2012

Riparian understory dynamics and relationship to dams on the Elwha River, Washington

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Riparian understory dynamics and relationship to dams

on the Elwha River, Washington

A thesis presented to

Eastern Washington University

Cheney, Washington

In partial fulfillment of the requirements

for the degree

Master of Science in Biology

By Aaron J Clausen

Spring 2012

ABSTRACT

Dams alter the dynamics inherent to river systems by displacing natural

hydrologic and sediment regimes, which can fundamentally alter riparian ecosystem

function. However, with better understanding of how dams negatively impact river

systems, and as many dams approach the end of their lifespan, dam removal is being used

to facilitate ecosystem restoration. Whereas researchers have successfully illustrated the

negative impacts dams have on biological communities, the long-term ecological

implications of dam removal are not well understood. At present, two dams are being

removed along the Elwha River (Washington, USA), providing a valuable window for

ecological studies concerning the effects of dams, and their removal, on biotic

communities.

In this study I described plant community dynamics along the twice-dammed

Elwha River for use as a baseline in assessing the long-term effects of dam removal on

this river system. I determined the relationships between understory and overstory

riparian plant communities and how they vary across geomorphic landforms relative to

the dams over a five-year period (2005 to 2010). I also evaluated the relative utility of

under- and overstory species as indicators of plant community type, reach location and

geomorphic landform.

Vegetation and environmental surveys were conducted in 2005 and 2010 on 100-

m^2 plots located along 15 perpendicular transects on river reaches above, below and

between the Glines Canyon and Elwha dams. I used multivariate analyses to define plant

communities along transects by assessing species composition within each plot (via

frequency and abundance of species), and characterized their distribution. I used a general linear models approach to assess compositional change in plant communities along river reaches over the five-year interval to determine the stability of understory and overstory plant communities. Finally, I used an indicator species analysis to examine the distributions of individual plant species.

I found that plant community composition along the Elwha River was heavily influenced by the distribution of geomorphic landforms. Physical factors (e.g. soil depth, substrate size, ground cover) were strongly correlated with longitudinal location and geomorphic position. River reaches delineated by the dams had markedly different plant communities. The reach between both dams had the fewer early successional communities associated with younger landforms, perhaps due to sediment starvation; this suggests the dams have played a role in plant community distribution.

In reaches above and below the dams there were greater differences between understory and overstory community composition as compared to the middle reach. Understory communities were less stable, meaning they had greater species compositional changes over time, compared to overstory communities, which were more stable. These data suggest the dams may have attenuated natural disturbance events in the middle reach.

Overstory species were the more useful for indicating the overall plant community, however, understory species were more reliable indicators of reach location suggesting the dams may have more of an impact on species distributions in the understory than the overstory.

These data provide a useful baseline for post-removal comparisons evaluating the long-term effects of dam removal on the Elwha River. My results concur with others that have suggested that reaches downstream of the dams will be most affected post-removal by the influx of sediments from the former reservoirs. I predict that, in addition to the reestablishment of younger landforms, dam removal will result in an increase of early-sere, disturbance-tolerant communities in downstream reaches. Also I anticipate that the stability of the understory and overstory communities will become more reminiscent of natural conditions (more stable overstory than understory) along all reaches. I also suggest that understory species not be neglected from indicator analyses, as they can be accurate, even exclusive, indicators for factors such as plant community type, geomorphic landform and reach location.

ACKNOWLEDGEMENTS

graduate school. Also, many thanks to the other biology graduate students for support, helpful criticism, and camaraderie, and for allowing the occasional conversation shift to topics other than plant ecology. I appreciate the support offered by Eastern Washington University during my time there; the faculty and staff were notably helpful and knowledgeable, and I was fortunate to have had such a nurturing environment for academic study. I am also thankful for the funding for this project, which was provided by an Eastern Washington University Foundation Faculty Research grand to Rebecca Brown.

The field crew from Eastern Washington University in 2005 included: Jeremiah Dung, Malcolm Havis, and Moose Sanders. From 2010 it included: Nathan Drake, Jake Ponce, and Devin Sontag. Without these students this research would have taken much longer than a Master's project would allow; I appreciate their interest in river ecology and thank them for their assistance in the field.

The National Park Service staff at Olympic National Park provided logistical support and permitting for this research. In particular I thank Steve Acker, Joshua Chenoweth, and James Michel for contributing their time and insight into helping this research along. Affiliates from the U.S. Geological Survey that provided valuable field assistance and data for this project include (besides Pat Shafroth): James Bromberg and Leanne Hanson.

Finally I would like to express my gratitude to Sonja Christensen for constant encouragement, sanity checks, and help preparing presentations and documents, as well

as my family, without whose support I would not have been able to manage my transit to

Washington and produce work presented here.

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INTRODUCTION

Riparian zones, the interface between aquatic and terrestrial systems along rivers, are highly diverse and complex ecosystems. The importance of riparian vegetation for wildlife habitat, bank stabilization, nutrient and energy sources, and buffering of sediment and pollutants has been well established (Likens *et al.* 1970, Hupp 1992, Naiman and Decamps 1997, Tabacchi *et al.* 1998, Naiman and Decamps 2005). Environmental gradients, such as elevation and moisture, change abruptly in riparian zones; as does flood disturbance, which creates environmental heterogeneity at multiple spatial scales. As a result one can observe markedly different plant communities in relatively small areas, which contributes to high biological diversity (Van Pelt *et al.* 2006).

Plant communities are typically described in terms of their dominant strata; in forested communities the temporal and compositional dynamics of the understory have not been thoroughly studied. The role environmental gradients (elevation, moisture, disturbance) play in shaping plant communities has been investigated in many systems; but only a handful of studies have examined the understory constituent independent of the overstory (Halpern and Spies 1995, Pabst and Spies 1998, McKenzie *et al.* 2000, Merritt and Cooper 2000, Bartels and Chen 2010, Chávez and Macdonald 2010, McEwan and Muller 2011). Although overstory communities typically dominate in terms of cover and resource acquisition, understory plants contribute most to biodiversity (Halpern and Spies 1995). The understory can also regulate succession to some degree (Royo and Carson 2006) and can play a significant role in nutrient and energy cycling (Nilsson and Wardle 2005). In spite of this, understory vegetation has historically been under-

emphasized in studies of plant communities, with some exceptions (Gilliam 2007). The overstory, which regulates light and nutrient availability to the understory, is thought to be a proxy for the environmental gradients that ultimately determine composition (McKenzie *et al.* 2000). The reliability of linkages observed between the overstory and understory strata has been questioned (Lyon and Sagers 1998, Decocq 2002), but there is more recent evidence supporting predictable relationships between these layers and emphasizing the usefulness of studying understory plant communities.

Gilliam and Roberts (2003) suggested that interpretations of entire plant communities not be made without considering the understory, and recently this has become more common practice. Understory vegetation has been related to broad environmental gradients; for example Pabst and Spies (1998) related understory plant communities to landform and canopy cover along several coastal riparian areas in Oregon and found that topographic moisture gradients seem to drive vegetation patterns. Other studies have shown that variation in the understory plant community can be explained by and related to overstory variables such as cover and basal area (McKenzie *et al.* 2000, Stromberg *et al.* 2010). For example, Chávez and Macdonald (2010) found differences in understory composition between four overstory patch types and suggested a mosaic of canopy patches promotes a range of understory seral stages. With respect to diversity, Berger and Puettmann (2000) observed a positive correlation between the understory and overstory, while Kirchner *et al.* (2011) found a higher presence and density of understory species in canopy gaps (where overstory diversity is low). Several studies have further examined understory species with respect to "micro"-conditions (climate, habitat, topography) (Dibble *et al.* 1999, Gilliam 2002, Chávez and Macdonald 2010, Kirchner *et*

al. 2011); these smaller-scale responses to environment (compared to overstory) are likely due understory plants' relatively small stature. Very few of these studies have been applied in riparian areas, where further empirical evidence is required to develop an understanding of the relationships between understory and overstory plant communities and the environmental drivers that shape them.

Although several studies have examined the distribution of understory plants relative to disturbance or canopy characteristics, the nature of riparian understory community succession, and how it relates to the overstory type and local physical gradients, has seldom been described. The composition of riparian plant communities is driven by succession, defined here as "change in communities following a disturbance (Connell and Slatyer 1977)". The dynamic fluvial processes of a river make succession a constant process in riparian systems, where a patchwork of environmental gradients is established by the intermittent destruction and creation of habitats. Plant communities are distributed according to these gradients (Hupp and Osterkamp 1985) and contribute to future successional processes (competition, debris deposition, etc.). The plants that colonize the riparian zone often have life history strategies that coincide with the seasonal flows and disturbance regime of the river (Mahoney and Rood 1998). Studies have examined the stability of plant communities in response to anthropogenic (Halpern 1988, Halpern 1989) and hydrologic disturbance in watersheds (Bornette and Amaros 1996, Dovčiak and Halpern 2010). For example, Dovčiak and Halpern (2010) found a positive relationship between diversity and stability in both herbaceous and woody vegetation stages, and noted reduced stability in 'colonizing' compared to 'forest' species. Similarly, Bornette and Amaros (1996) observed increased diversity and stability of aquatic plants

in the frequently disturbed channel. In riparia, the stability of plants likely correlates with the disturbance regime and life history characteristics of individual species, with communities that are in active channels or composed of shorter-lived species being less stable.

