness did not differ between savanna plots (mean=22.8, sd=8.8) and forested plots (mean=24, sd=8.6) (two sample t-test; p=0.49), nor was it correlated with canopy cover (Figure 3.6. However, species richness was negatively correlated with the second axis of the

NMS ordination (Table 3.5; Figures 3.4, 3.5), suggesting a greater association with a soil moisture gradient than canopy cover. This relationship was supported by the raw dataset in which richness was negatively correlated with CTWI (r=-0.57; Figure 3.7). Mean exotic cover was greater in savanna plots (65±29%) than in forested plots (29±28%; two sample t-test, p<0.01;), and was negatively correlated with canopy cover (r=0.58; Figure 3.8). Exotic cover was not correlated with CTWI scores (r<0.001; Figure 3.9). Overall, exotic cover was negatively correlated with the first ordination axis, which represented a gradient in canopy cover. However, exotic species abundance and composition was heterogeneously distributed according to position on the ordination (Figure 3.4). *Agrostis capillaris, Anthoxanthum odoratum,* and *Mentha pulegium* were negatively correlated with axis 1, and had high Indicator values in savanna plots (Table 3.3; Figures 3.1, 3.2). *Phalaris arundinacea* was strongly positively correlated with axis two and was found in both prairie and forest plots (Table 3.3; Figures 3.1, 3.2). Exotic *Rubus spp.* and *Geranium lucidum*, which were both indicator species in forest plots, were somewhat positively correlated with axis one, and negatively correlated with axis 2.

DISCUSSION

OREGON ASH COMMUNITIES

Sampled Oregon ash forests and wetland savannas with an Oregon ash component hosted species-rich understory communities. Species richness in forest plots (147, 47 of which were exotic) was comparable to that reported in other regional broadleaf forests. Thysell and Carey (2001) reported a similar number of vascular plant species (171, 53 of which were exotic) in Oregon white oak communities of the Puget Trough in western Washington, and found that those communities were somewhat less diverse than associated upland grasslands. Fierke and Kauffman (2006) also identified a similar number of species (151, 60 of which were exotic) in black cottonwood-dominated gallery forests along the Willamette River in western Oregon. Species richness in all sampled wetland plots (216) was also consistent with that reported in other studies of Willamette Valley wetlands (Schooler et al. 2006). Beta-diversity is difficult to

compare among studies due to broad differences in sampling and analytical methodologies. However, the number of identified forested wetland site types was higher than has been reported for regional upland hardwood communities (Thilenius 1968, Thysell and Carey 2001).

The observed diversity of site types reflects a high level of between-plot species diversity, and can be at least partially explained by the broad soil moisture gradient found in Oregon ash forests. Heinitz and Frenkel (1987) found a generally bi-modal distribution of species dominance associated with local soil moisture regime in ash forests of William L. Finley National Wildlife Refuge. The authors of that study found that on relatively dry sites, communities were dominated by *Symphoricarpos albus*, while more wet sites were dominated by *Carex obnupta*. The understories of many sites sampled for this study were dominated by those species, and their CTWI scores reflected the associated soil moisture patterns previously observed. Several of the native species found on dry sites, especially *Ranunculus uncinatus* and *Tellima grandiflora,* were associated with *Symphoricarpos* in both this study and Heinitz and Frenkel (1987). However, this study further divided dry site communities. Many relatively dry sites that were dominated by *Rubus ursinus* (site type one) had communities distinct from those previously described. An additional "dry" site type (site type three) was dominated by *Oemlaria cerasiformis* and *Camassia leichtlinii*. This site type greatly overlapped site type two in NMS ordinations, and so likely shared many species. In addition to *Carex obnupta*, relatively wet sites were often dominated by *Phalaris arundinacea,* a species hardly mentioned in Heinitz and Frenkel (1987). One other "wet" site type (site type five) was uncommon, and did not appear to reflect any community previously described.

Compositional differences among site types with similar soil moisture regimes appear to be at least somewhat associated with stand structural development. Stand density was the second most highly correlated environmental variable in NMS ordinations. Lower stand density is associated with older, more structurally diverse overstory characteristics, while higher stand density is characteristic of younger, more structurally homogeneous overstories (Franklin et al. 2002). Furthermore, composition was significantly different between "young" (stem exclusion and understory initiation) and "old" (young multi-strata and old growth) forests. Stand age and overstory structure also influence understory composition in other regional forest types. Halpern and Spies (1995) found that understory diversity increased slowly over time in conifer forests west of the Cascade crest, and posited that in those systems individual species' association with

particular developmental stages are largely a product of sensitivity to disturbance and the changing light regimes that accompany overstory succession. Fierke and Kauffman (2006) found that stand age and structural diversity is also related to understory diversity and composition in Willamette Valley cottonwood forests. This study did not quantify stand ages at a scale fine enough to test correlations between age and species richness. However, that stand age and overstory structure is apparently associated with understory composition suggests that the maintenance of heterogeneous age classes in Oregon ash forests on a landscape scale is important for the conservation of both within- and between-stand plant diversity.

EXOTIC PLANT SPECIES

This study found that exotic species are widespread in Oregon ash forests, though exotic species distribution differed according to site type. In general, wetlands are vulnerable to invasion by exotic species, and often undergo a transition to monotypic dominance following invasion by particularly aggressive species (Zedler 2004). Schooler (2006) found that community diversity and native species abundance were both negatively correlated with exotic species abundance in Willamette Valley wetlands. Fierke and Kauffman (2006) observed a similar phenomenon in regional cottonwood forests. In both of those studies, *Phalaris arundinacea* was a problematic exotic species, and could potentially disrupt tree species regeneration and successional dynamics (Fierke and Kauffman 2006). *Phalaris arundinacea* has been found in both experiments (Green and Galatowitsch 2002; Kercher and Zedler 2004) and observational field studies (Werner and Zedler 2002) to be capable of displacing native wetland plants and forming monotypic patches. This is often the case in a newly formed gap in vegetation and/or where nutrient deposition has become particularly concentrated (Zedler 2004). *P. arundinacea* should be of particular concern in aging ash forests or those with overstory mortality, as it was often dominant in ash forests and savannas sampled for this study, and was associated with low species richness.

More mesic ash forests were often invaded by *Rubus spp.* and/or *Geranium lucidum*. Each of these species has been identified as a threat to upland oak and prairie habitat in the Pacific Northwest, and all have the potential to displace native species (Dennehy et al. 2011). Most exotic grass species were limited on mesic sites where there was a closed forest canopy,

and were much more prominent in open wetlands. However, where they occur, exotic grass species such as *Poa pratensis, Dactylis glomerata, Anthoxanthum odoratum, Agrostis spp., Holcus lanatus,* and *Schedonorus arundinaceus* have the potential to increase litter and alter nutrient cycling processes in understory communities and displace native annual and perennial forbs (GOERT 2009; Dennehy et al. 2011).

Control of most exotic species in Oregon ash forests would likely be difficult. Herbicide treatments can be effective, but often negatively impact native populations (Boersma et al. 2006), and would only be appropriate in the areas where exotic species have formed monotypic patches. Mowing and hand-pulling to shift community dominance toward native species has had mixed results in open Willamette Valley wetland and upland site (Clark and Wilson 2001, Thorpe et al. 2008, Dennehy et al. 2011, Ensley 2015), though the effects and appropriateness of these treatments within forested wetlands have not been previously tested. The apparent ability of a closed canopy forest to at least partially suppress the spread of exotic plant populations suggests that the conservation of overstory communities might be one of the most effective tools in also conserving understory native abundance.

