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Riparian vegetation and the soil seed bank five years after dam removal on the Elwha River, Washington

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RIPARIAN VEGETATION AND THE SOIL SEED BANK FIVE YEARS AFTER DAM REMOVAL ON THE ELWHA RIVER, WASHINGTON

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ABSTRACT

Damming of rivers is widespread and can profoundly impact riparian areas by altering the fluvial processes that drive riparian vegetation communities. Dam removal may reverse these effects; however, very few studies have examined the response of riparian vegetation to large dam removal and associated disturbances, such as the release of sediment. Understanding how dam removal impacts downstream riparian vegetation is crucial as dam removal becomes more common. The Elwha River, Washington, is the location of the largest dam removals to date and provides an unprecedented opportunity to explore questions related to dam removal and riparian vegetation. The objectives of this study were to 1) look at how riparian vegetation species richness and community composition changed five years after the removal of two large dams on the Elwha, and 2) examine how the soil seed bank relates to riparian landforms and location above and below the former dam sites. To do this I surveyed plant species richness, community composition, and soil seed bank species richness and seed abundance on three riparian landforms (bars, floodplains, and terraces) located above, between, and below the dams. I surveyed the above ground vegetation in 2016 and 2017 and compared it to data collected before dam removal (2005 and 2010) and immediately after removal (2012, 2013, and 2014). The soil seed bank was collected in 2017. Native species richness increased five years after removal on certain landforms, and sediment deposition following dam removal does not negatively impact species richness downstream. Community composition differed above and below the dams five years after removal. The soil seed bank had more species and was more abundant above the dams on floodplains and bars but was sparse below the dams. I expect that native species richness will continue to increase, as sediment continues to work its way through the system and perturbations begin to fall within natural levels. This study represents the largest dataset collected on riparian vegetation following dam removal and provides evidence that removal may increase native species richness, while sediment deposition may limit the soil seed bank.

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1.1 INTRODUCTION

Over half of the large river systems in the world have been impacted by dams (Nilsson et al. 2005) and in the U.S. only ~2% of rivers remain unmodified by dams and levees (Lytle and Poff 2004). Dams alter key hydrologic and geomorphologic processes (Nilsson and Berggren 2000, Poff and Hart 2002, Graf 2006) and consequently impact riparian zones (Poff et al. 2007). These zones contain diverse and complex biological communities and provide a range of ecological functions and services (Naiman et al. 1993, Naiman and Decamps 1997, Tabacchi et al. 2000, Sweeney et al. 2004, Arthington et al. 2010). Many of these functions depend on riparian vegetation (Tabacchi et al. 2000) and fluvial processes, such as flooding and sediment deposition. These processes create different riparian landforms, such as bars, floodplains, and terraces, which often have distinct vegetation communities due to differences in flow regime and sediment characteristics (Hupp and Osterkamp 1996, Bendix and Hupp 2000, Lytle and Poff 2004, Latterell et al. 2006, Merritt et al. 2010).

By trapping sediment within reservoirs, dams limit the amount of sediment traveling downstream (Nilsson and Berggren 2000, Poff and Hart 2002, Rood et al. 2005). Sediment starvation below dams can cause channel incision (Kondolf 1997), which can limit overbank flooding and intensify the disconnect between the river and the floodplain (Schneider et al. 2003, Pollock et al. 2007, Jacobson et al. 2011). By altering natural flow regimes and the river-floodplain connection, dams can impact the biota that has adapted to certain flood intensity, frequency, and timing (Poff et al. 1997, Bendix and Hupp 2000, Shafroth et al. 2002, Lytle and Poff 2004, Solari et al. 2016). Removing over-bank flooding and the lateral exchange of materials (such as sediment and nutrients) can drastically impact floodplain species (Rood et al. 2005), possibly by allowing them to progress to a later successional community and become more like upland vegetation (Merritt and Cooper 2000). Dams have also been shown to limit hydrochory (seed dispersal by water) and downstream propagule dispersal which negatively effects recruitment of native species and allows for invasive or non-native plant invasions (Greet et al. 2012, Cubley and Brown 2016). Dams may also indirectly impact vegetation through other means, such as blocking of fish movement (Nilsson and Berggren 2000), which can limit marine derived nitrogen in the system (Duda et al. 2011a).

As many dams approach the end of their intended lifespan it often makes economic and environmental sense to remove them (Bednarek 2001, Babbitt 2002, Poff and Hart 2002, Doyle et al. 2003). However, there have been few completed studies looking at the effects of dam removal on riparian vegetation downstream of the dams. It is unknown whether the return of the drivers of riparian vegetation, such as flooding, fluvial change, and hydrochory, will translate to a return to pre-dam riparian vegetation communities. Additionally, dam removal may introduce addition perturbations to the system.

The removal of dams can cause increased downstream sediment movement (Bednarek 2001), which may temporarily raise channel bed height, alter over-bank flood frequency, change riparian landforms, and alter soil characteristics (Pizzuto 2002). For example, the removal of the Condit Dam on the White Salmon River, Washington, exposed 1.8 million m^3 of sediment, of which 1 million m^3 was transported out of the drained reservoir within fifteen weeks, raising the channel bed height by over a 1 meter (Wilcox et al. 2014). Abundant sedimentation can bury existing understory vegetation and provide nutrients and a bare surface for plant recolonization, potentially by invasive species (Jurik et al. 1994, Gleason et al. 2003, Asaeda and Rashid 2012). As little as 0.5 cm of sediment can reduce seedling emergence by 91.7% (Gleason et al. 2003). However, the release and deposition of fine-grained sediment may also increase herbaceous vegetation encroachment, especially if the sediment is high in total nitrogen content (Asaeda and Rashid 2012). Furthermore, some riparian tree species may be killed by heavy sediment deposition, while some may experience compensatory growth (Kui and Stella 2016). The characteristics of the sediment (such as texture and nutrient content) may also play a role in how species adapt to deposition. This change in sediment dynamics following dam removal is expected to lessen with time, as the old reservoir beds incise and stabilize. However, it may take years or decades for downstream areas to recover from impacts of this sedimentation (Pizzuto 2002), and it is unknown how this change in the sediment regime related to large dam removals may impact downstream vegetation.

The Elwha River on the Olympic Peninsula in Washington State is the site of the largest dam removal project to date and provides a rare opportunity to examine how large dam removals affects downstream vegetation. Two dams impounded the Elwha River; the lower Elwha Dam (33m), which was built between 1910 and 1913, and the Glines Canyon Dam (64 m), which was built between 1925-1927. From 1945 until their removal the dams were operated to allow water to flow out of the reservoir at the rate it flowed in. The dams blocked hydrochory (Brown and Chenoweth 2008), as well as sediment, which decreased the presence of newly deposited land forms and led to later successional floodplain forests (Kloehn et al. 2008, Shafroth et al. 2016). Both dams were removed in stages between 2010 and 2014, beginning with the Elwha Dam and ending with the larger Glines Canyon Dam. While the final piece of the Glines Canyon Dam was not removed until 2014, both reservoirs were drained by 2012.

Before dam removal, native species richness was 45% lower and community composition differed compared to their reference sites above the dams (Clausen 2012). In the first two years after dam removal, species richness and community composition did not change significantly from pre-removal conditions (Cubley 2015); however, hydrochory was restored (Cubley and Brown 2016). Examining the immediate impact of dam removal is not sufficient to understand how removal may impact downstream vegetation in the long term. While riparian areas may respond quickly to change, it can still take many decades for the communities associated with specific landforms to change to new types, with regular disturbance limiting succession (Latterell et al. 2006). However, in areas that experience significant geomorphic and hydrologic change, vegetation may respond in as short as five years (Lisius et al. 2018). Large movement of sediment downstream may delay the recovery of riparian vegetation. Thus, long-term monitoring is needed to better understand the effects of large dam removal on downstream vegetation.

The objective of my research was to test the hypothesis that dam removal can restore riparian vegetation communities downstream, and that evidence of this can be observed as soon as five years after dam removal. I tested this by documenting changes to riparian vascular plant communities five years after dam removal on the Elwha River. My specific research questions were: 1) would native plant species richness increase, and community composition change downstream from the dams five years after removal 2) what environmental factors drive vascular plant community composition after dam removal, and 3) does sediment negatively impacted plant species richness? I predicted that after five years, native species richness would increase below the dams, and community composition would become more like upstream reference cites. I also predicted that nonnative species richness would increase downstream of dams, particularly on the bar and floodplain landforms. Furthermore, I expected sediment deposition to impact both native and nonnative species, with lower native species and higher nonnative species on landforms with more sediment deposition.

1.2 METHODS

Study area

The Elwha River is located on the north side of the Olympic Peninsula in western Washington State, and runs south to north into the Strait of Juan de Fuca (Figure 1.1). It is 72 km long and drains a watershed of 833 km^2, 80% of which lies within Olympic National Park (East et al. 2015). The lower segment of the river is owned by the Washington Department of Fish and Wildlife, private land owners, and the Lower Elwha Klallam Tribe. The river alternates between steep canyons and wide valleys and experiences a wide rainfall gradient of around 600 cm to 100 cm from the headwaters in the Olympic Mountains to the mouth of the river near Port Angeles, Washington (Duda et al. 2011). The Elwha Dam was located 7.1 river kilometers above the mouth and the Glines Canyon dam was located at river kilometer 21.6. Over their lifetime, the dams trapped 21 ± 3 million m^3 of sediment (Randle et al. 2015), starving the downstream segments of fine-grained sediment, which led to a more cobble-dominated riverbed. The removal of the dams released roughly 7.3 million m^3 of sediment (as of 2015), and raised the channel bed by ~1 m, with much of the erodible sediment expected to work its way through the system within a few years (East et al. 2015, Warrick et al. 2015).

The presence of the dams created three river segments—the upper segment, which is located above both dams (~28-32 river kilometers above the mouth), the middle segment, which is located between the two dams (~15-21 river kilometers above the mouth), and the lower segment, which is located below both dams (~2-7 river kilometers above the mouth). The upper segment, unimpacted by the dams, served as my reference site. An ideal reference would have been an undammed reference river, but undammed rivers in the area had substantially different geomorphology, climate, or land use making them unsuitable.

Field sampling

At each river segment (upper, middle, and lower), five valley-wide transects were set up perpendicular to the river, as described in Shafroth et al. (2016; Figure 1.1). Each transect was placed to represent common riparian landforms and vegetation patch types. Landforms were determined using stand age and vegetation types, and further classified into bars, floodplains, and terraces. At each transect, 100 m^2 vegetation plots were established, randomly stratified across riparian landforms, and spaced to represent separate vegetation patch types and to avoid pseudoreplication.

At each plot we measured vascular plant species composition and cover. Vegetation was identified to species level using Hitchcock and Cronquist (1979). Species names and native status were updated using the ITIS and USDA Plants Databases, respectively (ITIS 2018, USDA 2018). Species cover was estimated using midpoints of modified Braun-Blanquet (1964) cover classes (trace, 0-1%, 1-2%, 2-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95%, 95-100%). Within each plot, we estimated ground cover percentage of water, sand/soil, bedrock, gravel, bryophytes/lichens, wood, and litter/organic matter, measured soil depth at each corner using a 119 cm soil probe, and estimated surface sediment grain size using a Wolman pebble count (Wolman 1954). Plot elevation was measured using a total station and a Real Time Kinematic GPS. Surveying was done two years before dam removal (in 2005 and 2010) and five times after dam removal (in 2012, 2013, 2014, 2016, and 2017). A list of plots sampled by year is provided in Table 1.1. Not all plots were sampled in all years; some plots were lost to erosion and channel movement, lost due to construction of engineered logjams in the lower river segment or created due to bar development. Furthermore, not all plots were sampled each year due to different sampling priorities in some years (e.g. in 2014, when plots with new sediment deposition were prioritized).

In 2016, soil samples were collected from each plot. Soil subsamples were collected a depth of 10 cm after removing the litter layer, from eight locations surrounding the vegetation plot. The subsamples were pooled by plot and stored in a cooler before being transported back the Eastern Washington University where they were dried at 60°C for 48 hours. They were then sieved and sent to Brookside Laboratories Inc. (New Bremen, OH) to test texture (percent clay, silt, sand, and organic matter), and common metrics of fertility and soil development, including: total exchange capacity, pH, estimated nitrogen release, S, P, Bray II P, Ca, Mg, K, Na, H, B, Fe, Mn, Cu, Zn, Al, NO_3-N, and NH_4-N.

Data analysis

To determine whether species richness increased on landforms downstream from dams, the effect of river segment, year, and landform on native and nonnative species richness was analyzed using a mixed model analysis (PROC MIXED in SAS) on all plots sampled each year. In each mixed model I nested transect, a random factor, into river segment, a fixed effect, and used the Satterthwaite method to calculate degrees of freedom to account for departures from homoscedasticity. A subset of this data was used to compare change in species richness from before and after the dam removals and sediment deposition (Table 1.1). To determine estimated sediment deposition, I calculated the difference in elevation at each plot before and after the dams were removed from 2010 to 2016. Plots from year 2016 were used instead of 2017 to increase sample size as elevation was measured for a smaller number of plots in 2017. Change in species richness was calculated for both native and nonnative species between 2010 and 2017. Change in elevation was square-root transformed and compared to change in native and nonnative species richness on the middle and lower river segment and across all landforms using linear models in R version 3.3.2 (R Core Team 2018) and graphed using the ggplot2 package (Wickham and Chang 2016).

We used a non-metric multidimensional scaling ordination (NMDS) and permutational multivariate analysis of variance (PERMANOVA) to compare species composition between 2010 and 2017, river segment, and landform.

Individual plants that could not be identified to species level and species that occurred in less than 5% of the plots in each year were removed from the community analysis. Bray Curtis distance measures and a Wisconsin double standardization were used. Environmental variables were compared to determine which ones were correlated, and then the vectors were plotted onto the NMDS. I used an indicator species analysis to determine what species could be used as indicators for each river segment and landform for 2010 and 2017. I also calculated the relative frequency of occurrence of each species between 2010 and 2017. NMDS plots were created in R version 3.3.2 (R Core Team 2018) using the Vegan package (Oksanen et al. 2018), and the PERMANOVA was performed in Primer 7 and PERMANOVA+ (Clarke and Gorley 2015). The indicator species analysis was performed in R version 3.3.2. (R Core Team 2018) using the indicspecies package (De Caceres and Legendre 2009).

1.3 RESULTS

Species richness

Overall, mean native species richness per plot was 21.8 species and nonnative species richness per plot was 6.5 species. Native species represented 75% of all species, across all landforms, river segments, and years. Across all years, there was higher native species richness in the upper river segment compared to the middle and lower (Table 1.3), however there was no difference in nonnative species richness between river segments across all years (Table 1.4).

Total native species richness increased from both years before removal (2005 and 2010) to 2017 (Figure 1.2, Table 1.2). Native species richness increased from 2010 and 2017 on the middle segment only (Figure 1.3, Table 1.3). Nonnative species richness did not change significantly with time (Figure 1.4, Table 1.4). Both native and nonnative species varied between landform, with higher native species richness in the floodplain and the lowest on the bars (Table 1.3), but with higher nonnative species richness on bars and floodplains than terraces (Table 1.4).

The most sediment deposition occurred on the lower river segment, with a significant difference between the lower river segment and the upper segment (Figure 1.5, Table 1.5), particularly on floodplains (Table 1.5). There was no correlation between change in native or nonnative species richness and sediment deposition on any landform or river segment below the dams (Figure 1.6; Figure 1.7).