Riparian zones are increasingly threatened by global alteration of hydrologic regimes (Naiman and Decamps 1993, Nilsson *et al.* 2005, Poff and Zimmerman 2010), particularly through river damming. More than 2.5 million dams impede rivers in the United States, of which more than 40,000 are at least 25 m high (Graf 1999, USACE 2011). Most of these were constructed in a time when societal benefits outweighed the known ecological impacts of damming, and have become a problem for maintaining natural ecosystems (Nilsson and Berggren 2000, Duda *et al.* 2008). Dams can alter downstream habitats by altering flow regimes and water temperature, trapping sediment, incising channels, and limiting fish migration (Poff and Hart 2002, Poff and Zimmerman 2010, Shafroth *et al.* 2002). In addition to trapping sediment, reservoirs created by dams also inundate large areas of habitat behind the dam. This transformation from lentic to lotic system changes the frequency of certain plant species (Johansson *et al.* 1996, Nilsson *et al.* 2002). Damming homogenizes environmental gradients, diminishing the natural continuity of the riparian system and limiting longitudinal interactions (Jansson *et al.* 2000, Poff *et al.* 2007, Ward and Stanford 1983). Dams impede hydrochory (Andersson *et al.* 2000, Brown and Chenoweth 2008), an important community-structuring process and the dispersal method many riparian plant are adapted for (Johansson *et al.* 1996, Jansson *et al.* 2005, Merritt *et al.* 2010). Spawning salmonids can contribute significantly to the nutrient content of riparian vegetation (Helfield and

Naiman 2001), a process impeded by damming. By altering the natural flood regime, dams induce stress in certain plant species that are adapted to a particular regime (Naiman and Decamps 1997). Stromberg *et al.* (2010) found lower understory diversity in all forest types along the regulated Bill Williams River, Arizona, compared to a free-flowing tributary. The decreased floristic diversity and increased number of invasive species often observed in dammed rivers is likely the result of reduced fluctuation in flow and disturbance (Hill *et al.* 1998, Poff *et al.* 1997). Dams control rivers, making them more predictable and reducing their inherent dynamism that drives heterogeneity and diversity.

Now that many dams have surpassed their lifespan due to deterioration and sediment accumulation, and their ecological effects are better understood, dam removal is increasingly considered as a means of ecosystem restoration (Hart *et al.* 2002, Stanley and Doyle 2003, Duda *et al.* 2008). Such is the situation with the Elwha and Glines Canyon Dams on the Elwha River, Washington, U.S.A. In the 1992 the U.S. Congress called for the restoration of the Elwha River ecosystem, with dam removal later being named the most effective approach (DOI 1995). The dam removals, among the largest in US history, began in September of 2011 and are expected to take around two years (DOI 1995, Woodward *et al.* 2008). The removals present a unique opportunity to study plant community responses, and much of the research done to this point will be valuable for post-removal comparison.

Objectives

The objective of my research was to determine how understory plant community dynamics relate to dams and to provide a baseline vegetation survey for comparison following dam removal. I examined the following specific questions and hypotheses:

1) How do the understory and overstory communities vary with:

A.) Geomorphic landform?

Hypothesis: Because plant community succession is related to landform succession in riparian areas, plant communities will be associated with particular geomorphic landforms. Understory communities will be more precisely tied to landform than overstory communities because those species interact over finer spatial scales.

B.) Damming?

Hypothesis: Due to the effects of the dams on sediment flux and geomorphic dynamics, the landforms and plant communities associated with them will be unevenly distributed in reaches above, between, and below the dam; with fewer early successional species in sediment-starved reaches (between, below dams).

C.) One another?

Hypothesis: Because overstory and understory species, to some extent, respond similarly to environmental gradients, understory community groups will be correlated with overstory patch type.

2) How do the understory and overall communities change through time?

Hypotheses: Flood-prone landforms, because they are generally shorter-lived, will have more compositional change over time. In flood-prone areas the

understory will be less stable than the overstory (more compositional change)

because it is composed of relatively short-lived species and is often disturbed.

3) Are understory species better indicators for environmental change than overstory species?

Hypothesis: Understory species, because they respond to the environment on a smaller scale due to their size, will be more reliable indicators of change in longitudinal (altered disturbance/sediment regimes) and horizontal (moisture, elevation gradients) environmental conditions.

METHODS

Study area

The Elwha River is 72 km long and lies on the northern edge of Olympic National Park (ONP, USA). The river is fed by 330 km of tributaries, and its entire watershed area is 833 km^2 (about 20% of ONP). A majority of the Elwha River Basin lies within Olympic National Park and has been relatively protected since 1938; the downstream 15 km of the Elwha River lies outside the park boundary on land belonging to the Washington Department of Fish and Wildlife and the Lower Elwha Klallam Tribe. The Elwha River flows through a variety of valley forms, including constrained areas where the river is restricted to steep canyons and unconstrained areas where the river can migrate across wide floodplains (Kloehn *et al.* 2008). Annual rainfall averages 100 cm at the river mouth and 550 cm at the headwaters of the river (Phillips and Donaldson 1972). Rainfall at a monitoring station about 3 km downstream of Glines Canyon Dam averages 140 cm annually (WRCC 2012). In 2007 daily average flow peaked at 520.8 m^3/s, and peak instantaneous discharge reached 1005.2 m^3/s; events with 10 and 49-year recurrence intervals, respectively, based on USGS real-time water data (Figure 1, Figure 2).

This field study was conducted in the downstream 32 kilometers of the Elwha River valley (Figure 3). The Elwha and Glines Canyon dams, located at river kilometer (rkm) 7.9 and 21.7 respectively, divide this segment of the Elwha into three reaches, which will hereafter be referred to as: lower (below Elwha Dam, from rkm 0.0 to rkm 7.9), middle (between Elwha and Glines Canyon Dams, from rkm 7.9 to rkm 21.7), and upper (above Glines Canyon Dam, from rkm 21.7 to rkm 32.0). The process most

affected by the dams, which are operated as run-of-river and therefore do not greatly alter hydrology, is sediment transport. The dams hold an estimated 19 million m^3 of sediment in their impoundments (DOI 1996, Gregory *et al.* 2002, Duda *et al.* 2011). In the lower reach, the river has been shown to migrate laterally between 2 and 10 m each year (Draut *et al.* 2008). The lower reach also experiences more anthropogenic influence in the form of channel structures (engineered log jams), residential and commercial development, logging, agriculture, and recreation, than the other reaches. Due to sediment retention in the reservoirs, the lower and middle reaches have larger bed material. Also, the channel in the middle reach migrates less resulting in community patches that are relatively less disturbed. The upper reach is the closest to 'natural condition' of the three reaches as it is still highly influenced by seasonal floods carrying large quantities of sediment; as such it has the associated geomorphic complexity and fluvial disturbance that results mosaic of vegetation patches more characteristic of natural riparia. For the purposes of this study, which has no undammed reference river, the upper reach is considered a natural control.

Study Design

In 2003 and 2004 fifteen transects were established across the river; five each in the lower, middle, and upper reaches. The transects spanned most to all of the bottomland, and thus were of variable length depending on local geomorphic conditions. Along each transect plot locations were located randomly within different patches defined by a combination of geomorphic position and overstory vegetation. Thus, the number of plots in each reach was variable. Vegetation presence and abundance were measured within 100-m^2 (typically 10 m by 10 m) nested diversity plots (Brown and Peet 2003). In July of

2005 122 such plots were sampled across the 15 transects. In July of 2010 68 of these

plots were resampled.

Vegetation survey

A nested-quadrat method, adopted from the Carolina Vegetation Survey, was used

to sample vegetation in each 100-m^2 plot (Peet and Wentworth 1998). Presence and

abundance (estimated using midpoints of Braun-Blanquet [1964] cover classes) of each

vascular plant species was recorded. I identified plants to species level using Hitchcock

and Cronquist (1976) and confirmed and updated names using ITIS (2012). I determined

native status by first referencing the USDA Plants Database (USDA 2012), then cross

referencing with a state list of noxious plants (WANWCB 2012). I used 7-character

species codes to simplify species references (Appendix I).

Environmental variables

In each 100-m^2 plot ground cover of sand/soil, gravel, bedrock,

bryophytes/lichens, litter/organic matter, decaying wood, and water was visually

estimated. Soil depths were measured for each plot by averaging the depths (via soil

probes) of points 1 m inside the four plot corners, and sediment particle-size distribution

was determined using a pebble count survey adopted from Wolman (1954). Using these

data I calculated median grain size, percent sand, and percent silt substrate size in each

plot. Points were surveyed along transects, documenting major topographic breaks,

vegetation plot locations, and right and left water's edge using a combination of Pentax

PCS-325 Total Station and a real-time kinematic Global Positioning System (Trimble R8

rovers with a Trimble 5800 base station and High Powered Broadcast 450 radio and Trimble Survey Controller model 2 controllers).