EFFECT OF FOREST CANOPY ON WETLAND COMMUNITIES

The results of this study suggest that the development of a forest canopy drastically alters plant community composition in Willamette Valley wetlands. Previous studies in open wetlands where anthropogenic disturbance is used to exclude woody plant growth have suggested that succession of Willamette Valley wetlands to a forested state has the potential to reduce species diversity and native species abundance (Pendergrass 1995; Clark and Wilson 2001). However, the distribution and diversity of native and exotic species in Willamette Valley wetlands may be more nuanced than previously thought. Wetland forests do not appear to be less species rich than open wetlands, and often have lower exotic species cover. Furthermore, rare species with federal or state protection in Oregon were located in both wetland types. *Lomatium bradshawii* and *Erigeron decumbens* are two species that are considered endangered in Oregon (Oregon Department of Agriculture 2016), and were only located in wetland savannas. Two additional species with state level protection (Oregon Department of Agriculture 2016), *Delphinium oreganum* and *Sidalcea nelsoniana* were only located in wetland forests. While continued

anthropogenic disturbance is necessary to prevent woody plant encroachment and maintain critical early seral wetland communities, it is important to note that adjacent wetland forests harbor equally species rich communities, often suppress exotic species, and can potentially provide habitat for otherwise rare species. The maintenance of both wetland savanna and wetland forest habitats is crucial for landscape scale biological diversity.

POTENTIAL IMPACTS OF THE EMERALD ASH BORER ON WETLAND COMMUNITIES

Overstory mortality in Willamette Valley forested wetlands could potentially drastically alter understory composition and increase exotic species abundance. In forests where it has already invaded, the emerald ash borer (EAB) tends to cause decline of overstory trees over just three to four years (Klooster et al. 2014). This leads to the formation of canopy gaps that are larger and more quickly generated than those that naturally occur in forests unaffected by EAB. Overstory structure and composition influences both the intensity and duration of solar radiation penetration into forest understories (Canham et al. 1990). The loss of overstory trees alters understory light regimes, which in turn can favor otherwise light-inhibited species (Hausman et al. 2010). In Ohio forests, canopy gaps created by ash tree removal has led to increased exotic understory species diversity and abundance (Hausman et al. 2010). Similar findings have been reported in eastern forests impacted by the hemlock woolly adelgid (Orwig and Foster 1998). Eschtruth et. al (2006) found that hemlock mortality caused by the hemlock wooly adelgid actually increased understory species richness in some forests, though many of the gained species were exotic.

Gap formation size following EAB introduction is largely a factor of host species dominance (Gandhi and Herms 2010). Ash mortality in the Willamette Valley and other areas where Oregon ash forms closed canopy forests could potentially create canopy gaps larger than those observed in eastern forests where tree diversity is higher. Oregon ash was the dominant species in all sampled forests, and appears to be the most important tree species in all stages of forest succession. On particularly wet sites, entire forest canopies may be lost following EAB infestation. This study suggests that the loss of a forest canopy in regional wetlands will have profound effects on understory composition and diversity. Furthermore, shifts in community composition is likely dependent on the local soil moisture regime. Drier sites may maintain some

overstory oak trees, but risk further invasion of exotic trees such as *Pyrus communis* and *Crataegus monogyna,* exotic shrubs such as *Rubus armeniacus* and exotic *Rosa spp.,* and exotic grasses such as *Agrostis capillaris* and *Schedonorus arundinaceus*. Reduced canopy cover on wet sites may lead to increased *Phalaris arundinacea* invasion, which is particularly troubling as that species appears to be associated with very low species richness.

ACKNOWLEDGEMENTS

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TABLES

Table 3.1 Diversity measures for all sampled Willamette Valley Oregon ash communities by forest plots, savanna plots, and all plots. Measures of richness are based on presence/absence counts collected on 0.2 ha plots. α = mean species richness per plot; γ = species richness for all plots; $\beta = \gamma/\alpha$ (Whittaker 1960).

	α	β	γ
All plots	23.5	9.18	216
Forest plots	24.0	6.12	147
Savanna plots	22.8	6.22	142

Table 3.2 Pairwise MRPP results comparing compositional similarity among developmental stages in Willamette Valley Oregon ash forest plots. Average distance is a measure of within-group similarity on a scale of 0-1, with 1 indicating 100% compositional similarity among sample units. The *A* statistic describes the effect size of compositional differences between groups, where *A*=0 is the chance-corrected within group agreement. The *A* statistic is reported with corresponding *p*-value, which represents the probability that the observed differences occur by chance.

	Avg. Dist.	LSE	UI	YMS	OG
LSE	0.40	-	-	-	-
UI	0.31	0.008 (0.152)	-	-	-
YMS	0.36	0.023 (0.034)	0.003 (0.324)	-	-
OG	0.37	0.045 (0.002)	0.022 (0.014)	-0.001 (0.461)	-

Table 3.3 List of species found in 25 m^2 species abundance plots located in Willamette Valley Oregon ash forests and savannas. N = number of plots in which the species was found. ST = site type the species was most associated with according to indicator species analysis (more than one is listed when ISA scores are nearly equal among two or more site types); nine site types were identified using cluster analysis of species abundance estimates on all plots. IV = indicator value for listed site types. O = IV's for "old forests" (young multi-strata and old growth); Y = IV's for "young forests" (stem exclusion and understory initiation); S = IV's for savannas. IV's are on a scale from 0-100 with higher values indicating higher frequency and/or abundance of that species within a site type or stage of structural development. Bolded IV's were significant at α = 0.05 based on a randomized permutation test. * indicates exotic species.

Species	N	ST	IV	Forest Plots O	Y	S
Acer macrophyllum	1	1	6	4	0	0
Achillea millefolium	1	7	17	0	0	2
Agrostis capillaris*	27	7	**81**	0	1	**48**
Agrostis exerata	1	9	6	0	0	2
Aira caryophylla*	11	8, 7	25, 23	0	0	**26**
Allium amplectens	4	8	7	0	0	9
Alopecurus pratensis*	6	9, 8	9, 9	0	4	4
Amalanchier alnifolia	12	2	15	5	14	0
Anthoxanthum odoratum*	22	8	**63**	0	0	43
Apocynum cannabinum	2	8	13	0	0	5
Asclepias speciosa	1	9	6	0	0	2
Aster hallii	9	9, 8	13, 15	0	0	**21**
Beckmannia syzigachne	7	9	**19**	0	0	16
Bidens cernua	1	9	6	0	0	2
Bidens vulgata	1	9	6	0	0	2
Brachypodium sylvaticum*	12	1	13	0	3	0
Briza minor	2	8, 7	17, **28**	0	0	**28**
Brodiaea coronaria	5	9, 7	4, 3	0	1	7
Brodiaea elegans	2	8	13	0	0	5
Bromus hordeaceus*	4	7	12	0	0	9
Calandrinia ciliata	1	9	6	0	0	2
Camassia leichtlinii	10	3	**37**	9	6	0
Camassia quamash	18	9, 5	16, 10	0	6	19
Carex densa	9	2	**25**	0	11	3
Carex feta	2	2	5	0	2	1
Carex hendersonii	2	2	4	0	6	0
Carex leporina	9	2	**39**	0	**20**	0
Carex leptopoda	27	1, 5	13, **29**	12	**35**	0

Carex obnupta	25	4	**49**	18	21	0
Carex pachystachya	12	2	**41**	0	**26**	0
Carex pellita	3	9	7	0	0	7
Carex praticola	3	2	6	0	2	1
Carex stipata	1	2	7	0	3	0
Carex unilateralis	17	9, 5	21**, 61**	0	4	18
Centaurium erythrea*	14	7	**42**	0	0	**29**
Chamerion angustifolium	1	9	6	0	0	2
Cinna latifolia	1	1	6	0	3	0
Circea alpina	2	1	13	8	0	0
Cirsium vulgare*	3	2	5	3	0	1
Clarkia spp.	3	9	**17**	0	0	7
Claytonia siberica	4	1	**18**	2	4	0
Cornus sericea	3	1	11	**12**	0	0
Crataegus monogyna*	8	2	5	5	4	0
Crataegus spp.	12	7	**20**	9	0	8
Cynosuros echinatus*	1	7	17	0	0	2
Dactylis glomerata*	1	2	7	4	0	0
Danthonia californica	12	8	21	0	0	**25**
Daucus carota*	2	7	14	0	0	5
Delphinium oreganum	1	3	10	0	3	0
Deschampsia cespitosa	20	8	**65**	0	0	**47**
Deschampsia elongata	1	4	11	0	3	0
Downingia ynia	5	9	**19**	0	0	**12**
Eleocharis acicularis	4	5	**30**	0	5	1
Eleocharis palustris	4	9, 6	7, 6	0	0	9
Elymus glaucus	11	3	**49**	4	**16**	0
Epilobium densiflorum	5	4	7	0	0	**12**
Epilobium spp.	18	2	**25**	3	17	2
Erigeron decumbens	1	8	7	0	0	2
Eriophyllum lanatum	8	8	**28**	0	0	19
Eryngium petiolatum	1	9	6	0	0	2
Galium aparine	39	3, 2	18, **27**	27	**34**	0
Galium oreganum	1	4	11	4	0	0
Galium parisiense*	4	8	6	0	0	9
Galium trifidum	6	5	**25**	3	5	0
Geranium dissectum*	4	2	9	1	4	0
Geranium lucidum*	9	3	**55**	17	2	0
Geranium robertianum*	1	1	6	0	3	0
Geum macrophyllum	22	1, 2	16, 22	16	22	0