Species composition

Plant species composition changed from 2010 and 2017 (Figure 1.8) on lower river segment bars, lower river segment floodplains, and middle river segment floodplains (Table 1.6). In 2010, the lower river segment contained mostly nonnative species as indicators, including *Leucanthemum vulgare, Hypericum perforatum, Digitalis purpurea, and Lapsana communis,* but also contained native species indicators, such as *Oemleria cerasiformis, Rubus parviflora, and Populus trichocarpa.* In 2017 it only contained two nonnative species as indicators (*Cytisus* *scoparius* and *Rubus bifrons*), with *Oemleria cerasiformis, Rubus parviflora, Artemisia suksdorfii, Lonicera involucrata*, and *Dicentra formosa* as native indicators. Nonnative indicator species increased on bar landforms after dam removal, with only native species indicators in 2010 (*Salix sitchensis, Populus trichocarpa, Alnus rubra, Equisetum arvense, and Deschampsia elongata*), and mostly nonnative species indicators in 2017 (*Aira caryophyllea, Senecio sylvaticus, Vulpia myuros, Plantago lanceolata, Senecio jacobaea, and Sonchus asper).* The few native species indicators on bars in 2017 included herbaceous species such as: *Epilobium brachycarpum, Agrostis exarata, Eriophyllum lanatum, Epilobium minutum, and Mimulus guttatus*. The full list of indicator species can be found in Appendix 1.1 and 1.2.

While indicator species are useful for determining which species differentiate different landforms and river segments, they are not necessarily the dominant species in those categories. The dominant species (defined as those having the relatively highest cover – though some of these may still cover less than 20% of the plot) varied among river segments and landforms and are listed in Appendix 1.3. The upper river segment had higher cover of native conifer species, such as *Pseudotsuga menziesii* and *Tsuga heterophylla*, particularly on the terraces. The shrub layer for each landform in the upper segment was dominated by *Rosa* spp. and *Rubus* spp. The herbaceous layer varied by landform, with *Achlys triphylla* dominating the terraces, *Nemophila parviflora* and *Claytonia sibirica* in the floodplains, and grasses (such as *Deschampsia elongata* and *Elymus glaucus)* as well as *Equisetum arvense* dominating the bars.

The dominant species in the middle river segment also varied across landforms, primarily in the herbaceous layer. *Polystichum munitum* was dominant on the terraces, *Equisetum arvense* and nonnative *Dactylis glomerata* dominated the floodplain, and *Agrostis* species were dominant on the bar landforms. The middle segment also contained many nonnative species as dominant species in the herbaceous layer, such as *Phalaris arundinacea*, *Geranium robertianum*, and *Lathyrus latifolius*. The dominant trees and shrubs varied little among the landforms, with *Acer* species, *Alnus rubra*, and *Salix sitchensis* as the dominant tree species and *Symphoricarpos albus*, *Rosa* species, and *Rubus* species as the dominant shrubs across all landforms.

Dominant species on the lower river segment also varied among landforms. *Acer macrophyllum* was the most dominant tree on the terraces, while *Alnus rubra*, *Populus balsamifera*, and *Salix sitchensis* were more dominant on the floodplain and bar landforms. *Oemleria cerasiformis* and *Symphoricarpos albus* were highly dominant shrubs for both the terrace and floodplain landforms, while *Rubus* and *Rosa* species were the dominant shrubs on bar landforms. Herbaceous species were highly variable between landforms, with *Polystichum munitum* dominant on terraces; *Urtica dioica*, *Equisetum arvense*, and nonnative *Geranium robertianum* on the floodplains; and nonnative *Leucanthemum vulgare*, *Hypericum perforatum*, *Phalaris arundinacea*, and native *Equisetum arvense* on the bar landforms.

The dominant species in each river segment and landform generally remained similar between 2010 and 2017, particularly in the terrace landforms and among tree and shrub species. The biggest change in dominant species composition occurred in the herbaceous species on the floodplain and bar landforms. In the upper segment the dominant herbaceous floodplain species changed from *Nemophila parviflora* to *Claytonia sibirica*, and *Deschampsia elongata* to *Equisetum arvense* on the bars. The nonnative grass, *Aira cayophyllea*, also became the second-most dominant herbaceous species on the bars in the upper segment in 2017. On the middle segment the dominant herbaceous species changed from *Dactylis glomerata* and *Polystichum munitum* before the dams were removed, to *Equisetum arvense* and *Phalaris arundinacea* after removal. The middle bars changed from *Agrostis exarata* (a native grass), to *Agrostis stolonifera* (a nonnative grass). Similarly, the dominant species in the lower segment changed from *Urtica dioica* to *Equisetum arvense* on the floodplains, and *Leucanthemum vulgare* to *Equisetum arvense* on the bars. Furthermore, *Equisetum arvense* increased in its relative frequency of occurrence by 30% following dam removal (Appendix 1.4).

In 2017, plant community composition differed among landforms and segments (Table 1.6). The difference in landform is shown on axis 1 of the ordination, while the difference in segment is shown on axis 2 (Figure 1.9). Community composition was correlated with a number of environmental variables including: percent cover of bryophytes/lichens, percent cover litter/organic matter, percent cover of sand/soil, percent cover of gravel/cobble, median particle size, soil depth, percent clay, silt, sand, and organic matter, total exchange capacity, pH, estimated nitrogen release, S, P, Bray II P, Ca, Mg, K, Na, H, B, Fe, Mn, Cu, Zn, Al, No3-N, and NH4-N (Figure 1.9). Most environmental vectors were strongly correlated with axis 1, which was associated with landform. Gravel size and presence of gravel and sand, percent sodium, and pH tended to be higher on bar landforms (Figure 1.9b). All other variables (with the exceptions of copper and percent cover of bryophytes) were higher on plots in the floodplains and terraces (Figure 1.9a).

1.4 DISCUSSION

The increase in native species richness and the changes in community composition below the dams in the five years since their removal suggest that dam removal is gradually restoring downstream riparian plant diversity on the Elwha by increasing the heterogeneity of landforms in the middle river segment, where increased native species richness was primarily seen. This was likely the result of an increase in newly deposited landforms following sediment deposition from dam removal (East et al. 2014). Before dam removal, the middle segment had few newly formed, fine-grained bar surfaces (Kloehn et al. 2008, Shafroth et al. 2016). This pattern is similar to the results of a sediment release on the Kurobe River in Japan where Asaeda and Rashid (2012) found that the thickness of the fine-grained layer following deposition was positively correlated with herbaceous biomass. However, the riverbed is still equilibrating post-dam removal as 7.3 million m^3 of sediment works through the system (Magirl et al. 2015), so these landforms may continue to change.

Regular flood disturbance and sediment deposition/erosion is often a driver of riparian plant diversity (Poff et al. 1997, Brown and Peet 2003), thus increasing flood and sediment disturbance on these landforms may increase species richness. Increases in native species may also be explained by the restoration of hydrochory following dam removal. Three species that became indicators of the lower river segment in 2017 were also found to be transported via hydrochory following dam removal (*Epilobium brachycarpum, Mimulus guttatus, and Senecio sylvaticus*) (Cubley and Brown 2016).

While native species richness increased in the middle segment, it did not increase in the lower segment. This may be due to the sediment deposition downstream following dam removal. In the two years following dam removal, sediment loads were 3 and 20 times higher than the yearly average (Magirl et al. 2015), as more than 7.3 million m^3 of sediment moved its way through the system. While it is unknown how much of this sediment was deposited in the riparian areas, deposition patterns varied across landforms and segments. The upper segment saw little deposition. The middle segment experienced deposition on the bars and floodplains, but to a lesser extent than the lower segment, which experienced the highest amount of deposition across all landforms. Substantial sediment deposition can negatively impact riparian species (Kui and Stella 2016), especially those not adapted to this type of disturbance. Three terraces on the lower segment had deposition above 0.2 meters, whereas no terraces in the middle or upper segment had sediment deposition. This suggests that the lower segment is experiencing the brunt of the sediment deposition, and this may be delaying restoration.

There was no negative correlation between native species richness and sediment deposition. This is contrary to my predictions; I hypothesized that the sediment flux following dam removal would lead to a decrease in native species and an increase in nonnative species. The proportion of native species to nonnative species remained similar to what it was before the dams were removed (Clausen 2012) and is likewise similar to other rivers on the Olympic Peninsula (Planty-Tabacchi et al. 1996). This suggests that plant communities on these landforms are resilient to higher amounts of sediment deposition and flooding, which is consistent with some descriptions of riparian plant species dynamics (Hupp and Osterkamp 1996, Naiman and Decamps 1997, Bendix and Hupp 2000, Lytle and Poff 2004). Furthermore, we may not be seeing an effect of sediment deposition due to the possible timing of the deposition; if it occurred multiple years prior, the plants species may have had time to recover, or if it occurred slowly it may not have been a significant disturbance like it would have been if it occurred during a short period.

Overall, the difference in native species richness among river segments is likely due to the historic presence of the dams. This would also explain the higher species richness in the upper river segment across all years. Before the dam removal, Clausen (2012) found that native species richness was 45% lower below the dams. While native species richness is increasing below the dams, it is still higher in the upper segment. Other possibilities for the difference in native species richness between river segments include land-use, precipitation, or differences due to patterns along the river. Nilsson et al (1989) found that species richness was highest in the middle reach of two rivers in Sweden. This was also found in other studies (Dunn et al. 2006). Our upper segment falls right along the middle of the length of the Elwha, so it is possible that species richness is highest in the upper river segment due to this pattern. This would explain the higher species richness on terrace landforms in the upper segment, which I would expect to be similar across segments if the lower species richness on bars and terraces in the middle and lower segment were do only to the dams. Time will tell whether species richness in the middle segment continues to rise to upstream levels, and if it does, it will be strong evidence that the low diversity of the middle segment was driven by the dams.

Native species richness was highest on the floodplains and lowest on the bars. This is consistent with the intermediate disturbance hypothesis, which suggests that the highest diversity will be found in areas with intermediate levels of disturbance (Connell 1978). This has also been observed in other riparian studies (Biswas and Mallik 2010, Mligo 2016) However, some studies have found the highest species richness on the most frequently flooded landforms, such as bars (Brown and Peet 2003).

Community composition also differed between each landform and segment and was correlated with a subset of environmental variables that were consistent with what Clausen (2012) found before dam removal. This finding is also consistent with riparian ecological theory; riparian zones often have different species communities at different landforms (Hupp and Osterkamp 1996, Bendix and Hupp 2000, Lytle and Poff 2004, Merritt et al. 2010), and this difference is likely due to a difference in abiotic factors (Tabacchi et al. 1998) and disturbance (Brown and Peet 2003). Other studies have shown similar findings on the Elwha and other rivers of the Olympic Peninsula. Shafroth et. al. (2016) found different riparian forest composition and structure associated with landforms on the Elwha, and Latterell et al. (2006) found different vegetation patch types at different riparian landforms on the Queets River. The difference in community composition among river segment is likely due to legacy dam effects, much like species richness.

The highest change in dominant species across each river segment occurred in the herbaceous species of the floodplain and bar landforms, which maybe because the tree and shrub species are longer lived and less likely to experience a change in dominant species in five years following dam removal. Interestingly, nonnative species did not become dominant following dam removal. In fact, on the lower bar, lower floodplain, and middle floodplain, the native *Equisetum arvense* replaced a nonnative species as either the first or second most dominant herbaceous species by cover. However, a few nonnative species did become more dominant after dam removal: *Aira caryophyllea* replaced *Elymus glaucus* as the second most dominant herbaceous species on upper bars, and *Agrostis stolonifera* replaced *Agrostis exarata* as the most dominant herbaceous species on middle bars.

Conclusion

This study represents the largest dataset gathered on riparian vegetation before and after dam removal, and the results suggest that dam removal may increase native species richness downstream of the dams, possibly by creating newly formed landforms and increasing disturbance through flooding and sediment deposition. While no change was observed in the first two years following removal (Cubley 2015), the significant change after five years suggests that it may take more than two years for riparian plant communities to respond to the changes in flow regime, sediment dynamics, and seed supply following dam removal. Furthermore, this provides stronger evidence that the lower levels of native species found below the dams prior to removal (Clausen 2012) was due to the dams, rather than another factor, such as land-use or precipitation.

1.5 TABLES AND FIGURES

Table 1-1. Table showing the number of plots sampled per year for each river segment and landform. To compare change in species richness with sediment deposition I had to look at a smaller subset of data (using 2016 for sediment deposition and 2017 for change in species richness). The number of plots can be seen in the bottom most table.

Year		*Bar*	*Flood*	*Ter*	**Total**
2005	*Up*	15	13	9	**37**
	Mid	3	13	22	**38**
	Low	8	24	11	**43**
	Total	**26**	**50**	**42**	**118**
		Bar	*Flood*	*Ter*	**Total**
2010	*Up*	10	8	7	**25**
	Mid	3	10	16	**29**
	Low	5	17	6	**28**
	Total	**18**	**35**	**29**	**82**
		Bar	*Flood*	*Ter*	**Total**
2013	*Up*	15	11	6	**32**
	Mid	13	10	13	**36**
	Low	11	15	6	**32**
	Total	**39**	**36**	**25**	**100**
		Bar	*Flood*	*Ter*	**Total**
2014	*Up*	7	4	5	**16**
	Mid	8	6	6	**20**
	Low	10	8	4	**22**
	Total	**25**	**18**	**15**	**58**
		Bar	*Flood*	*Ter*	**Total**
2016	*Up*	11	11	4	**26**
	Mid	6	10	9	**25**
	Low	12	15	8	**35**
	Total	**29**	**36**	**21**	**86**
		Bar	*Flood*	*Ter*	**Total**
2017	*Up*	10	10	4	**24**
	Mid	6	10	8	**24**
	Low	8	14	8	**30**
	Total	**24**	**34**	**20**	**78**
		Bar	*Flood*	*Ter*	**Total**
2017 sediment /change	*Mid*	2	10	3	**15**
	Low	1	15	7	**23**
	Total	**3**	**25**	**10**	**38**

Table 1-2 The results from the mixed model analysis looking at the effect of year, river segment, and landform on total species richness. Only significant Tukey pairwise comparisons are shown.

Species Richness (2005, 2010, 2014, 2016, 2017) - Mixed Model Results

Type 3 Tests of Fixed Effects				*Tukey Pairwise Comparison*			
Effect	**DF**	**F**	***p***	**Effect**	**Estimate**	**DF**	**Adj *p***
Year	5	3.04	0.0103	2005:2017	-4.9986	466	0.0343
Segment	2	20.77	<.0001	2010:2017	-5.7037	466	0.0198
Year*Segment	10	1.11	0.3544	Lower:Upper	-7.0285	466	<.0001
Landform	2	27.08	<.0001	Middle:Upper	-6.2361	466	<.0001
Year*Landform	10	0.69	0.7359	Middle (2010):Middle(2017)	-12.0328	466	0.0443
Segment*Landform	4	0.39	0.8133	Bar:Floodplain	-7.8236	466	<.0001
Year*Segment*Landform	20	0.93	0.545	Floodplain:Terrace	6.2015	466	<.0001

Table 1-3 The results from the mixed model analysis looking at the effect of year, river segment, and landform on native species richness. Only significant Tukey pairwise comparisons are shown.

