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The effect of large woody debris, direct seeding, and distance from the forest edge on species composition on novel terraces following dam removal on the Elwha River, WA.

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The effect of large woody debris, direct seeding, and distance from the forest edge on species composition on novel terraces following dam removal on the Elwha River, WA.

By

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Accepted in Partial Completion
of the Requirements for the Degree
Master of Science

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Master's Thesis

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Presented to
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Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Sara Cendejas-Zarelli
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Abstract

The removal of two dams on the Elwha River, Washington, exposed over 300 hectares of reservoir sediments and created primary successional habitats that posed challenges to revegetation efforts. In order to meet Elwha restoration goals, coarse sediment deposits would require revegetation methods aimed at quickly restoring native vegetation while deterring exotic species invasions. I examined the effect of two restoration treatments—large woody debris translocations and native seed enhancements—on plant species composition on novel terraces in the former Lake Mills reservoir four years after dam removal. I sampled vegetation in seeded and unseeded treatment areas with and without large woody debris. I also examined species composition and seed dispersal mechanisms to determine whether distance limited native plant recruitment from the nearby forest edge. I used two-way analysis of variance, NMDS ordinations, and permutational multivariate analysis of variance to determine whether wood placements, seeding treatments, and distance from the forest influenced species composition on novel terraces. My results revealed that Shannon-Weiner diversity, species richness, and percent exotics increased on plots containing wood, compared with surrounding bare sediments, but plant establishment did not substantially increase on wood plots. Plots located in seeded treatment areas had higher species richness and plant abundance, with decreased exotic species recruitment. As distance from the forest edge increased, Shannon-Weiner diversity, species richness, and percent exotics on unseeded plots declined, but plant abundance did not change significantly with distance. In addition, a greater proportion of plants were wind-dispersed at greater distances, while plants dispersed by gravity and ballistic mechanisms were associated with closer distances to the forest edge. This study's results help fill a knowledge gap regarding the efficacy of using translocated large woody debris and direct seeding to restore vegetation in primary successional habitats following dam removal and helps inform best practices regarding the use of these restoration methods at future dam removal projects.

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1.0 Introduction

1.1 Successional Trajectories of the River Forest Ecosystem

Primary succession is characterized by natural disturbance events such as volcanic activity, large-scale flooding events, and retreating glaciers, which results in exposed substrates devoid of soil and biological legacies (Clements 1916; Walker and del Moral 2008). Human-induced disturbances, such as resource extraction, urbanization, and dam removal, can also create large-scale disturbances (Walker and del Moral 2008). Depending on the nature and extent of the disturbance, primary successional landscapes can be stressful environments and challenging to restore to historic vegetative conditions. These landscapes are often prone to intense solar radiation, subject to wind and water erosion, and lack structural complexity (del Moral and Bliss 1993). And, depending on the scale of the disturbance, potential sources of propagules may be distant, which can limit natural colonization (Del Moral and Wood 1993). Furthermore, substrates lack fully-functioning microbial communities, adequate soil nutrients, and organic matter, which compromise plant and water relations (Walker and del Moral 2003). In addition, climate change adds new uncertainties to historic conditions that might further complicate this slow, natural process.

Large dam removals exemplify a human-induced disturbance that presents challenges for land managers and restoration ecologists. Primary successional landscapes in de-watered reservoirs are characterized by coarse sediments and unpredictable flooding regimes, which result in low plant recruitment and the threat of exotic species invasion (Shafroth et al. 2002; Woodward et al. 2011; Chenoweth et al. 2011). This contrasts with natural river disturbances in the Pacific Northwest (PNW), where floodplain and riparian forest succession generally follow secondary successional pathways that lead to faster plant recovery (Van Pelt et al. 2006). Early plant colonization of herbaceous species quickly succeed to black cottonwood (*Populus balsamifera*), red alder (*Alnus rubra*), and willow species (*Salix*). Over time, smaller flooding events introduce nutrient-rich sediments that help support the establishment of later-arriving species, such as big-leaf maple (*Acer macrophyllum*) and western red cedar (*Thuja plicata*). However, given the abundance of coarse sediment deposits that have been impounded behind dam structures for decades, it remains unclear how successional trajectories typical of PNW riparian forests will unfold on novel terraces in recently de-watered reservoirs.

1.2 The Elwha River Dam Removal Project

The Elwha River dams inundated 3.15 km^2 of floodplain habitats and acted as barriers to anadromous fish migration for more than a century. In the years following dam construction, populations of native fish, including all five species of Pacific salmon, plummeted by 99% (Pess et al. 2008). In 1992, the U.S. Congress passed the Elwha River Ecosystem and Fisheries Restoration Act (Public Law 102-495), which mandated dam decommissioning and dam removal to restore salmon populations and the riparian habitats that support them (DOI 1995). The deconstruction of two dams on the Elwha River represents the largest dam removal and ecosystem restoration effort to date. Between 2011 and 2014, two hydroelectric dams—the Elwha dam (32 meters high) and the Glines Canyon Dam (64 meters high)—were removed to restore the Elwha River ecosystem and its' severely degraded native anadromous fisheries (DOI 1995, Figure 1). Whereas there is a growing body of scientific research related to the effects of dam removal, much of that research has centered on small dams and focused on sediment transport (Grant and Lewis 2015, O'Connor et al. 2015). However, large dams (>30 meters high) impound larger reservoirs and store more sediment than small dams, and, therefore, exert greater and more prolonged environmental impacts (Doyle et al. 2003; Foley et al. 2017).

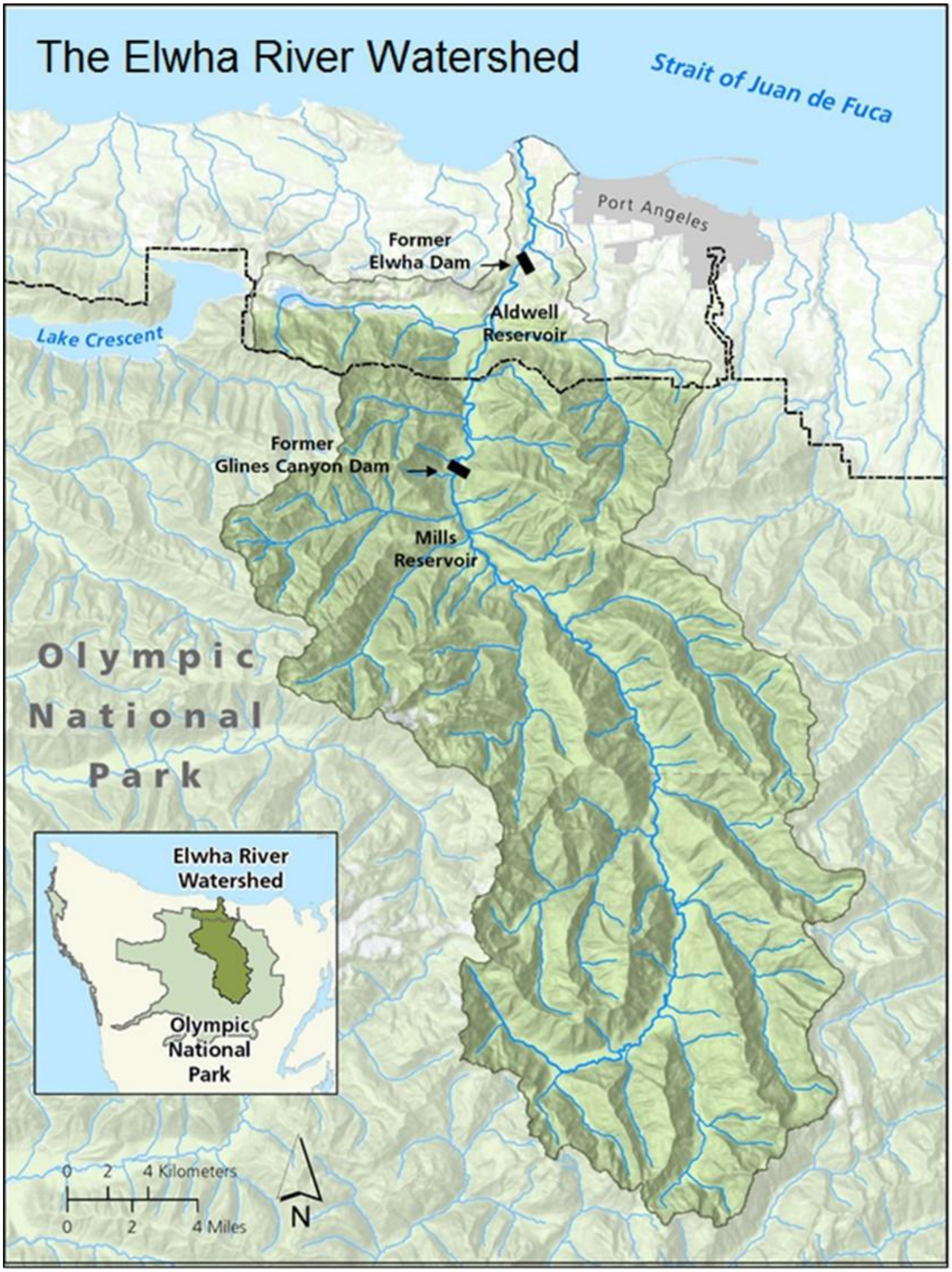

Figure 1. Study area within the former Lake Mills reservoir on the Elwha River, WA. Image credit: Olympic National Park.

1.3 Elwha Restoration

Over the Elwha dams' lifespan, an estimated 21 million m^3 of sediment accumulated within the reservoirs, with most sediment (~76%) trapped behind Glines Canyon Dam in the former Lake Mills reservoir (hereafter, Mills; Warrick et al. 2015). The Elwha River is expected to erode much of the impounded sediment over time; however, an estimated 10-40% of the total accumulated sediment will likely persist as permanent, novel landscape features within the two former lakebeds (Randle et al. 2015; Warrick et al. 2015). These permanent landscape features, the valley walls and terraces (Figure 2), comprise differing sediment types with contrasting plant communities. The valley walls are composed of fine, clay and silt-sized soils and sediments and are covered by abundant naturally regenerating vegetation via secondary succession. In contrast, the terraces model primary succession and are comprised of thick deposits of well-drained, coarse sediments that lie atop fine sediment deposits.

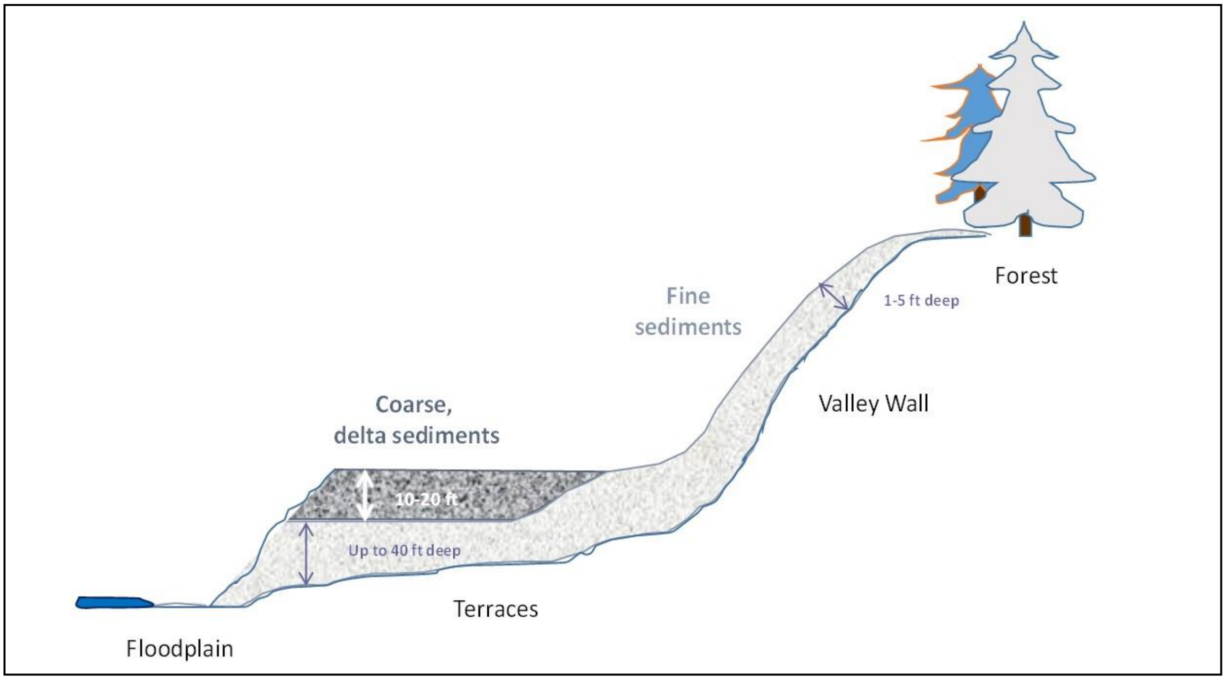

Figure 2. Schematic of landscape features in the former Lake Mills reservoir, Elwha River, WA. Image credit: J. Chenoweth, ONP.

The overarching goal of the Elwha River Restoration project was to restore historic salmon runs. Success requires removing the barriers to fish migration as well as restoring the riparian forests critical for salmon habitat within the river and tributaries of the Elwha River Valley. If left unaided, natural plant succession will be a slow process and may impede habitat recovery required for healthy salmon populations. Therefore, a key component of Elwha River recovery will be the acceleration of plant succession in sediments within the former Lake Aldwell and Lake Mills reservoirs. Three primary objectives of the revegetation program are to (1) stabilize floodplain sediments to reduce sediment erosion and improve water quality, (2) encourage the rapid development of native forests for shade and large wood recruitment, and (3) minimize the threat of invasive exotic species (Chenoweth et al. 2011). Beginning in 2011, restoration biologists with Olympic National Park (ONP) and the Lower Elwha Klallam Tribe (LEKT) partnered to meet those goals.

Vegetation restoration on novel terraces along the Elwha River will be challenging. As is common in primary successional habitats, there are few biological features to support plant growth, including a lack of seeds and vegetative propagules, micro and macronutrients, beneficial soil microbes, and organic matter (Chenoweth et al. 2011; Cortese and Bunn 2017). Coarse terrace sediments are also extremely well-drained and are often perched far above the water table, resulting in water stress (Chenoweth 2013). Moreover, the entire Mills basin frequently experiences strong, anabatic winds and intense sun exposure, contributing to drought stress as sediment temperatures and evaporation rates increase (Chenoweth and McHenry 2015). Another potential impediment to natural forest succession is whether seed dispersal from the forest edge limits plant recruitment along the Elwha. Together, these combined effects are suspected of limiting natural plant recruitment and recovery on novel terraces in Mills (Chenoweth 2013).

Another substantial threat posed to newly formed habitats is the invasion of exotic species, which can influence successional pathways by outcompeting native species for light and water resources and can significantly alter the chemical and biological conditions of soils (Jean-Baptiste et al. 2018; Holl 2020). Therefore, restoring the former reservoir to historic forested habitats will require active methods that accelerate natural succession by promoting vegetation trajectories that lead to native plant communities (Shafroth et al. 2002; Chenoweth et al. 2011).

1.4 Restoration Techniques Employed in the Elwha Lakebeds

To combat exotic species invasion and accelerate native plant succession, ONP restoration crews sowed 2,525 kilograms of native seeds, covering 0.7 km^2 of floodplain and upland habitats within the former Lake Aldwell and Lake Mills reservoirs (Chenoweth pers. comm.). Seed mixtures contained a combination of ten locally harvested and produced grass and forb species (Chenoweth et al. 2020). These species included common yarrow (*Achillea millifolium*), spiked bentgrass (*Agrostis exarata*), Suksdorf’s sagewort (*Artemisia suksdorfii*), Pacific brome (*Bromus pacificus*), sedge mixtures (*Carex pachystachya & Carex deweyana*), slender hairgrass (*Deschampsia elongata*), blue wild-rye (*Elymus glaucus*), Oregon sunshine (*Eriophyllum lanatum*), and riverbank lupine (*Lupinus rivularis*; Appendix Table A). Direct seeding is a standard method for revegetating habitats following disturbance, and often results in increased vegetative cover, increased species richness (Barr et al. 2017), and results in plant communities that are more resilient to stress (Witko 2006).