Glyceria elata	2	1	13	3	1	0
Glyceria occidentalis	1	4	11	0	0	2
Gnaphalium palustre	1	9	6	0	0	2
Grindelia integrifolia	6	8	**18**	0	0	**14**
Heracleum lanatum	4	3	**17**	1	8	0
Holcus lanatus*	19	8	**27**	0	4	**22**
Hordeum brachyantherum	3	9	9	0	0	7
Hypericum perforatum*	6	2	15	1	3	2
Hypochaeris radicata*	3	8	6	0	0	7
Juncus effusus	6	9	11	1	1	5
Juncus ensifolius	2	8	4	0	0	5
Juncus patens	15	3, 2	18, **24**	4	**24**	0
Juncus tenuis	14	8	**23**	0	0	**26**
Koeleria macrantha	2	8	5	0	0	5
Lapsana communis*	2	6	**15**	2	1	0
Lathyrus aphaca*	1	2	7	0	3	0
Lathyrus latifolius*	1	2	7	4	0	0
Leontodon taraxacoides*	10	8	**59**	0	0	**23**
Leucanthemum vulgare*	5	8	**21**	1	0	6
Linum bienne*	3	8	**20**	0	0	7
Lomatium bradshawii	1	9	6	0	0	2
Lonicera hispidula	2	2	14	2	2	0
Lonicera involucrata	6	1	10	7	3	0
Lotus corniculatus*	1	6	8	0	0	2
Lotus unifoliolatus	3	8	12	0	0	7
Lupinus spp.	1	7	17	0	0	2
Luzula multiflora	5	9	11	0	0	**12**
Lycopus americanus	1	9	6	0	0	2
Lycopus uniflorus	1	4	11	0	3	0
Lysimachia nummularia*	8	5	**22**	2	**14**	0
Madia glomerata	10	7	**25**	0	0	**23**
Madia sativa	1	8	6	0	0	2
Mahonia aquifolium	1	2	10	4	0	0
Malus fusca	1	8	7	0	0	2
Melissa officinalis*	3	4	8	0	**9**	0
Mentha arvensis*	2	4, 2	5, 4	0	2	1
Mentha pulegium*	23	9	**60**	0	0	**53**
Microseris laciniatus	8	8	**23**	0	0	**19**
Mimulus dentatus	8	1	**27**	8	5	0
Mimulus guttatus	1	8	7	0	0	2

Mosotis laxa	13	5	**51**	1	**28**	0
Myosotis discolor*	13	9	12	0	0	**27**
Navarretia intertexta	1	8	7	0	0	2
Nemophila parviflora	1	1	6	0	3	0
Oemlaria cerasiformis	7	3	**42**	3	10	0
Oenanthe sarmentosa	15	4	**58**	14	6	1
Orthocarpus bracteosus	1	9	6	0	0	2
Panicum occidentale	3	8	**20**	0	0	7
Parentacelia viscosissimum*	13	7	**45**	0	0	**30**
Perideridia gairdneri	21	2, 7	24, **25**	0	**24**	6
Persicaria maculosa	1	9	6	0	0	2
Phalaris arundinacea*	28	6	**82**	15	5	9
Phleum pratensis*	4	9	15	0	0	7
Physocarpus capitatus	2	1	13	4	0	0
Plagiobothrys scouleri	2	9	**20**	0	0	**5**
Plantago lanceolata	5	8	13	0	0	12
Poa pratensis*	26	2	**46**	13	**32**	0
Polypodium glycyrrhiza	2	3	8	8	0	0
Polystichum munitum	18	1	**33**	6	**26**	0
Potentilla gracillis	12	7	**57**	0	0	**28**
Prunella vulgaris	1	8	**20**	0	3	0
Prunus avium*	19	1	6	0	6	17
Pyrus communis*	9	2	11	1	5	4
Ranunculus alismifolius	5	5	**65**	0	9	0
Ranunculus orthorhynchus	2	9	11	0	0	5
Ranunculus repens*	2	1	13	0	6	0
Ranunculus uncinatus	20	2	**22**	17	17	0
Rhamnus purshiana	8	1	**26**	10	2	0
Ribes divaricatum	1	2	7	0	3	0
Rorippa curvisiliqua	2	9	11	0	0	5
Rosa (exotic)*	11	1, 9	8, 5	10	1	3
Rosa (native)	39	1, 4, 9, 2, 8, 7	5, 6, 4, 7, 10, 14	4	17	19
Rubus armeniacus*	18	2	**21**	10	8	1
Rubus laciniatus*	2	4	9	0	2	0
Rubus ursinus	23	1	**70**	41	6	0
Rubus vestitus*	1	3	10	0	3	0
Rumex acetosella	3	8, 7	4, 4	0	0	7
Rumex spp.	24	2	**20**	5	**23**	2
Salix spp.	2	4, 6	2, 5	0	0	5
Sanicula crassicaulis	1	1	6	0	3	0

Species						
Saxifraga oregana	1	8	7	0	0	2
*Schedonorus arundinaceus**	10	2	**49**	0	**18**	0
*Senecio jacobea**	3	3, 8	5, 7	2	0	2
Sidalcea virgata	1	7	17	0	0	2
Sisyrinchium idahoense	4	9	9	0	0	9
*Solanum dulcamara**	3	4	**21**	2	8	2
Spirea douglasii	11	5	**24**	6	1	0
Stachys spp.	9	2, 6	7, 7	1	**19**	0
Stellaria calycantha	9	3	10	5	10	0
Stellaria crispa	3	3	**19**	0	9	0
Symphoricarpos albus	25	2	**74**	**28**	15	0
*Taraxacum officinale**	1	2	10	0	3	0
Tellima grandiflora	11	2	**29**	18	4	0
Thalictrum fendleri	12	2	**43**	4	**18**	0
*Torilis arvensis**	1	2	10	0	3	0
Toxicodendron diversilobum	17	2	**47**	8	**17**	0
Toxicoscordion venenosum	1	8	7	0	0	2
Trillium albidum	1	3	10	0	3	0
Triteleia hyacinthina	12	2	**25**	1	11	3
Typha latifolia	2	4	**22**	0	0	5
Veratrum sp.	3	1	8	7	0	0
Veronica americana	3	6	6	3	0	0
Veronica scutellata	14	9, 2	10, 11	0	7	9
Viburnum ellipticum	7	3	**51**	5	7	0
*Vicia sativa**	5	2	**36**	1	9	0
*Vicia tetrasperma**	17	9, 3, 2, 8	4, 3, 11, 6	1	6	12
Wyethia angustifolia	5	8	**33**	0	0	**12**

Table 3.4 Environmental variables and their means±sd for each of nine Willamette Valley Oregon ash community site types derived from cluster analysis. Site types 1-4 occurred only in forest plots; site types 7-9 occurred only in savanna plots; site types 5 and 6 occurred in both wetland types. RD = relative dominance of tree species (only ash and oak are reported as they were the only trees observed dominating forest canopies); Richness = number of species per plot; % Exotic = percent exotic species cover per plot; CTWI = community type wetland index scores; CC = canopy cover; St/ha = stand density.