Native Species Richness (2005, 2010, 2014, 2016, 2017) - Mixed Model Results

Type 3 Tests of Fixed Effects				*Tukey Pairwise Comparison*			
Effect	**DF**	**F**	**P**	**Effect**	**Estimate**	**DF**	**Adj P**
Year	5	3.12	0.0089	2010:2017	-3.8086	455	0.0256
Segment	2	13.39	0.0005	Lower:Upper	-8.2455	13.2	0.0006
Year*Segment	10	1.97	0.0349	Middle:Upper	-6.583	15.2	0.0036
Landform	2	37.69	<.0001	Middle (2010):Middle (2017)	-8.9155	456	0.0171
Year*Landform	10	0.9	0.5359	Bar:Floodplain	-7.309	466	<0.0001
Segment*Landform	4	1.02	0.396	Bar:Terrace	-5.0706	453	<0.0001
Year*Segment*Landform	20	1.02	0.4397	Floodplain:Terrace	2.2385	446	0.0209

Table 1-4. The results from the mixed model analysis looking at the effect of year, river segment, and landform on nonnative species richness. Only significant Tukey pairwise comparisons are shown.

Nonnative Species Richness (2005, 2010, 2014, 2016, 2017) - Mixed Model Results

Type 3 Tests of Fixed Effects				*Tukey Pairwise Comparison*			
Effect	**DF**	**F**	**P**	**Effect**	**Estimate**	**DF**	**Adj P**
Year	5	2.05	0.0707	Bar:Terrace	4.1574	450	<0.0001
Segment	2	1.87	0.1904	Floodplain:Terrace	4.4431	441	<0.0001
Year*Segment	10	0.5	0.8882				
Landform	2	46.85	<.0001				
Year*Landform	10	0.46	0.9161				
Segment*Landform	4	3.52	0.0076				
Year*Segment*Landform	20	0.66	0.8636				

Table 1-5. The results from the mixed model analysis looking at the effect of landform and river segment on the change in elevation, a measure of deposition. Only significant Tukey pairwise comparisons are shown (alpha = 0.05)

Change in Elevation (Before [2010] - After [2016]) - Mixed Model Results

Type 3 Tests of Fixed Effects				*Tukey Pairwise Comparison*			
Effect	**DF**	**F**	**P**	**Effect**	**Estimate**	**DF**	**Adj P**
Landform	2	1.81	0.1742	Lower: Upper	0.3632	18.7	0.0032
Segment	2	7.55	0.0043	Lower Floodplain: Upper Floodplain	0.3877	21.9	0.0392
Segment*Landform	4	0.31	0.8726				

Table 1-6 Table showing the results from a PERMANOVA comparing species composition between year, river segment (sect), and landform (land). River segments include upper (up), middle (mid), and lower (low). Landforms include terrace (ter), floodplains (flood) and bars.

PERMANOVA Results		*Pair-Wise Comparisons*			
Factors	**P (perm)**	**Groups Being Compared**	**Avg. Similarity**	**t**	**P (perm)**
Year	< 0.001	2010:2017	24.234	1.882	<0.001
Sect	< 0.001	Low:Mid	25.256	2.371	<0.001
Land	< 0.001	Low:Up	19.985	3.993	<0.001
Year:Sect	0.006	Mid:Up	22.846	2.579	<0.001
Year:Land	0.696	Bar:Flood	25.246	2.883	<0.001
Sect:Land	< 0.001	Bar:Ter	13.345	4.723	<0.001
Year:Sect:Land	0.083	Flood:Ter	23.154	3.967	<0.001
--	--	Low:Mid (2017)	26.763	1.905	<0.001
--	--	Low:Up (2017)	20.000	2.978	<0.001
--	--	Mid:Up (2017)	23.762	1.958	<0.001
--	--	Bar:Flood (2017)	26.451	2.342	<0.001
--	--	Bar:Ter (2017)	13.277	3.641	<0.001
--	--	Flood:Ter (2017)	23.15	2.778	<0.001
--	--	2010:2017 (Low)	29.394	1.900	<0.001
--	--	2010:2017 (Mid)	27.989	1.291	0.046
--	--	2010:2017 (Up)	27.002	1.335	0.022
--	--	2010:2017 (Bar)	29.379	1.382	0.016
--	--	2010:2017 (Flood)	31.114	1.555	0.005
--	--	2010:2017 (Ter)	28.706	1.015	0.378
--	--	2010:2017 (Low Bar)	21.664	1.570	0.007
--	--	2010:2017 (Low Flood)	38.847	1.550	0.016
--	--	2010:2017 (Low Ter)	39.925	1.145	0.224
--	--	2010:2017 (Mid Bar)	42.787	1.267	0.14
--	--	2010:2017 (Mid Flood)	31.325	1.332	0.038
--	--	2010:2017 (Mid Ter)	33.493	0.946	0.524
--	--	2010:2017 (Up Bar)	33.684	1.192	0.128
--	--	2010:2017 (Up Flood)	39.144	1.098	0.224
--	--	2010:2017 (Up Ter)	44.584	0.989	0.457

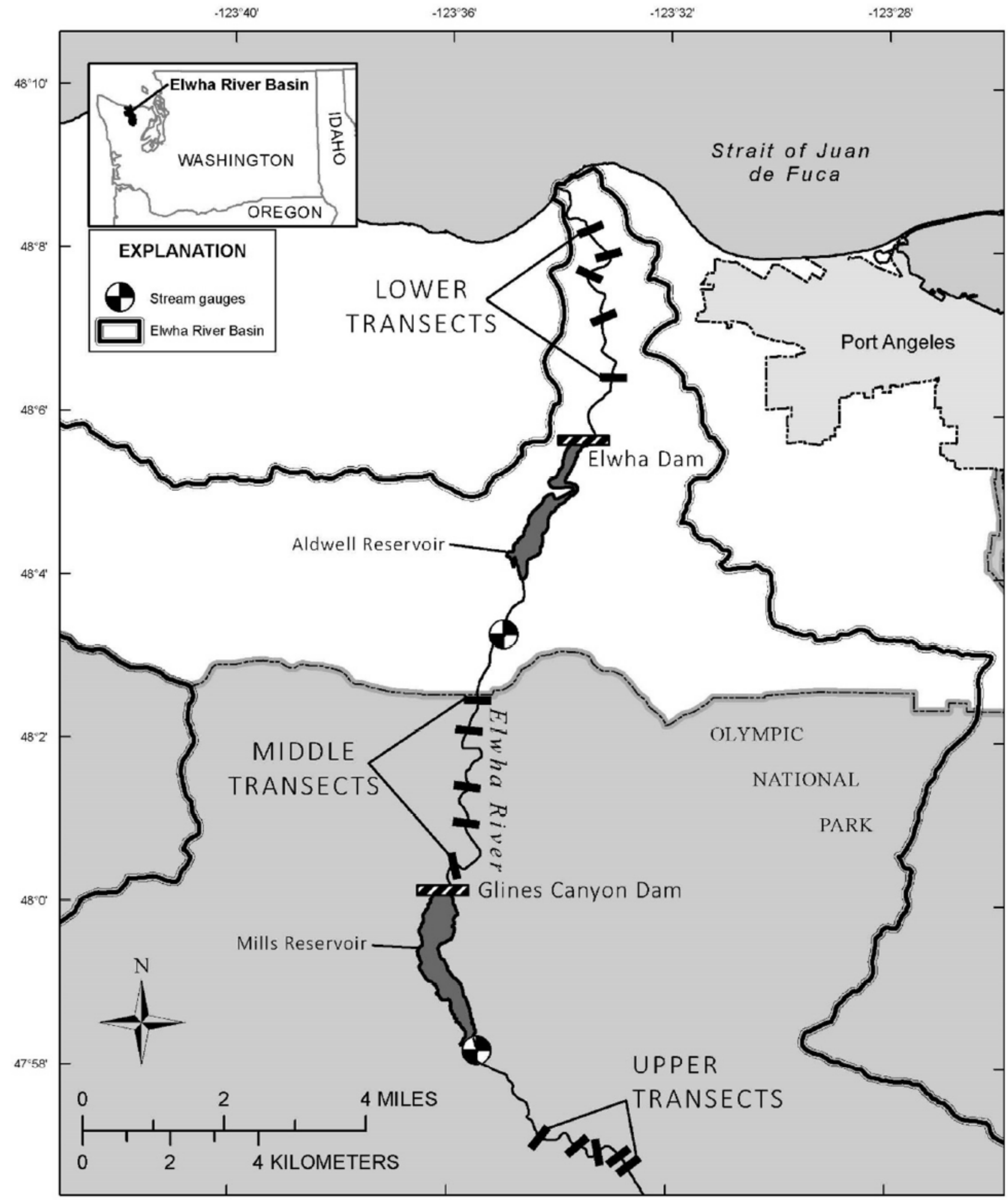

Figure 1.1. A map of the Elwha River and the location of our study sites. Transects are located in the lower, middle, and upper river segment. Map credit: Shafroth et al. (2016).

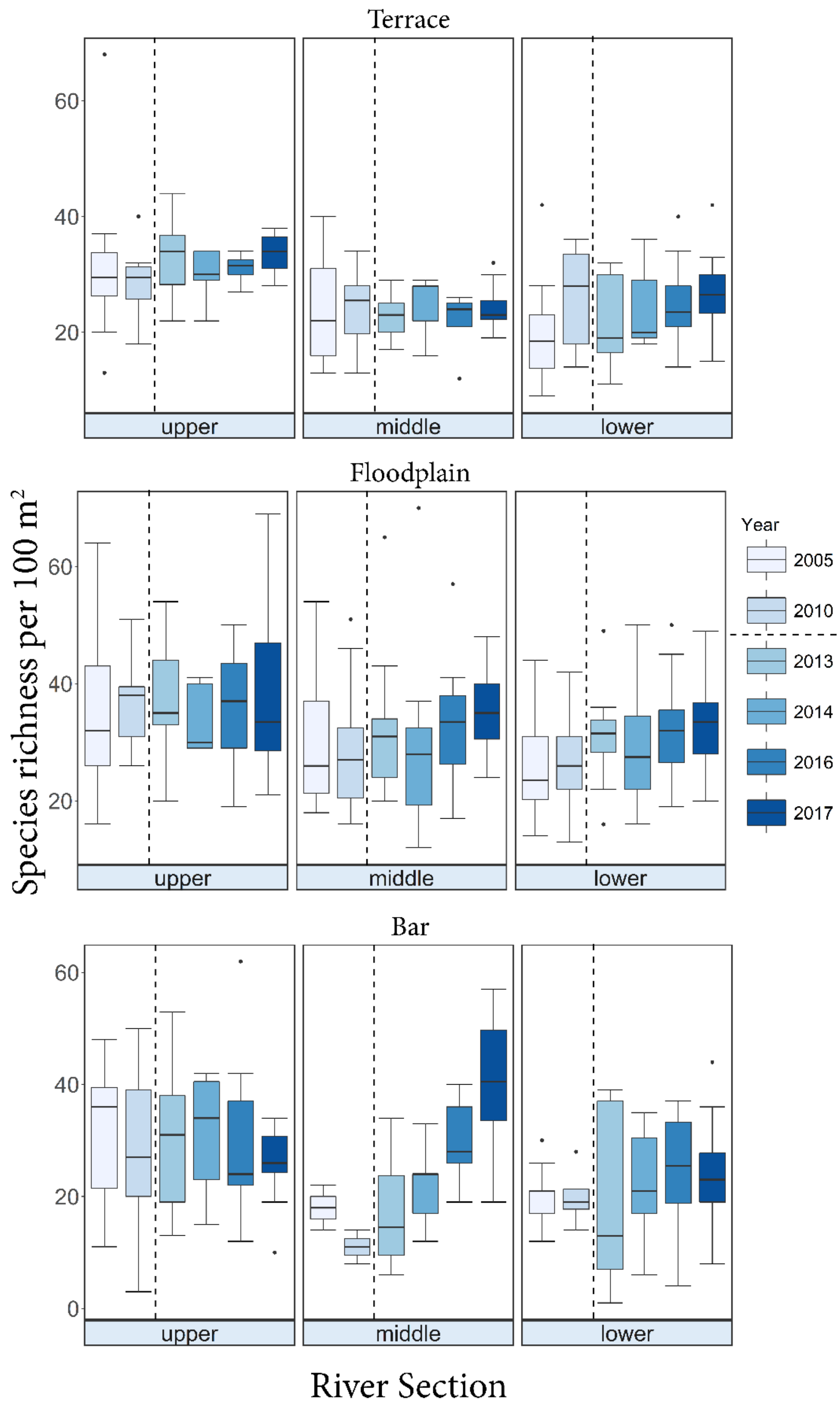

Figure 1.2. Native species richness across all years, by river segment and landform. The dotted line indicates when the dams were removed.

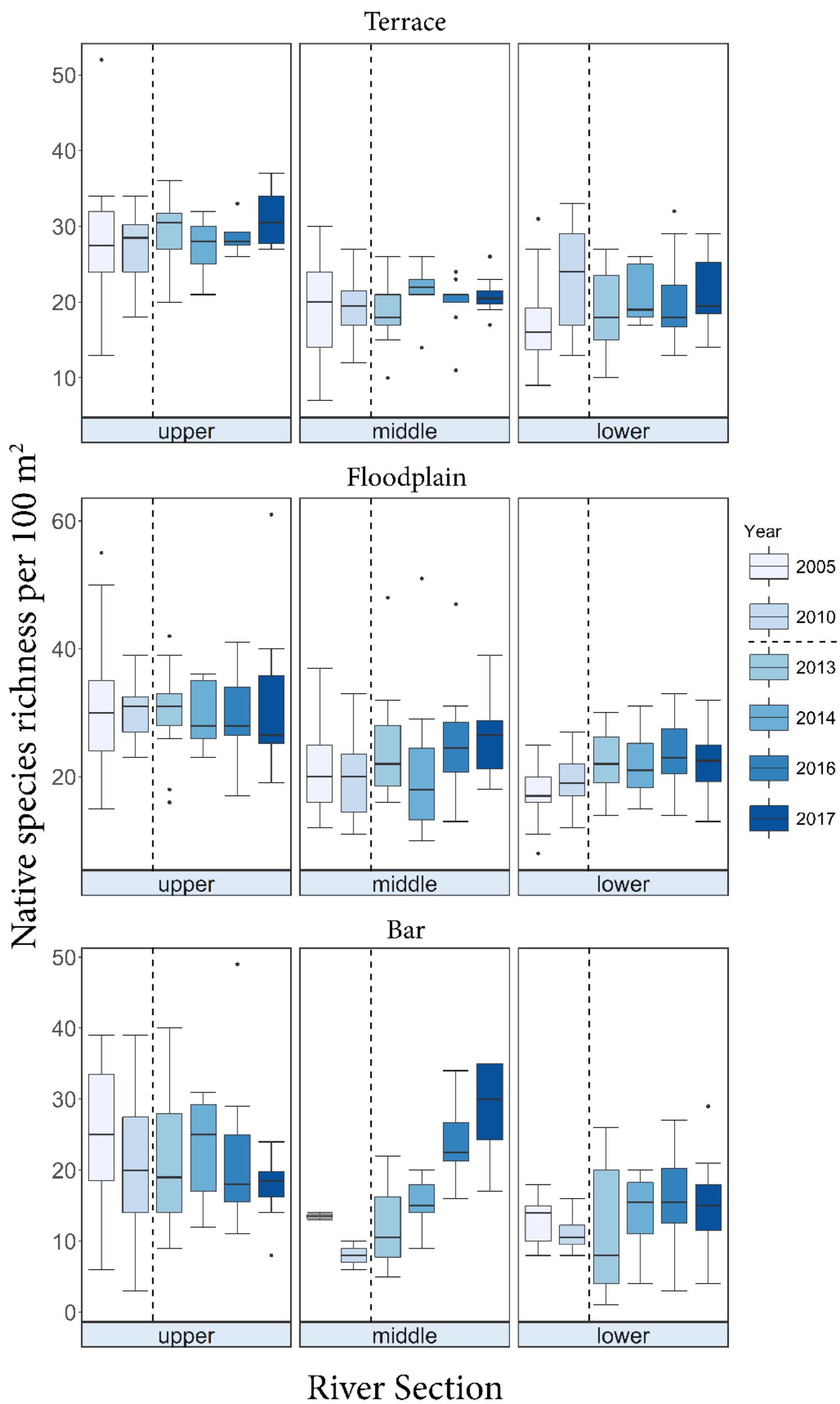

Figure 1.3. Native species richness across all years, by river segment and landform. The dotted line indicates when the dams were removed.