Shafroth *et al.* (*In* prep) classified each plot as one of six geomorphic landforms using a combination of geomorphic position and stand age; these closely follow those described for Queets River (ONP, WA) by Latterell *et al.* (2006) and Van Pelt *et al.* (2006) (Table 1). Also, Shafroth *et al.* (*In* prep) classified each plot as one of seven overstory patch types based on independent analysis of overstory plant species.

Data analyses

I compiled species presence and cover, with cover-class values replaced by midpoint percentages, and environmental information from each plot into a data matrix for analyses (SAS 2011). I then created individual datasets to examine the composition of overall plant communities separately from understory communities. The overall community includes all vascular plant constituents; the understory includes all the species that are not overstory trees.

First, I described the overall and understory plant communities using a combination of one-way hierarchical cluster analysis and indicator species analysis (ISA) in PC-Ord to create vegetation groups based on the entire plant community from both years. For the cluster analyses, I analyzed log-transformed species cover values with Relative Sørenson distance measures and a flexible beta (= -0.25) linkage method. I selected for maximized percentage of incorporated information and significance of the Indicator Value (IV, from ISA) when determining the ideal number of groups (12 for overall and 14 for understory plant community). In naming the groups I modified a

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convention established by Grossman *et al.* (1998), using the 3 most abundant species in each group as well as species that were consistently significant indicators (significant IV in both sample years) for each group. I then abbreviated cluster group names to the dominant genus, or dominant genera if a single genus was not unique, and occasionally included other pertinent information (reflecting unique composition or landform).

I next examined the distributions of overall and understory communities with respect to geomorphic landform and reach location using non-metric multidimensional scaling (NMS). To this end I used NMS to ordinate species cover values from each plot (McCune and Mefford 2011). This allowed for visualization of compositional similarities between plots. I did this for the entire community as well as the understory constituents only. For the understory community NMS I overlaid the geomorphic landform, understory community group, and reach location variables onto the ordinations. For the overall community NMS I overlaid the grouping variables of overall community group (from cluster analysis), geomorphic landform, and reach location onto the ordinations. To simplify interpretation of relationships between plant communities, geomorphic landform, and reach location I used correspondence analysis (Proc corresp, SAS version 9.3), which evaluates correspondence between categorical variables (SAS 2011). I also used correspondence analysis to evaluate the correlation between my understory plant community grouping and the overstory patch types indicated by Shafroth *et al.* (*In prep*).

For NMS, I used Relative Sørensen measures to calculate ordination distances, with a starting seed of 17, 100 runs with real data, and 200 iterations. PCOrd selected the number of dimensions that adequately reduced stress, stopping when adding an additional dimension would reduce stress by less than 5 (McCune and Mefford 2011). Varimax

rotation was selected to maximize loading of species cover onto ordination axes. I examined Pearson-Kendall correlation coefficients for relationships between species cover, environmental variables, and the ordination axes. I also calculated species scores (Plexus values, via weighted averaging) so chi-square distances between species could be observed and species associations could be estimated. I applied this NMS procedure throughout the study.

To evaluate change in plant communities over time I used PC-Ord to visualize successional vectors between the two sampling years on NMS ordination plots and calculate the percent dissimilarity between plots sampled both years. To evaluate the relative stability of the understory and overstory communities I first created separate data sets for each layer; I then used the dissimilarity matrix to determine each plot's similarity to itself after 5 years (McCune and Mefford 2011). I averaged plot dissimilarity within reach and geomorphic landform for each layer, and tested for significant differences using Proc glm in SAS (2011). Here stability is referring to how much a plot changed (as a percentage calculated from species frequency and abundance) from 2005 to 2010; low stability indicates high compositional change, high stability indicates low compositional change.

To determine the reliability of indicator species from the overstory and understory I used ISA to calculate IVs for each species with respect to geomorphic landform, overall plant community, and reach location (Dufrêne and Legendre 1997). I performed ISA for both years combined as well as individual years. The significance of each species' highest IV was tested with 4,999 Monte Carlo random permutations of sample units (plots) within groups (landform class), with the null hypothesis that the species had no

indicator value. Only species that were consistently significant indicators of a group (p <

0.05 in both sample years) are reported here.

General

In the two years of survey 278 species were recorded; of these 77 were exotic (Appendix I). Over 40% of total vegetation cover, in 2005 and 2010, was from four native overstory species: *Alnus rubra*, *Populus balsamifera s*sp. *trichocarpa, Acer macrophyllum,* and *Pseudotsuga menziesii* (Table 2). The native understory species *Polystichum munitum, Symphoricarpos albus,* and *Oemleria cerasiformis* contributed a combined 10% of total cover both years (Table 2). Two exotic herbaceous species, *Geranium robertianum* and *Dactylis glomerata* contributed a combined 4% of total cover both years; no other exotic species had more than 1% of total vegetation cover in either year, and I observed no exotic overstory species (Table 3).

Very few open bar or mature fluvial terrace landforms were sampled in either sample year in the lower reach; other landforms were nearly equally distributed (Figure 4, Figure 5). Some landforms (e.g. open bars) were not sampled because they were destroyed by construction projects, others (e.g. mature fluvial terraces) because the floodplains were so expansive that the transects did not extend to the terraces. The middle reach had very few bar or developing floodplain landforms, reflecting the relatively high stability of the reach; it was composed of nearly 50% transitional fluvial terrace landforms. In the upper reach no established floodplains were observed, few woody bars or transitional fluvial terraces, and nearly equal distributions of the remaining landforms.

Understory community composition

Cluster analysis organized the understory species into 14 groups based on similarities in species composition, incorporating 37% of the species data (Table 4). With two exceptions (the *Oemleria* and *Symphoricarpos* communities), most understory groups were found in similar numbers of plots each year. Understory community group appears to be strongly related to geomorphic landform and overall community.

The first NMS ordination axis, which explained the most variance of all the axes (26%, Appendix II), appears correlated with geomorphic landform (Figure 6). There is a general trend of increasing landform successional stage as one moves across axis 1 from left to right. To some extent landforms delineate compositional similarities. When overlaid with understory plant community type the ordination again appears stratified along axis 1 (Figure 7). Because group central tendencies are more clustered near the older landforms in the correspondence analysis, understory communities appear less distinct on older landforms compared to younger ones (Figure 8). Some understory plant communities were related to specific geomorphic landforms, such as the *Equisetum* understory community being associated with the open bar landform. Reach location also appears to delineate unique understory plant communities (Figure 9). Of the 14 understory community groups, 8 appear associated with particular reach locations (Figure 10). Across these analyses the presence of younger landforms were positively related to plant diversity, estimated (visually) sand/soil cover, and estimated gravel cover, and inversely related to elevation ($r^2 > 0.20$). This trend translates to communities (e.g. *Poa pratensis, Equisetum*) that colonize these landforms and reaches (e.g. the upper reach) where these landforms are abundant. These results are summarized for each understory

community group in Table 5. Tables illustrating the variance explained by each of the ordinations in this study can be found in Appendix II.

Overall community composition

Cluster analysis organized the plot data into 12 groups (hereafter communities) based on similarities in species composition, incorporating 38% of the species data (Table 6). With two exceptions (the *Alnus-Populus* and *Polystichum* communities), most communities were found in similar numbers of plots each year. Geomorphic landform appears strongly related to vegetation community composition. The clustered groups for overall community correlated closely with the overstory patch type determined by Shafroth *et al.* (*In prep*) (Figure 11).

The second axis of the NMS ordination, which explained the most variance of all the axes (29%, Appendix II), appears correlated with geomorphic landform (Figure 12). There is a general trend of increasing landform age as one moves up axis 2. Landforms appear to delineate compositional similarities more distinctly for overall community than for understory community groups. The transition between successive landform stages is much clearer in ordinations of the overall community compared to those for the understory. When overlaid with overall plant community the ordination again appears stratified along axis 2 (Figure 13). Group central tendencies for the overall community are more clustered near the older landforms in the correspondence analysis; overall communities appear less distinct on older landforms compared to younger ones (Figure 14). Some overall plant communities were related to specific geomorphic landforms; as in the case of *Alnus*-bar overall communities being associated with the open bar landform. Reach location appears to delineate distinct understory plant

communities along axis 1 (which explained 21% of variation, Appendix II) (Figure 15).

Of the 12 overall community groups, 8 appear associated with particular reach locations

(Figure 16). Across these analyses the presence of younger landforms was positively

related to exotic plant diversity, and inversely related to elevation ($r^2 > 0.20$). This trend

translates to communities (e.g. *Salix*) that colonize these landforms and reaches (e.g. the

upper reach) where these landforms are abundant. The results are summarized for each

overall community group in Table 7. Of the 14 understory community groups, 5 appear to

be related to particular overall plant communities (Figure 17).

Response to reach location

Reaches separated by the dams appear to have unique environmental conditions

and plant communities. These trends are summarized for each reach in Table 8. In

particular, the middle reach has very few bar landforms and an abundance of terraces.