	Forest Plots				Both		Savanna Plots		
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
# of plots	16	14	9	7	3	10	5	15	15
Ash RD	89±24	94±15	87±24	99±1	85±13	87±24	4±8	30±39	72±37
Oak RD	2±5	5±15	10±16	0±0	6±11	1±5	0±0	5±18	0±0
Richness	12±5	17±5	14±4	9±3	7±2	6±4	12±5	18±7	13±5
% Exotic	12±14	39±26	30±21	20±21	05±17	73±30	85±21	67±29	49±28
CTWI	46±15	53±8	53±13	87±8	79±7	83±13	47±4	49±11	71±12
CC	79±7	72±11	72±9	61±35	78±2	48±40	0±0	2±9	3±11
St/ha	480±157	1446±1016	740±451	504±397	1987±227	340±497	7±16	19±54	29±79

Table 3.5 Environmental variables for Willamette Valley Oregon ash communities with their means, ranges, and correlation with NMS ordination axes. Values are presented for both the entire data set (All plots) and with savanna plots removed (Forest plots).

Variable	Forest plots Mean (range)	All plots Mean (range)	Forest plots NMS Axis 1	Axis 2	All plots NMS Axis 1	Axis 2
Canopy cover	75.2 (27-93)	44.3 (0-93)	-0.09	-0.10	0.91	0.04
CTWI	59 (27-100)	61 (27-100)	-0.19	0.70	-0.09	0.74
% Exotic cover	29 (0-94)	44 (0-116)	-0.01	0.00	-0.51	-0.07
Species richness	24 (7-42)	23.5 (7-42)	0.50	-0.61	-0.12	-0.66
St/ha	854 (60-4320)	503 (0-4320)	0.63	-0.10	0.44	-0.11

Table 3.6 Significant indicators of six Willamette Valley Oregon ash forest site types and their correlations with NMS ordination axes. Axis 1 represents a stand density gradient; axis 2 represents a soil moisture gradient; axis 3 did not appear to represent an additional measured gradient. * indicates exotic species.

| Species	Axis 1	Axis 2	Axis 3
Camassia leichtlinii	0.30	-0.51	0.27
Carex densa	0.46	-0.22	-0.06
Carex leporina	0.44	-0.18	-0.07
Carex leptopoda	0.19	-0.13	-0.18
Carex obnupta	-0.36	0.38	-0.17
Carex pachystachya	0.43	-0.13	-0.08
Carex unilateralis	0.25	0.03	0.23
Claytonia siberica	0.02	-0.26	0.15
Eleocharis acicularis	0.33	-0.05	0.04
Elymus glaucus	0.43	-0.37	0.18
Epilobium spp.	0.25	0.07	-0.13
Galium trifidum	0.09	-0.04	0.20
*Geranium lucidum**	0.55	-0.30	0.43
Juncus patens	0.37	-0.57	0.05
*Lysimachia nummularia**	0.23	0.25	0.27
Mimulus dentatus	-0.46	0.19	-0.34
Myosotis laxa	0.32	0.30	0.24
Oemlaria cerasiformis	-0.03	-0.30	0.10
*Phalaris arundinacea**	-0.38	0.48	0.25
*Poa pratensis**	0.50	-0.49	-0.06
Polystichum munitum	-0.07	-0.59	-0.06
Ranunculus alismifolius	0.22	0.12	0.11
Ranunculus uncinatus	0.15	0.05	0.02
Rhamnus purshiana	0.14	-0.39	-0.26
*Rubus armeniacus**	0.10	-0.39	-0.26
Rubus ursinus	-0.59	0.07	0.07
*Schedonorus arundinaceus**	0.49	-0.31	-0.18
*Solanum dulcamara**	-0.28	0.57	-0.08
Spirea douglasii	-0.05	0.25	-0.26
Symphoricarpos albus	0.06	-0.55	0.30
Tellima grandiflora	0.26	-0.38	0.44
Thalictrum fendleri	0.32	-0.47	0.46
Toxicodendron diversilobum	0.19	-0.61	0.06
*Vicia sativa**	0.31	-0.47	-0.15