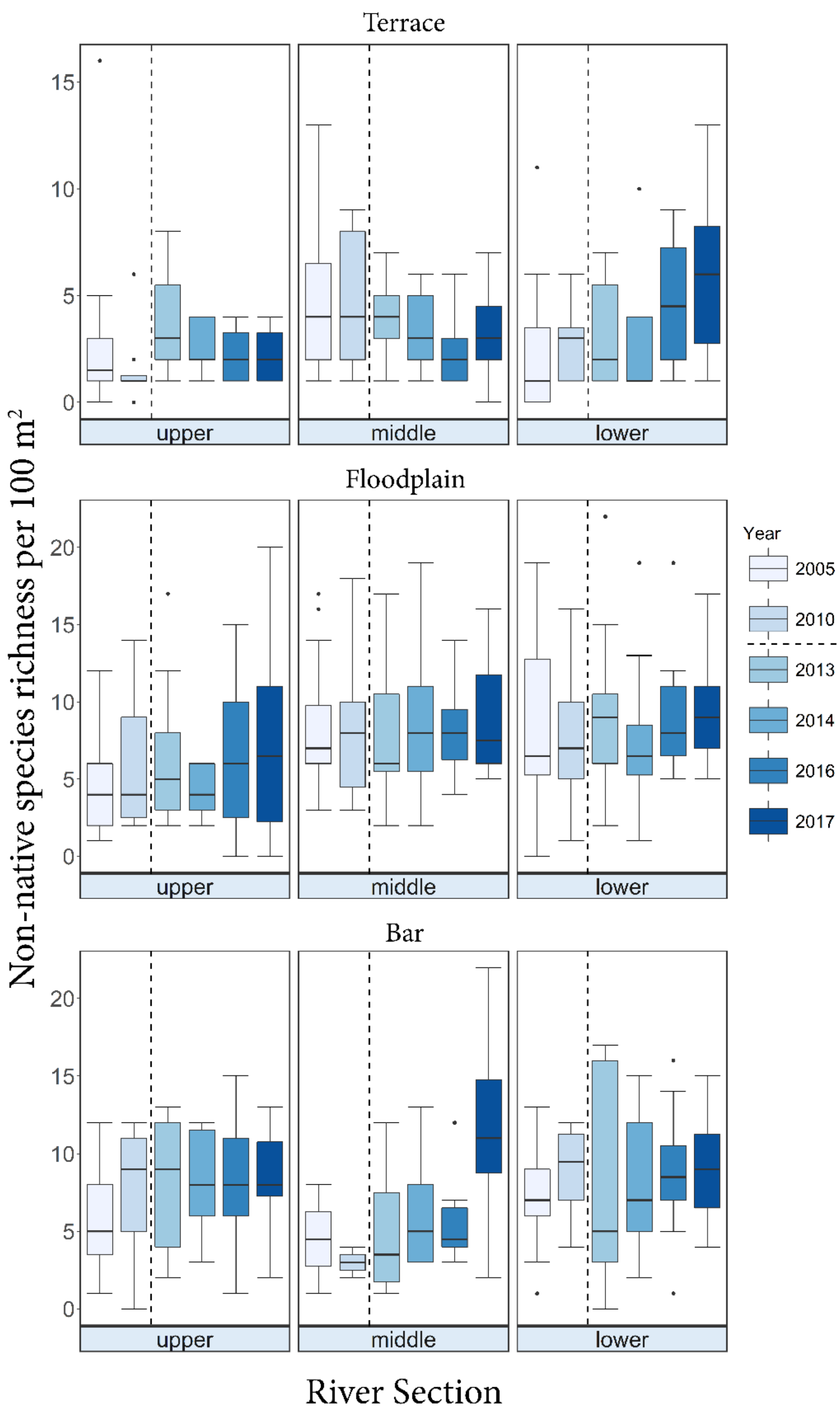

Figure 1.4. Nonnative species richness across all years, by river segment and landform. The dotted line indicates when the dams were removed.

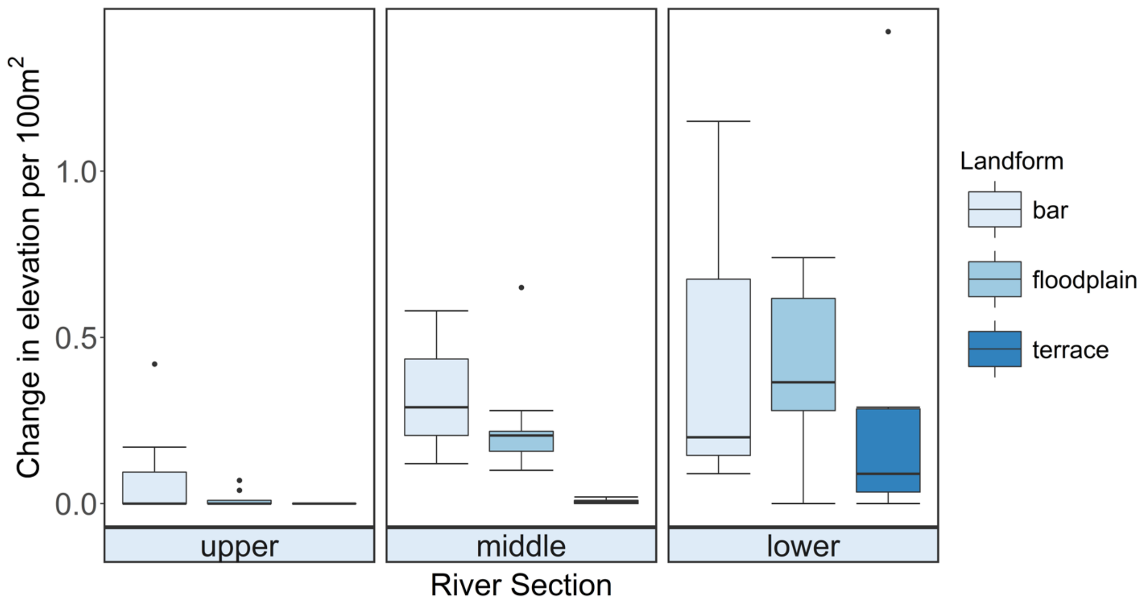

Figure 1.5. Boxplots showing the average change in elevation (between 2010 and 2016) for each plot, by river segment and landform.

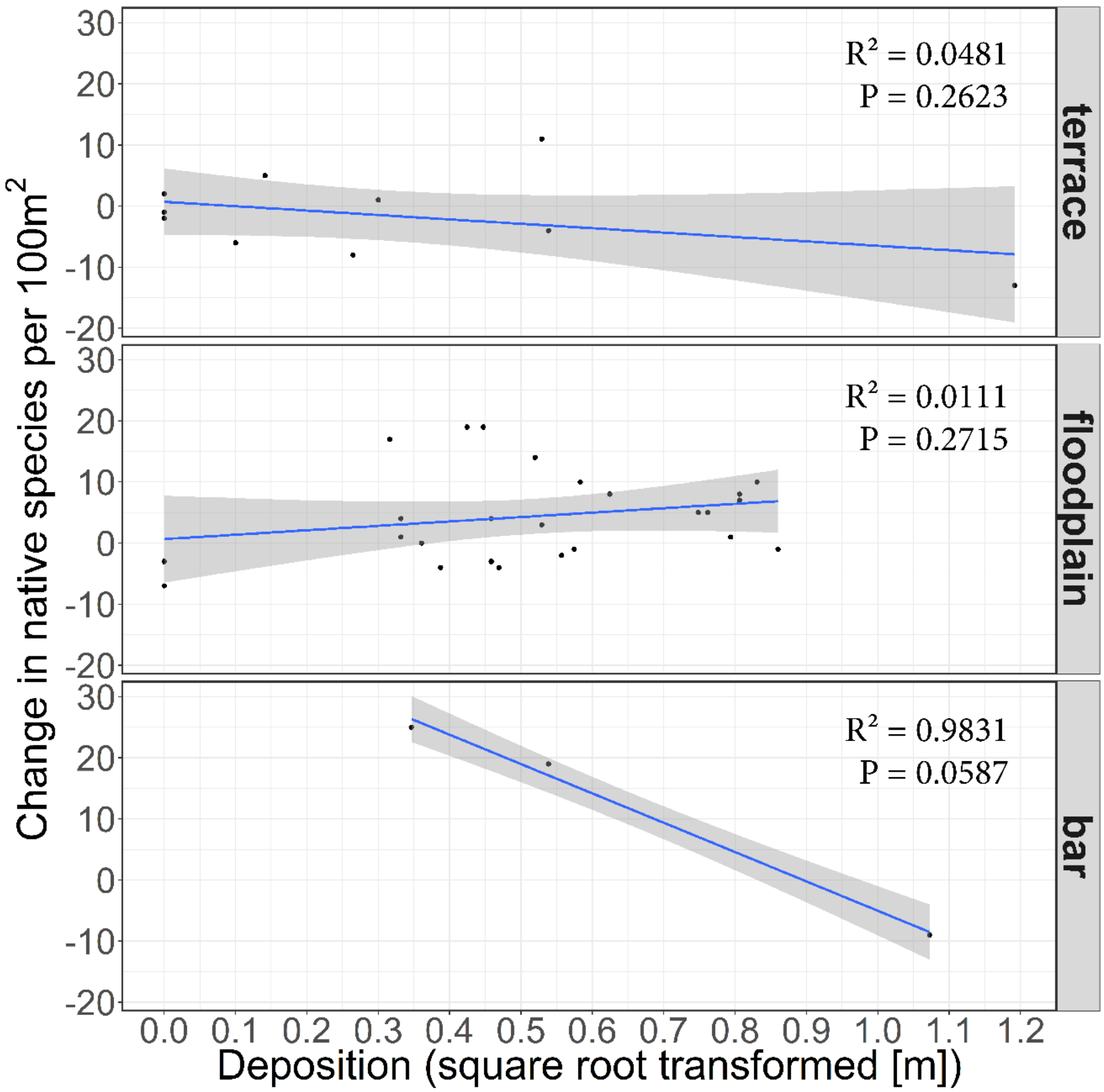

Figure 1.6. Scatter plots and the results from a linear regression showing the relationship between change in native species and deposition downstream of the dams. The shaded area represents the 95% confidence interval.

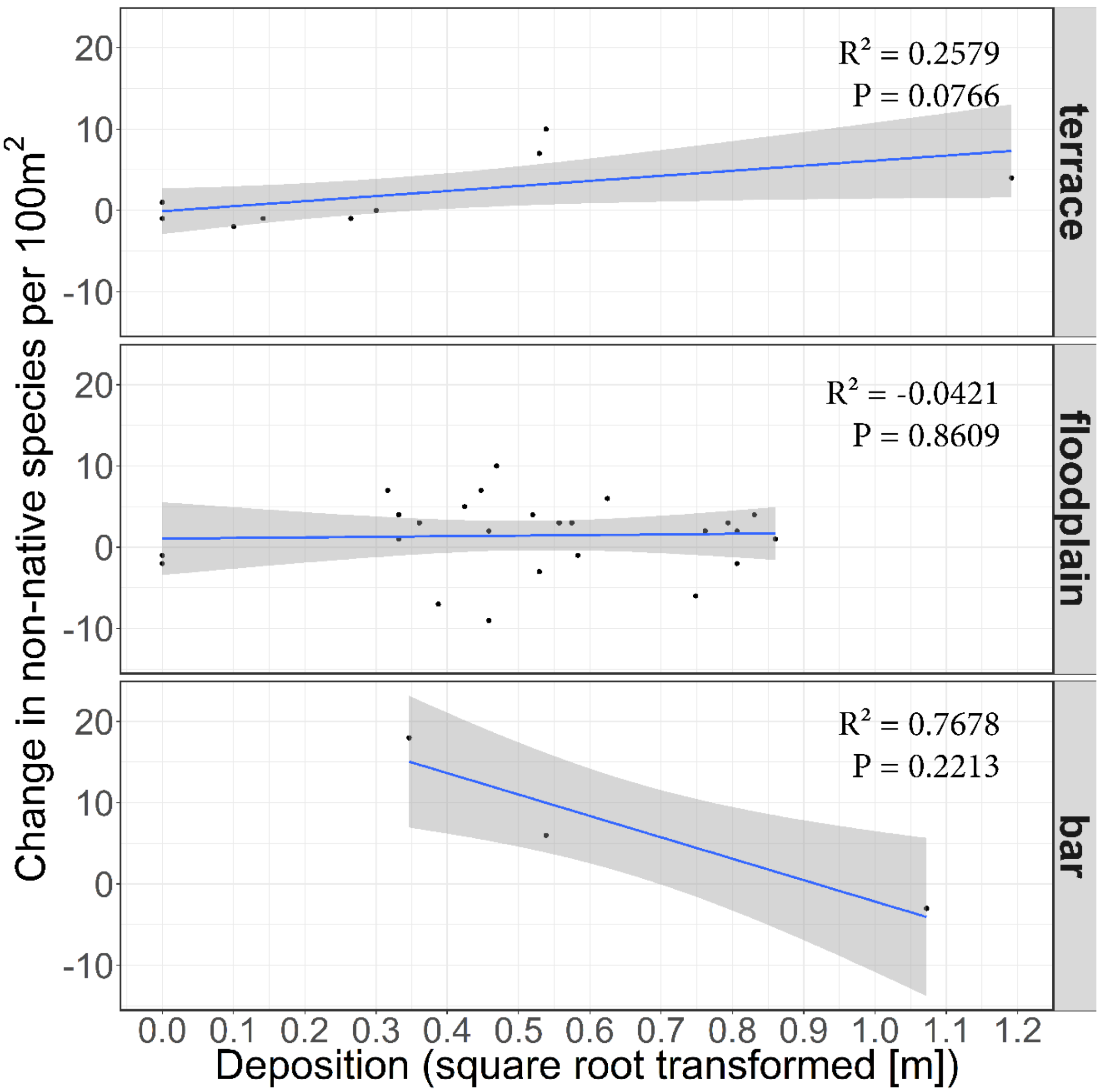

Figure 1.7. Scatter plots and the results from a linear regression showing the relationship between change in non-native species and deposition downstream of the dams. The shaded area represents the 95% confidence interval.