Communities associated with bars (*Alnus*-bar, *Equisetum*) are not found in the middle

reach, while *Polystichum* communities (found on terraces) are abundant. *Populus*

balsamifera ssp. *trichocarpa* (black cottonwood) was a significant indicator of the lower

reach below Elwha Dam; while species indicating the upper control reach included

Equisetum arvense (field horsetail) and *Achlys triphylla* (vanilla leaf). Invasive *Dactylis*

glomerata (orchard grass) was an indicator for the sediment-starved middle reach.

Change through time

Stability was measured on a gradient of compositional change, with the smallest

compositional changes (determined by percent dissimilarity) being the most stable.

Younger landforms appeared to be less stable than the older ones (Figure 18).

Communities associated with landforms had similar trends, with the *Polystichum* understory plant community being among the most stable. The overall community ordination displayed different trends, with the floodplain and woody bar landforms appearing relatively stable compared to the transitional fluvial terrace and open bar landforms (Figure 19). The most stable of overall communities included *Alnus, Acer, Populus,* and *Alnus-Populus.* There was a general trend for the stability in understory and overstory communities to be more similar with increasing landform age (open bar → mature fluvial terrace). Overstory plant communities on the woody bar and developing floodplain landforms were 2.7 and 2.1 times more stable (GLM, $p < 0.05$) than understory communities, respectively (Figure 20). Trends of less stable understory on the open bar, established floodplain, and transitional fluvial terrace landforms were not significant (GLM, $p > 0.05$).

Understory communities in the upper reach appear to have changed composition the most (**Figure 21**). For the overall community the reaches appear to have similar stability (**Figure 22**). The overstory plant communities in the lower and upper reaches were 1.8 and 2.1 times more stable (GLM, $p < 0.05$) than the understory communities, respectively (**Figure 23**). A trend of less stable understory in the middle reach was not significant (GLM, $p > 0.05$).

Reliability of understory indicators

Species from both overstory and understory communities were strong indicators of geomorphic landforms (Figure 24). The understory species *Equisetum arvense* and *Holodicsus discolor* were indicators of the open bar and established floodplain landforms,

respectively. Where both overstory and understory species were indicators for landform there was no community that produced the best indicators. For instance, *S. sitchensis* and *P. munitum* were the best indicators for the woody bar and mature fluvial terrace landforms, respectively.

Where both overstory and understory species were indicators for overall community the overstory provided the best indicator species (Figure 25). For example, *A. macrophyllum* and *T. plicata* were indicators for the *Acer* and *Thuja* communities, respectively. Some overall communities were exclusively indicated by overstory species, such as *A. grandis* for the *Abies* community, others by understory species, such as *S. albus* for the *Populus* community.

Where both overstory and understory species were indicators for geomorphic landform the understory provided the best indicator species (Figure 26). *P. balsamifera* ssp. *trichocarpa* was the only overstory species consistently indicating a reach, that being the lower, however *O. cerasiformis* had an IV for the lower reach nearly twice as large. The best indicators for the middle and upper reach were *D. glomerata* and *O. berteroi*, respectively.

With the exception of the *Populus* overstory patch type, which had no indicators, all overstory patch types were consistently indicated by at least one of the overstory species used to describe them (Figure 27). However the overstory species were not always the best indicators, and several patch types had many indicators from the understory community. For instance: the *Acer, Pseudotsuga-Alnus*, and *Pseudotsuga-Tsuga* overstory patch types were best indicated by *Urtica dioica, Bromus inermis*, and *Achlys triphylla*, respectively.

DISCUSSION

Community composition

My results support the hypothesis that mechanisms facilitating plant community composition appear to be strongly driven by factors associated with geomorphic landforms, a pattern that has previously been described for riparian systems (e.g., Hupp and Osterkamp 1985, Hupp and Osterkamp 1996, Latterell *et al.* 2006, Shin and Nakamura 2005). Pabst and Spies (1998) conducted a similar study relating the distribution of understory plant communities to landforms (defined more broadly on a gradient from ridge-top to valley bottom) and the environment in riparian forests along near Oregon coast; they found hillslope processes (namely soil moisture, moisture stress, and humidity) were major drivers of vegetation patterns, and certain groups of species were located occupied distinct locations along environmental gradients. My results concur with these, with elevation (an analog for hillslope gradients) being correlated with geomorphic landform and plant community patterns. I also found that certain communities tend to occupy particular niches along landform gradients. Latterell *et al.* (2006) documented a re-cycling of patch types (referred to as landforms in my study), and corresponding alteration of the patch characteristics (e.g., stem density/volume, soil depth/nutrients, etc.) caused by flood disturbance. A similar successional flow can be illustrated for plant communities (Figure 28). By understanding how the driving mechanisms behind plant community distribution (hydrologic disturbance, soil texture, etc.) are being altered by dams, one can predict responses of vegetation to dam removal.

My hypothesis that landforms would be unevenly distributed between the dams proved correct. In particular, the middle reach has fewer landforms composed of finer sediments (bars) compared to the upper reach. These findings are consistent with observations implicating the dams as the source of reduced channel meandering and fine sediment deposition in this reach (DOI 1995) and with Kloehn *et al.* (2008) who found the regulated (lower and middle) reaches had higher proportions of old floodplains. Based on their associations with these landforms, certain plant communities (e.g., the *Equisetum* understory, *Alnus*-bar overall) were absent or reduced at study sites in the middle and lower reaches. Bar landforms were present on the lower reach, though few had open canopies; this likely resulting from reduced disturbance as the floodplain flattens out near the delta. Also in the lower reach, severe anthropogenic disturbance between sampling periods destroyed several of the open bar landforms, removing them from the analyses.

Plant communities, both overall and understory, differed across the three reaches, validating my hypothesis. This result is consistent with that of Jansson *et al.* (2000), who found reduced floristic similarity between impoundments along rivers in northern Sweden relative to within them. The differences in community composition between the reaches may be attributed to dam-imposed sediment restrictions, as mentioned earlier, with communities being indirectly excluded from reaches based on their association with particular landforms. Hydrochory, a process Brown and Chenoweth (2008) found to be interrupted on the Elwha River, likely plays a role as well; limitations in downstream seed supply from particular species could alter community composition below the dams. In any case, without undammed reference reaches at the same longitudinal positions one

cannot rule out the possibility that these differences are due to natural variation in longitudinal gradients (e.g., elevation) unrelated to the dams.

As I expected, certain understory community types were associated with overall communities. The mechanism behind these associations is likely a result of adaptations to disturbance or species interactions, although without knowledge about species physiology and interactions this is speculative. For example, the frequent occurrence of the *Equisetum* understory with the *Alnus*-bar overstory (both found preferentially on open bar landforms) may relate to those communities' ability to colonize bare sediments after disturbance events, whereas the *Achlys* understory association with the *Abies* overstory (on mature fluvial terraces) might be the result of canopy closure limiting the understory to herbaceous species.

Change through time

Although many of the most flood-exposed plots were not resampled, the changes in plant communities from 2005 to 2010 may be attributable to the large flood event mentioned earlier. Because the intervening years included 49-year peak flow event, I expect some compositional change may be due to natural fluvial process (flooding, sediment erosion/aggradation). As this study lack a non-flooded reference river, natural dynamics cannot be ruled out as a driver of compositional change.

Very few landforms transitioned in the 5-year period, and those that did so only progressed to the next landform in successional age. One landform was returned to an open bar state from a developing floodplain, likely due to flood disturbance. Having multiple years of data is valuable for studies of succession in response to disturbance,

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however 5 years is a relatively short time period for observing landform succession. I have provided some context for interpretations of successional processes; however because the successional stages of vegetation and landforms along the Elwha River are likely several decades or centuries these conclusions are limited. Other studies of vegetation succession following disturbance typically had several temporal samples spread across at least a decade (Bornette *et al.* 1996, Dovčiak and Halpern 2010, Halpern 1988, Halpern 1989).

Stability of understory communities (characterized here as species compositional change over time) was inversely related to landform successional age, with stability being lowest on the most flood-disturbed landforms (where diversity was general higher); this partially confirmed my expectations. My result contrasts with Dovčiak and Halpern's (2010), who observed increased stability with higher diversity in both herbaceous and woody stages of clear-cut watersheds. However, they did not sample flood-disturbed landforms, where very diverse communities were observed (possibly due to a lack of interspecific competition). If the most flood-disturbed landforms were removed from analyses, one would likely observe a similar trend. Dovčiak and Halpern (2010) also observed reduced stability in 'colonizing' compared to 'forest' species; in my study the most flood-disturbed landforms had higher proportions of initial colonizing species. Bornette and Amoros (1996) observed both diversity and stability of aquatic plants to be high in the frequently disturbed channel, again contrasting my finding of decreased stability on disturbed landforms.

The overstory maintained relatively constant stability across the geomorphic landforms, with the open bar and mature fluvial terrace landforms being the most stable.

In the case of open bars this is likely due to the limited number of overstory species capable of colonizing flood-disturbed bars (e.g. *Salix, Alnus*). In the case of mature fluvial terraces overstory stability is likely due to the resistance of mature communities to compositional change.