FIGURES
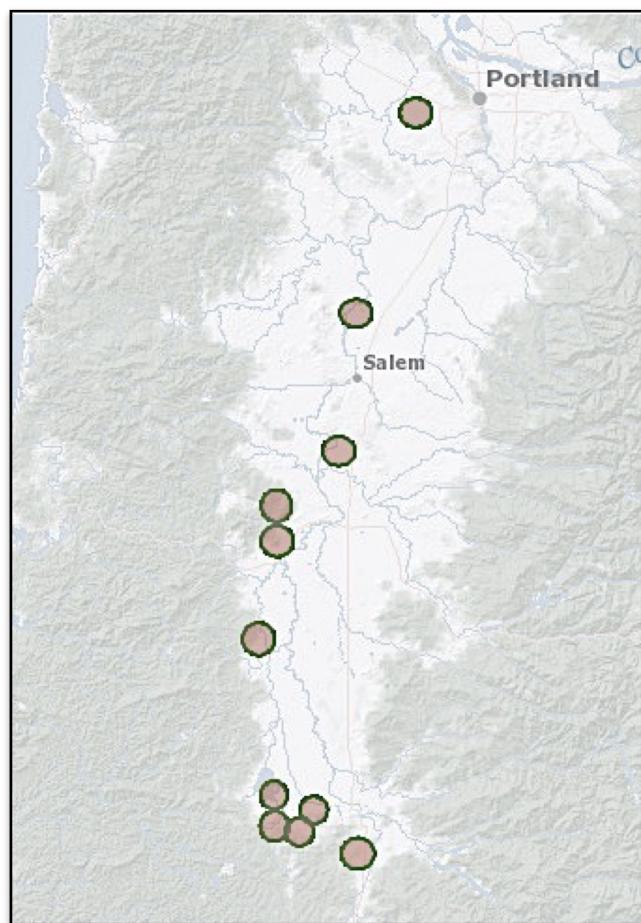
Figure 3.1 Map of Willamette Valley, OR with locations of sampled Oregon ash forests and savannas. Locations sampled were: Lane County Quamash Prairie Restoration Site (forest), Willow Creek Preserve (forest and savanna), Coyote-Spencer Wetlands (forest and savanna), Fern Ridge Wildlife Management Area (forest and savanna), William L. Finley National Wildlife Refuge (forest and savanna), Jackson Frazier Wetlands (forest and savanna), OSU Soap Creek Ranch (forest), Ankeny National Wildlife Refuge (forest), Willamette Mission State Park (forest), Tualatin Hills Nature Park (forest).
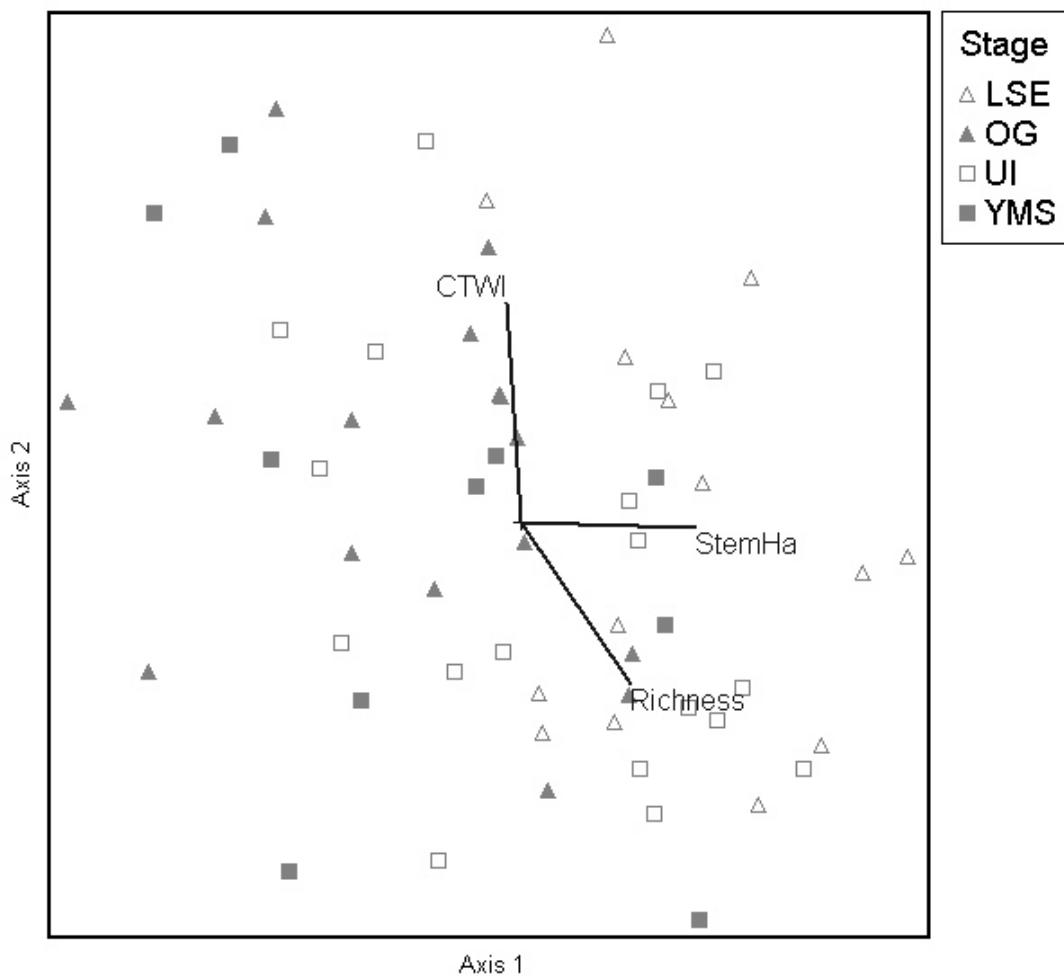
Figure 3.2 NMS ordination of Willamette Valley Oregon ash forest plots in species space. A joint plot overlay indicates strength and direction of environmental gradients with $r > |0.15|$. Community Type Wetland Index (CTWI), which represents an approximated soil moisture gradient, was the environmental gradient most highly correlated with Axis 2 of the ordination. Stand density was the gradient most highly correlated with Axis 1. Species richness was nearly evenly correlated with both axes. Younger forest plots (stem exclusion and understory initiation) tended to group toward the right of the ordination, while older plots (young multi-strata and old growth) tended to group toward the left. LSE = stem exclusion; UI = understory initiation; YMS = young multi-strata; OG = old growth.
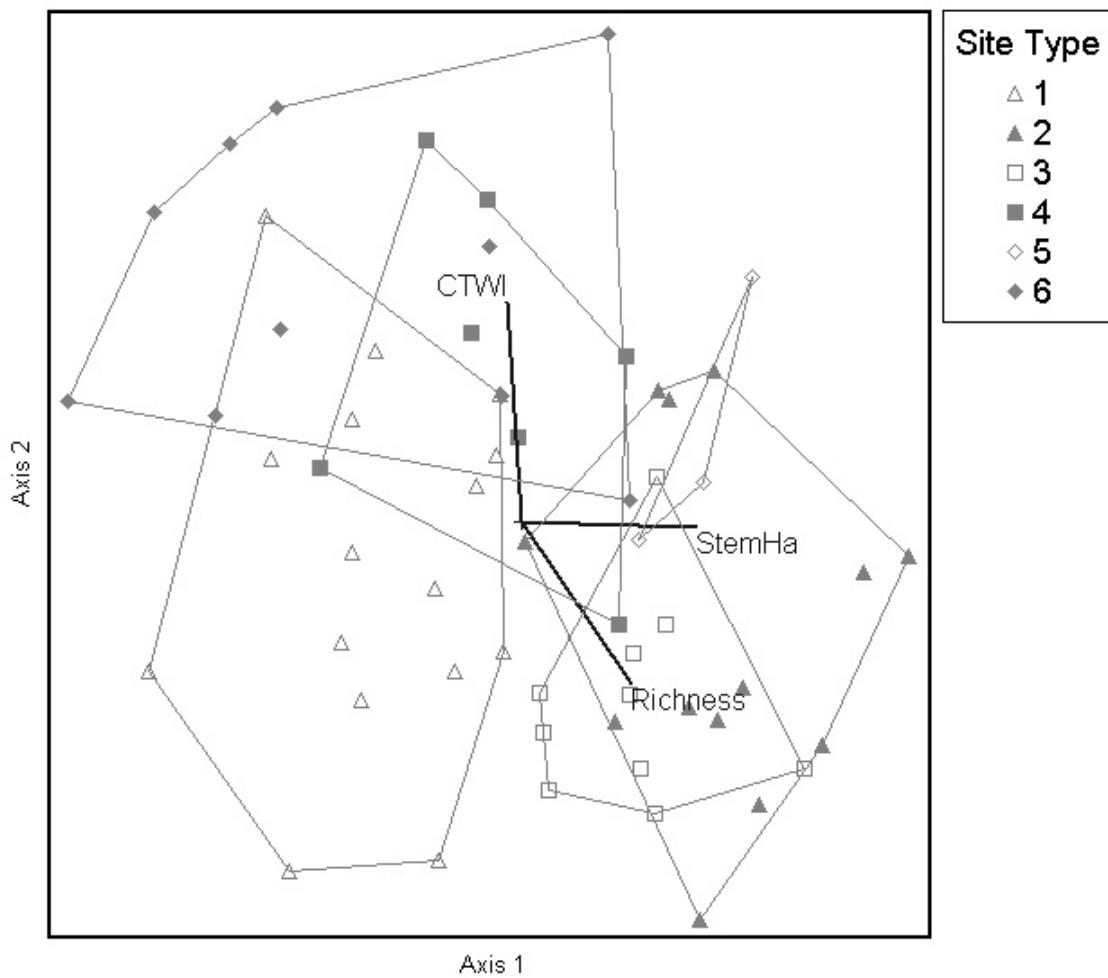