Figure 1.8. NMDS ordination showing the vegetation community composition in 2010 and 2017. k = 3. Stress = 0.18. The two years are significantly different (PERMANOVA: $p < 0.001$)

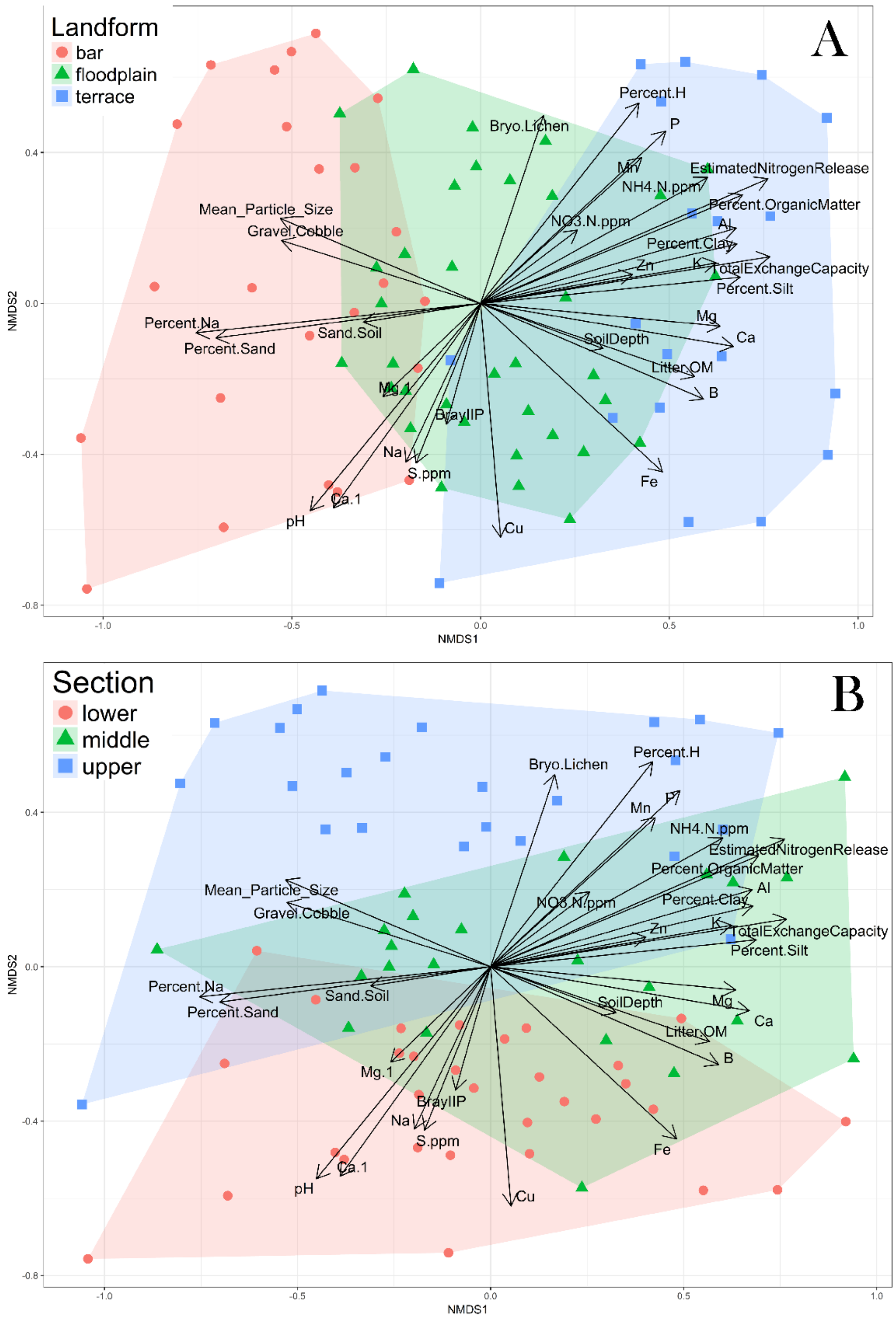

Figure 1.9. NMDS ordination showing 2017 vegetation communities shaded by landform (A) and river segment (B). Significantly correlated environmental vectors are plotted. The direction of the vector indicates the direction of the association, and the length of the line indicates the strength of the correlation. Element units are in mg/kg unless otherwise noted. k = 3. Stress = 0.16.

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Chapter 2 : Riparian soil seed bank characteristics following dam removal on the Elwha River, Washington.

2.1 INTRODUCTION

While dam removals are becoming an increasingly common method to restore rivers, it is still relatively unknown how riparian vegetation downstream of the removed dams will respond (Poff and Hart 2002, Shafroth et al. 2002). Soil seed banks, which can be defined as the collection of viable seeds found in the soil, may play a key role in recolonization and early succession of disturbed landforms following dam removal; however, their dynamics in riparian zones are not well understood (Goodson et al. 2001a). While several studies have stressed the importance of the soil seed bank in wetlands, few have looked at their role in riparian areas or their influence on restoration (Goodson et al. 2001a, Williams et al. 2008a). Most research has found soil seed banks of riparian zones dominated by annual ruderal species (Lu et al. 2010, Greet et al. 2013, O'Donnell et al. 2016), suggesting that they may play a role in early succession following a disturbance. Soil seed banks may also serve as biodiversity reservoirs (Vandvik et al. 2016). Riparian soil seed bank composition may be unique based on riparian landform, similar to above ground vegetation, although this has not been shown in all instances (Williams et al. 2008b, Schwab and Kiehl 2017).

The potential for seed banks to help to restore pre-dam plant communities is relatively unknown. Lu et al. (2010) found a low abundance of species that made up the pre-dam vegetation community in the soil seed bank of the drawdown zone of the Three Gorges Reservoir in China. However, Boudell and Stromberg (2008) found that the soil seed bank of a long-dewatered floodplain contained riparian species, suggesting that riparian vegetation may emerge if fluvial processes are restored. Goodson et al. (2002) found a substantial soil seed bank in old channel segments, which often experience heavy sediment deposition. The soil seed bank has also been shown to correlate with riparian zone health, with less altered riparian systems having a more diverse and less exotic soil seed bank than more disturbed systems (Williams et al. 2008a, Greet et al. 2013).

Dam removal often releases high volumes of sediment (Bednarek 2001), which can blanket riparian landforms (Cubley 2015), bury existing vegetation, and provide nutrients and a bare surface for recolonization (Jurik et al. 1994, Gleason et al. 2003a, Asaeda and Rashid 2012). Sediment carried downstream can contain seeds, often picked up through hydrochory, and these seeds become part of the soil seed bank when the sediment is deposited, while the deposition limits the germination of seeds in the pre-existing soil below (Jurik et al. 1994, Gleason et al. 2003a, Goodson et al. 2003a). Because this sedimentation on top of existing vegetation may reduce local seedling emergence, the seeds that are carried in the sediment may be more likely to germinate than local seed (Goodson et al. 2003). The impact of sediment deposition following dam removal may make the soil seed bank a vital component of restoration following removal. Furthermore, the composition of the seed bank may ultimately determine the success of a river restoration; a seed bank dominated by invasive species may contribute to undesirable recolonization (Williams et al. 2008a), while one with native and desirable species may drive passive restoration (Rubio et al. 2014).

The removal of two large dams on the Elwha River in Washington, provides a rare opportunity to examine the riparian soil seed bank following large dam removal. The Elwha River passed through two dams, Elwha Dam (33 m) and Glines Canyon Dam (64 m). Both dams were built in the early 1900's. The dams trapped sediment, altered downstream morphology (Kloehn et al. 2008), and limited hydrochory (Brown and Chenoweth 2008). They were removed in stages between 2010 and 2014, with most of the reservoirs drained by 2012. In the initial two years following removal hydrochory was restored (Cubley and Brown 2016), but no change in species richness and composition was seen below the dams (Cubley 2015). Five years following removal, species richness had increased, and community composition had shifted as described in Chapter 1.

In this study, I examined the soil seed bank of riparian landforms on the Elwha River five years after dam removal. I aimed to evaluate how the soil seed bank differed above, between, and below the dams, and on different riparian landforms with various levels of sediment deposition. I tested two hypotheses: 1) there would be higher seedbank species richness and germinated seed abundance on landforms above the dams, and 2) there would be lower seedbank species richness and seed abundance on landforms with larger amounts of sediment deposition.

2.2 METHODS

Study area

The 72 km long Elwha River is located in Northwest Washington State on the Olympic Peninsula (Figure 2.1), where it flows south to north from the headwaters in the Olympic Mountains to the Strait of Juan de Fuca, alternating between steep canyons and wide valleys. It encompasses a watershed of approximately 833 km^2, of which about 80% lies within Olympic National Park (East et al. 2015). The rest of the river lies within private, state, and tribal land. The Elwha experiences a wide rainfall gradient, roughly 600 cm annually at the headwaters to around 100 cm annually at the mouth, near Port Angeles, Washington (Duda et al. 2011).

The Elwha was previously impounded by two dams, the upper Glines Canyon dam (located at river kilometer 21.6) and the lower Elwha Dam (located at river kilometer 7.1), which were built in 1927 and 1914 respectively. They were constructed to provide power for local lumber mills and were operated to allow water to flow out as it flowed into the reservoirs (Duda et al. 2008). The dams trapped sediment and woody debris, preventing them from being transported downstream. This altered channel morphology, decreased the presence of newly formed landforms, and may have led to a shift of riparian communities to later successional forests (Kloehn et al. 2008, Shafroth et al. 2016). The dams also blocked hydrochory, potentially limiting downstream seed recruitment (Brown and Chenoweth 2008).

The dams were removed between 2010 and 2014 in stages to allow for sediment to be distributed across the reservoirs, limiting the amount and intensity of sediment movement downstream, and to provide breaks during times when anadromous fish were migrating upstream. The dam removal exposed an estimated 21 ± 3 million m^3 of sediment, of which around 7.3 million m^3 eroded within years of removal, blanketing riparian landforms and causing bed aggradation of approximately 1 m (Cubley 2015, East et al. 2015, Randle et al. 2015, Warrick et al. 2015).

Study design

My study utilized long-term vegetation transects that were established before the dam removal (Clausen 2012). Sets of five transects were located within three different segments of the Elwha River: above the dams (upper), between the dams (middle), and below the dams (lower) (Figure 2-1). The upper segment served as our reference, due to its relatively undisturbed state, natural levels of flooding and sediment transport. Each transect was oriented perpendicular to the river channel, spanning across the riparian landforms in the river valley. Landforms were classified by vegetation patch type and geomorphic surface age class (see Shafroth et al. 2016), and grouped into terrace, floodplain, and bar landform classes. Seventy-four 100 m^2 vegetation plots were located in a stratified random fashion across the vegetation patch types crossed by the transect. Only one plot was positioned in each vegetation patch type crossed by a transect to avoid psuedoreplication.

Field Sampling

Soil was collected from each plot during the summer of 2016 and 2017. A soil core was used to collect soil from 0 to 10 cm deep at 8 locations just outside each vegetation plot, avoiding previously sampled locations. Surface litter was lightly brushed away to expose the soil below before it was collected. This was done to ensure that I collected only seeds found in the soil, rather than recently deposited surface seeds. Each subsample was pooled and mixed thoroughly, before being placed in a cooler. The samples were then cold stratified for 12 weeks until October 2017 in order to break seed dormancy. Plot elevation data was collected using a Real Time Kinematic GPS in 2010 and 2016.

Greenhouse Methods

In October 2017 the seed bank soil was sieved (4 mm) to remove large stones and roots. Three hundred ml of each sample was spread across a 27.94 cm W x 54.28 cm L x 6.20 cm D greenhouse flat filled with five cm of potting soil. Each flat was randomly placed on tables at the Eastern Washington University research greenhouse. Control flats, containing only potting soil, were placed at each table to account for seeds present in the potting soil and seed drift in the greenhouse. No species germinated in the controls. The flats were bottom watered twice weekly and subjected to ambient light for two weeks, two hours of supplemental light during the day for four weeks, and four hours of supplemental light a day for the rest of the study to account for changing season. Supplemental lighting was used to simulate late spring day lengths and was provided by overhead grow lights.

Seeds were allowed to germinate from October 2017 to May 2018. Germinated seedlings were counted and identified to species where possible, using Hitchcock and Cronquist (1973). Flowering individuals were removed to avoid overcrowding and discarded or pressed as a voucher specimen. Species classification (native or nonnative) was obtained from the USDA Plants National Database and scientific names were checked and updated using ITIS (ITIS 2018, USDA 2018).

Data Analysis

A mixed model analysis (PROC MIXED in SAS) was used to compare the effect of landform and river segment on seed bank richness (number of species per plot) and abundance (total number of germinated seeds per plot). In both mixed models I nested transect, a random factor, into river segment, a fixed effect. To account for departures from homoscedasticity in my data, the Satterthwaite method was used to calculate degrees of freedom. A Tukey-adjusted least square means test was used to look at pairwise comparisons. The mixed model analysis was done in SAS 9.4 and graphed in R (R Core Team 2018), using the ggplot2 package (Wickham and Chang 2016).

General linear models (using a Poisson distribution) were used to compare seed bank species richness and abundance to sediment deposition on plots located below the dam sites. Plots from the upper river segment were removed to isolate the effect of deposition following dam removal. To determine estimated sediment deposition, I calculated the difference in elevation at each plot before (2010) and after (2016) the dams were removed. Plots from year 2016 were used instead of 2017 to increase sample size as elevation was measured for a smaller number of plots in 2017. This resulted in a smaller data set for the sediment and seed bank analysis. Species richness and abundance were plotted against sediment deposition. These analyses were performed and graphed in R (R Core Team 2018).

2.3 RESULTS

Overall, 367 total seeds germinated representing 34 species in the seed bank of the 76 plots sampled (Table 2-1). Twenty-one taxa were identified to family, and of those, 12 are classified as nonnative (57%). The most common species found was the native little western bittercress (*Cardamine oligosperma*), followed by multiple grass species and a sedge (*Carex sp.*) that I was unable to identify to species because they did not flower. The most common nonnative species included wall-lettuce *(Mycelis muralis*) and oxeye daisy (*Leucanthemum vulgare*). Only two woody species germinated, thimbleberry (*Rubus parviflorus*) and an unknown blackberry (*Rubus sp*.).

Floodplains contained the most species and seeds. Nonnative species are indicated by NN. *Cerastium arvense, Cirsium vulgare (NN), Crepis capillaris (NN), Galium trifidum, Geranium robertianum (NN), Mimulus sp., Rubus parviflorus, Rumex crispus (NN),* and *Stellaria media (NN)* were all unique to the upper river segment. *Epilobium ciliatum*, *Geranium molle (NN)* and *Holcus lanatus (NN)* were unique to the middle segment. *Rubus sp.* and *Stachys sp.* were unique to the lower segment. The soil seed bank differed from the above ground vegetation (see Chapter 1), with relatively more annual herbaceous species represented. *Cardamine oligosperma* was not found above ground in any plot in 2017. Other species, such as *Mycelis muralis (NN)* and *Leucanthemum vulgare (NN),* were present in the extant vegetation, however there was no consistent pattern between their presence in the soil seed bank and their presence above-ground.

Soil seed bank species richness and abundance was higher in the upper river segment (Table 2.2, Table 2.3). Both species richness and abundance were higher in the upper segment floodplains (Table 2.2, Table 2.3); abundance only was also higher on the upper bars compared to bars in other segments (Figure 2.3). Abundance was similar in upper floodplains and upper bars (Figure 1.3; Table 2.3). There was no significant difference in species richness between bars, floodplains, and terraces on the lower and middle river segment, or bars and terraces on the upper river segment (Figure 1.3; Table 2.2).