Large woody debris (LWD) was also utilized as a restoration tool within Mills to create safe sites for vegetation, improve growing conditions for plants, increase landscape complexity, and slow the erosion of floodplain sediments (Chenoweth and McHenry 2015). Large woody debris serves many important ecological functions in riparian and forest ecosystems (Harmon et al. 1986; Schreiner et al. 1996) and has been shown to improve seedling survival rates in restoration projects (Heinemann and Kitzberger 2006, Campilong 2014). Some of the benefits of LWD for improving plant survival are an increase in sediment moisture levels and a decrease in wind velocities (Colton 2018). Arrays of LWD placed on perched terraces may act as nucleation sites for regenerating plants by attracting seed dispersers and creating safe sites for seedlings (Schreiner et al. 1996). Also, when placed in overlapping arrays, LWD may protect vegetation by acting as a barrier against browsing deer and elk, which can alter plant growth forms and survival rates (Harmon et al. 1986; Chenoweth and McHenry 2015).

1.5 Study Objectives

Collectively, revegetation methods such as direct seeding and the incorporation of LWD may contribute to natural succession by increasing native plant establishment while deterring exotic species invasions. However, when large-scale dam removal exposes hundreds of hectares of coarse-textured sediments, the efficacy of both direct seeding and translocated LWD to promote plant establishment within these newly formed habitats, is poorly understood. This study’s objective is to examine the effect of these restoration treatments four years after dam removal within the former Lake Mills reservoir. This study also seeks to understand the influence of seedling recruitment from intact vegetation at the forest edge.

My research questions and hypotheses are as follows: 1) is plant establishment greater at sites with LWD? Logs act as an effective seed trap for wind-blown propagules and create favorable micro-sites leading to increased plant survival rates; therefore, I hypothesize that plots containing LWD will possess higher plant abundance, Shannon-Weiner diversity, and species richness than sites without wood. 2) Is direct seeding an effective method for revegetating novel terraces, and does seeding influence native pioneer herbaceous and woody species recruitment? There are inherently more seeds at seeded sites; therefore, I hypothesize that seeded areas will have greater native plant abundance, higher species richness, and fewer exotic species. 3) Does distance from the forest edge and mechanisms of seed dispersal limit natural plant recruitment and herbaceous and woody species composition following dam removal and reservoir drawdown? Mature vegetation at the forest edge provides a seed source for early successional habitats. I hypothesize that plant abundance will decline with increasing distance from the forest edge and species composition will also differ with distance. The results of this study will help fill a knowledge gap regarding the efficacy of using LWD and direct seeding to restore vegetation in primary successional habitats after dam removal, and help inform best practices regarding the use of these restoration methods at future dam removal projects.

2.0 Methods

2.1 Study System

The Elwha River is located west of the city of Port Angeles on the Olympic Peninsula in Washington State. Roughly 87% of the Elwha watershed (830 km^2) lies protected within the boundary of Olympic National Park. The Elwha River flows north for over 80 kilometers from its headwaters in the Olympic Mountains to the Strait of Juan de Fuca. The region has an oceanic climate with relatively cool, wet winters and dry summers.

The Elwha dam, located at river mile 4.9, impounded the former Lake Aldwell (108 ha). The Glines Canyon dam, located at river mile 13.4, impounded the former Lake Mills (168 ha). The Mills basin covers an area of approximately 2 km^2, extending 3.4 km in length and 570 meters in width. I conducted my research in Mills for several reasons, including its large size and great restoration need, abundant deposits of coarse terrace sediments, and an abundance of translocated and naturally deposited LWD on terrace surfaces.

My sampling area was primarily located on novel terraces along the west side of the Mills basin (Figure 3). Most of my sampling occurred on a large perched terrace composed of coarse sediment deposits. The adjacent valley walls to the west of the terraces are almost completely covered in vegetation consisting of dense stands of black cottonwood (*Populus balsamifera*), red alder (*Alnus rubra*), and willow (*Salix* spp.), with an understory of common rush (*Juncus effusus*). To the west of the valley walls lay adjacent forests with vegetation that includes a mixture of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*), with an understory of salal (*Gaultheria shallon)*, Oregon grape (*Berberis nervosa*), salmonberry (*Rubus spectabilis*), and swordfern (*Polystichum minutum*).

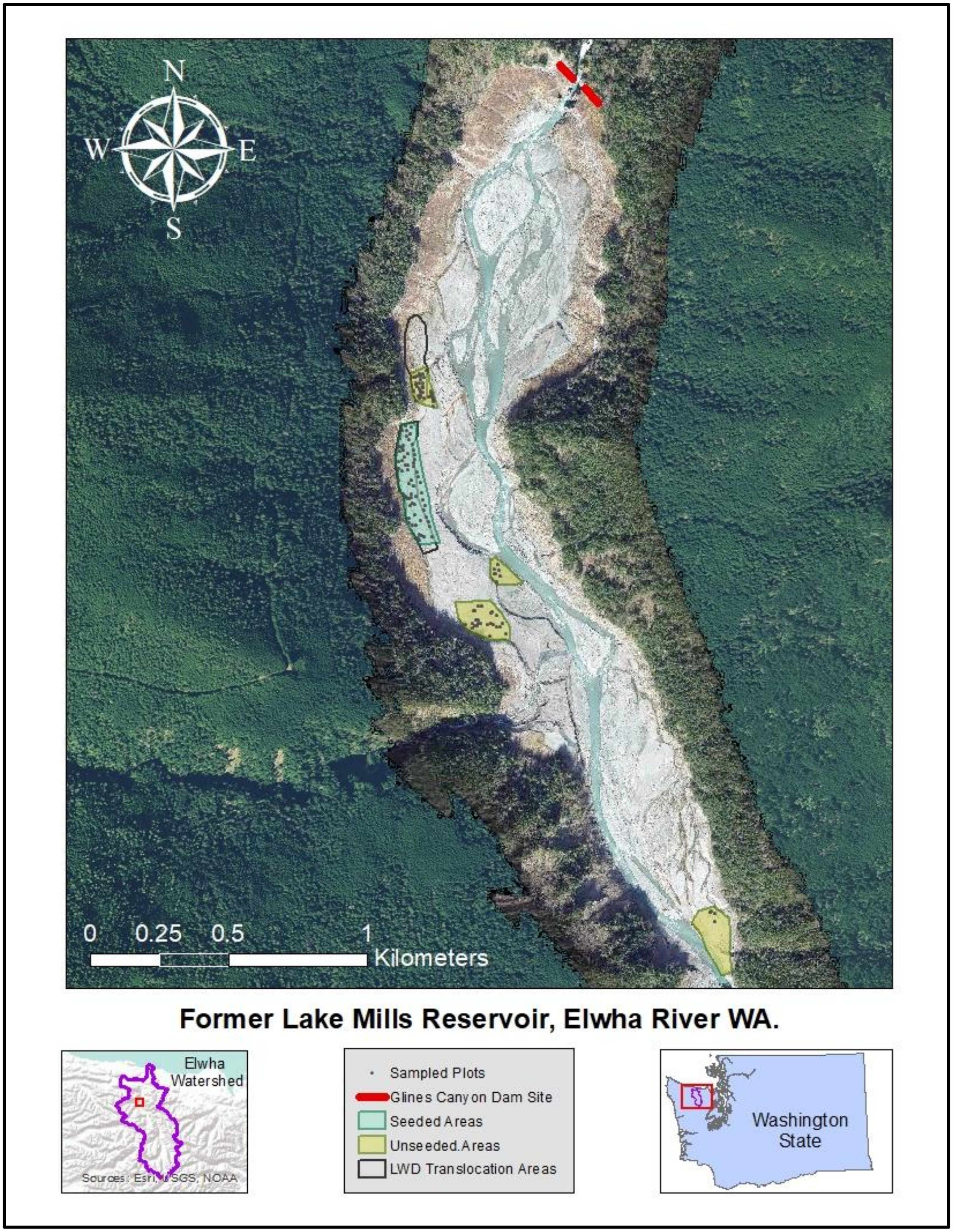

Figure 3. Sampling locations within the former Lake Mills reservoir on the Elwha River, WA. Plots were located in seeded and unseeded areas with naturally deposited and translocated LWD.

2.2 Restoration Treatments

ONP restoration biologists applied several revegetation and restoration treatments to coarse sediments on the west side of the Mills basin where terraces were expected to remain as permanent landscape features. Some of these restoration treatments included direct seeding of native grasses and forbs, translocated LWD, and untreated control sites (Chenoweth 2015). From 2013 to 2015, restoration biologists applied 2,333.1 kilograms of native seeds to coarse sediments in Mills. In order to guide where seeds fell in windy habitats, crews applied seeds by hand (Chenoweth et al. 2020). A list of seeded species applied by ONP is located in Appendix Table A.

In 2012 and 2014, ONP and LEKT staff translocated 835 logs to novel terraces along the west side of the Mills basin (Appendix Table B; Chenoweth and McHenry 2015). Translocated LWD consisted of log boles and logs with attached root-wads. Restoration crews arranged logs in single or parallel configurations and in overlapping arrays, or "clusters" (Chenoweth 2015). In 2013, roughly two-thirds of the 2012 LWD translocation area was augmented with native seeds; the remaining LWD translocation area was left unseeded. No active planting occurred in the 2012 translocation area. I established the majority of my plots within and adjacent to the 2012 LWD translocation area in seeded and unseeded areas. The remaining plots were located in seeded and unseeded areas with naturally occurring LWD (Figure 3).

2.3 Variable Selection

I measured the following response variables: Shannon-Weiner diversity, species richness, plant abundance, and percent exotic species. My treatment groups included: (1) LWD plot type,

(2) seeding treatment, and (3) control plots (Table 1). I also examined the effect of distance from the forest edge on species composition and seed dispersal mechanisms.

Table 1. Description of variables and treatment groups.

Variable	**Description**
LWD Plot Type	(1) Non-wood—plot contains no LWD. (2) Cluster—2 or more overlapping logs. (3) Simple—1 single, or 2-3 parallel logs. (4) Root-wad—root structure at the end of a log.
Seeding Treatment	(1) Seeded area. (2) Unseeded area.
Control plots	Non-wood plots in unseeded areas.
Distance from Forest	The distance (meters) of each plot from the nearest forest edge.

2.4 Sampling Design

I determined plot location using a stratified random sampling design, with strata defined by LWD plot type. I used aerial imagery from Giga-pan (Ritchie 2016) to identify logs and adjacent non-wood areas using ArcGIS (Figure 3; Version 10.3; Environmental Systems Research Institute, Redlands, CA). Using Universal Transverse Mercator (UTM) coordinates determined in ArcGIS, I mapped plots and navigated to them in the field using a hand-held global positioning system (GPS) unit. I then determined whether each plot met sampling criteria, which included: (1) log diameter had to be ≥ 50 centimeters—consistent with LWD sampling in previous Elwha studies; (2) logs had to have ≥ 3 meters of their total length in contact with the ground—sampling along logs only occurred where logs were in full contact with the ground to ensure trapping effects of LWD; (3) root-wads had to be in reasonable contact with the ground to ensure trapping effects of LWD; and (4) non-wood plots had to be ≥ 10 meters from LWD to minimize any effects from logs. Previous studies in Mills indicated that plant survival increased within one meter of LWD (Calimpong 2014, Colton 2018); therefore, I used a 1 m^2 quadrat to sample vegetation.

2.5 Plot Establishment and Vegetation Sampling

Sampling strategy varied by LWD plot type. Wood plots included LWD cluster, LWD simple, and LWD root-wad plots (Table 1). LWD clusters consisted of aggregations of two to five overlapping logs (Figure 4, inset A). LWD simple plots consisted of one single or two to three logs arranged parallel to each other (Figure 4, inset B). LWD root-wad plots consisted of a log bole with an attached root-wad (Figure 4, inset C). For LWD cluster and simple plots, I randomly selected and sampled three 1 m^2 quadrats from the total log length available on both sides of each log for a total of six quadrats per plot (Figure 5, inset A).

At LWD cluster plots, I randomly selected and sampled just one log in the cluster of logs in the same fashion. At LWD simple plots that contained two or more parallel logs, sampling occurred along the two outside logs within the log group. On LWD root-wad plots, plant sampling occurred within a 1 m^2 quadrat at the end and on both sides of the root-wad for a total of three quadrat samples per plot (Figure 5, inset B).

Figure 4. Examples of LWD cluster (A), simple (B), and root-wad (C) plots.

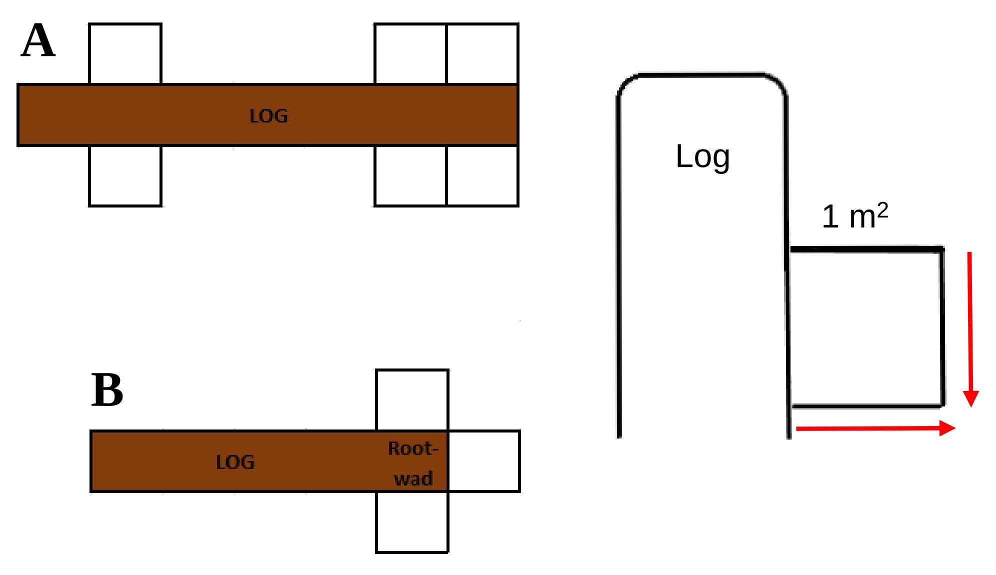

Figure 5. Examples of quadrat samples around logs (A) and logs with attached root-wads (B).

I established non-wood plots within seeded and unseeded treatment areas by first selecting a random starting location at the northern end of each of treatment area in ArcGIS. I then navigated to that location in the field using a GPS unit. I randomly selected a compass bearing (out of 360°) to determine the orientation of each plot's transect line. I then used a three-meter long tape measure to represent the transect line and laid it on the ground at the selected orientation (Figure 6). Plant sampling occurred within three 1 m^2 quadrats along both sides of the transect line for a total of six quadrats per non-wood plot (Figure 7). I used a random number generator to determine the distance and direction of travel between adjacent non-wood plots.

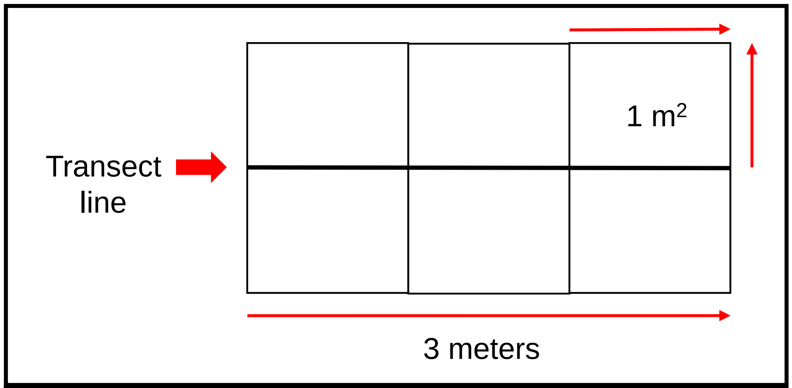

Figure 6. Example of a non-wood plot with six quadrats located along a transect line.