Figure 3.3 NMS ordination of Willamette Valley Oregon ash forest plots in species space with convex hulls representing plot membership in each of the six understory community site types derived from cluster analysis. Joint plot is the same as in Figure 3.2.
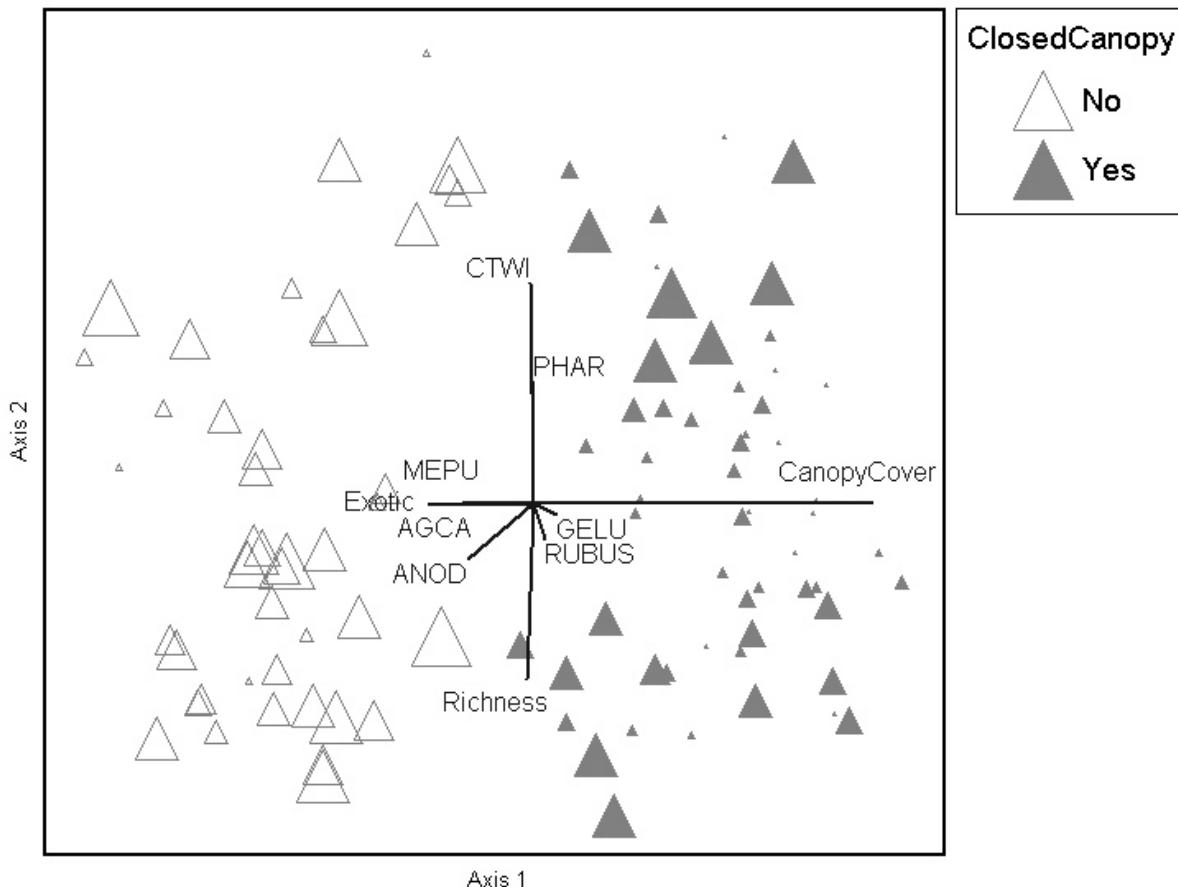
Figure 3.4 NMS ordination of Willamette Valley Oregon ash forest and savanna plots in species space. Plot symbols distinguish between closed canopy forest and savanna plots. Joint plot indicates direction and strength of environmental gradients. Canopy cover was the gradient most highly correlated with Axis 1. CTWI (Community Type Wetland Index) was the gradient most highly correlated with Axis 2. Species richness was negatively correlated with Axis 2. While exotic cover was negatively correlated with Axis 1, this was not a linear relationship. Exotic cover and composition had a heterogeneous distribution throughout the ordination. Larger symbol sizes indicate higher exotic cover, and joint plot lines indicate correlations between ordination axes and the cover of particularly common exotic species. GELU = *Geranium lucidum*, RUBUS = combined abundance of *Rubus armeniacus* and *Rubus laciniatus*, PHAR = *Phalaris arundinacea*, MEPU = *Mentha pulegium*, AGCA = *Agrostis capillaris*, and ANOD = *Anthoxanthum odoratum*.
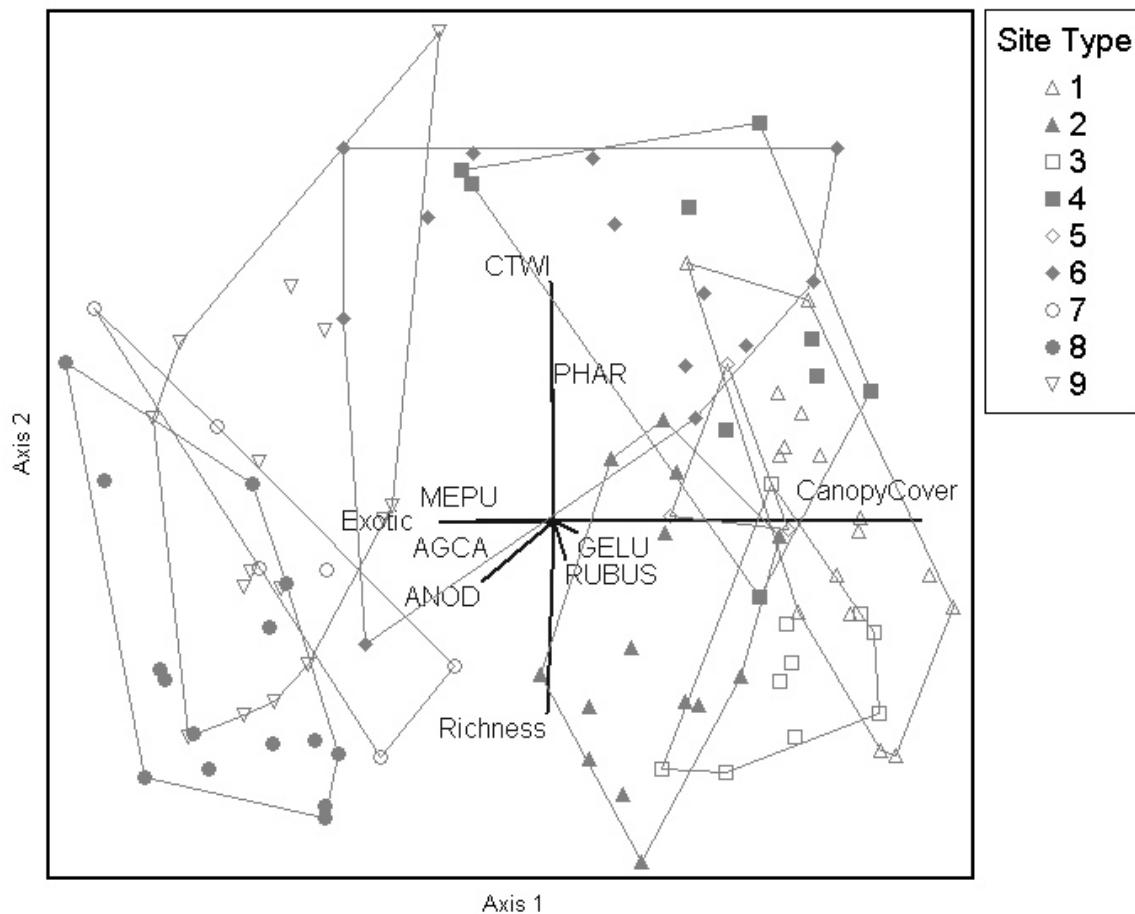