Upper river segment floodplains contained higher species richness than all other segment landforms, representing 62% of the species found (Table 2.1). The upper bars and floodplains also contained higher seed abundance, with 67% of all seeds counted (Table 2.1). Soil seed bank species richness and germinated seed abundance both had a negative correlation with newly deposited sediment depth across all riparian landforms on both the middle and lower river segments (Figure 2.4; Figure 2.5). However, the effect of sediment depth on seed species richness or abundance did not vary among the different river segments or landforms.

2.4 DISCUSSION

The high seed bank richness and abundance in the upper floodplains and bars relative to the downstream river segments indicates that dam removal may have altered the downstream soil seed bank on the Elwha River. This may be a legacy of the dams, as similar patterns were found before dam removal in 2005 Brown (2007).

The very limited seed bank below the dams following dam removal could also be explained by the high sediment depth on many of our sites, which may limit the soil seed bank by depletion. Disturbance following sediment deposition on downstream sites created exposed substrate, which may have allowed species to germinate, depleting the soil seed bank. It is possible that this explains patterns in the seed bank that were seen on the Lake Mills Delta before dam removal, where seed bank species richness and abundance decreased with surface age (Hulce 2009). Furthermore, disturbance in agricultural soils that create exposed surfaces has been shown to increase emergence, thus lowering the number of seeds in the seed bank (Feldman et al. 1996, Mulugeta and Stoltenberg 1997). The soil seed bank may have also been limited due to burial and mixing with sediment, or by loss of seed viability.

While many seed bank studies show that the majority of seeds can be found in the top 10 cm of soil, it may be different for riparian areas, due to the frequent cycles of erosion and deposition (Goodson et al. 2001). A study by O'Donnell et al (2014) examined the seed bank at different soil depths on rivers in Australia and found that the highest propagule abundance and species richness was found 20-30 cm deep on landforms that experience frequent fluvial disturbance. This suggests that I may not have sampled deeply enough. However, it is questionable how ecologically viable seeds at that depth are: as little as 0.25 to 0.5 cm of sediment has been shown to significantly reduce seedling emergence (Jurik et al. 1994, Gleason et al. 2003). Unless further erosion occurs, it is unlikely that seeds at that depth will germinate.

It is also possible that the sites with sediment deposition simply did not contain many seeds. Brown and Chenoweth (2008) found that the sediment trapped behind Glines Canyon Dam contained few seeds and Michel et al. (2011)

found low seed rain on the exposed sediments behind Glines Canyon dam and downstream floodplains. However, downstream hydrochory has increased following dam removal (Cubley and Brown 2016), and seeds from hydrochory can mix with sediment and be deposited together (Goodson et al. 2003b). Some of the most prevalent species found in the soil seed bank, *Cardamine oligosperma* and *Mycelis muralis,* were also represented in the hydrochorous seeds trapped following removal (Cubley and Brown 2016).

The patterns I found in seed bank species richness and abundance among landforms (higher on floodplains and terraces) are similar to other studies, where higher species richness and abundance are often found in riparian areas that experience intermittent flooding. Bornette et al. (1998) found the lowest propagule species richness in sites with frequent flooding, with the highest species richness in sites with intermediate flood frequency. Schwab and Kiehl (2017) found highest seed density and species richness in areas with fluctuating water levels, and less in sites with stable conditions. Many other studies had similar findings, with higher seed density in flooded areas of a drawdown zone (Zhang et al. 2016), and higher seed abundance in flooded sites (Capon and Brock 2006). Additionally, O'Donnell et at. (2014) found the highest species richness on river benches (a raised bar, similar to an early developing floodplain), but highest seed abundance on bars, similar to my findings.

These results suggest that in natural conditions, fluvial processes, such as flooding and sediment deposition, are a major driver of soil seed banks in riparian zones. The soil seed bank may have fewer species on the terraces due less mixing of soil and sediment; seeds may not have had any mechanism to enter the soil from the litter layer. Furthermore, seeds in the soil of more mature landforms may have been there for a longer time period and may no longer be viable. Hulce (2009) found less species richness and germinated seeds on older landforms on the Lake Mills delta before the dams were removed on the Elwha.

Over all I found a relatively sparse seed bank on the Elwha River (34 species and 367 germinated seeds) compared to other seed bank studies which have found around 50 to 125 species, with seed abundance in the thousands, using similar methodology and replicate sizes (Capon and Brock 2006, Boudell and Stromberg 2008, Araujo Calçada et al. 2015, O'Donnell et al. 2016, Schwab and Kiehl 2017), but in differing ecoregions. However, this discrepancy may be explained by the unusually high sediment depth on many of our sites below the dam, as explained above. Another explanation for the low seed abundance may be the timing of soil collection. Most seed bank studies reviewed collected soil in the winter and spring. Collecting in the summer may limit the number of spring germinating species in the seed bank. However, seasonal variation may not be important in some cases. Soil seed banks are often dissimilar to the above ground vegetation (Goodson et al. 2001b, Hopfensperger 2007), suggesting that seed banks may not noticeably contribute to above ground vegetation communities in stable areas. This further suggests that seeds in the soil seed bank may stay dormant through growing seasons if conditions are not right for germination, limiting the effect of season on seed bank species richness and abundance. However, when conditions are right, such as after a disturbance, the seed bank can germinate and contribute more to the community.

It is also worth noting that the seed bank germination method I used only allowed observation of germinated seeds and does not necessarily account for all seeds in the soil. Furthermore, the watering regime may encourage germination of some species, while inhibiting others (Gurnell et al. 2007). Therefore, I may have only observed a fraction of the soil seed bank present in my samples.

In conclusion, the soil seed bank of the Elwha River five years after dam removal exhibited a limited seed bank downstream of the dams compared to our reference segment. This is likely due to a combination of legacy dam effects and increased deposition on landforms that generally contain the majority of the seed bank species richness in riparian zones, such as bars and floodplains. This is supported by the relatively abundant seed bank in the upper segment floodplain and bars, which was not impacted by the dams and experienced little to no sediment deposition in the five years following dam removal. It is unclear whether the limited seed bank found in areas with high sediment deposition is caused by low seed availability in the sediment, seed burial by the sediment, or depletion caused by seeds germinating immediately after deposition.

I predict that the seed bank will increase in species richness and abundance as sediment stabilizes and the natural flow and sediment dynamics return. As the riparian landforms stabilize and the vegetation communities mature, there may be more inputs than losses through germination, leading to an increase in seeds present in the soil. If the landform were to develop into communities typical of terrace landforms, seed bank species richness may level off with only a few dominant species contributing seeds. However, abundance may continue to increase as those species continue to add seeds year after year. Long term monitoring of the soil seed bank following dam removal would give us valuable insights into how the soil seed bank changes through time in areas with sediment deposition and few seeds.

2.5 TABLES AND FIGURES

Table 2.1. Plant species found in the soil seed bank by landform and river segment. Total number of species, seed count, and number of plots for each landform is summarized at the bottom. Nonnative species are marked with (NN).

	Upper			Middle			Lower		
	Bar	Flood	Ter	Bar	Flood	Ter	Bar	Flood	Ter
Agrostis sp.					x	x			
Bromus sp.		x		x					
Cardamine oligosperma	x	x	x		x	x	x	x	
Carex sp.		x				x		x	
Cerastium arvense		x							
Cirsium vulgare (NN)		x							
Crepis capillaris (NN)	x	x							
Dactylis glomerata (NN)					x	x			
Dicot 1	x							x	
Dicot 2		x							
Dicot 3		x			x				
Epilobium ciliatum					x				
Festuca sp.	x	x		x	x		x	x	x
Galium aparine						x			
Galium trifidum		x							
Geranium molle (NN)					x				
Geranium robertianum (NN)		x							
Holcus lanatus (NN)					x				
Hypericum perforatum (NN)							x		
Leucanthemum vulgare (NN)	x	x					x	x	
Mimulus sp.	x								
Montia parvifolia		x							
Mycelis muralis (NN)		x	x						x
Phalaris arundinacea (NN)	x						x		
Poacae sp. 1	x	x	x	x	x	x		x	
Poacae sp. 2	x	x	x					x	
Rorippa islandica		x		x				x	
Rubus parviflorus		x							
Rubus sp.									x
Rumex crispus (NN)		x							
Stachys sp.							x		
Stellaria media (NN)		x							
Stellaria sp.		x							
Urtica dioica					x			x	
Total number of species	9	21	4	4	10	6	6	9	3
Total seed count	112	136	11	7	27	14	8	21	8
N	9	10	4	6	9	8	8	14	8

Table 2.2. The results from a mixed model analysis looking at the effect of river segment and landform on soil seed bank richness. Only statistically significant pairwise comparisons are shown.

Seed bank species richness - Mixed Model Results

Type 3 Tests of Fixed Effects				*Tukey Pairwise Comparison*		
Effect	**DF**	**F**	**P**	**Effect**	**Estimate**	**Adj P**
Segment	2.000	12.380	< 0.001	Low:Up	-1.899	< 0.001
Landform	2.000	6.180	0.003	Mid:Up	-1.522	0.001
Reach*Landform	4.000	3.100	0.021	Bar: Flood	-1.169	0.006
--	--	--	--	Flood:Ter	1.026	0.030
--	--	--	--	LowBar:UpFlood	-3.650	< 0.001
--	--	--	--	LowFlood:UpFlood	-3.543	< 0.001
--	--	--	--	LowTer:UpFlood	-3.775	< 0.001
--	--	--	--	MidBar:UpFlood	-3.733	< 0.001
--	--	--	--	MidFlood:UpFlood	-2.956	< 0.001
--	--	--	--	MidTer:UpFlood	-3.150	< 0.001
--	--	--	--	UpBar:UpFlood	-2.622	0.002
--	--	--	--	UpTer:UpFlood	2.650	0.033

Table 2.3. The results from a mixed model analysis showing the effect of river segment and landform on the soil seed bank seed abundance. Only significant pairwise comparisons are shown.

Seed bank species count - Mixed Model Results

Type 3 Tests of Fixed Effects				*Tukey Pairwise Comparison*		
Effect	**DF**	**F**	**P**	**Effect**	**Estimate**	**Adj P**
Segment	2.000	19.080	< 0.001	Low:Up	-8.532	< 0.001
Landform	2.000	4.310	0.017	Mid:Up	-7.726	< 0.001
Reach*Landform	4.000	2.690	0.039	Flood:Ter	4.300	0.013
--	--	--	--	LowBar:UpBar	-11.444	< 0.001
--	--	--	--	LowBar:UpFlood	-12.900	< 0.001
--	--	--	--	LowFlood:UpBar	-10.944	< 0.001
--	--	--	--	LowFlood:UpFlood	-12.400	< 0.001
--	--	--	--	LowTer:UpBar	-11.444	< 0.001
--	--	--	--	LowTer:UpFlood	-12.900	< 0.001
--	--	--	--	MidBar:UpBar	-11.278	0.002
--	--	--	--	MidBar:UpFlood	-12.733	< 0.001
--	--	--	--	MidFlood:UpBar	-9.444	0.005
--	--	--	--	MidFlood:UpFlood	-10.900	< 0.001
--	--	--	--	MidTer:UpBar	-10.694	0.001
--	--	--	--	MidTer:UpFlood	-12.150	< 0.001
--	--	--	--	UpTer:UpBar	9.694	0.046
--	--	--	--	UpTer:UpFlood	11.150	0.010

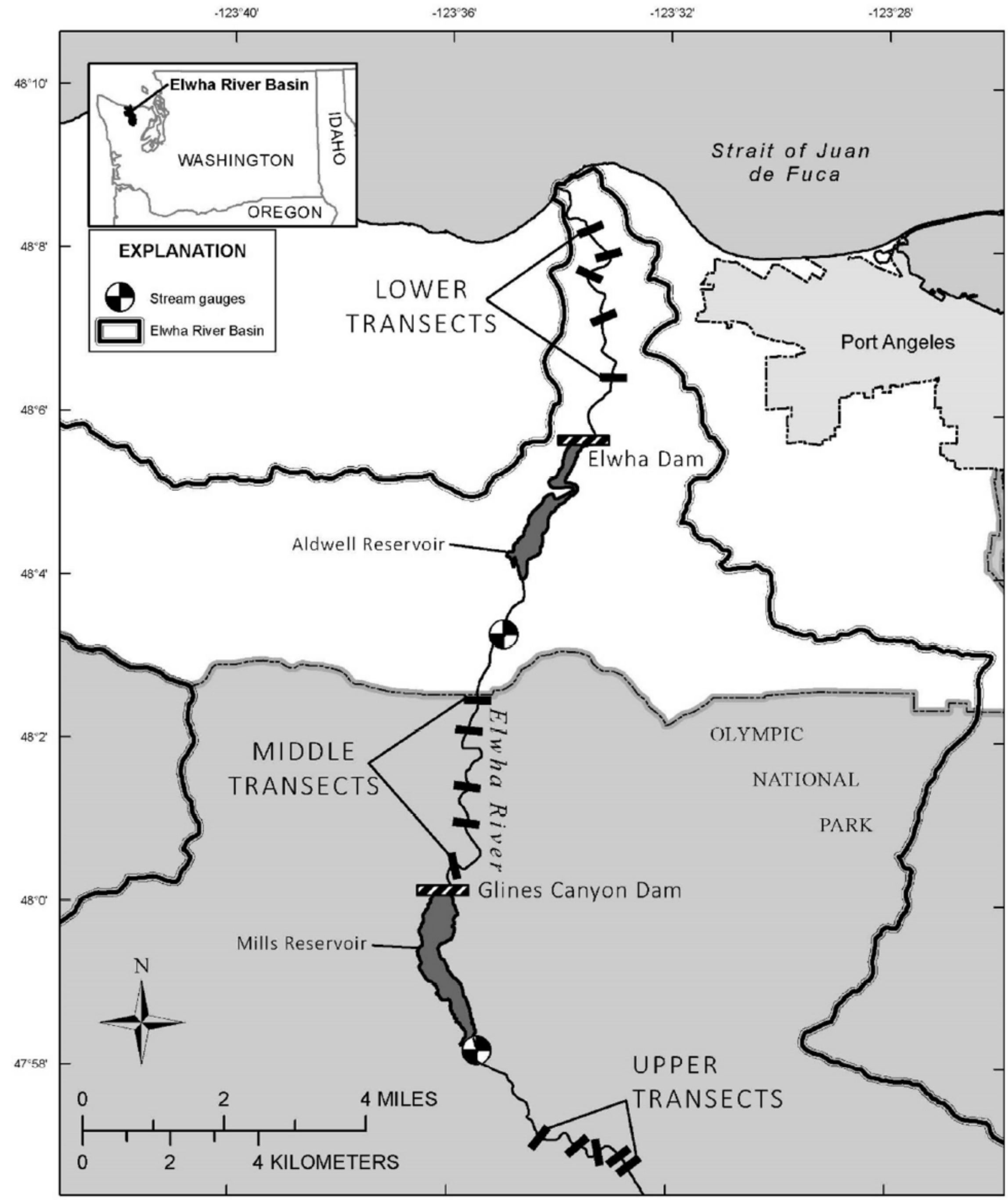

Figure 2.1. A map of the Elwha River and the location of our study sites. Transects are located in the lower, middle, and upper river segment. Map credit: Shafroth et al. (2016).