Figure 7. Example of a non-wood plot with a three-meter tape measure representing the transect line along which six quadrats were placed and plant sampling occurred.

2.6 Distance from the Forest Edge

I used measuring tools in ArcGIS to determine the distance, in meters, of each plot from the nearest forest edge. All plots within seeded and unseeded areas ranged between 28 and 248 meters from intact vegetation at the forest edge (Appendix Table C).

2.7 Field Sampling

Plant sampling occurred from June-July, 2016, during which time I sampled a total of 143 plots, consisting of 34 clusters, 35 simple, 35 root-wad, and 39 non-wood plots on novel terraces in Mills. Forty-six percent of all plots were located in seeded treatment areas, and 54% were located in unseeded areas. I identified plants to species and classified them based on primary seed-dispersal mechanism and life form (Burns and Honkala 1990, Pojar and McKinnon 1994, USDA) using a field guide (Pojar and Mackinnon 1994) and assistance from ONP's restoration botanist (J. Chenoweth pers. comm.). I identified four primary dispersal mechanisms from field guides and primary literature. These included seeds with wind, ballistic, gravity, and animal dispersal mechanisms. Wind-dispersed plant species consisted of those with physical structures adapted for wind dispersal (e.g., winged seeds, pappus, spores, etc.). Gravity dispersed species are those lacking known seed dispersers or sophisticated dispersal mechanisms. Species exhibiting ballistic dispersal have seed pods that forcibly expel seeds when the seed pod dries. And, seeds dispersed by animals are those with seeds contained in fleshy fruits which are directly consumed by animals, or when seeds attached externally to animal feathers, fur, etc. Out of all species with known dispersal mechanisms, wind-dispersed species were most common (N=33 species), with fewer species dispersed by gravity (N=18 species), by animals (N=six species), and by ballistic mechanisms (N=three species).

2.8 Data Analysis

I conducted all statistical analyses in R (R Core Team; Version 3.2.4 for Windows). I assessed plant sampling efficacy using the *specpool* function to determine whether model estimates of species richness across my entire study area were similar to observed plant data. I calculated mean Shannon-Weiner (H') diversity and species richness for wood plot types and seeding treatments using the *Shannon-Weiner diversity result* function in the Biodiversity R package.

To confirm whether my data met assumptions of normality and homogeneity of variance, I used a Shapiro-Wilks and Levene's test. These tests revealed that Shannon-Weiner diversity, species richness, plant abundance, and percent exotics had non-normal distributions and violated the assumption of equal variance. As a result, I performed a square-root transformation on Shannon-Weiner diversity and log-transformed species diversity, plant abundance, and percent exotics to meet the assumptions of an Analysis of Variance (ANOVA). I used a two-way ANOVA to compare Shannon-Weiner diversity, species richness, plant abundance, and percent exotics across wood plot types, seeding treatments (seeded vs. unseeded), and their interaction. I used a Tukey's HSD post-hoc test to determine which levels of categorical variables differed significantly with respect to Shannon-Weiner diversity, species richness, plant abundance, and percent exotics. A variety of biotic and abiotic factors, including plot location, sediment composition, and water availability, contributed to highly variable vegetation within each sampling area and at each plot. However, to avoid pseudo-replication and ensure a balanced sampling design, I nested quadrats within plots and took the mean of plant abundance at each plot (Crawley 2007).

To examine the effect of dispersal distance on natural plant recruitment, I examined unseeded plots only. All variables failed to meet the assumptions of normality and equal variances; therefore, I used non-metric Kendall's tau correlations to determine whether Shannon-Weiner diversity, species richness, plant abundance, and percent exotics were significantly correlated with distance from the forest edge.

To determine whether species composition differed significantly due to my variables, I conducted a permutational multivariate analysis of variance (PERMANOVA; 9,999 permutations; Anderson 2001) using the function *Adonis*, and also preformed post-hoc comparisons using *pairwise.adonis*. I used non-metric multi-dimensional scaling (NMDS) ordinations to illustrate patterns in species composition on terrace sediments. I performed NMDS ordinations for wood plot type and seeding treatment on a data matrix consisting of species with known seed dispersal mechanisms and species that occurred in 5% or more plots (N=28 species, 143 plots). I removed all other species from community analyses. The NMDS ordination for distance from forest consisted of a data matrix of 52 species and 77 plots, with seeded plots removed from community analyses. I converted all datasets into distance matrices using Bray-Curtis dissimilarity distances, and obtained NMDS solutions using 100 permutations and k=2 dimensions. Stress values provide a measure of support for ordinations. Values <0.05 provide an excellent representation, values <0.1 indicate good ordination, values < 0.2 are potentially useful, and values >0.3 indicate poor fit (Clarke 1993). Stress values obtained for both of my ordinations indicated a potentially useful picture (≈0.16). I conducted all NMDS ordinations using the *metaMDS* function in the Vegan package (Oksanen et al. 2019).

To identify indicator species of LWD plot types and seeding treatments, I performed indicator species analysis using multi-level pattern analysis (De Cáceres et al. 2010), which determines indicator species by assessing the relative abundance and frequency of species within each group. Indicator species analysis is useful for identifying species that distinguish different wood and seeding treatments. Indicator species analysis was conducted using the *multipatt* function in the *indicspecies* package using 9999 permutations and a significance level of $\alpha=0.05$.

To identify where statistically high (hot) and low (cold) values of plant abundance clustered spatially, I conducted spatial “hot-spot” analysis in ArcGIS. Hot-spot analysis calculates the Getis-Ord Gi* statistic, which produces a Z-score and P-value. A high Z-score combined with a small P-value indicates strong spatial clustering. Hot-spot analysis references neighboring plots when determining clusters of high or low plant abundance. That is, a significant hot-spot will have high plant abundance and will be surrounded by other plots with high abundance. The analytical output created in ArcMap bins significant hot and cold spots into three high and three low categories, at the 90%, 95%, and 99% confidence level, and a zero bin, which indicates a lack of significant clustering (ESRI). Before performing hot-spot analysis, I tested spatial autocorrelation in plant abundance on wood and non-wood plots using Global Moran’s I in ArcGIS and found a lack of autocorrelation on LWD plots (Moran’s I=0.060, Z=1.081, P=0.280) and non-wood plots (Moran’s I=0.021, Z=0.7578, P=0.449). Hot-spot analysis was conducted using inverse distance sampling and a Euclidean distance band set to 40.004 meters. To reduce critical p-values to account for spatial dependence and multiple testing, I applied no standardization and a false discovery rate.

3.0 Results

3.1 Vegetation

During this study, I identified 49,345 individual plants, comprising 74 different species, on terrace sediments in Mills. I identified 58 of the 74 to either the species or genus level; and identified the remainder to family or life-form (Table 2). I confirmed sampling efficacy using Bootstrap and first- order Jackknife species richness estimators. Both methods indicated that the number of species present in the study area was likely greater than 74, with Bootstrap estimating 84 +/- 4.0 species and Jackknife estimating 98 +/- 7.0 species.

Herbaceous species comprised the majority of individual plants identified. Treatments notwithstanding, the most abundant plant species were the native annual, small-flowered willow-herb (*Epilobium minutum*; 35%), the native seeded grass, blue wild-rye (*Elymus glaucus*; 23%), and the seeded biennial, riverbank lupine (*Lupinus rivularis*; 15.4%; Table 2). Sampling also included a total of 490 woody plant counts comprising 14 different species. Regardless of treatment, the two most abundant woody species were black cottonwood (*Populus balsamifera*) and Douglas fir (*Pseudotsuga menziesii*; Table 2). Two exotic hair grass species (*Aira praecox, Aira caryophyllea*) were present on 92% of all sampled plots. Due to their small size and great abundance, they were challenging to count accurately, so they were assessed as either present or absent and were not included in analyses.

I identified seven seeded species applied by ONP restoration crews during vegetation sampling (Table 2). The two most abundant seeded species were blue wild-rye and riverbank lupine. Seeded species comprised 73% and 27% of total plant abundance in seeded and unseeded treatment areas, respectively, and constituted 49% of total plant abundance.

Table 2. List of species identified in terrace sediments following dam removal on the Elwha River, WA. 2015. Primary seed dispersal mechanism is listed for each species. Percent abundance is listed for each plant group and represents the abundance of each species out of all (49,345) plants sampled. * Indicates seeded species.

Botanical name	**Common name**	**Origin**	**Dispersal mechanism**	**% Abundance**
Ferns and allies			**% Total =**	**2.99**
Cryptogramma crispa	Parsley fern	Native	Wind	0.01
Equisetum arvense	Common horsetail	Native	Wind	2.98
	Unknown Ferns			0.00
Forbs			**% Total =**	**66.99**
**Achillea millefolium*	Common yarrow	Native	Wind	1.89
Agoseris spp.	*Agoseris* spp.		Wind	0.16
**Anaphalis margaritacea*	Pearly everlasting	Native	Wind	0.16
Cardamine pensylvanica	Few-seeded bittercress	Native	Ballistic	0.01
**Chamerion angustifolium*	Fireweed	Native	Wind	0.16
Cirsium arvense	Canada thistle	Exotic	Wind	0.10
Cirsium spp.	*Cirsium* spp.		Wind	0.20
Claytonia sibirica	Siberian spring-beauty	Native	Gravity	0.00
Collomia heterophylla	Vari-leaved collomia	Native	Ballistic	0.68
Crepis capillaris	Smooth hawksbeard	Exotic	Wind	0.02
Epilobium ciliatum	Purple-leaved willow-herb	Native	Wind	0.70
Epilobium minutum	Small flowered willow-herb	Native	Wind	35.17
**Eriophyllum lanatum*	Oregon sunshine	Native	Wind	4.36
Galium aparine	Cleavers	Native	Animal	0.00
Geranium spp.	*Geranium* spp.			0.01
Gnaphalium palustra	Lowland cudweed	Native	Wind	0.49
Hypochaeris glabra	Smooth cat's ear	Exotic	Wind	0.32
Hypochaeris radicata	Hairy cat's ear	Exotic	Wind	2.39
**Lupinus rivularis*	Riverbank lupine	Native	Ballistic	15.38
Madia spp.	Tarweed spp.		Wind	0.04
Mimulus guttatus	Yellow monkey flower	Native	Gravity	0.01
Mycelius muralis	Wall lettuce	Exotic	Wind	0.21
Petasites palmatus	Palmate coltsfoot	Native	Wind	0.04
Rumex acetosella	Sheep sorrel	Exotic	Gravity	1.73
Rumex occidentalis	Western dock	Native	Gravity	0.01
Sedum spp.	*Sedum* spp.			0.01
Senecio sylvaticus	Wood groundsel	Exotic	Wind	2.40

Table 2. (Continued)

Botanical name	**Common name**	**Origin**	**Dispersal mechanism**	**% Abundance**
Forbs				
Solidago canadensis	Canada goldenrod	Native	Wind	0.02
Spergularia rubra	Red sandspurry	Exotic	Gravity	0.07
Stachys cooleyae	Cooley's hedge nettle	Native	Gravity	0.01
Stellaria crispa	Crisp sandwort	Native	Gravity	0.03
Tanacetum spp.	Tansy spp.			0.00
Trifolium repens	White clover	Exotic	Gravity	0.03
Veronica americana	American brooklime	Native	Gravity	0.05
	Unknown Forbs			0.12
Graminoids			**% Total =**	**29.02**
Agrostis spp.	*Agrostis* spp.			0.01
Carex spp.	Sedge spp.			0.10
Dactylis glomerata	Orchard grass	Exotic	Gravity	0.07
**Deschampsia elongata*	Tufted hair grass	Native	Gravity	3.90
**Elymus glaucus*	Blue wild-rye	Native	Gravity	23.26
Holcus lanatus	Common velvetgrass	Exotic	Gravity	1.44
Juncus balticus	Baltic rush	Native	Gravity	0.01
Juncus effusus	Common rush	Native	Gravity	0.00
Juncus spp.	Rush spp.			0.00
	Unknown Grasses			0.22
Woody shrubs and trees			**% Total =**	**0.99**
Abies grandis	Grand fir	Native	Wind	0.00
Acer spp.	Maple spp.	Native	Wind	0.00
Alnus rubra	Red alder	Native	Wind	0.03
Alnus sinuata	Slide alder	Native	Wind	0.00
Holodiscus discolor	Oceanspray	Native	Wind	0.00
Ribes sanguineum	Red flowered currant	Native	Animal	0.00
Rubus leucodermis	Blackcap raspberry	Native	Animal	0.00
Rubus parviflorus	Thimbleberry	Native	Animal	0.00
Rubus spp.	*Rubus* spp.		Animal	0.03
Rubus ursinus	Trailing blackberry	Native	Animal	0.01
Populus balsamifera	Black cottonwood	Native	Wind	0.61
Pseudotsuga menziesii	Douglas Fir	Native	Wind	0.19
Salix spp	*Salix* spp.	Native	Wind	0.10
Tseuga heterophylla	Western hemlock	Native	Wind	0.00

3.2 Comparison of Restoration Treatments

I compared Shannon-Weiner diversity, species richness, plant abundance, and percent exotics across large wood plots, seeding treatments (seeded vs. unseeded), and their interaction (Table 3).

Table 3. Comparison of Shannon-Weiner diversity, species richness, plant abundance (number of stems), and percent exotics across wood plot types and seeding treatments. Raw values represent means and standard errors. Means with common letters do not differ significantly ($\alpha = 0.05$), determined by Tukey's HSD. Due to the interaction between wood plot types and seeded treatments, related to species richness, a post-hoc test was not applied.

Variable	**Shannon-Weiner diversity**	**Species Richness**	**Abundance**	**% Exotics**
Wood Plot Type				
Cluster	1.41^{a} +/- 0.07	11.71 +/- 0.67	63.80^{a} +/-8.97	14.04^{a} +/- 3.05
Non-wood	0.89^{b} +/- 0.05	6.61 +/- 0.40	62.89^{a} +/- 9.93	4.48^{b} +/- 1.09
Root-wad	1.47^{b} +/- 0.05	9.66 +/- 0.45	56.76^{a} +/-6.94	16.07^{a} +/- 2.99
Simple	1.43^{b} +/- 0.06	11.89 +/- 0.50	71.19^{a} +/- 9.40	13.20^{a} +/- 2.42
Seeding Treatment				
Seeded	1.29^{a} +/- 0.05	2.31 +/- 0.04	4.12^{a} +/- 0.10	4.80^{a} +/- 0.73
Unseeded	1.28^{a} +/- 0.05	2.13 +/- 0.05	3.55^{b} +/- 0.11	17.66^{b} +/- 2.05

Shannon-Weiner diversity varied significantly by wood plot type, with non-wood plots having significantly lower Shannon-Weiner diversity (two-way ANOVA, $F_{(3,1)}$=24.193, P<0.001), but did not vary by seeding treatment (two-way ANOVA, $F_{(1,138)}$=0.128, P=0.721; Figure 8), with no interaction.