There was a trend for stability to be more similar between understory and overstory communities with increased landform age. On the woody bar and developing floodplain landforms understory stability was much lower than that of the overstory. In the lower and upper reaches (where these landforms were abundant) the same trend was observed. On the mature fluvial terrace landform stability between the overstory and understory was nearly equal. I found very few studies in riparian zones that have examined the temporal stability of plant communities (Bornette *et al.* 1996, Dovčiak and Halpern 2010, Halpern 1988, Halpern 1989), and none in any system that observed differential stability between the overstory and understory plant communities. Alternatively, it could be that the understory and overstory normally have similar stability, and that intervening time between sampling periods coincided with unusual changes (perhaps caused by the record flooding).

Older, more elevated landforms are considered more stable with decreased proximity to the river channel. These results suggest that older landforms are not only geologically stable, but also botanically stable relative to the younger landforms. Further, variability in botanical stability along the Elwha River appears to stem from changes in understory stability, as overstory community stability is relatively consistent across landforms.

Reliability of indicators

My expectation that understory species would be more reliable indicators than those of the overstory was met for reach location but not for geomorphic landform or overall plant community. Because they were used in the definition of certain groups, it was not surprising to find that overstory species were consistently the best indicators for overall plant community. However, understory species also consistently indicated several communities, and for two were the exclusive indicators. Despite being described by overstory species, overstory species were not always the best indicators for overstory patch type (Shafroth *et al. In prep*). Chávez *et al.* (2010) also observed indicator species for canopy type, though their classes were more broadly defined and they did not evaluate the relative indicator ability of overstory and understory species. They observed the shrub *Amelanchier alnifolia* to be an indicator for broadleaf canopy patches (mainly *Populus tremuloides*), contrasting with my finding that it indicates overstory patches dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* (conifers). This suggests that specific interactions between overstory and understory species may be system-specific or driven by mechanisms not accounted for here.

Understory species are valuable, but underrepresented, indicators of environmental change. Studies have used understory species as means to indicate environmental conditions, such as: anthropogenic disturbance (Dale *et al.* 2002), canopy type (Chávez *et al.* 2010), fire regime (Keith *et al.* 2010), forest regeneration (Dibble *et al.* 1999, McLachlan *et al.* 2001), landform-ecosystem type (Meilleur *et al.* 1992), and soil moisture (Lookingbill *et al.* 2004). No studies were found that focused on riparia or

compared the efficacy of understory and overstory species as indicators of environmental change. Overstory species have inherent advantages as indicator species: they are much easier to observe and identify, are widely used as indicators for habitat type, and are much easier to classify for someone without intimate knowledge of a system as many species have congeners that occupy similar niches worldwide. However, it is likely that understory species respond to gradients on a smaller scale, both spatially and temporally, because they are typically smaller and shorter-lived. Therefore they are potentially more accurate indicators, depending on the environmental condition being observed (small-scale changes would be difficult to interpret across landscape-scale gradients). Because they were consistently significant, and at times exclusive, indicators of several environmental conditions I suggest understory species not be excluded from analyses of plant community distributions.

CONCLUSION

I found that plant communities were organized according to environmental conditions that vary with geomorphic landform, a pattern observed in previous studies of riparian zone vegetation. Along the Elwha River, areas separated by the Elwha and Glines Canyon dams contain distinct plant communities. I also found that the stability over time of understory communities to be much less than overstory communities on the most flood-disturbed landforms, and in reaches where these landforms were abundant. Finally, I have shown that understory species to be more accurate indicators of reach location than overstory species, suggesting they may be more impacted by dams.

It has been predicted that sediment will be redistributed throughout the lower reaches following dam removal (Kloehn *et al.* 2008, Duda *et al.* 2011); in the context of my study this model would be supported if the substrate conditions in the middle reach approach those observed for the upper control reach. If this is the case, I predict the return of early-sere, disturbance-tolerant plant communities (*Alnus, Equisetum*). I also predict that the differential stability between the overstory and understory plant communities in the middle reach will become more similar to that of the upstream control reach; with the understory being significantly less stable on the newly formed landforms.

The restoration of the Elwha River will be a valuable case study of the effects of river fragmentation and dam removal on river ecosystems. Although vegetation monitoring and restoration was not part of the decision to remove the dams (Winter and Crain 2008) it has since become a necessary part of the rehabilitation plan (Chenoweth *et al.* 2011). After the dam removal there will be large disturbed and newly exposed areas

which could become colonized by exotic species (Michel *et al.* 2011, Woodward *et al.* 2011, Chenoweth *et al.* 2011), thus managing non-natives will be a top priority. Successful revegetation of the exposed deltas and prevention of exotic invasion will be a fundamental part of the Elwha River restoration and will greatly benefit from the insight gained by pre-removal analyses.

Geomorphic Landform	Age	Dominant Vegetation
Open Bar	Young (near channel, often disturbed)	Herbaceous early colonizers
Woody Bar	1-5 years	Red alder, willow
Developing Floodplain	5-20 year s	Red alder, willow
Established Floodplain	15-40 years	Red alder

Transitional Fluvial Terrace	25-70 years			Red alder, cottonwood			
Mature Fluvial Terrace	100-300 years			Spruce, hemlock, maple			

Table 1 – Table listing age and vegetation characteristics of each geomorphic landform type (Latterell *et al.* 2009)

Natives							
2005				**2010**			
Species	**# of Plots**	**% of Natives**	**% of Total**	**Species**	**# of Plots**	**% of Natives**	**% of Total**
ALNURUB	81	21.1	18.6	ALNURUB	68	23.2	21.3
POPUBALT	56	8.37	7.37	POPUBALT	51	10.8	9.92

ACERMAC	93	8.07	7.1	ACERMAC	72	8.1	7.43
PSEUMEN	55	6.23	5.49	PSEUMEN	41	7.08	6.49
POLYMUN	82	5.97	5.25	POLYMUN	66	6.76	6.2
SYMPALB	80	4.61	4.06	OEMLCER	51	5.34	4.9
OEMLCER	63	3.9	3.43	SALISIT	26	5.1	4.68
ABIEGRA	70	3.74	3.29	SYMPALB	65	3.78	3.46
THUJPLI	29	3.32	2.92	ACERCIR	27	3.37	3.09
ACERCIR	41	3.12	2.75	ABIEGRA	54	3.06	2.8

Table 2 - Table of ten most abundant native species from each sample year.

Exotics							
2005				**2010**			
Species	**# of Plots**	**% of Exotics**	**% of Total**	**Species**	**# of Plots**	**% of Exotics**	**% of Total**
GERAROB	43	25.1	3.00	DACTGLO	49	36.5	3.04
DACTGLO	53	25.0	2.99	GERAROB	52	13.4	1.12
LEUCVUL	32	6.68	0.80	AGROCAP	44	6.64	0.55
MYCEMUR	87	6.51	0.78	LEUCVUL	29	5.6	0.47
CYTISCO	14	5.98	0.72	LATHLAT	22	4.56	0.38
POA_TRV	30	5.59	0.67	MYCEMUR	69	4.26	0.35
PHALARU	29	4.03	0.48	LAPSCOM	25	3.99	0.33
RANUREP	22	3.71	0.44	RUBUULM	6	3.47	0.29
HOLCLAN	24	2.77	0.33	HYPEPER	19	2.85	0.24
AGROSTO	14	2.12	0.25	RANUREP	26	2.72	0.23

Table 3 - Table of ten most abundant exotic species from each sample year.

Grp #	Group Name	Landforms	Reaches	2005 Plots	2010 Plots
1	SYMPALB-ROSANUT-GERAROB	Woody bars to transitional fluvial terraces	50% lower, 50% middle	7	5
2	**OEMLCER**-	Floodplains, mature	88% lower,	5	11

Group	Species	Habitat	Location		
	SYMPALB-POLYMUN	fluvial terraces	12% middle		
3	**DACTGLO**-GERAROB-RANUREP	Established floodplains to transitional fluvial terraces	6% lower, 94% upper	8	8
5	**GERAROB**-OEMLCER-SYMPALB	Woody bars to developing floodplains	100% lower	2	1
11	**HOLODIS**-OEMLCER-SYMPALB	Established floodplains to fluvial terraces	60% lower, 40% middle	3	2
14	**POLYMUN**-TOLMMEN-ACHLTRI	Fluvial terraces	21% lower, 63% middle, 16% upper	8	11
19	**LATHLAT**-CYTISCO-LEUCVUL	Woody bars to floodplains	80% lower, 20% middle	2	3
21	**ACHLTRI**-BROMVUL-TIARTRI (TRIELAT, CAMPSCO)	Developing floodplains, fluvial terraces	10% lower, 10% middle, 80% upper	6	4
25	**SYMPALB**-POLYMUN-OEMLCER	Established floodplains to fluvial terraces	43% lower, 57% middle	9	5
27	**URTIDIO**-OEMLCER-CAREMER	Transitional fluvial terraces	100% lower	1	3
38	**TOLMMEN**-URTIDIO-AGROSTO (CIRCALP)	Fluvial terraces	57% middle, 43% upper	3	4
79	**CAREDEW**-PHALARU-CIRCALP	Open bars, mature fluvial terraces	50% middle, 50% upper	2	0
87	EQUIARV-ELYMGLAG-DESCELO	Open bars	100% upper	2	2
95	POA_TRV-ELYMGLAG-AGROCAP	Bars to developing floodplains	100% upper	9	8

Table 4 - Understory community groups as determined by cluster analysis. Underlined species were significant understory community indicators in 2005 and 2010, bolded species made up 20% or more of total understory vegetation abundance within each group, and species in parentheses were significant indicators both years but were not among the highest in abundance.