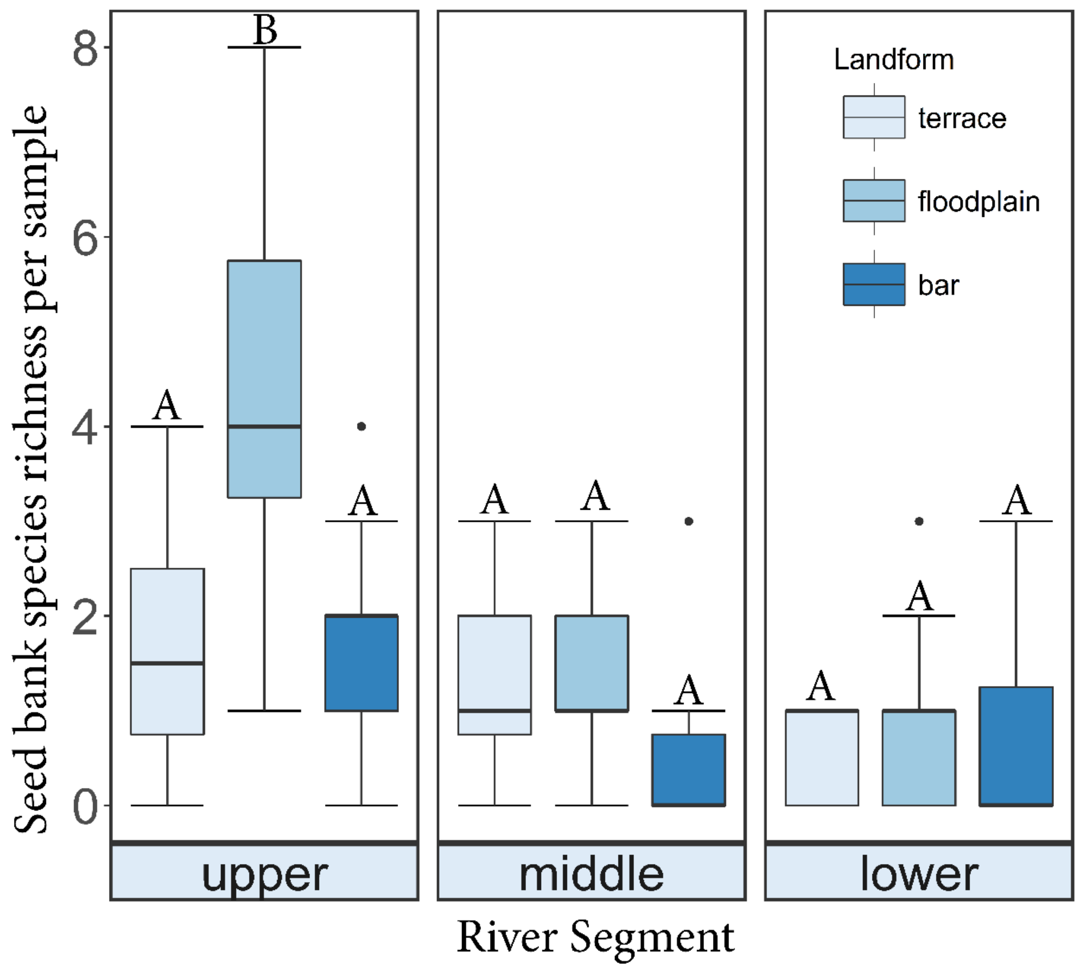

Figure 2.2. Boxplot showing the average seed bank species richness (per sample collected from 100 m² plot) between river segment and landform. Different letters denote significance between groups. The effect of river segment and landforms was tested using a mixed model analysis.

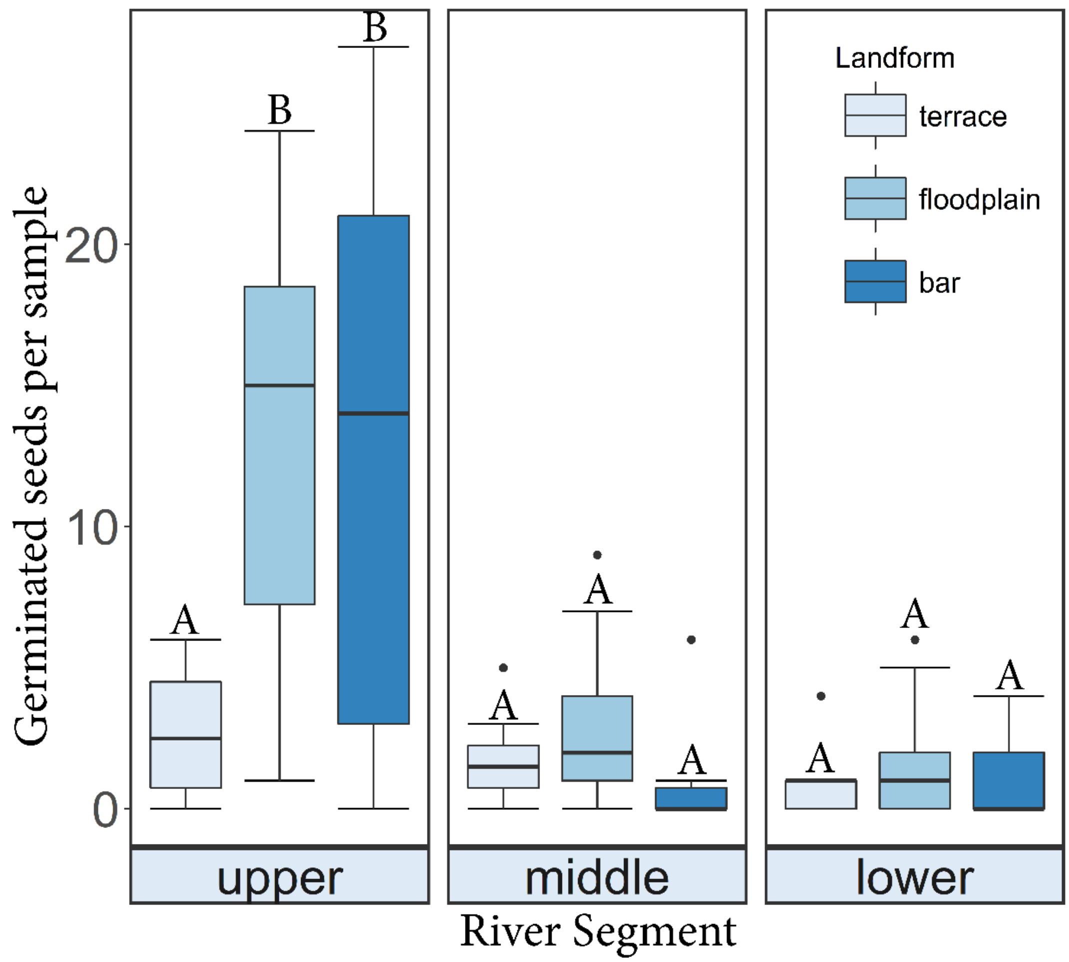

Figure 2.3. Boxplot showing the average seed bank germinated seed abundance (per sample collected from 100 m² plot) between river segment and landform. Different letters denote significance between groups. The effect of river segment and landforms was tested using a mixed model analysis.

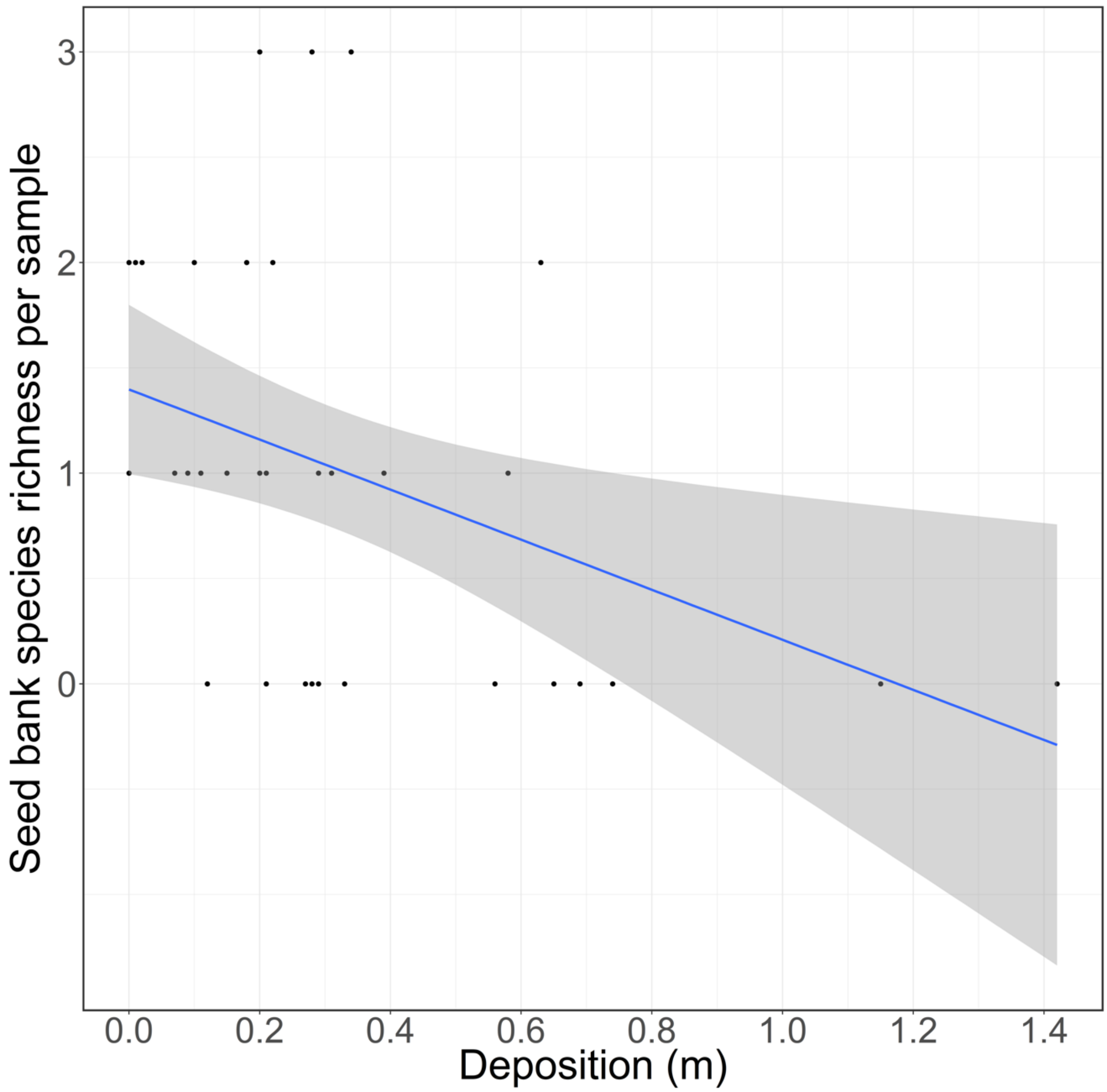

Figure 2.4. Scatter plots showing the relationship between seed bank species richness and deposition below the dams (Poisson regression; slope = -1.771; p = 0.029).

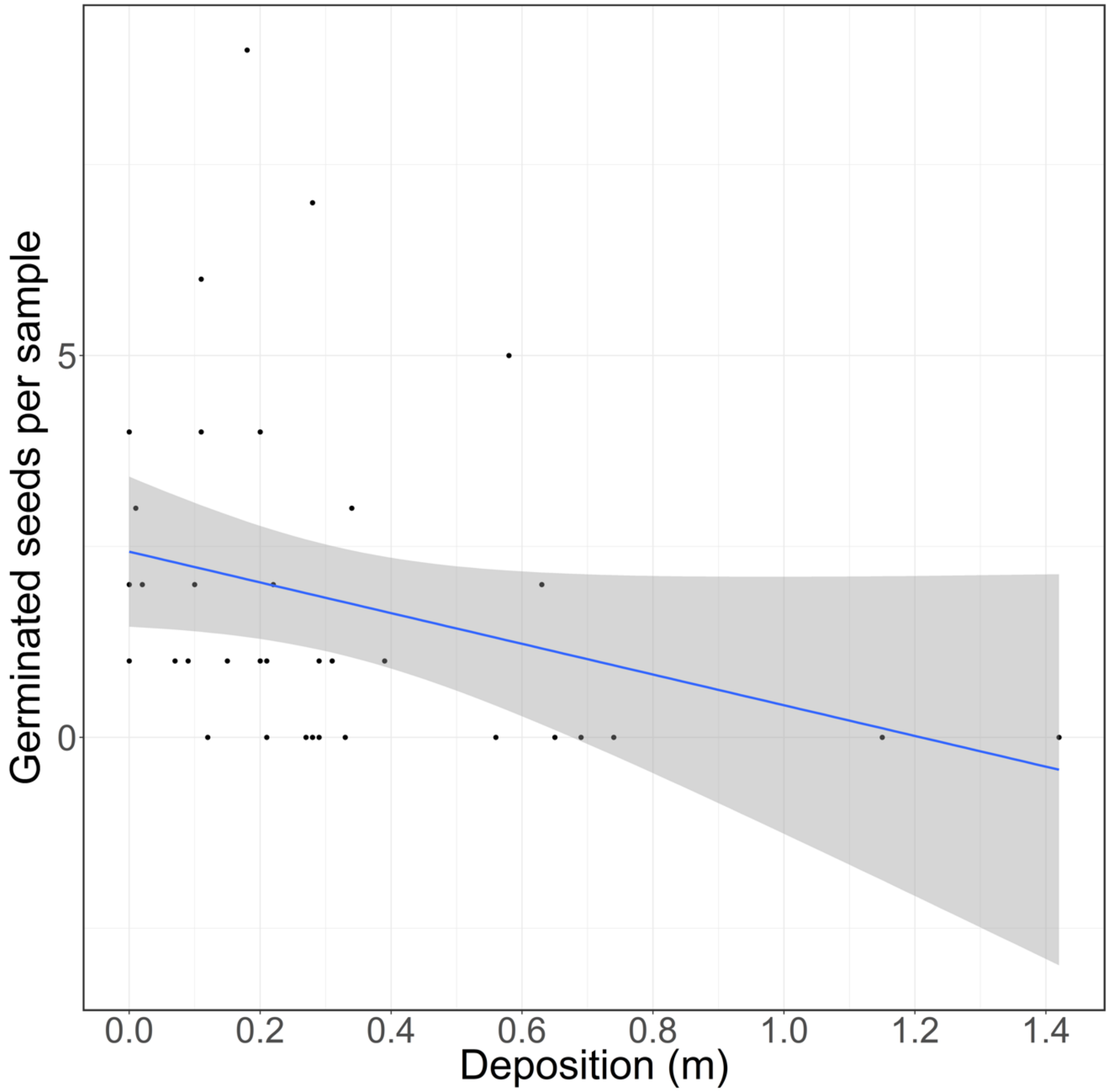

Figure 2.5. Scatter showing the relationship between seed bank and germinated seed abundance and deposition below the dams (Poisson regression; slope = -1.671; p = 0.005).

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APPENDIX I

Appendix 1.1 The results of the indicator species analysis for 2017.