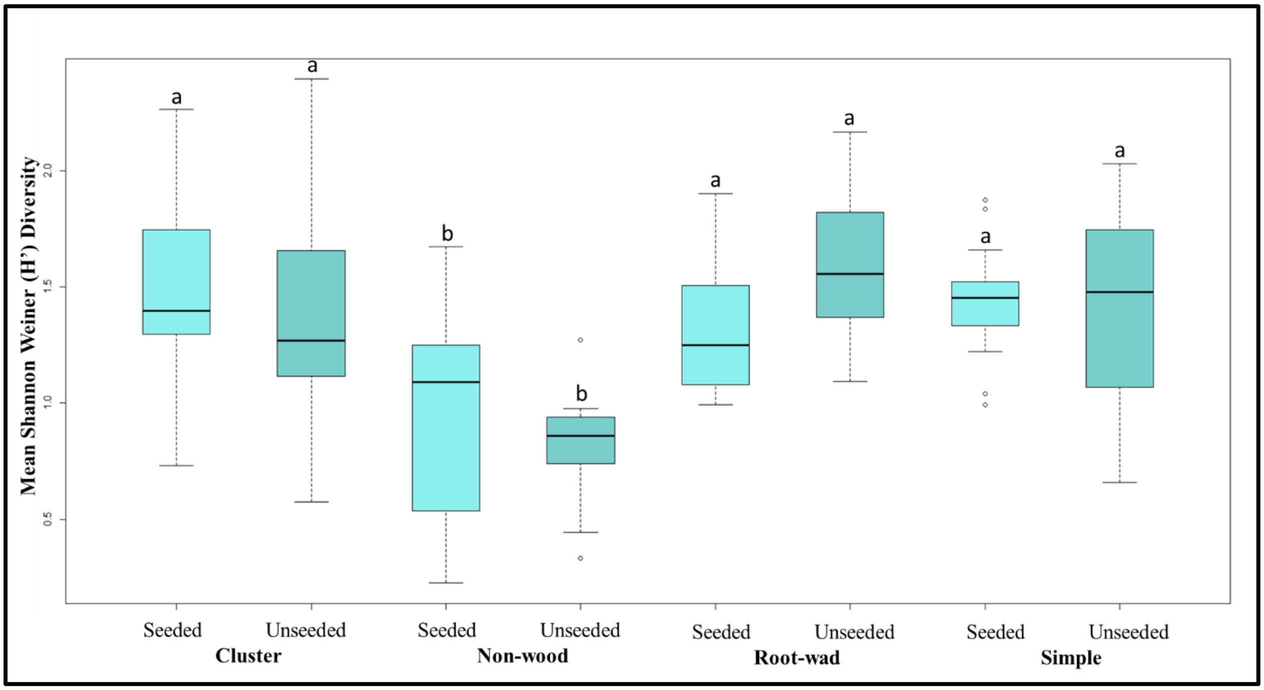

Figure 8. Boxplots illustrating the combined effects of wood plot type and seeding treatment on mean Shannon-Weiner diversity in the former Lake Mills reservoir following dam removal on the Elwha River, WA. All plots containing wood had significantly higher Shannon-Weiner diversity than non-wood plots in both seeded and unseeded treatment areas. Boxplots represent median Shannon-Weiner diversity with 95% CI. Medians with common letters do not differ significantly ($\alpha = 0.05$), determined by Tukey's HSD. N=143.

Species richness varied by wood plot type, with highest richness found on cluster and simple plots ($F_{(3,1)}$=36.910, P<0.001; Table 3). Species richness also varied significantly by seeding treatment, with lower species richness on unseeded plots (two-way ANOVA, $F_{(1,3)}$=14.455, P<0.001). Finally, the interaction between wood plot type and seeding treatment was also significant ($F_{(3,135)}$=3.877, P=0.011). An interaction plot revealed that this interaction was driven by root-wad and simple plots (Appendix Table D). Of all the wood treatments, non-wood plots were the only plot type showing an increase in species richness in response to seeding (Figure 9).

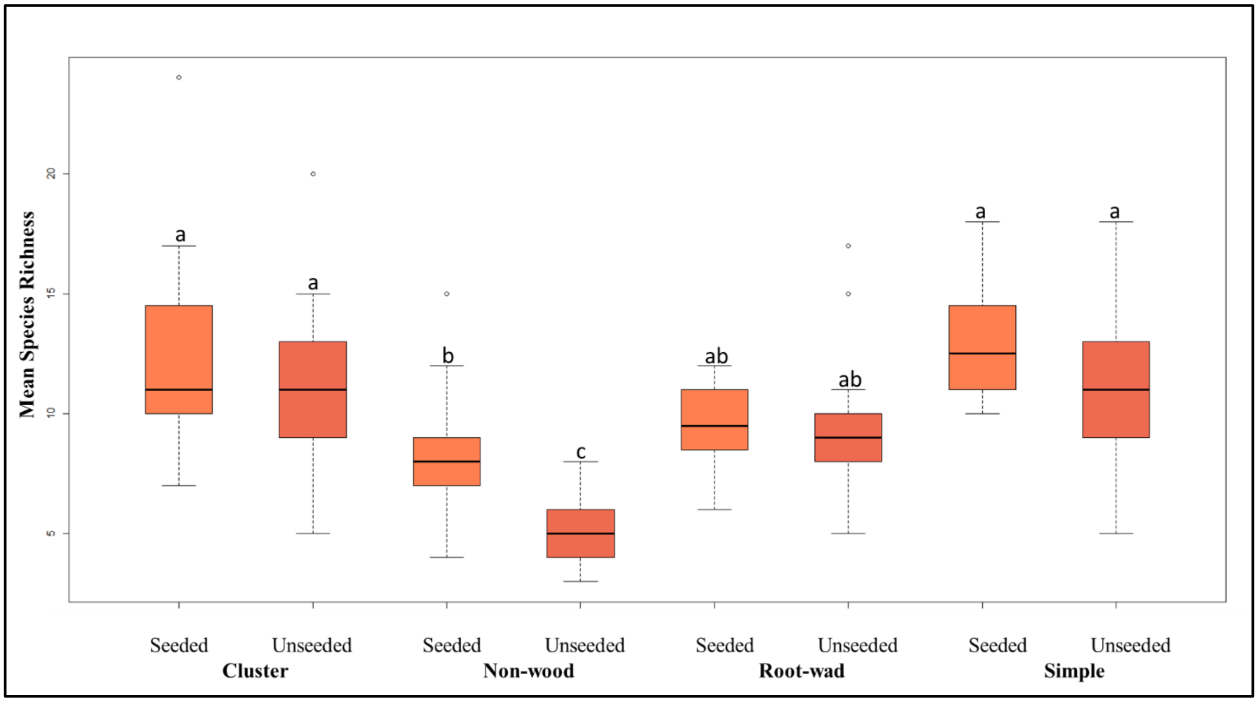

Figure 9. Boxplots illustrating the combined effects of wood plot type and seeding treatment on mean species richness in the former Lake Mills reservoir following dam removal on the Elwha River, WA. Species richness was highest on cluster and simple plots, with non-wood seeded plots and seeded and unseeded root-wad plots having median levels of species richness, and unseeded non-wood plots having lowest species richness. Boxplots represent median species richness with 95% CI. Medians with common letters do not differ significantly (α = 0.05), determined by Tukey's HSD. N=143.

Mean plant abundance did not differ significantly by plot type ($F_{(3,1)}$=0.375, P=0.772), but did differ significantly by seeding treatment ($F_{(1,138)}$=15.291, P<0.001), with seeded root-wad and simple plots having significantly more stems, with no interaction (Figure 10).

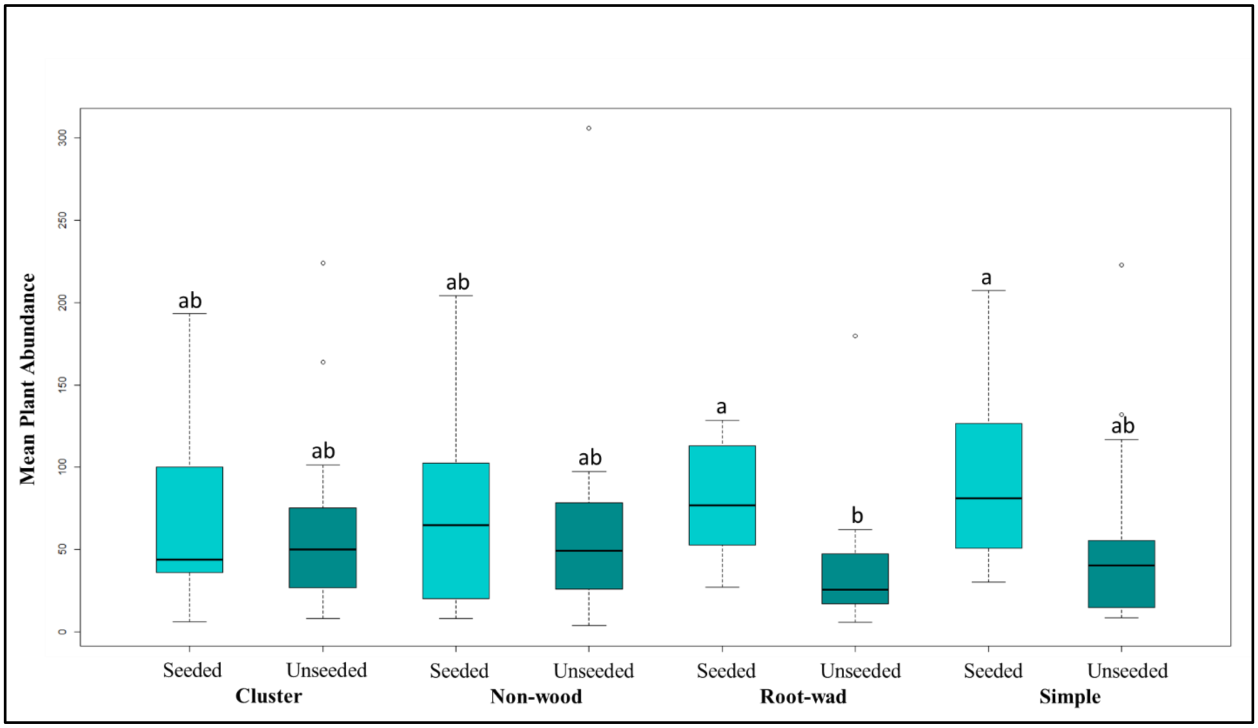

Figure 10. Boxplots illustrating the combined effects of wood plot type and seeding treatment on mean plant abundance in the former Lake Mills reservoir following dam removal on the Elwha River, WA. Mean plant abundance did not differ significantly by plot type, but was significantly lower on unseeded plots. Boxplots represent median species richness with 95% CI. Medians with common letters do not differ significantly ($\alpha = 0.05$), determined by Tukey’s HSD. N=143.

Percent exotic species differed significantly by wood plot type ($F_{(3,1)}= 11.488$, $P<0.001$), with wood plots having significantly more exotics than non-wood plots. Exotics also differed by seeding treatment ($F_{(1,138)}=56.923$, $P<0.001$), with unseeded areas having significantly more exotic species than seeded areas, with no interaction. Seeded non-wood plots had significantly fewer exotic species compared to all other treatment combinations (Figure 11).

I also examined total exotic plant abundance at each plot to ensure that patterns in percent exotics were not implicitly tied to mean plant abundance at each plot. A two-way ANOVA comparing total exotics by wood plot type, seeding treatment, and their interaction, yielded statistically similar results as percent exotics, with wood plots ($F_{(3,1)}= 7.927$, $P<0.001$) and unseeded treatment areas ($F_{(1,138)}=17.523$, $P<0.001$) having more exotics compared to non-wood plots and seeded treatment areas, respectively, with no interaction.

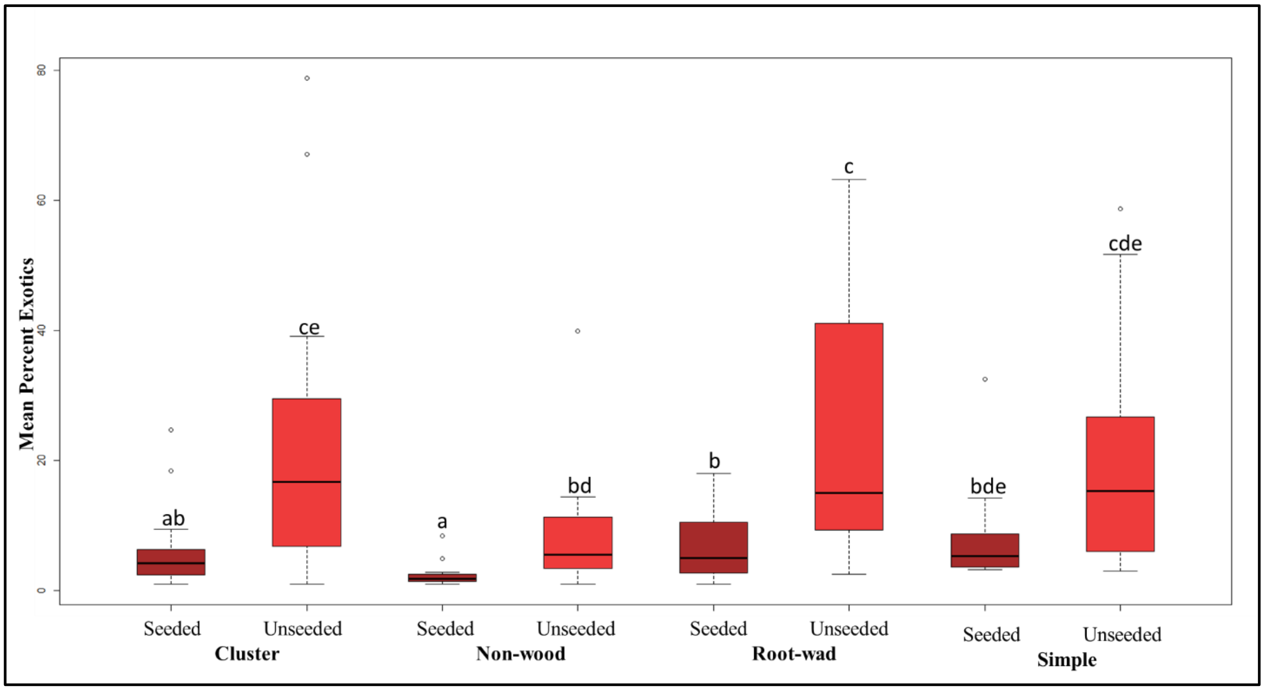

Figure 11. Boxplots illustrating the combined effects of wood plot type and seeding treatment on percent exotic species in the former Lake Mills reservoir following dam removal on the Elwha River, WA. Percent exotics were higher in unseeded treatment areas and on plots containing wood. Boxplots represent median percent exotics with 95% CI. Medians with common letters do not differ significantly ($\alpha = 0.05$), determined by Tukey's HSD. N=143.

3.3 Community Composition among LWD Treatments

PERMANOVA results indicate that species composition differed significantly by wood plot type ($F_{(3,139)}$=5.080, P=0.001). A multivariate post-hoc test revealed that all plots containing LWD differed significantly from non-wood plots (all P-values<0.05; Table 4). I also conducted post-hoc PERMANOVAs and pairwise comparisons to examine the effect of wood plot type on species composition within seeded and unseeded areas separately. The results revealed that species composition differed significantly with respect to wood plot type in both seeded ($F_{(3,62)}$=3.550, P<0.001) and unseeded areas ($F_{(3,73)}$=4.775, P<0.001); however, the effect of wood on species composition in seeded and unseeded areas was not as clear as the results for all plots, regardless of treatment. Appendix Tables G-I provides results of these pairwise comparisons and NMDS ordinations.

Table 4. Post-hoc pairwise comparisons of species composition among all plot types in the former Lake Mills reservoir following dam removal on the Elwha River, WA. Pairwise comparisons reveal that species composition among plots containing wood did not differ, but all wood plots differed significantly from non-wood plots, based on adjusted *P-values* (in bold text).

Plot Comparisons	**Df**	**SS**	***F***	**R^2**	***P***
Cluster vs. Non-wood	1	1.021	7.778	0.099	**0.006**
Cluster vs. Root-wad	1	0.199	1.215	0.018	1.000
Cluster vs. Simple	1	0.169	1.236	0.018	1.000
Non-wood vs. Root-wad	1	0.923	6.190	0.079	**0.006**
Non-wood vs. Simple	1	1.647	13.237	0.155	**0.006**
Root-wad vs. Simple	1	0.315	2.022	0.029	0.306

An NMDS ordination plot provides results that are consistent with post-hoc pairwise comparisons for all plots. The ordination shows a high degree of overlap among wood plots, which illustrates that species composition among wood plots was similar. Along the NMDS2 axis, non-wood plots, symbolized by pink plus signs, appear to separate from other wood plot types and are more clustered near the bottom of the ordination, illustrating the significant difference in species composition among wood and non-wood plots (Figure 12). Species such as wall lettuce, thistles, and willowherbs were more abundant on those non-wood plots. Interestingly, while these species are all wind-dispersed, non-wood plots did not have an associated dispersal mechanism.