Figure 3.5 NMS ordination of plots in species space using presence absence data collected in Willamette Valley Oregon ash forests and savannas. Convex hulls show arrangement of understory community site types. Joint plot is the same as in Figure 3.4. Joint plot lines indicate correlations between ordination axes and the cover of particularly common exotic species. GELU = *Geranium lucidum*, RUBUS = combined abundance of *Rubus armeniacus* and *Rubus laciniatus*, PHAR = *Phalaris arundinacea*, MEPU = *Mentha pulegium*, AGCA = *Agrostis capillaris*, and ANOD = *Anthoxanthum odoratum*.
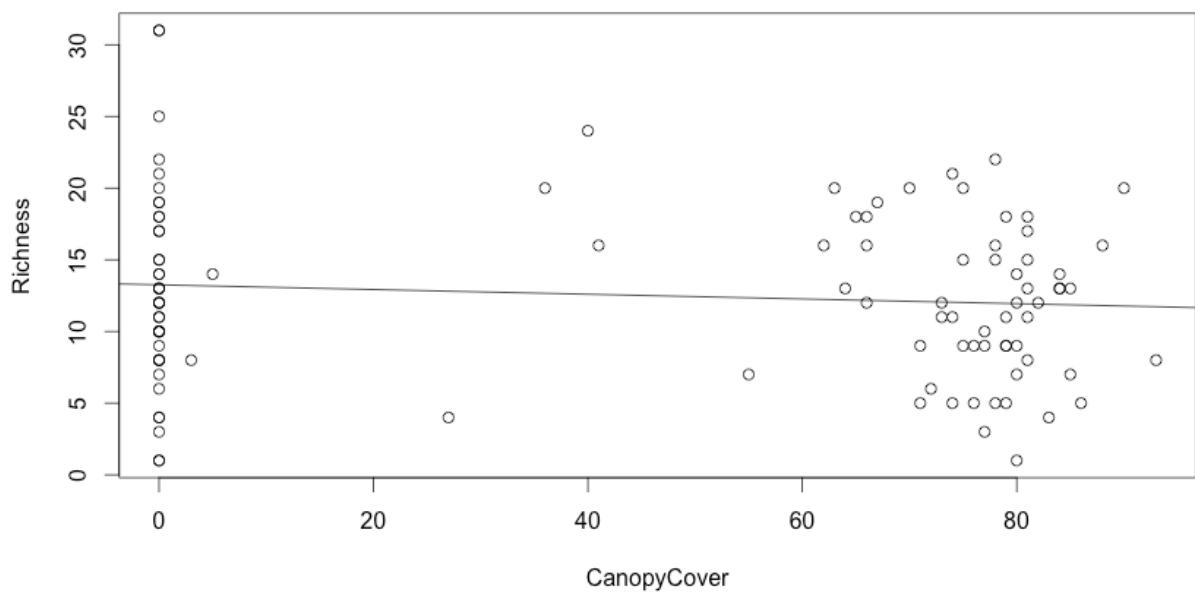
Figure 3.6 Scatter plot of species richness vs canopy cover for all 102 sampled Willamette Valley Oregon ash forest and savanna plots with regression line. Many savanna plots had no canopy cover, while most forest plots had high canopy cover. However, some plots were intermediate. Species richness was not correlated with canopy cover (r=-0.1).
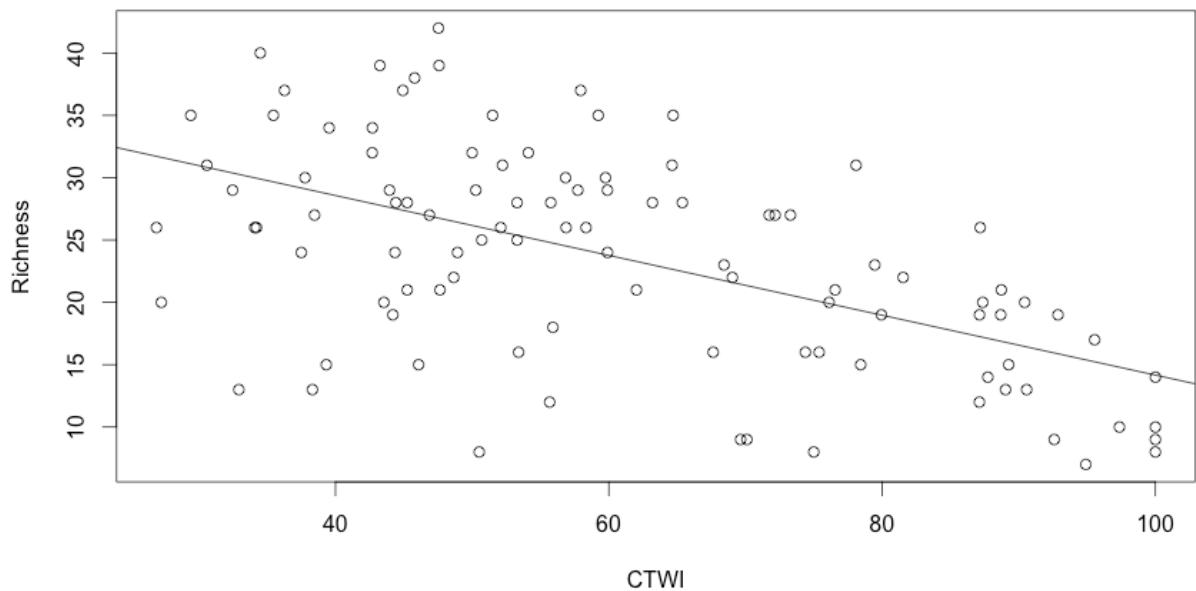
Figure 3.7 Scatter plot of species richness vs CTWI scores for all 102 sampled Willamette Valley Oregon ash forest and savanna plots with regression line (*r*=-0.57).
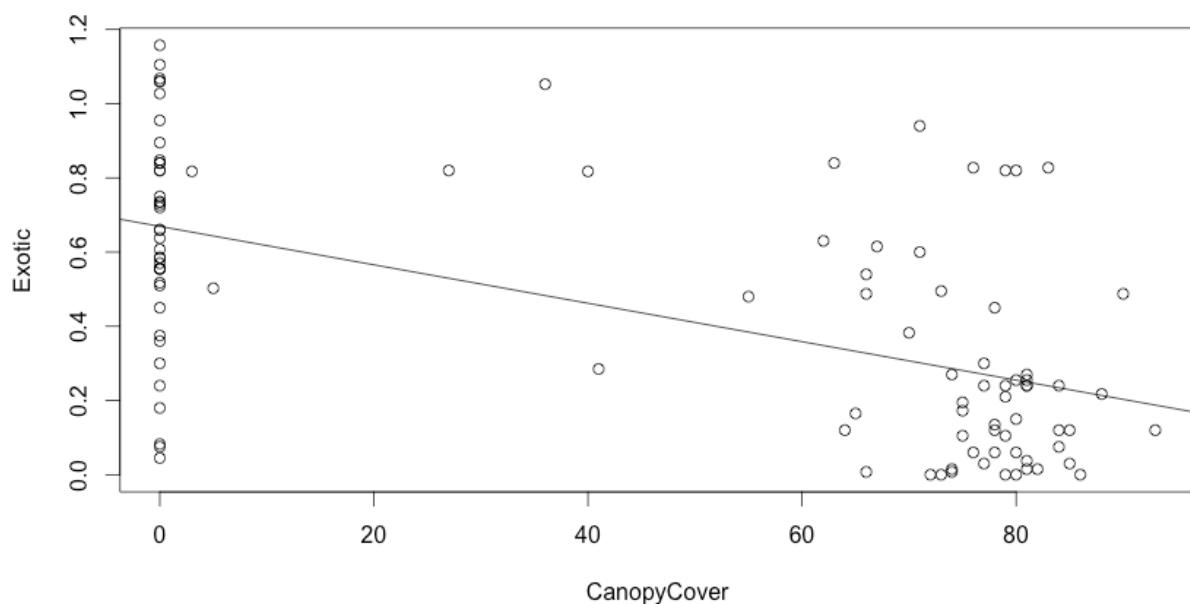
Figure 3.8 Scatter plot of exotic species cover vs canopy cover for all 102 sampled Willamette Valley Oregon ash forest and savanna plots with regression line. Exotic species cover was negatively correlated with canopy cover (*r*=-0.58), though exotic species cover was highly variable.
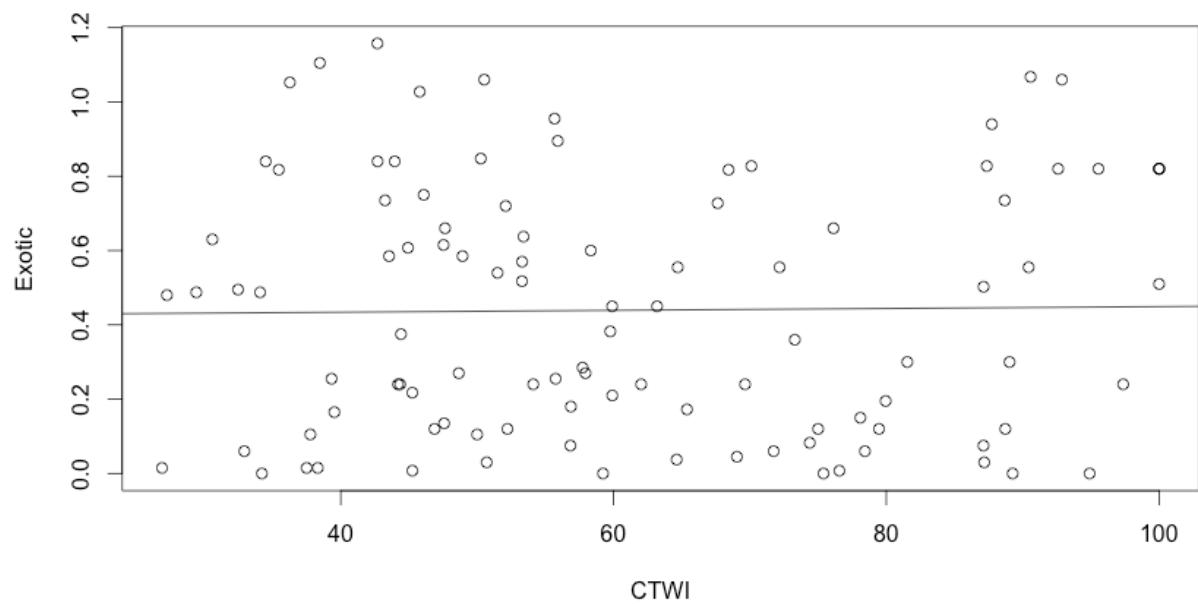
Figure 3.9 Scatter plot of exotic species cover vs CTWI scores for all 102 sampled Willamette Valley Oregon ash forest and savanna plots with regression line. Exotic species cover was not correlated with CTWI scores (r=0.01).