Group (abbrev.)	Positive Relation	Negative Relation	Indicator species	Overall Community	Reach Location
Symphoricarpos-Rosa				*Alnus*	
		Elevation			
Oemleria		Plant diversity	*Oemleria*		Lower

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			cerasiformis		
			Dactylis glomerata		Middle
Dactylis		Elevation			
Geranium		Plant diversity, elevation		Alnus	Lower
Holodiscus		Plant diversity	*Holodiscus discolor*		
Polystichum	Elevation	Exotic plant diversity	*Polystichum munitum*	*Polystichum*	Middle
Lathyrus latifolius	Exotic plant diversity	Elevation	*Lathyrus latifolius, Cytisus scoparius*	*Salix*	Lower
Achlys	Elevation		*Achlys triphylla, Trientalis latifolia, Campanula scouleri*	*Abies*	Upper
Symphoricarpos		Plant diversity	*Symphoricarpos albus*	*Alnus*-exotic	
Urtica		Plant diversity		*Thuja*	Lower
Tolmeia			*Tolmeia menziesii, Circaea alpina*	*Alnus-Populus*	
Carex deweyanna					
Equisetum	Plant diversity			*Alnus*-bar	Upper
Poa pratensis	Native plant diversity			*Salix*	Upper

Table 5 - Table summarizing trends, indicator species, and associated overall community and reach location, for each understory community group.

Grp #	Group Name	Landforms	Reaches	2005 Plots	2010 Plots
1	**ALNURUB-POPUBALT/** OEMLCER	Developing/established floodplains to transitional fluvial terraces	71% lower, 29% middle	12	6
3	**ALNURUB/**	Woody bars to	32% lower,	15	13

	GERAROB-SYMPALB	developing and established floodplains	25% middle, 43% upper		
8	ALNURUB/ GERAROB-OEMLCER (EQUIARV)	Open bars	8% lower, 8% middle, 83% upper	7	5
11	**POPUBALT**-ABIEGRA/ SYMPALB	Established floodplains to transitional and mature fluvial terraces	40% lower, 60% middle	8	7
15	**SALISIT**-ALNURUB-POPUBALT	Open and woody bars to developing floodplains	50% lower, 10% middle, 30% upper	4	6
30	**ACERMAC**-ACERCIR/ **POLYMUN**	Transitional and mature fluvial terraces	47% lower, 47% middle. 5% upper	9	10
31	**THUJPLI**-PSEUMEN/ POLYMUN (GAULSHA-VACCPAR)	Transitional and mature fluvial terraces	71% lower, 29% middle	3	4
45	ALNURUB/ POLYMUN-SYMPALB	Established floodplains and mature fluvial terraces	100% middle	1	4
53	**ABIEGRA**-PSEUMEN-ACERCIR	Transitional and mature fluvial terraces	50% lower, 50% middle	3	3
58	**ALNURUB/** DACTGLO-GERAROB	Established floodplains to transitional fluvial terraces	11% lower, 67% middle, 22% upper	5	4
66	**PSEUMEN/**POLYMUN-DACTGLO (HIERALB)	Transitional and mature fluvial terraces	56% lower, 44% middle	4	5
105	**TSUGHET/ACHLTRI**-TIARTRI	Mature fluvial terraces	100% upper	1	1

Table 6 - Overall community groups as determined by cluster analysis. A "-" indicates species in common strata, while a "/" indicates strata differentiation. Underlined species were significant community indicators in 2005 and 2010, bolded species made up 20% or more of total vegetation abundance within each group, and species in parentheses were significant indicators both years but were not among the highest in abundance.

Group (abbrev.)	Positive Relation	Negative Relation	Indicator species	Reach Location
Alnus-Populus		Elevation		Lower
Alnus		Elevation	*Alnus rubra*	
Alnus-bar	Exotic plant diversity		*Equisetum arvense*	Upper
Populus			Symphoricarpos albus	Middle
Salix	Exotic plant diversity		*Salix sitchensis*	Lower
Polystichum				Middle

Acer	Elevation	Exotic plant diversity	*Acer macrophyllum, Polystichum munitum*	
			Thuja plicata, Vaccinium parvifolium,	Lower
Thuja		Exotic plant diversity	*Gaultheria shallon*	
Abies	Elevation		*Abies grandis*	
Alnus-exotic				Middle
Pseudotsuga	Elevation		*Pseudotsuga menziesii, Hieracium albiflorum*	
Tsuga	Elevation			Upper

Table 7 - Table summarizing trends, indicator species, and associated overall community and reach location, for each overall community group.

Reach Location	Geomorphic Landforms	Overall Communities	Understory Communities	Indicator Species
Lower	No open bars	*Alnus-Populus, Salix, Thuja, Pseudotsuga*	*Oemleria, Geranium, Holodiscus, Lathyrus latifolius, Urtica*	*Populus balsamifera* ssp. *trichocarpa, Oemleria cerasiformis, Rubus parviflorus, Holodiscus discolor*
Middle	> 70% fluvial terraces, < 5% bars	*Populus, Polystichum, Alnus*-exotic	*Polystichum, Symphoricarpos, Tolmeia*	*Dactylis glomerata, Symphoricarpos albus, Carex deweyanna, Circaea alpina*
Upper	35-40% bars, no	*Alnus, Alnus*-bar,	*Dactylis, Achlys,*	*Osmorhiza berteroi,*

established floodplains	*Tsuga*	*Equisetum, Poa pratensis*	*Galium trifidum, Achlys triphylla, Equisetum arvense*

Table 8 - Table summarizing landform trends, overall communities, understory communities, and indicator species, associated with each reach.
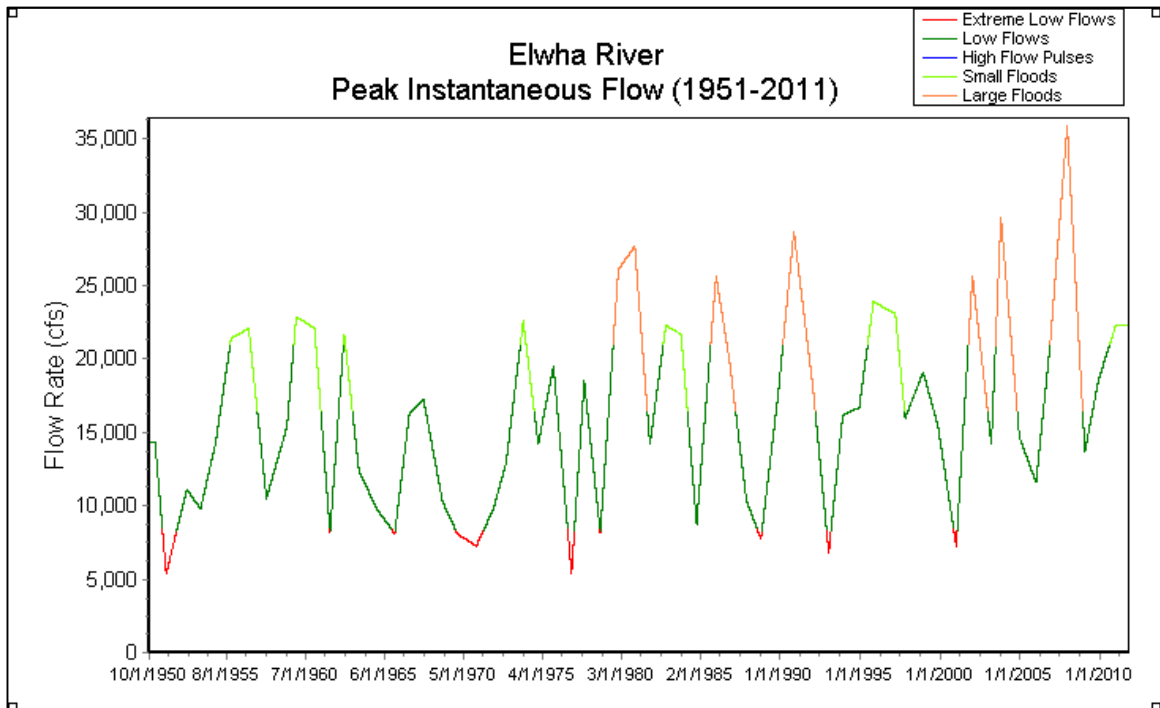
Figure 1 - Graph of annual peak in instantaneous surface flow since 1950, notice peak in December of 2007 (USGS 2012).
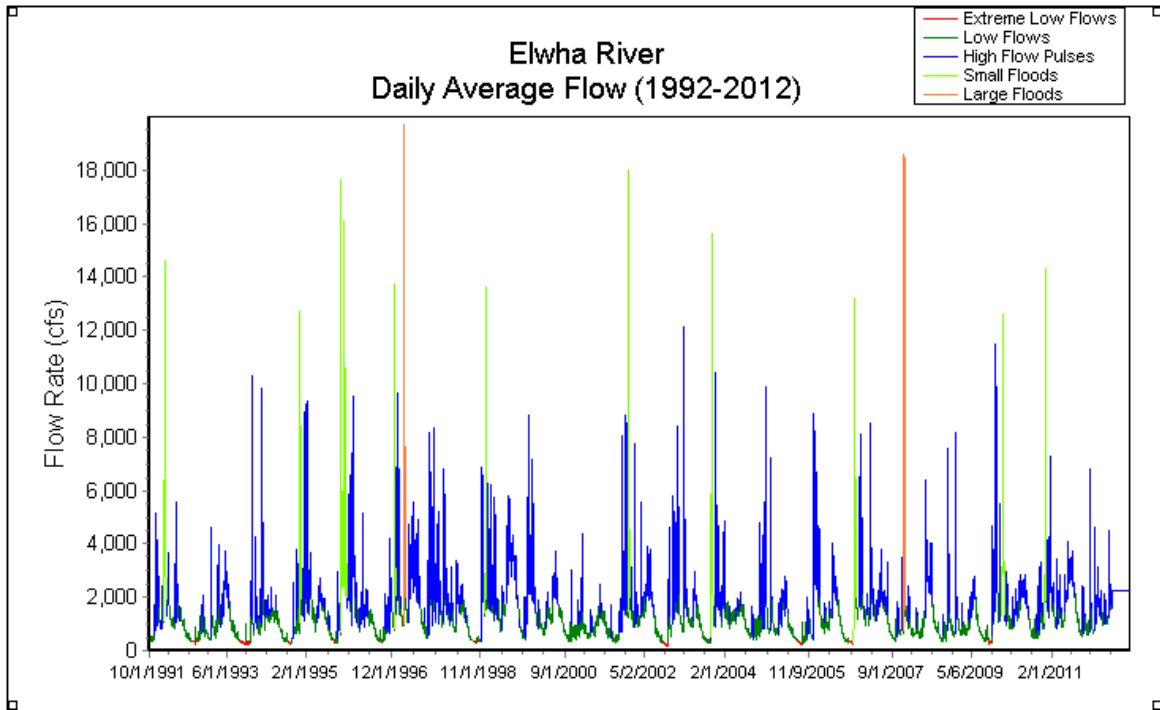
Figure 2 - Graph of daily average discharge between 1991 and 2011, notice peak in December of 2007 (USGS 2012).