Vectors for each dispersal mechanism are also plotted on the ordination. Each vector's length is directly related to the strength of the association, with longer vectors signifying a stronger, more significant relationship. Along the NMDS1 axis, blue vectors for wind, gravity, and ballistic seed dispersal mechanisms illustrate the relationship between dispersal mechanism and species composition among my plots. For example, on the left-hand side of the ordination, long-distance (wind) dispersal was associated with wind-dispersed species such as willows, wood groundsel, and hairy cat's ear. On the right-hand side of the ordination, short-distance dispersal (gravity and ballistic) was associated with species such as riverbank lupine and common velvetgrass. Animal dispersal modes were not significantly correlated with species composition ($P > 0.05$).

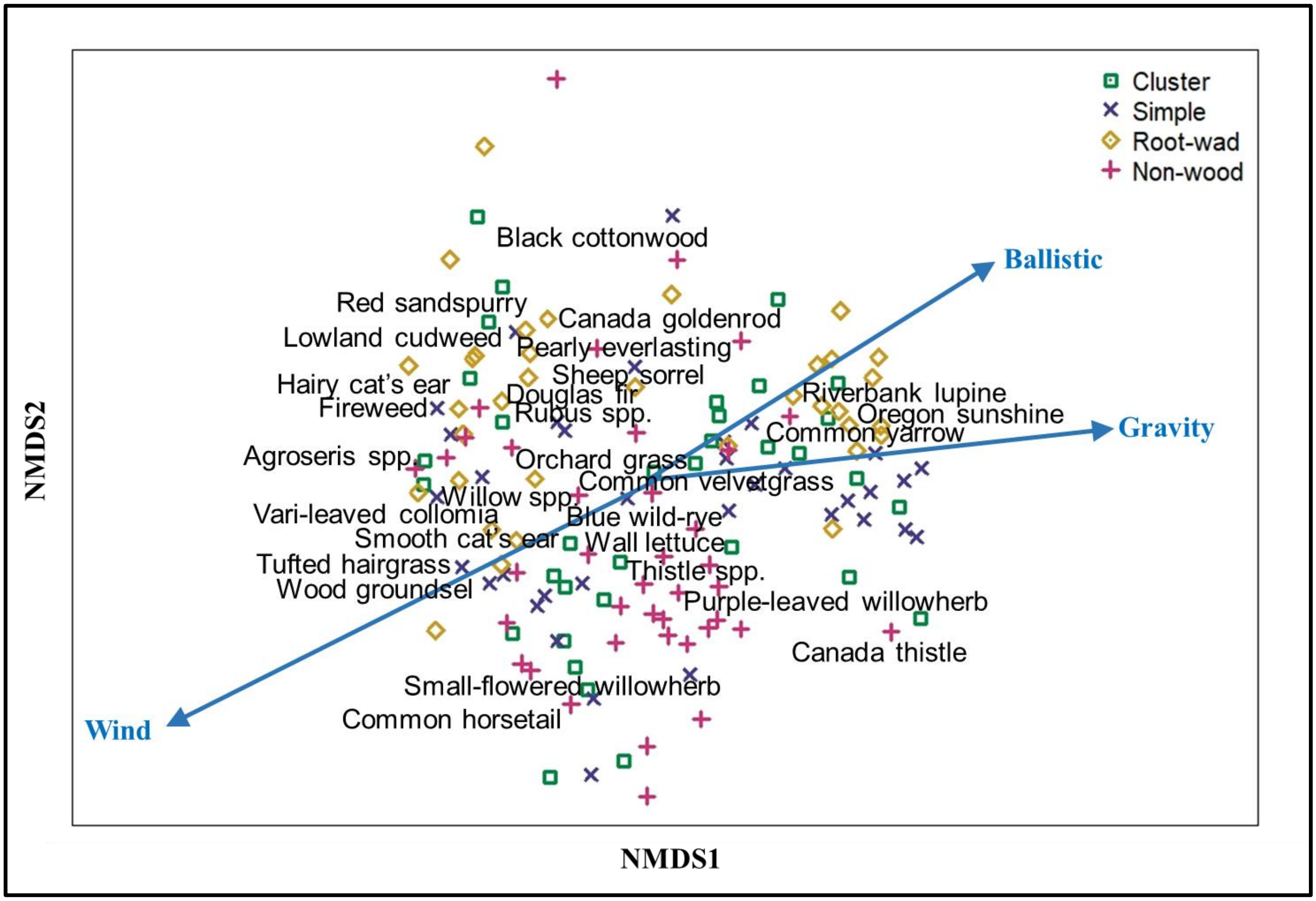

Figure 12. Nonmetric multidimensional scaling (NMDS) ordination of species composition in the former Lake Mills reservoir following dam removal on the Elwha River, WA, with unique symbols for each plot type. While symbols show a high degree of overlap for all plot types, post-hoc test results indicate that species composition on non-wood (NW) plots differed significantly from all LWD plots (*P*=0.006) for all LWD-NW comparisons, Table 5), and all LWD plots were similar. Blue vectors illustrate the relative influence of seed dispersal mechanisms on community composition. Animal dispersal was not significant (*P*> 0.05). Vector length indicates strength of association. Points represent individual plots (N=143). Stress value=0.16.

Indicator species analysis identified different species associated with the various wood plot types (Table 5). On cluster plots, five significant indicator species were identified, with common horsetails and small-flowered willowherb having the strongest association with cluster plots. Seven species were identified as indicators of simple plots; the exotic hairy cat's ear had the strongest association with simple plots. Other significant indicators of simple plots included two other exotics—wall lettuce and smooth hawksbeard. Thistles (*Cirsium* spp.) of unknown nativity were identified as significant indicators of root-wad plots. The majority of indicator species of wood plots were wind-dispersed. No significant indicator species were identified for non-wood plots.

Table 5. List of indicator species and nativity status by wood plot type in residual sediments in the former Mills reservoir, Elwha River, WA. 2015. Nativity status: N=native, E=exotic, U=unknown. Only significant indicator species are shown. *Indicates species was applied by seed in seeded treatment areas.

Plot Type	**Indicator species**	**Common name**	**Nativity**	**Indicator value**	***P***
Cluster	*Equisetum arvense*	Common horsetail	N	0.567	0.001
	Epilobium ciliatum	Small-flowered willowherb	N	0.535	0.013
	Carex spp.	*Carex* spp.	U	0.433	0.014
	Salix spp.	*Salix* spp.	N	0.354	0.037
	Sedum spp.	*Sedum* spp.	U	0.286	0.034
Simple	*Hypochaeris radicata*	Hairy cat's ear	E	0.783	0.001
	Chamerion angustifolium	Fireweed	N	0.505	0.015
	Mycelius muralis	Wall lettuce	E	0.469	0.031
	Unknown grass A		U	0.464	0.002
	Collomia heterophylla	Vari-leaved collomia	N	0.444	0.023
	Crepis capillaris	Smooth hawksbeard	E	0.307	0.039
	Unknown grass B		U	0.289	0.036
Root-wad	*Cirsium* spp.	Thistle spp.	U	0.408	0.027
Non-wood		*No significant indicator species*			

3.4 Community Composition among Seeding Treatments

Species composition varied by seeding treatment with distinct plant communities represented in seeded and unseeded treatment areas (PERMANOVA, $F_{(1,141)}$=22.492, P<0.001). An NMDS ordination plot (Figure 13) illustrates that the two seeding treatments are separated from one other in ordination space, which indicates a strong influence of seeding on species composition. Vectors on the NMDS ordination illustrate the association of individual plots with native versus exotic species. Along the NMDS1 axis, species applied as seed, including riverbank lupine, Oregon sunshine, and common yarrow, occur on the right-hand side of the ordination and are more abundant on seeded plots. On the left-hand side of the ordination, exotic species including hairy cat’s ear, smooth cat’s ear, and wood groundsel were more abundant on unseeded plots.

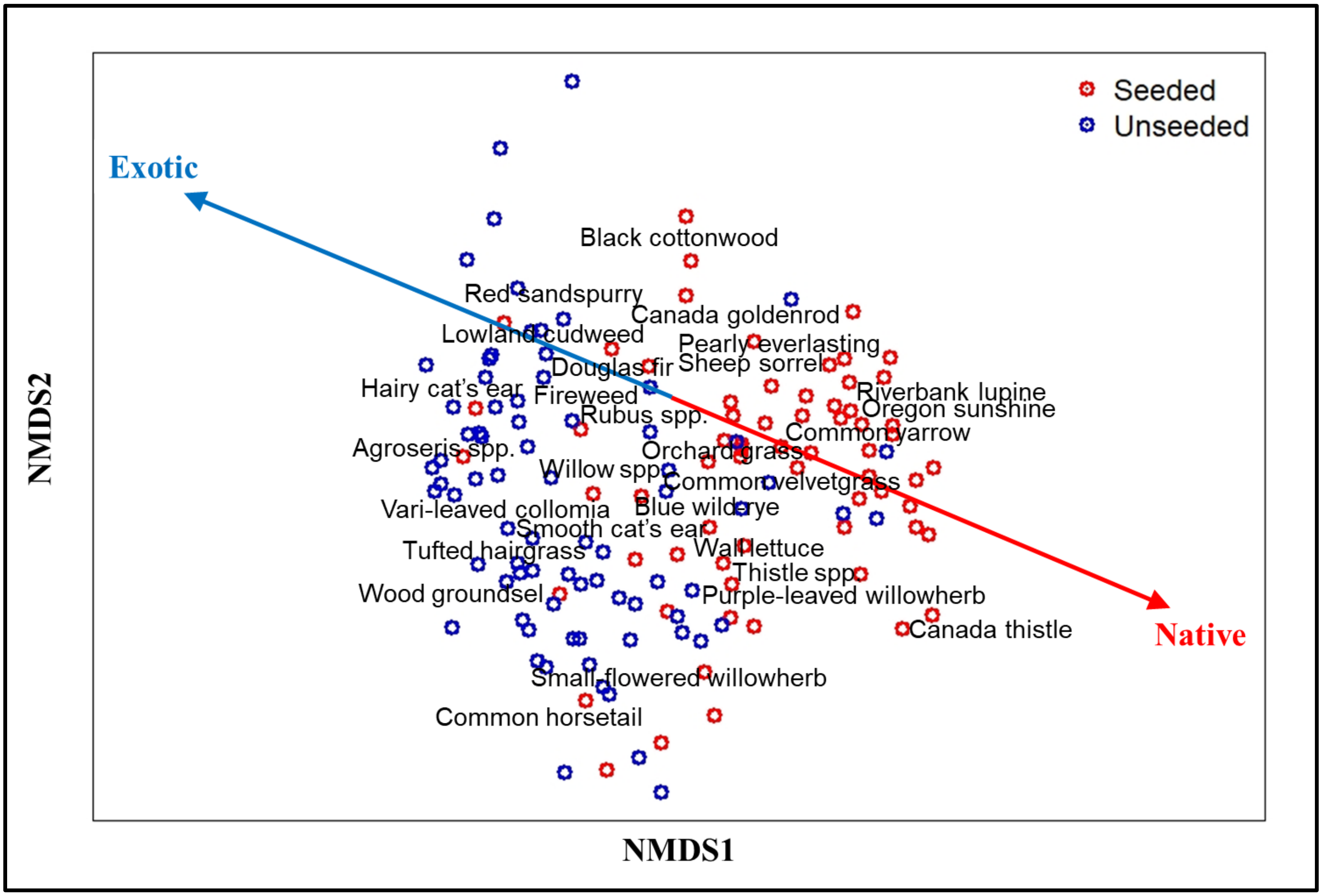

Figure 13. NMDS ordination of species composition in the former Lake Mills reservoir following dam removal on the Elwha River, WA. PERMANOVA results indicate that applying native seed stock had a significant effect on species composition ($F_{(1,141)}$=22.492, P<0.001). Vectors illustrate the association of individual plots with native versus exotic species (α = 0.05). Points represent individual plots (N=143). Stress value=0.16.

Indicator species analysis identified several indicators of seeded treatment areas, which consisted primarily of species seeded by ONP staff. Riverbank lupine, Oregon sunshine, and common yarrow were all strongly associated with seeded areas (Table 5). Common horsetail was identified as the only indicator species of unseeded plots, and consistent with results of indicator species analysis for plot type were most abundant on unseeded cluster plots.

Table 6. List of indicator species and nativity status by treatment type in residual sediments in the former Mills reservoir, Elwha River, WA. 2015. Nativity status: N=native, E=exotic, U=unknown. Only significant indicator species are shown. *Indicates species was applied by seed in seeded treatment areas.

Seeding Treatment	**Indicator species**	**Common name**	**Nativity**	**Indicator value**	***P***
Seeded	**Lupinus rivularis*	Riverbank lupine	N	0.842	0.000
	**Eriophyllum lanatum*	Oregon sunshine	N	0.794	0.000
	**Achillea millifolium*	Common yarrow	N	0.751	0.000
	Carex spp.	Sedge spp.	U	0.376	0.028
Unseeded	*Equisetum arvense*	Common horsetail	N	0.457	0.030

3.5 Distance from the Forest Edge

A PERMANOVA was used to test whether distance from seed sources influenced species composition on unseeded plots. Results indicate that distance had a significant effect on species composition ($F_{(1,75)}$=3.176, *P*=0.001). Results of Kendall's tau correlations revealed that Shannon-Weiner diversity (τ = -0.262, *P*<0.001), species richness (τ = -0.200, *P*=0.013), and percent exotics (τ = -0.346, *P*<0.001) were significantly negatively correlated with distance; all three variables declined as distance from the forest increased (Figure 14). Total plant abundance was not significantly correlated with distance (*P-value* >0.05).