Figure 3.10 Wetland savanna with Oregon ash regeneration. Ash is maintained in a small, shrubby form via repeated mowing, burning, and/or herbicide use. Plant communities are dominated by native and exotic grasses as well as wildflower species. Overall, exotic species cover tends to be high on these sites. Willow Creek Natural Area, Lane County, Oregon.

Figure 3.11 Young closed canopy Oregon ash forest. Plant community composition differs greatly from adjacent open wetlands. Coyote Management Unit at Fern Ridge Wildlife Area, Lane County, Oregon.

Figure 3.12 Canopy gap in a relatively dry Oregon ash forest. Vegetation is dominated by exotic species such as *Rubus armeniacus, Schenodorus arundinaceus, Pyrus communis,* and *Leucanthemum vulgare.*

CHAPTER 4: CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE WORK

The results of this study suggest that Oregon ash is a keystone species in many Willamette Valley wetlands, and that its presence or absence largely determines a site's structural and compositional characteristics. Willamette Valley wetland plant communities are dynamic systems whose successional trajectories are largely mediated by human management. The maintenance of both open and forested wetlands on the landscape is critical for the conservation of regional biological diversity. While Oregon ash forest is likely the climax community type on most wetland sites within the Valley, most portions of the Valley with hydric soil conditions suitable for ash growth have been highly altered, degraded, or converted to urban use. The conservation of existing ash-dominated wetland forests, and their inclusion in wetland restoration planning should be considered as a regional land management priority. Additionally, threats to ash species in North America should be further recognized as a conservation issue that is relevant to western forests.

This study quantified successional dynamics among stands in varying stages of structural development, and compared ash forest community composition to that of regional wetlands where forest development has been suppressed via anthropogenic disturbance. Nearly 70% of sampled ash-dominated stands initiated more than 80 years ago, and are in advanced stages of successional and structural development. The remainder typically initiated between 30 and 80 years ago in small, isolated wetlands that have been designated for conservation. Ash was the sole overstory tree species in approximately 76% of sampled stands, with Oregon white oak being the only other dominant tree species observed. All forests exhibited moderate levels of tree or partial crown mortality, though understory ash regeneration, primarily in the form of vegetative sprouting, was also abundant. Plant communities within these forests were typically dominated by native species and exhibited high levels of between-stand (beta) diversity. Together, the sampled forests covered just a few hundred hectares. However, their associated soil series cover approximately 11% of the Willamette Valley, suggesting that the potential extent of regional ash forests has been greatly suppressed by human activity.

Sampled Oregon ash stands initiated on deep, poorly drained, and fine textured soils where anthropogenic disturbance has been abandoned or is otherwise absent. Changes in tree

community structure followed patterns previously described in other forest types. More recently initiated stands were relatively dense and were dominated by smaller trees with little size class variation. Over the course of several decades, stands became markedly less dense, average tree size increased, and size class composition became more heterogeneous. However, in contrast to other forest types in which different species characterize various successional stages, limited tree species diversity and the ability of Oregon ash to regenerate under a forest canopy made that species dominant or co-dominant regardless of stand age. Overstory diversity was low in all stands, but was dependent on local soil moisture regime. On sites with a relatively high average annual water table, Oregon ash was often the only tree in overstory canopies. More mesic sites were often co-dominated by Oregon white oak, though understory regeneration for that species was greatly lower than it was for Oregon ash. Other tree species were infrequent and were typically minor understory species.

More than any other measured environmental variable, the presence or absence of a forest canopy influenced plant community composition in sampled Willamette Valley wetlands. While Oregon ash was present at all sampled sites, in more open prairies and savannas it was largely reduced to a shrubby form by periodic mowing or burning. Where these disturbances were absent, ash forest development drastically altered local community composition. Both community composition and diversity were also associated with a soil moisture gradient; differences in composition between open and closed canopy wetlands were highly dependent on site-specific soil moisture conditions.

Sites with an open (or no) canopy had significantly higher exotic species cover, though exotic species composition was also dependent on local soil moisture conditions. On drier sites, exotic grasses such as *Agrostis capillaris* and *Schenodorus arundinacea*, as well as exotic *Rubus* and multiple exotic forb species, were particularly prevalent where canopy cover was reduced or absent. On sites with an intermediate soil moisture regime, *Mentha pelugium*, *Anthoxanthum odoratum*, and exotic *Rosa spp.* attained high cover. Exotic trees, including *Crataegus monogyna* and *Pyrus communis* were also observed invading canopy gaps and grasslands under mesic to intermediate soil moisture conditions. On the wettest sites, *Phalaris arundinacea* was common and occasionally formed near monocultures. Species richness was not correlated with exotic species cover, but was negatively correlated with Community Type Wetland Index. However, it is unclear whether this was due to the increasing influence of *Phalaris arundinacea* on wet sites,

or if inundated wetlands in the Willamette Valley are inherently prone to low levels of plant diversity.

Looming forest health threats, including the emerald ash borer (EAB), have the potential to drastically reduce or eliminate Oregon ash from regional forest canopies, which will likely have profound effects on wetland forest structure and associated plant communities. The ecological effects would likely include decreased landscape-scale biological diversity and the loss of forest habitat features. Many wetlands in the Willamette Valley have a water table that is seasonally high enough to exclude nearly all tree species. On these sites, the loss of Oregon ash would likely cause an overall decline in forested area and a shift in ecological states toward shrubland or grassland - though the development of management actions may be necessary to determine the specific state of these wetlands post-EAB invasion. On more mesic sites, Oregon white oak offers some overstory tree species redundancy that might mitigate the loss of overall forested area. However, in both cases, the potential for exotic species invasion following overstory ash mortality is high.

This research is particularly important as a baseline reference for Willamette Valley wetland restoration. Wetland restoration has become a national and regional land management priority, and the development of reference community descriptions is vital to guide future restoration plans and prescriptions. Ash-dominated forested wetlands in the Willamette Valley serve as refugia for native plant species and partially suppress the expansion of exotic species. Future restoration efforts should consider promoting the expansion of regional forested wetlands in addition to the currently prioritized wetland grasslands. Furthermore, research in the field of ash tree breeding might result in Oregon ash trees that are EAB resistant. If western ash forests are impacted by EAB, future restorationists may be able to utilize newly developed ash cultivars to reestablish previously forested sites. To help inform ash forest establishment and restoration, this study provides an initial assessment of historical ash forest locations, extent, ecological conditions, variability among associated plant communities, and how these characteristics relate to a soil moisture gradient.

While this study demonstrates the importance of Willamette Valley ash and ash/oak forests in supporting native plant diversity, and provides a description of the variation in forest structural conditions, additional research is necessary to understand how these systems interact with other biological communities, both aquatic and terrestrial. Old growth ash and ash/oak

forests produce large trees and snags that likely offer important habitat features. A quantification of these features, the vertebrate and invertebrate animal communities they support, and how they differ from upland forests and wetlands in earlier stages of structural development is needed. Willamette Valley forested wetlands also interact with aquatic systems where they boarder streams, creeks, sloughs, and small lakes/ponds. The extent to which Oregon ash trees contribute to in-stream wood recruitment, stream temperature regulation, and other hydrologic processes is unknown. Oregon ash is likely a crucial component of small stream restoration in wetlands and riparian areas currently under agricultural production, but more research is needed to quantify ash tree/stream interactions.

Finally, Oregon ash trees provide a unique aesthetic component within the Willamette Valley that could be lost with the arrival of the emerald ash borer. Valley bottom riparian corridors and wetland forests punctuate many of the Valley's pastoral landscapes, and Oregon ash is a major, if underappreciated, member of those forests. While not typically considered an economically important species in the region, Oregon ash has historically been used as a material for tool and furniture making as well as an important source of firewood (Peattie and Landacre 1991). Furthermore, Oregon ash, along with exotic species of ash, is increasingly planted as an urban "street tree" in the Pacific Northwest. These measures of cultural importance, along with the ecological characteristics explored in this study, highlight what is at stake if Oregon ash experiences mortality rates similar to those of its eastern relatives. The protection of existing ash stands, as well as future restoration efforts should the emerald ash borer invade the Willamette Valley, are important for the preservation of this piece of the region's natural and cultural heritage. Exploration of how these objectives can be accomplished should be ongoing if Oregon ash is to remain a prominent component of Willamette Valley landscapes.

LITERATURE CITED

Peattie, D. C., & Landacre, P. (1991). A natural history of western trees. Houghton Mifflin Harcourt.