Group	Species	Status	Indicator Value	p
Segment				
Upper	*Fragaria vesca*		0.795	0.005
	Aira caryophyllea	NN	0.674	0.005
	Osmorhiza berteroi		0.664	0.005
	Madia gracilis		0.612	0.005
	Nemophila parviflora		0.571	0.005
	Anaphalis margaritacea		0.564	0.005
	Epilobium brachycarpum		0.559	0.005
	Vulpia myuros	NN	0.547	0.005
	Aira praecox	NN	0.540	0.005
	Achlys triphylla		0.535	0.010
	Rumex acetosella	NN	0.514	0.005
	Tsuga heterophylla		0.493	0.010
	Rubus leucodermis		0.485	0.015
	Phleum pratense	NN	0.456	0.010
	Bromus pacificus		0.437	0.010
	Trientalis borealis		0.436	0.015
	Pteridium aquilinum		0.408	0.020
	Fragaria virginiana		0.381	0.045
	Claytonia perfoliata		0.354	0.050
Middle	*None*	--	--	--
Lower	*Oemleria cerasiformis*		0.848	0.005
	Rubus parviflorus		0.726	0.005
	Artemisia suksdorfii		0.666	0.005
	Cytisus scoparius	NN	0.539	0.005
	Lonicera involucrata		0.504	0.010
	Rubus bifrons	NN	0.503	0.020
	Dicentra formosa		0.491	0.015
Landform				
Terrace	*Polystichum munitum*		0.909	0.005
	Acer circinatum		0.834	0.005
	Thuja plicata		0.640	0.005
	Rosa gymnocarpa		0.624	0.010
	Maianthemum racemosum		0.606	0.005
	Achlys triphylla		0.594	0.005
	Tiarella trifoliata		0.575	0.010
	Adenocaulon bicolor		0.533	0.010

	Tsuga heterophylla		0.508	0.010
	Dicentra formosa		0.506	0.005
	Trientalis borealis		0.489	0.005
	Galium trifidum		0.473	0.020
	Goodyera oblongifolia		0.397	0.015
	Prosartes hookeri		0.397	0.015
	Viola glabella		0.397	0.020
	Pteridium aquilinum		0.396	0.015
	Linnaea borealis		0.375	0.030
Floodplain Bar	*Ranunculus repens*	NN	0.547	0.050
	Epilobium brachycarpum		0.613	0.005
	Aira caryophyllea	NN	0.605	0.005
	Agrostis exarata		0.557	0.030
	Eriophyllum lanatum		0.503	0.010
	Senecio sylvaticus	NN	0.500	0.005
	Vulpia myuros	NN	0.500	0.020
	Epilobium minutum		0.459	0.015
	Plantago lanceolata	NN	0.446	0.010
	Mimulus guttatus		0.404	0.020
	Senecio jacobaea	NN	0.384	0.035
	Sonchus asper	NN	0.377	0.030

Appendix 1.2. The results of the indicator species analysis for 2010.

Group	Species	Status	Indicator Value	p
Segment				
Upper	*Achlys triphylla*		0.704	0.005
	Pseudotsuga menziesii		0.665	0.005
	Osmorhiza berteroi		0.656	0.005
	Fragaria vesca		0.592	0.005
	Collomia heterophylla		0.588	0.005
	Montia parviflora		0.588	0.005
	Galium triflorum		0.587	0.010
	Equisteum arvense		0.586	0.005
Middle	*Geranium robertianum*	NN	0.741	0.005
	Dactylis glomerata	NN	0.725	0.005
	Circaea alpina		0.692	0.005
	Carex deweyana		0.668	0.005
	Symphoricarpos albus		0.658	0.005
	Rubus ursinus		0.653	0.005
	Polystichum munitum		0.061	0.010
	Adenocaulon bicolor		0.546	0.005
	Bromus inermis	NN	0.491	0.005
Lower	*Oemleria cerasiformis*		0.722	0.005
	Leucanthemum vulgare	NN	0.663	0.005
	Rubus parviflora		0.619	0.005
	Populus trichocarpa		0.605	0.015
	Hypericum perforatum	NN	0.600	0.005
	Digitalis purpurea	NN	0.559	0.010
	Lapsana communis	NN	0.547	0.005
Landform				
Terrace	*Acer macrophyllum*		0.712	0.005
	Polystichum munitum		0.699	0.005
	Adenocaulon bicolor		0.656	0.005
	Circaea alpina		0.616	0.050
	Galium triflorum		0.587	0.010
Floodplain	*Mycelis muralis*	NN	0.630	0.025
	Symphoricarpos albus		0.630	0.005
	Oemleria cerasiformis		0.610	0.005
	Rubus ursinus		0.610	0.040
	Dactylis glomerata	NN	0.605	0.010
Bar	*Salix sitchensis*		0.809	0.005
	Populus trichocarpa		0.689	0.005

Alnus rubra	0.658	0.005
Equisetum arvense	0.640	0.005
Deschampsia elongata	0.621	0.005

Appendix 1.3. The top two dominant tree, shrub, and herbaceous species at each river segment, landform, and year, measured by percent cover at 100 m² vegetation plot.

		Terrace		**Floodplain**		**Bar**	
		2010	2017	2010	2017	2010	2017
Upper	Tree	*Pseudotsuga menziesii* *Tsuga heterophylla*	*Tsuga heterophylla* *Pseudotsuga menziesii*	*Alnus rubra* *Salix sitchensis*	*Alnus rubra* *Acer macrophyllum*	*Alnus rubra* *Populus balsamifera*	*Populus balsamifera* *Alnus rubra*
	Shrub	*Mahonia nervosa* *Rosa gymnocarpa*	*Rosa gymnocarpa* *Rubus ursinus*	*Rubus leucodermis* *Rubus ursinus*	*Rubus leucodermis* *Rubus ursinus*	*Rosa nutkana* *Rubus ursinus*	*Rubus ursinus* *Rosa nutkana*
	Herb	*Achlys triphylla* *Linnaea borealis*	*Achlys triphylla* *Polystichum munitum*	*Nemophila parviflora* *Galium aparine*	*Claytonia sibirica* *Tolmiea menziesii*	*Deschampsia elongata* *Elymus glaucus*	*Equisetum arvense* *Aira cayophyllea**
Middle	Tree	*Acer macrophyllum* *Alnus rubra*	*Acer circinatum* *Acer macrophyllum*	*Alnus rubra* *Pseudotsuga menziesii*	*Alnus rubra* *Pseudotsuga menziesii*	*Alnus rubra* *Salix sitchensis*	*Alnus rubra* *Salix sitchensis*
	Shrub	*Symphoricarpos albus* *Rubus ursinus*	*Symphoricarpos albus* *Rubus ursinus*	*Rosa nutkana* *Symphoricarpos albus*	*Rubus ursinus* *Symphoricarpos albus*	*Symphoricarpos albus* *Rubus ursinus*	*Rubus ursinus* *Symphoricarpos albus*
	Herb	*Polystichum munitum* *Dactylis glomerata**	*Polystichum munitum* *Carex deweyana*	*Dactylis glomerata** *Polystichum munitum*	*Equisetum arvense* *Phalaris arundinacea**	*Agrostis exarata* *Geranium robertianum**	*Agrostis stolonifera** *Lathyrus latifolius**
Lower	Tree	*Acer macrophyllum* *Thuja plicata*	*Acer macrophyllum* *Thuja plicata*	*Alnus rubra* *Populus balsamifera*	*Populus balsamifera* *Alnus rubra*	*Salix sitchensis* *Populus balsamifera*	*Alnus rubra* *Salix sitchensis*
	Shrub	*Oemleria cerasiformis* *Symphoricarpos albus*	*Oemleria cerasiformis* *Symphoricarpos albus*	*Oemleria cerasiformis* *Symphoricarpos albus*	*Oemleria cerasiformis* *Symphoricarpos albus*	*Rubus parviflorus* *Symphoricarpos albus*	*Rubus bifrons** *Rosa nutkana*
	Herb	*Polystichum munitum* *Carex mertensii*	*Polystichum munitum* *Petasites frigidus*	*Urtica dioica* *Geranium robertianum**	*Equisetum arvense* *Urtica dioica*	*Leucanthemum vulgare** *Hypericum perforatum**	*Equisetum arvense* *Phalaris arundinacea**

*Nonnative species

Appendix 1.4. Species list for Elwha River including the relative frequency of occurrence for plant species between 2010 and 2017. Only species with a relative frequency of occurrence > 0.01 for either year are shown. The species are ordered by highest occurrence in 2017.

Species	**Relative frequency of occurrence**	
	2010	2017
Acer macrophyllum	0.8	0.77
Mycelis muralis	0.75	0.77
Rubus ursinus	0.69	0.73
Symphoricarpos albus	0.7	0.71
Alnus rubra	0.72	0.69
Elymus glaucus	0.75	0.65
Polystichum munitum	0.71	0.65
Populus balsamifera	0.54	0.62
Dactylis glomerata	0.49	0.58
Salix sitchensis	0.3	0.53
Galium aparine	0.51	0.51
Equisetum arvense	0.19	0.51
Geranium robertianum	0.55	0.5
Rubus spectabilis	0.4	0.5
Abies grandis	0.58	0.49
Oemleria cerasiformis	0.52	0.49
Agrostis stolonifera	0.01	0.46
Circaea alpina	0.36	0.45
Leucanthemum vulgare	0.27	0.42
Carex deweyana	0.39	0.41
Tolmiea menziesii	0.24	0.41
Petasites frigidus	0.14	0.41
Deschampsia elongata	0.17	0.4
Acer circinatum	0.31	0.38
Rosa nutkana	0.3	0.38
Rubus parviflorus	0.34	0.36
Epilobium ciliatum	0.05	0.36
Stachys mexicana	0.17	0.35
Bromus vulgaris	0.63	0.33
Pseudotsuga menziesii	0.46	0.33
Lathyrus latifolius	0.2	0.33
Holcus lanatus	0.14	0.33
Collomia heterophylla	0.11	0.33
Hypochaeris radicata	0.23	0.31
Achillea millefolium	0.07	0.31

Fragaria vesca	0.48	0.29
Claytonia sibirica	0.2	0.29
Phalaris arundinacea	0.06	0.28
Artemisia suksdorfii	0.05	0.28
Thuja plicata	0.29	0.27
Holodiscus discolor	0.27	0.27
Galium triflorum	0.39	0.26
Crepis capillaris	0.01	0.26
Rosa gymnocarpa	0.3	0.24
Agrostis exarata	0.13	0.24
Osmorhiza berteroi	0.33	0.23
Ranunculus repens	0.25	0.22
Trifolium repens	0.12	0.22
Stellaria crispa	0.11	0.22
Cirsium arvense	0.1	0.22
Adenocaulon bicolor	0.31	0.21
Prunella vulgaris	0.24	0.21
Anaphalis margaritacea	0.19	0.19
Poa trivialis	0.12	0.19
Lapsana communis	0.22	0.18
Urtica dioica	0.19	0.18
Tiarella trifoliata	0.13	0.18
Polypodium glycyrrhiza	0.16	0.17
Aira caryophyllea	0.02	0.17
Trifolium dubium	0	0.17
Agrostis capillaris	0.48	0.15
Nemophila parviflora	0.16	0.15
Micromeria douglasii	0.11	0.15
Stellaria calycantha	0.11	0.15
Ribes divaricatum	0.1	0.15
Hypericum perforatum	0.16	0.14
Cirsium vulgare	0.13	0.14
Achlys triphylla	0.29	0.13
Montia parvifolia	0.11	0.13
Rumex crispus	0.08	0.13
Dicentra formosa	0.04	0.13
Eriophyllum lanatum	0.04	0.13
Galium trifidum	0	0.13
Lupinus rivularis	0	0.13
Plantago lanceolata	0.16	0.12
Cytisus scoparius	0.08	0.12
Lonicera involucrata	0.08	0.12
Rumex acetosella	0.07	0.12

Madia gracilis	0.05	0.12
Tsuga heterophylla	0.04	0.12
Vulpia myuros	0.01	0.12
Rubus leucodermis	0.12	0.1
Maianthemum racemosum	0.1	0.1
Medicago lupulina	0.04	0.1
Epilobium minutum	0.02	0.1
Cardamine oligosperma	0.01	0.1
Trientalis borealis	0.23	0.09
Taraxacum officinale	0.13	0.09
Aira praecox	0.08	0.09
Bromus pacificus	0.07	0.09
Bromus sitchensis	0.06	0.09
Lathyrus nevadensis	0.02	0.09
Mimulus guttatus	0	0.09
Digitalis purpurea	0.13	0.08
Mahonia nervosa	0.13	0.08
Tellima grandiflora	0.13	0.08
Fragaria virginiana	0.12	0.08
Senecio jacobaea	0.04	0.08
Senecio sylvaticus	0.01	0.08
Athyrium filix-femina	0.1	0.06
Phleum pratense	0.08	0.06
Vaccinium parvifolium	0.07	0.06
Arctium minus	0.05	0.06
Veronica officinalis	0.05	0.06
Sonchus asper	0.02	0.06
Vicia hirsuta	0.02	0.06
Cerastium arvense	0	0.06
Clematis vitalba	0	0.06
Hieracium albiflorum	0.13	0.05
Pteridium aquilinum	0.1	0.05
Bromus inermis	0.08	0.05
Linnaea borealis	0.07	0.05
Chamerion angustifolium	0.05	0.05
Geum macrophyllum	0.02	0.05
Festuca subuliflora	0.01	0.05
Juncus effusus	0	0.05
Viola glabella	0.16	0.04
Prosartes hookeri	0.11	0.04
Goodyera oblongifolia	0.08	0.04
Hydrophyllum tenuipes	0.06	0.04
Vicia americana	0.06	0.04

Claytonia perfoliata	0.05	0.04
Ranunculus uncinatus	0.05	0.04
Sambucus racemosa	0.05	0.04
Carex hendersonii	0.02	0.04
Carex mertensii	0.02	0.04
Poa palustris	0.01	0.04
Disporum hookeri	0	0.04
Erigeron philadelphicus	0	0.04
Mentha arvensis	0	0.04
Poa compressa	0	0.04
Poa pratensis	0.24	0.03
Amelanchier alnifolia	0.1	0.03
Festuca rubra	0.06	0.03
Maianthemum stellatum	0.06	0.03
Vicia sativa	0.06	0.03
Aquilegia formosa	0.05	0.03
Gaultheria shallon	0.05	0.03
Lonicera ciliosa	0.02	0.03
Moehringia macrophylla	0.02	0.03
Picea sitchensis	0.02	0.03
Malus fusca	0.01	0.03
Viola sempervirens	0.01	0.03
Geranium molle	0	0.03
Juncus balticus	0	0.03
Linaria dalmatica	0	0.03
Oenanthe sarmentosa	0	0.03
Ribes lacustre	0.11	0.01
Campanula scouleri	0.08	0.01
Sedum spathulifolium	0.02	0.01
Cinna latifolia	0.01	0.01
Luzula parviflora	0.01	0.01
Asplenium viride	0	0.01
Epilobium brachycarpum	0.1	0
Festuca subulata	0.08	0
Epilobium glaberrimum	0.07	0
Luzula multiflora	0.07	0
Galium kamtschaticum	0.05	0
Asplenium trichomanes	0.04	0
Clematis ligusticifolia	0.04	0
Festuca occidentalis	0.04	0
Phacelia hastata	0.04	0
Aruncus dioicus	0.02	0
Collomia grandiflora	0.02	0

Danthonia californica	0.02	0
Cardamine occidentalis	0.01	0
Viola palustris	0.01	0

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