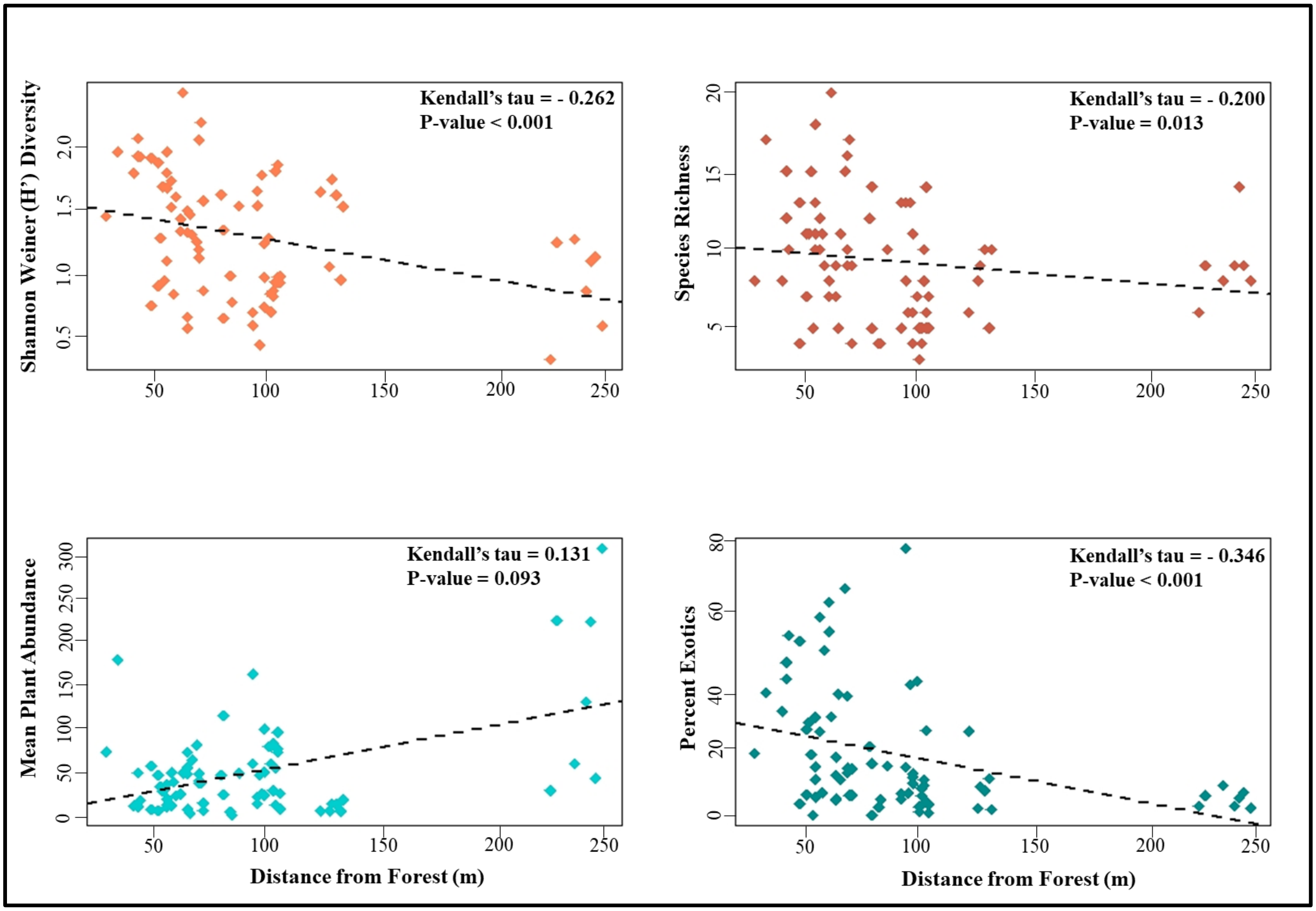

Figure 14. Kendall's tau correlations between distance from the forest edge and mean Shannon-Weiner diversity, species richness, plant abundance, and percent exotics on unseeded plots (N=77) in the former Lake Mills reservoir following dam removal on the Elwha River, WA. Shannon-Weiner diversity, species richness, and percent exotics were significantly negatively correlated with distance, while plant abundance was not correlated with distance ($\alpha = 0.05$).

An NMDS ordination plot illustrates patterns in species composition and dispersal mechanism related to distance on unseeded plots (Figure 15). The NMDS2 axis illustrates the influence of distance from the forest edge on species composition. For example, species located near the bottom right of the ordination, including oceanspray, western hemlock, and riverbank lupine, were more abundant closer to the forest edge. Conversely, species located near the top left of the ordination, including Siberian spring beauty, common horsetail, and orchard grass, were more abundant at greater distances. The NMDS ordination also illustrates the relationship between distance and seed dispersal mechanism. For example, short-distance dispersal modes (ballistic and gravity) were associated with closer distances to the forest edge and long-distance dispersal (wind) was associated with greater distances. Vectors were omitted from the ordination to improve readability; the red star near the center of the ordination plot represents the origin of vectors for seed dispersal. Animal dispersal was not significantly correlated with distance ($P >$ 0.05).

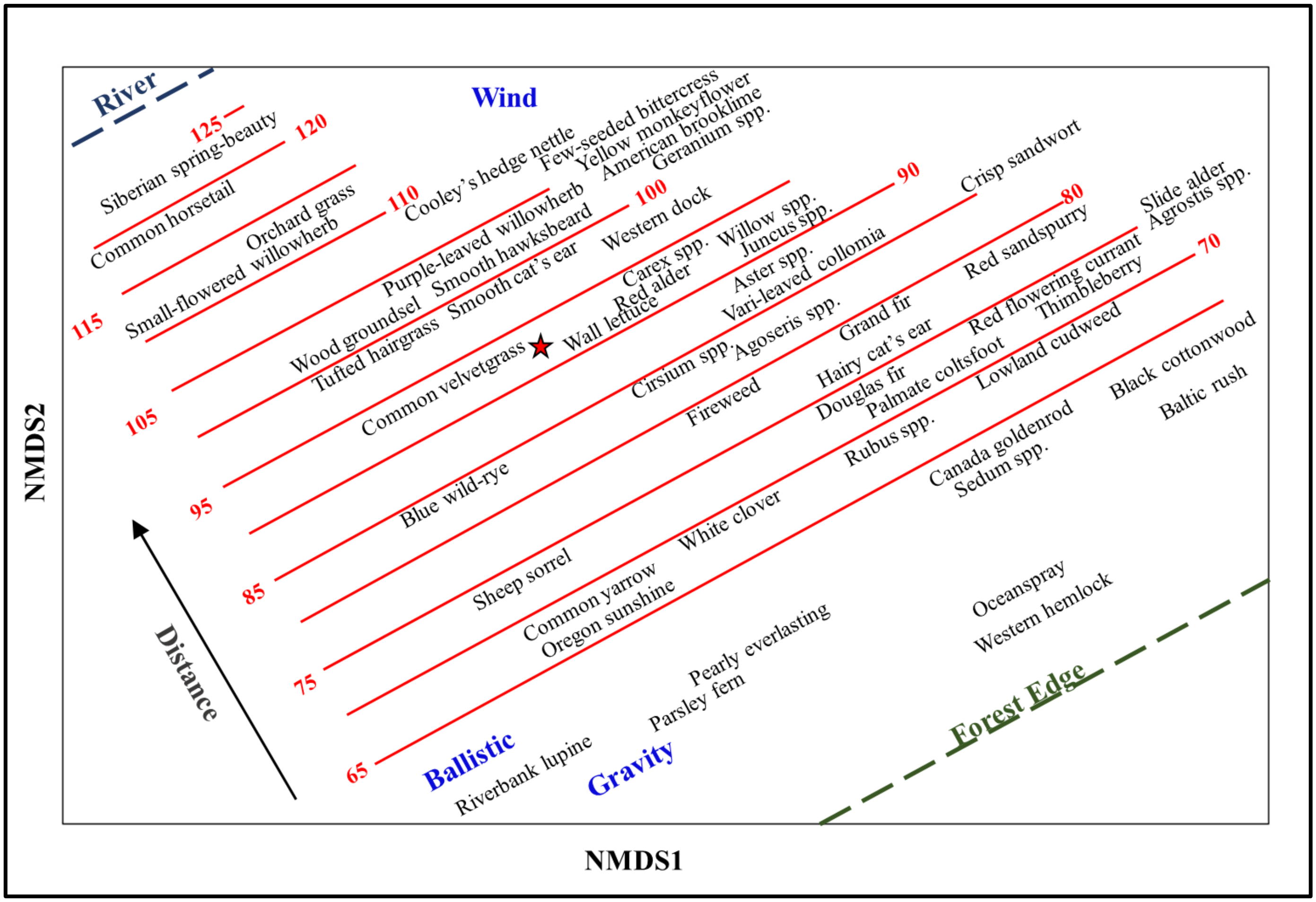

Figure 15. NMDS ordination of species composition on unseeded plots in the former Lake Mills reservoir following dam removal on the Elwha River, WA. PERMANOVA results indicate that distance (m) from the forest edge significantly influenced species composition in unseeded areas ($F_{(1,75)}=3.478$, $P<0.001$). Blue labels for each dispersal type illustrate the relative influence of each significant dispersal mechanism on species composition ($\alpha = 0.05$). All vector lines originated at the red star near the center of the ordination but were removed to improve readability. Wind dispersal was associated with greater distance from the forest edge, while gravity and ballistic dispersal modes were associated with closer distances. Animal dispersal was not significant. Stress value=0.16.

3.6 Spatial Analysis

A spatial analysis conducted on all plots identified five significant hot-spots; four LWD plots and one non-wood plot. Three of the LWD hot-spots were located within the large, seeded treatment area, and the fourth was located within an unseeded area on a low terrace on the river floodplain (Figure 16). The remaining non-wood hot-spot was also situated on the low floodplain terrace. No significant cold-spots occurred in the study area, which indicates that there were few areas where low plant abundance clustered spatially. Abundance on all other plots lacked significant high or low spatial clustering.

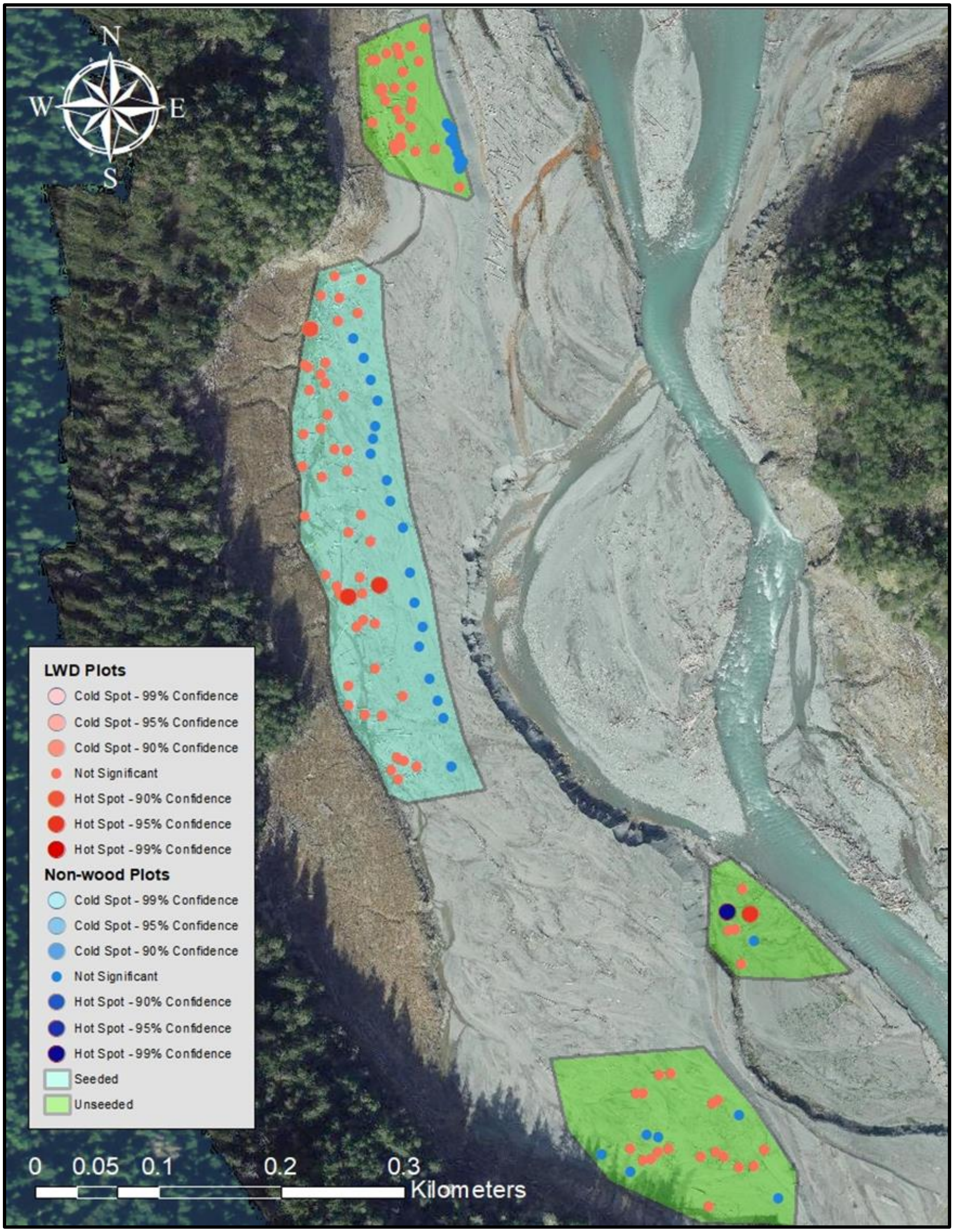

Figure 16. Hot-spot analysis generated in ArcGIS for plant abundance on LWD (N=104) and non-wood plots (N=39) located in seeded and unseeded treatment areas in the former Lake Mills reservoir, Elwha River, WA. 2015. Four significant hot-spots were identified on wood plots, three in seeded areas on the perched terrace, and one in an unseeded area on a lower terrace. Only one non-wood plot was identified as a hot-spot, which also occurred in the unseeded area on the lower terrace (all significant Z-scores >2.80, all *P-values* <0.004).

4.0 Discussion

The purpose of this study was to examine the effects of translocated LWD and direct seeding and limitations imposed by distance on species composition during the initial years of plant succession within the former Lake Mills reservoir. My findings as they relate to my research questions are as follows: 1) there was no difference in plant abundance in sites that had LWD compared to non-wood plots; however, Shannon-Weiner diversity, species richness, and exotic species were greater on plots that contained wood. 2) Seeded plots had an increase in species richness and plant abundance, and a decrease in exotic species; however, seeding did not influence Shannon-Weiner diversity. 3) Distance from the forest edge did not limit plant abundance; however, I noted a decrease in Shannon-Weiner diversity, species richness, and percent exotic species in response to distance from the forest edge. Using NMDS ordinations, indicator species analysis, spatial analysis, and knowledge of seed dispersal mechanisms, I illustrated that species composition differed with respect to LWD, seeding treatments, and distance from the forest.

4.1 LWD Treatments

The presence of LWD on novel terraces influenced species composition; plots containing LWD had higher Shannon-Weiner diversity and species richness. However, contrary to my prediction, plant establishment did not increase around LWD, as measured by stem counts; mean plant abundance was similar on plots with and without LWD. These results are consistent with those found following the eruption of Mount St. Helens, where logs and boulders had negligible effects on plant establishment in seral post-volcanic habitats (Halpern and Harmon 1983, Halpern et al. 1990). In contrast, other studies in primary successional habitats found an increase in seedling abundance near surface topography, such as cracks, rills, rocks, mounds, and depressions, compared to surrounding flat areas (del Moral and Wood 1993, Jumpponen et al. 1999, Titus and Tsuyuzaki 2003, Chad and del Moral 2005). Since plant abundance did not differ significantly among wood and non-wood plots, it may indicate that seeds, albeit from fewer species, are dispersing to and germinating in open, coarse sediments with and without wood. Coarse sediments that comprise terrace surfaces range from sand-sized particles to cobbles (Chenoweth 2013). Studies in post-glacial habitats found that coarse surface sediments, similar to those that occur in Mills, created favorable micro-sites for plant germination and establishment to occur (Jumpponen et al. 1999; Niederfriniger Schlag and Erschbamer 2000). Perhaps the interstitial spaces between coarse sediments create small micro-sites that trap seeds and retain moisture (del Moral and Wood 1993, Niederfriniger Schlag and Erschbamer 2000), allowing some species to germinate and establish on coarse terraces in Mills.

Whereas logs and root-wads did not have higher plant abundance than open sites, all plots containing wood had higher Shannon-Weiner diversity and species richness compared to open areas without wood. Increased Shannon-Weiner diversity and species richness around LWD are likely attributed to the structure that wood provides; when habitat structure is more diverse, species assemblages tend to follow that pattern of complexity (Brown and Naeth 2014). Using larger irregular surface topography such as cracks, rills, rocks, mounds, and depressions as imperfect analogs for LWD, studies have shown that these structures trap wind-blown seeds in early successional habitats, leading to increased seed deposition (Wood and del Moral 1988; Dale et al. 2005; Tsuyuzaki et al. 1997; Titus and Tsuyuzaki 2003; Jones et al. 2005; Walker et al. 2006).

4.2 LWD Treatments—Species Composition and Restoration Implications

A diverse array of wind-dispersed native and exotic forbs and grasses, as well as wind and bird-dispersed woody shrubs and trees, contributed to increased Shannon-Weiner diversity and species richness on plots containing wood. While bird-dispersed plant abundance was very low in this study (N=21), all woody plants dispersed by birds were found on plots containing wood, with the majority (60%) around elevated root-wads. Elevated wood structures likely promote species richness by attracting avian species that deposit seed-rich scat at LWD perch sites. In my study, the addition of logs to terrace surfaces along the Elwha created complex structures, contributing to increased Shannon-Weiner diversity and species richness of seeds trapped by LWD.