Figure 3 – Map of study area along Elwha River, Olympic National Park, WA.
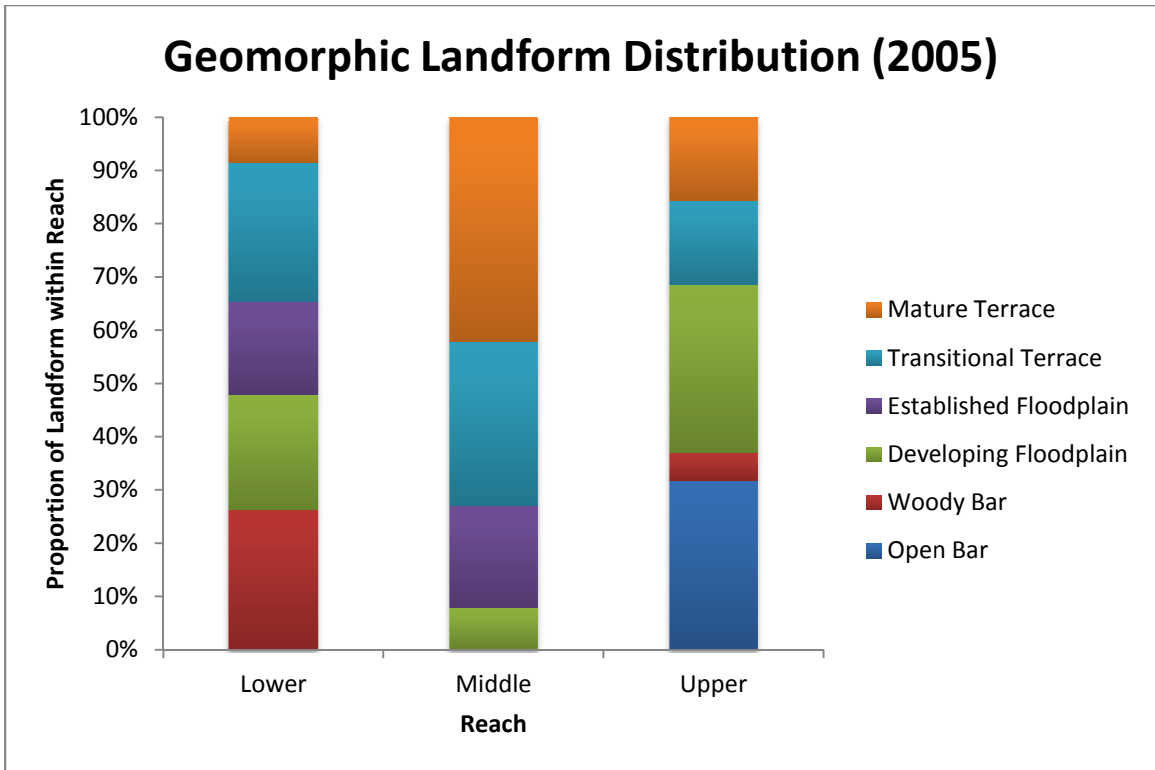
Figure 4 - Distribution of geomorphic landforms within reaches in 2005.
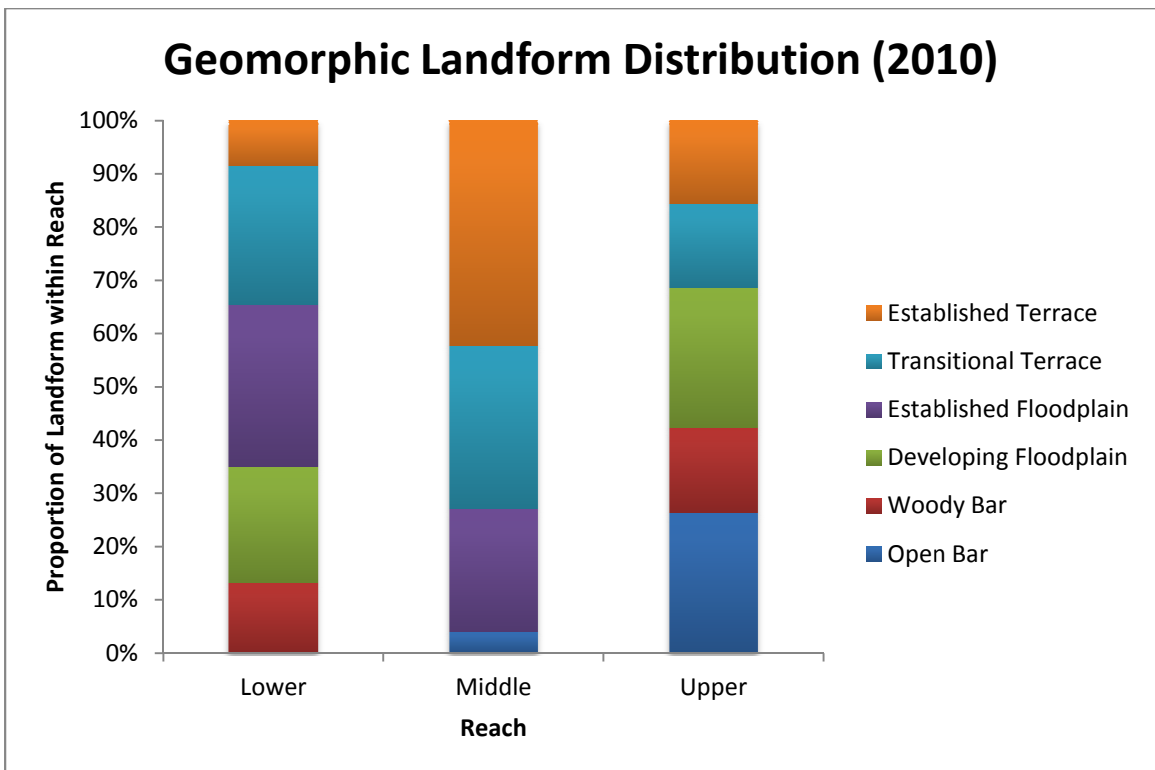
Figure 5 - Distribution of geomorphic landforms within reaches in 2010.

Figure 6 - NMS ordination biplot (axes 1 and 3) of understory species in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with r²>0.20. Plots grouped by geomorphic landform.