Exotic species also contributed to increased Shannon-Weiner diversity and species richness on plots containing wood. Because LWD creates favorable micro-sites and acts as an effective trap for wind-blown seeds, and because many of the exotics identified during this study were dispersed by wind, it led to an increase in exotics on wood plots, particularly when wood plots were unseeded. Indicator species analysis revealed that several exotic forbs were indicators of LWD simple plots. Other studies (Chenoweth 2015, Morgan 2018) found that small weedy annuals, such as *Aira* species and *Senecio sylvaticus,* were also indicators of coarse sediments in Mills; however, those studies also included planted sites. Many exotic species are excellent colonizers of degraded habitats and are adapted for growth in stressful environments (Walker et al. 2006). They complete their life cycles in a matter of weeks, germinating, flowering, and producing seeds before the onset of seasonal droughts (Grime 1979, Sakai et al. 2001). While exotic species were more abundant on plots containing wood, exotics represented a small portion of total plant abundance in my study area. These results are consistent with other Mills' studies

(Chenoweth 2013, Schuster 2015, Morgan 2018), which found that exotics were present, but not dominant. And, similar to results from Chenoweth (2013), I found no evidence of highly invasive species on novel terraces in Mills. However, other exotics, including Canada thistle, common velvetgrass, and hairgrass (*Aira praecox* and *A. caryophyllea*) were present. Other studies (Chenoweth et al. 2020; Kardouni 2020) have noted that these exotics increased in abundance on plots with sparse seeding. Because they are early and successful pioneers, exotic species can influence successional pathways by outcompeting native species, changing the chemical and biological conditions of soils, and negatively affecting the ability of surrounding vegetation to access water and nutrients (Jean-Baptiste et al. 2018, Holl 2020). Therefore, continual management of these terraces will be required to assure natural plant succession and native plant recovery over time (Shafroth et al. 2002; Chenoweth et al. 2020).

4.3 Seeding Treatments

On plots where native seed stock was sowed, plant abundance increased and exotic species declined. The prevention of exotic species invasions was one of the primary objectives of the Elwha revegetation plan (Chenoweth et al. 2011). Therefore, my results suggest that direct seeding on coarse sediments helps meet this objective. The ability of seeded species to promote native plant establishment while suppressing exotic invasions in Mills is consistent with other studies (Carter et al. 2012; Nemec et al. 2013; Chenoweth et al. 2020), which found that applying native seed stock to Elwha sediments led to higher vegetative cover, increased species richness, and reduced exotic species recruitment. Between 2013 and 2015, ONP restoration crews applied roughly 1,800 kilograms of native seed, most of which was applied to terrace sediments in Mills, with an average seeding rate of 323 seeds per square meter (Chenoweth et al. 2020). My study shows that this application rate effectively reduced exotic species' recruitment in recently dewatered habitats susceptible to exotic invasion.

4.4 Seeding Treatments—Species Composition and Restoration Implications

Several seeded species, including riverbank lupine, Oregon sunshine, yarrow, and unknown sedges, were identified as indicator species of seeded plots. ONP restoration biologists selected native seeded species to apply to reservoir sediments based on their ability to tolerate xeric habitats lacking organic matter and nutrients (Chenoweth 2013). As early colonizers, seeded species contribute vital organic matter and nutrients to terrace sediments through the annual decomposition of herbaceous stems, leaves, and roots, improving growing conditions for later successional species. For example, seeded cover crops, such as riverbank lupine, fix atmospheric nitrogen and modify soil nutrients. Kardouni (2020) found that riverbank lupine provided a cover crop that decreased the invasion of exotic grasses while increasing growth rates and foliar nitrogen levels of planted conifers in Mills. Several other studies have shown the benefits of seeded lupines in seral habitats, which include trapping seeds and leaf litter (Urbanska 1997; Dale et al. 2005), creating safe-sites (Urbanska 1997, Niederfriniger Schlag and Erschbamer 2000), reducing wind and water erosion (Niederfriniger Schlag and Erschbamer 2000), and increasing the establishment (Kardouni 2020) and survival rates of later successional woody species (Niederfriniger Schlag and Erschbamer 2000; Chenoweth et al. 2020). And as stated above, augmenting with native seeds increases the potential for seeded species to germinate and establish. Once established, seeded species can outcompete exotics for resources such as space and water, reducing the potential for invading exotics to establish.

Indicator species analysis identified common horsetail (*Equisetum arvense*) as the sole indicator species of unseeded plots. Two other studies (Chenoweth 2013, Whisman 2013) also noted horsetails to be early and abundant colonizers in moist sediments following reservoir drawdown in Mills. The widespread distribution of horsetails is likely due to wind and water-borne spores, stems, and roots being transported and deposited onto novel terraces during reservoir drawdown. Horsetails are indicative of moist riparian habitats, and their relative abundance on novel terraces in Mills is likely attributed to saturated sediments during reservoir drawdown. Horsetails have extensive rhizomes that can reach depths of four meters and extend laterally for tens of square meters, allowing them to access water in otherwise xeric surface conditions (Husby 2013). And, because their rhizomes are tolerant of deep burial, horsetails are often early colonizers of disturbed habitats where burial occurs (Husby 2013). For example, immediately following the 1912 and 1980 eruptions of Katmai volcano and Mount St. Helens, respectively, horsetails were abundant in deep tephra deposits (Bilderback 1987, Siegel and Siegel 1982, Rothwell 1996). Common horsetails are perennials but possess aerial stems that die back annually. In shrub wetland systems in Alaska, the deep and extensive rhizomes of horsetails allowed them to access soil nutrients such as calcium, phosphorus, and potassium in lower soil horizons (Marsh et al. 2000). Elevated levels of these vital nutrients were found in horsetail litter, which became available to surrounding vegetation and increased primary productivity in the wetland (Marsh et al. 2000). It is likely that horsetail are beneficial to surrounding vegetation by providing a source of these limited nutrients through the annual decomposition of their stems. Whether horsetails will persist on novel terraces over time will likely depend on their ability to continue to extract available moisture and nutrients from deep sediment deposits.

4.5 Distance from Forest and Seed Dispersal Mechanisms

Distance from seed sources at the forest edge influenced species composition on unseeded plots (seeded plots were excluded from distance analyses). Shannon-Weiner diversity, species richness, and percent exotics declined as distance from the forest increased. This result is similar to the results of a study on Mount St. Helens, which found that species richness decreased with distance (>500 meters) from established vegetation (del Moral and Wood 1993). In my study area, seed dispersal limitations likely prevented some species from colonizing distant unseeded areas, leading to lower Shannon-Weiner diversity and species richness at greater distances from the forest edge. However, plant abundance did not change significantly with distance, illustrating that some species are not limited by dispersal. The most abundant species (based on rank abundances at distances over 100 meters from the forest edge) were small flowered willowherb, blue wild-rye, tufted hair grass, common horsetail, and wood groundsel, in descending order of abundance. The consistency in stem counts in unseeded areas indicates that plants (albeit from fewer species as distance increased) colonize the terraces in relatively equal amounts, regardless of distance. This result contrasts with other studies that found declines in plant abundance as distance increased (del Moral and Wood 1993, Fuller and del Moral 2003, Dale et al. 2005, Halpern and Harmon 1983); however, distances in those studies were somewhat greater than my study area and ranged from hundreds of meters to several kilometers, while my sampling area ranged from 28-248 meters from established vegetation.

Regardless of distance, plants dispersed by wind were dominant in my study area, followed by gravity, ballistic, and animal dispersed plants. Wind-dispersed plant abundance was more closely associated with farther distances, while gravity and ballistic mechanisms were associated with closer distances. Lightweight, wind-dispersed species are often the earliest colonizers of disturbed habitats due to their excellent dispersal capabilities (del Moral and Wood 1993, Dale et al. 2005). Diaspores adapted for wind dispersal have significantly greater dispersal distances than gravity and ballistic dispersers (del Moral and Wood, 1993), and can travel up to 4 kilometers from their origin (Wilson 1993). Unseeded plots in my study area were well within the maximum dispersal capabilities of wind-dispersed species; however, seed sources at the forest edge are not the only source of plant propagules on terrace sediments. The narrow Elwha River valley funnels wind from the Strait of Juan de Fuca in the north to mountainous regions in the south. Winds that occur within the river corridor shift throughout the day as air masses warm and cool, resulting in strong winds that funnel up and down the river. While the forest edge, which lies to the east and west of our sampling area, provides the closest source of wind-dispersed propagules, plants dispersed by wind also originate from more distant seed sources to the north and south, in-line with dominant wind patterns (Woodward et al. 2011).

While herbaceous species comprised the vast majority of plants observed, several woody species were already established on novel terraces when this study was conducted, including black cottonwood, willows, and Douglas fir. Black cottonwood seedlings were particularly abundant in my study area (Figure 17). The early abundance of black cottonwood on novel terraces in Mills can be attributed to reservoir drawdown timing. Between October 2011 and

Figure 17. Black cottonwood (*Populus balsamifera*) seedlings growing on the large western terrace in the former Lake Mills reservoir. Elwha River, WA. Summer, 2015.

October 2012, there were numerous planned reservoir drawdown and hold periods during the deconstruction of Glines Canyon dam. The most prolonged hold period occurred for ten weeks in the spring of 2012, which coincided with the height of seed production for black cottonwood and willow (Bountry et al. 2015, Chenoweth 2015). A study in the Horsetooth reservoir found that reservoir drawdown that coincided with cottonwood seed dispersal led to increased cover of the species (Auble et al. 2007). Black cottonwood germination and seedling survival are dependent on sediment moisture levels during the first month (USDA 2002). Terrace sediments were completely saturated during these hold periods. As reservoir drawdown resumed, cottonwoods adapted to the lowering water table by growing deep tap roots to reach groundwater levels 6-18 meters below the perched terraces (Naiman et al. 2005, Chenoweth 2015). The rapid establishment of woody species, including black cottonwood, on novel terraces is fortunate. Where restoration goals include the rapid return of riparian forests to dewatered reservoirs, managers should consider timing reservoir drawdown and hold periods to coincide with cottonwood and willow seed dispersal to increase the potential for woody species to establish.

4.6 Spatial Analysis

Hot-spot analysis identified a few key areas where high plant abundance clustered spatially. These areas occurred on the western-most seeded treatment area and on the lower unseeded floodplain terrace (Figure 16). One low terrace was associated with the river floodplain, making it a unique example where floodplain dynamics are likely influencing species composition (Naiman et al. 2000); all plots sampled on that terrace were positioned greater than 200 meters from the forest edge. Higher levels of disturbance and moisture associated with this floodplain terrace may select species that are either more tolerant of flooding disturbance or are pioneering species after a flooding event. Species associated with the floodplain terrace included native and exotic grasses and native Cooley's hedge nettle, common horsetail, black cottonwood, and Sitka willow. Douglas fir was also detected on the distant terrace. In Elwha floodplain sediments, Douglas firs are considered a mid-seral species (Whisman 2013); seed rain from Douglas firs beyond 150 meters from the forest edge is considered unlikely (Chenoweth pers. comm.). It is more likely that Douglas firs on the distant floodplain terrace resulted from fir cones being transported by the river from upstream sources.

Spatial hot-spot analysis provides further support for seeded treatment areas having higher plant abundance. Of the few hot-spots identified, the majority occurred in seeded areas. However, hot-spot analysis reveals a lack of strong spatial patterns overall. In primary successional habitats following large-scale disturbance, vegetation spatial patterns can be highly variable, unpredictable, and slow to develop (del Moral et al. 2010). Low recruitment and survivorship due to environmental stress can further obscure plant spatial patterns (Robbins and Matthews, 2009). Given the early stage of plant succession on novel terraces along the Elwha, it is not surprising that few areas with particularly high or low plant abundance were identified during this study. As succession proceeds on novel terraces, it remains unclear whether plant abundance patterns will begin to reflect how LWD, seeding treatments, and distance from the forest will shape plant communities in these habitats.

4.7 Conclusions

This study examined plant establishment in a primary successional habitat during one growing season, four years after dam removal was initiated. Over this period, I characterized the early stages of plant community development on novel terraces. The influence of seeding was immediately apparent; native seed enhancements helped meet some of the primary goals of the Elwha revegetation plan by increasing plant abundance and deterring exotic species. Direct seeding also led to higher species richness, but richness increased most when paired with LWD treatments. Where restoration projects begin with primary succession, methods that promote rapid revegetation will ultimately accelerate soil development by adding organic matter, promoting nutrient cycling, and encouraging microbial activity.

The beneficial effects of LWD were less apparent. The addition of LWD led to increased Shannon-Weiner diversity and species richness, compared with surrounding bare sediments; however, LWD placements did not result in greater plant establishment, contrary to my prediction. In addition, wood plots had higher proportions of exotic species compared to bare sediments. I acknowledge that the benefits of LWD, including deterring ungulate herbivory, accumulating organic matter and nutrients, and serving as a substrate for vegetation as logs begin to decay, will take years to decades to detect. Therefore, future studies examining these vital resources and their impacts on plant communities surrounding LWD is recommended.

As distance from the forest edge increased, Shannon-Weiner diversity, species richness, and percent exotics on unseeded plots declined. However, plant abundance did not change significantly with distance, which indicates that some species' dispersal capabilities are not limited by distance in the Mills basin. In addition, floodplain dynamics are likely influencing seed dispersal modes and species composition at greater distances. Furthermore, understanding the timing of reservoir drawdown to compliment wind-dispersed species can be an important management technique that can accelerate the succession of native plant species required for the holistic recovery of forest habitats along river systems in the Pacific Northwest.

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Appendix

Table A. List of plant species applied by hand to coarse terrace sediments in Mills within the 2012 southern log translocation area during spring of 2012 and 2013 (Chenoweth et al. 2020).

Scientific Name	**Common Name**
Achillea millifolium	Common yarrow
Agrostis exarata	Spiked bentgrass
Artemisia suksdorfii	Suksdorf's sagewort
Bromus pacificus	Pacific brome
Carex mix *(C. pachystachya & C. deweyana)*	Sedge species
Deschampsia elongata	Slender hairgrass
Elymus glaucus	Blue wild-rye
Eriophyllum lanatum	Oregon sunshine
Lupinus rivularis	Riverbank lupine
Total amount applied to coarse sediments in Mills between 2012-2015	**709.6 kg**

Table B. Map of 2012 and 2014 LWD translocation areas on the west side on the Mills basin. Image courtesy ONP restoration manager, J. Chenoweth, and A. Ritchie (U.S.G.S.).

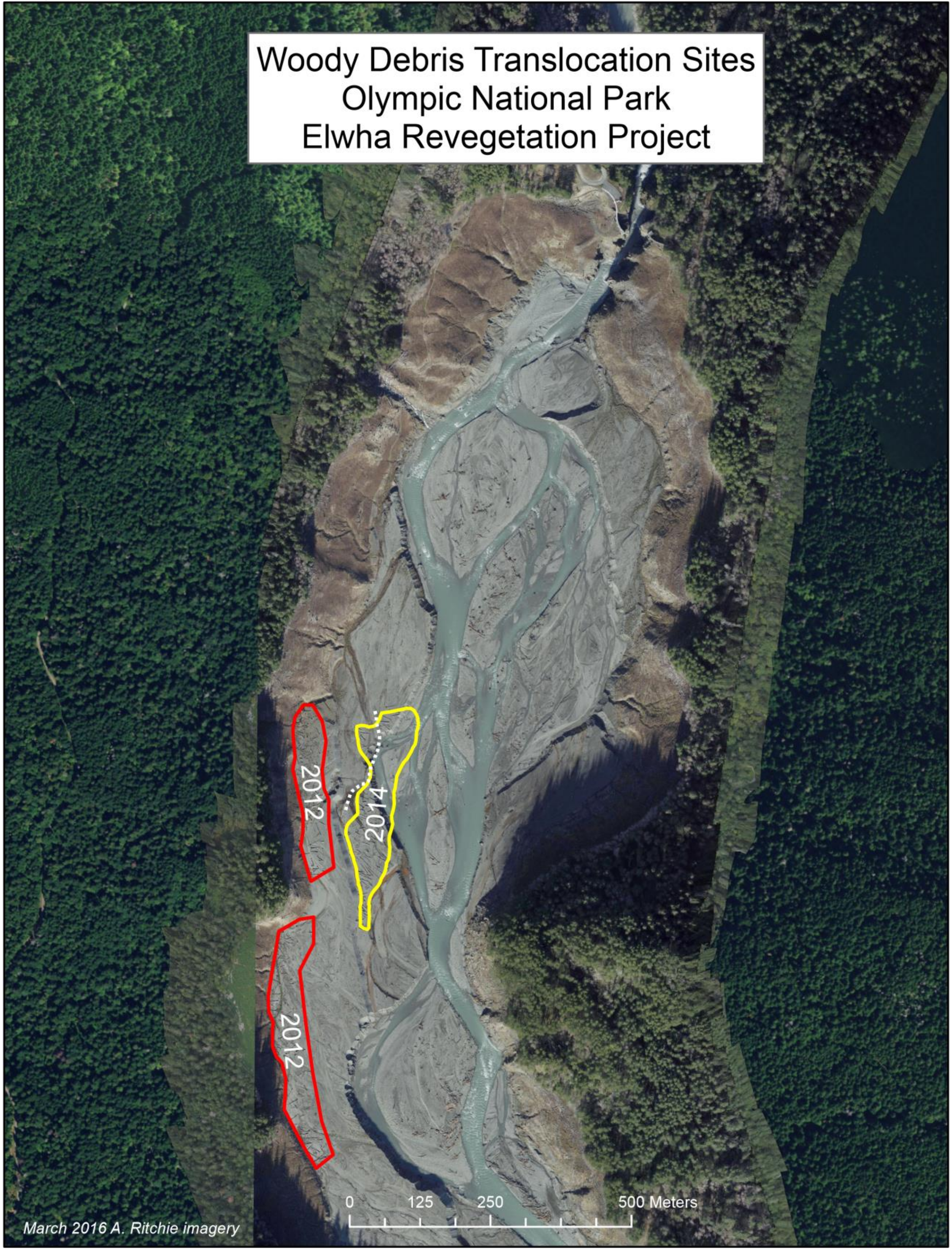

Table C. Ranges of values for distance from the forest edge (m). Distances were measured at the plot level and obtained using map tools in ArcGIS.

Variable	Mean	Min	Max	Std. Dev.
Distance to forest (m)	89.0	28.0	248.0	43.6

Table D. Interaction plot of log-transformed species richness by plot type and treatment type. Mean species richness was higher on seeded cluster and non-wood plots, but slightly lower on and seeded root-wad and simple plots.

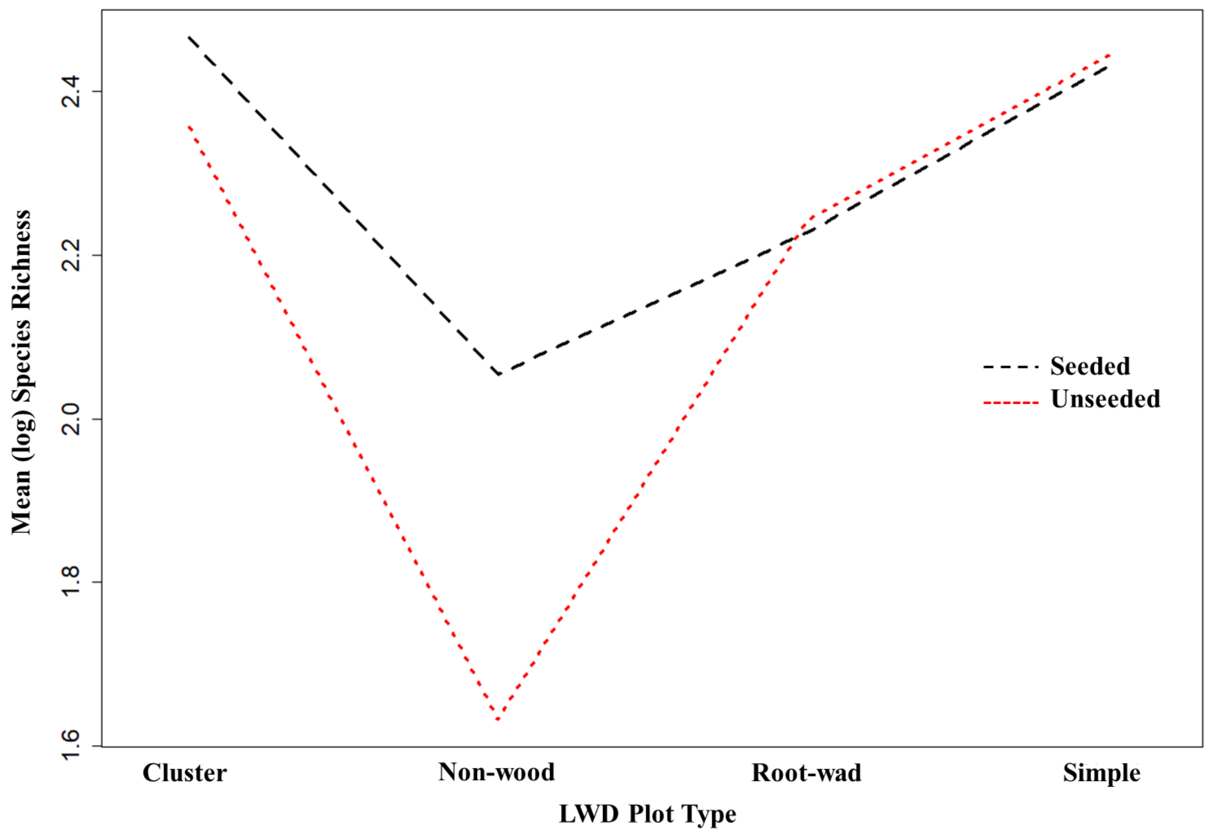

Table E. Kendall’s tau correlations between distance from forest and Shannon-Weiner diversity, species richness, plant abundance, and percent exotic species. Shannon-Weiner diversity, species richness, and percent exotics were all significantly negatively correlated with distance, while plant abundance was not correlated, based on p-values (α=0.05).

Response Variable	**Kendall's tau**	***P-value***
Shannon-Weiner diversity	-0.240	0.002
Species richness	-0.165	0.041
Plant abundance	0.026	0.738
Percent exotics	-0.276	<0.001

Table F. Nonmetric multidimensional scaling (NMDS) ordination of species composition on unseeded plots in the former Lake Mills reservoir following dam removal on the Elwha River, WA, with unique symbols for each wood plot type. Blue vectors illustrate the relative influence of seed dispersal mechanisms on community composition. Animal dispersal was not significant (*P*> 0.05). Vector length indicates strength of association. Points represent individual plots (N=77). Stress value=0.16.

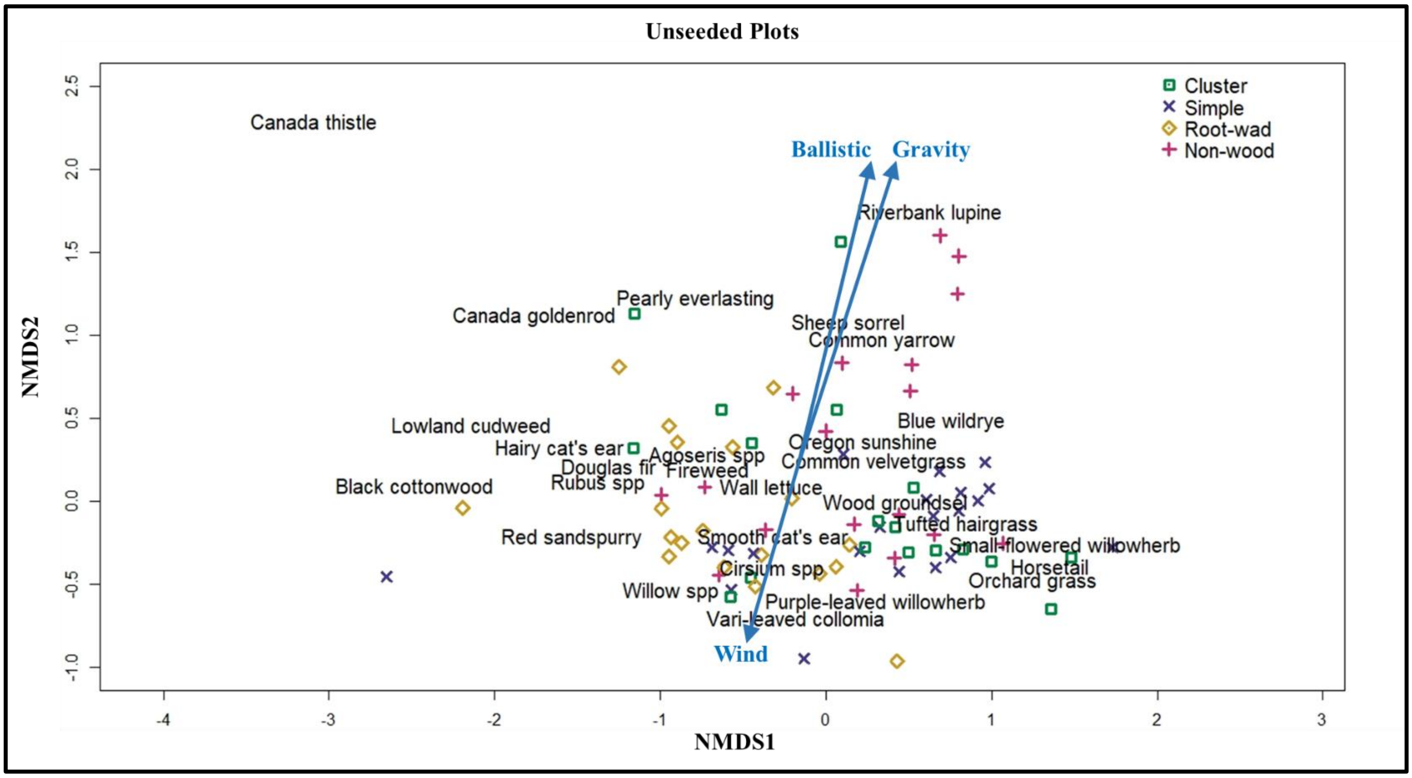

Table G. Post-hoc pairwise comparisons of species composition among wood plot types in unseeded treatment areas the former Lake Mills reservoir following dam removal on the Elwha River, WA. Pairwise comparisons reveal that species composition among cluster, simple, and non-wood plots did not differ, but cluster, simple, and non-wood plots differed significantly from root-wad plots, based on adjusted *P-values* (in bold text).

Plot Comparisons	**Df**	**SS**	**F**	**R^2**	**P**
Cluster vs. Non-wood	1	0.581	2.481	0.063	0.138
Cluster vs. Root-wad	1	1.078	4.455	0.113	**0.006**
Cluster vs. Simple	1	0.495	1.867	0.051	0.336
Non-wood vs. Root-wad	1	1.685	7.754	0.169	**0.006**
Non-wood vs. Simple	1	0.594	2.486	0.061	0.090
Root-wad vs. Simple	1	0.846	3.429	0.087	**0.018**

Table H. Nonmetric multidimensional scaling (NMDS) ordination of species composition on seeded plots in the former Lake Mills reservoir following dam removal on the Elwha River, WA, with unique symbols for each wood plot type. Blue vectors illustrate the relative influence of seed dispersal mechanisms on community composition. Animal dispersal was not significant (*P*> 0.05). Vector length indicates strength of association. Points represent individual plots (N=66). Stress value=0.16.

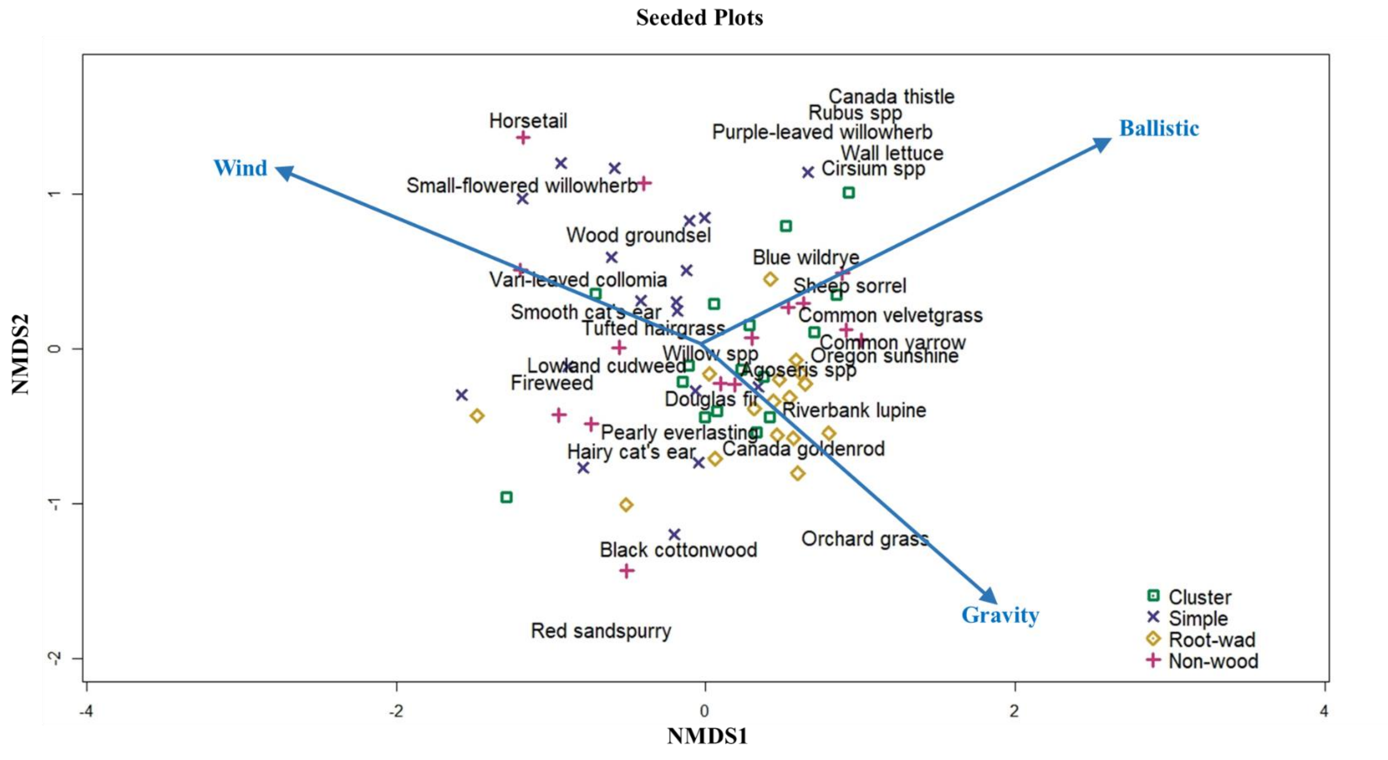

Table I. Post-hoc pairwise comparisons of species composition among wood plot types in seeded treatment areas the former Lake Mills reservoir following dam removal on the Elwha River, WA. Pairwise comparisons reveal that species composition among cluster and root-wad plots, cluster and simple plots, and non-wood and simple plots did not differ, but all other plot combinations differed significantly in composition, based on adjusted *P-values* (in bold text).

Plot Comparisons	Df	SS	F	R^2	P
Cluster vs. Non-wood	1	0.779	3.556	0.100	**0.012**
Cluster vs. Root-wad	1	0.262	1.477	0.047	1.000
Cluster vs. Simple	1	0.208	0.886	0.029	1.000
Non-wood vs. Root-wad	1	1.565	7.841	0.197	**0.006**
Non-wood vs. Simple	1	0.519	2.052	0.060	0.474
Root-wad vs. Simple	1	0.769	3.603	0.107	**0.030**