Figure 7 - NMS ordination biplot (axes 1 and 3) of understory species in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with r²>0.20. Plots grouped by understory community group.
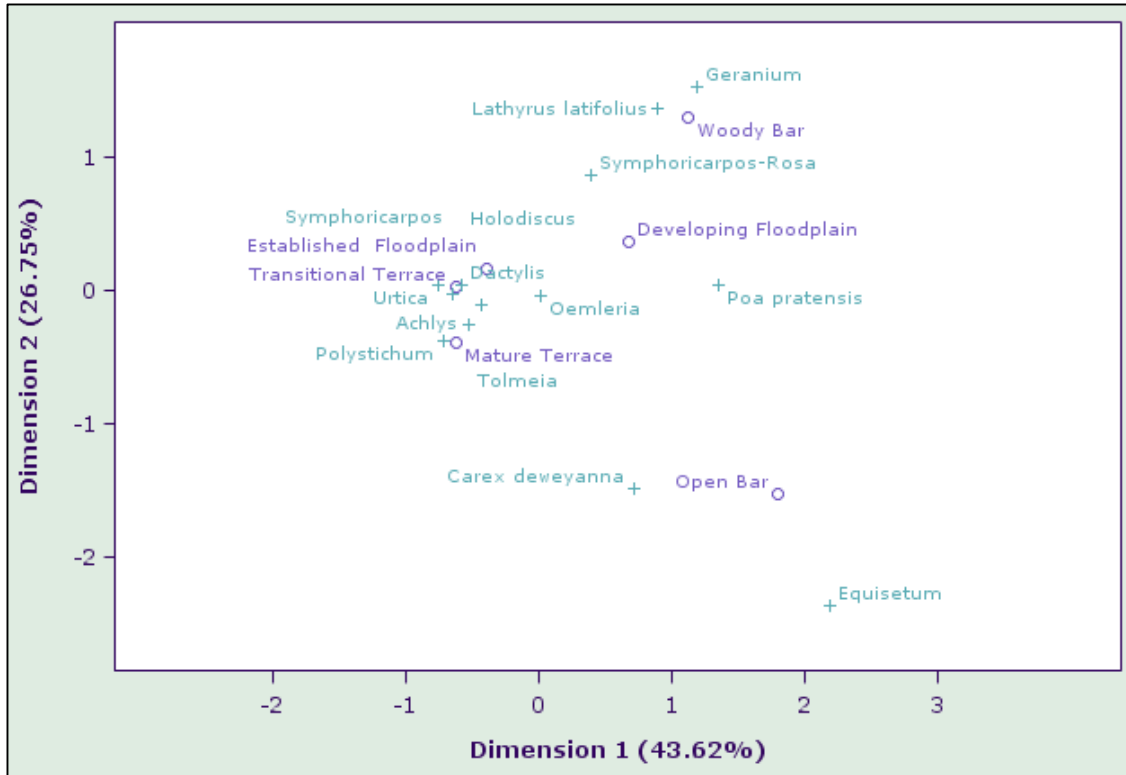
Figure 8 – Correspondence analysis showing the relationship (based on relative central tendencies between groups) between geomorphic landform and understory community group.

Figure 9 - NMS ordination biplot (axes 1 and 2) of understory species in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with $r^2 > 0.20$. Plots grouped by reach location.
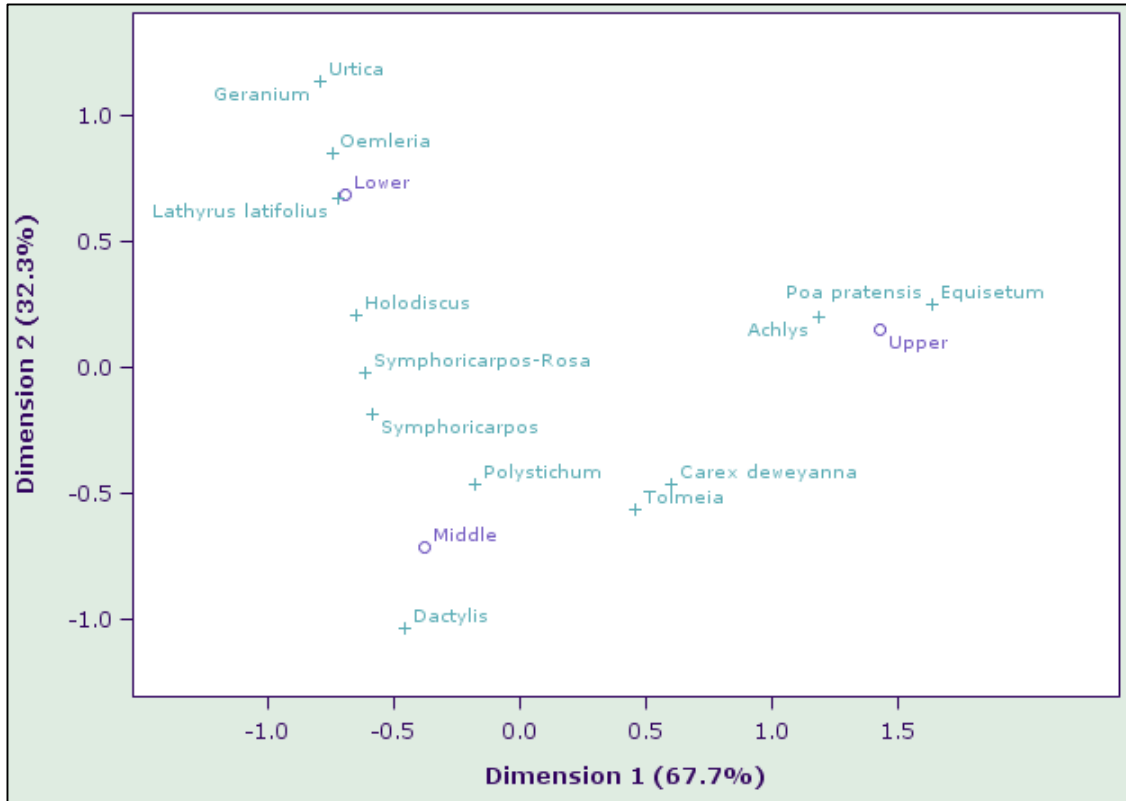
Figure 10 - Correspondence analysis showing the relationship (based on relative central tendencies between groups) between reach location and understory community group.
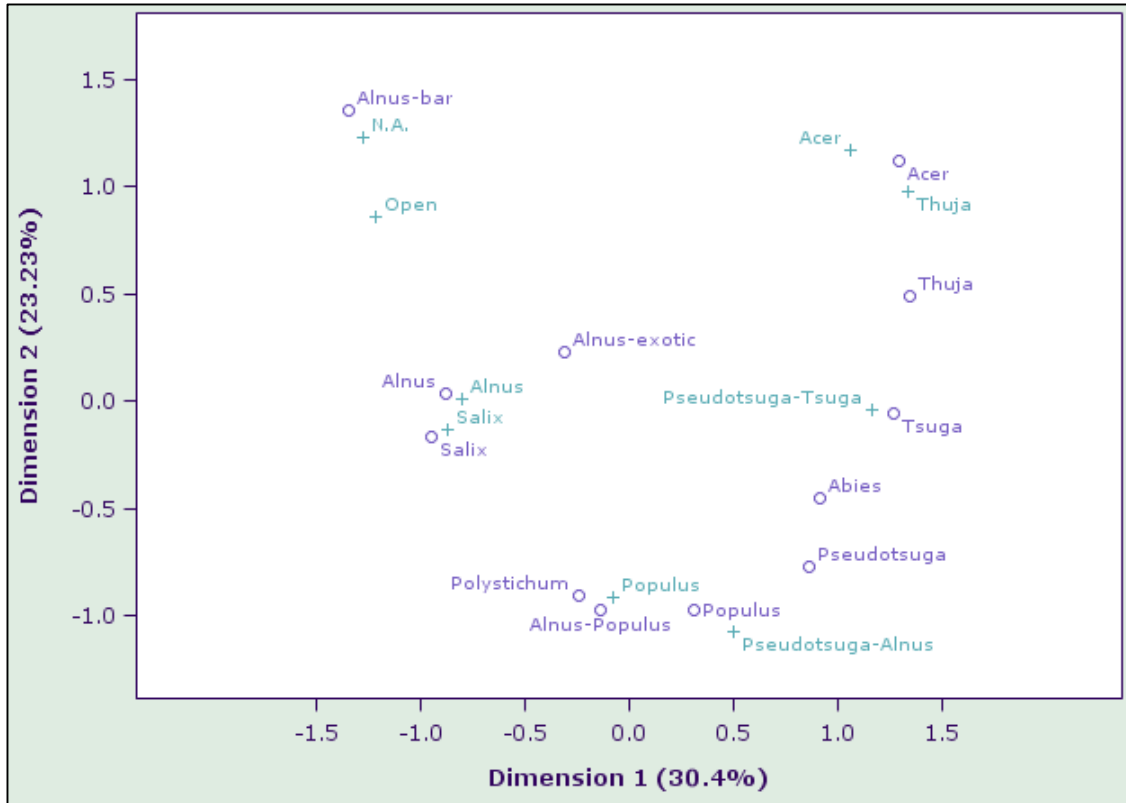
Figure 11 - Correspondence analysis showing the relationship (based on relative central tendencies between groups) between overstory patch type (Shafroth *et al. In prep*) and overall plant community.

Figure 12 - NMS ordination biplot (axes 1 and 2) of entire plant community in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with $r^2>0.20$. Plots grouped by geomorphic landform.
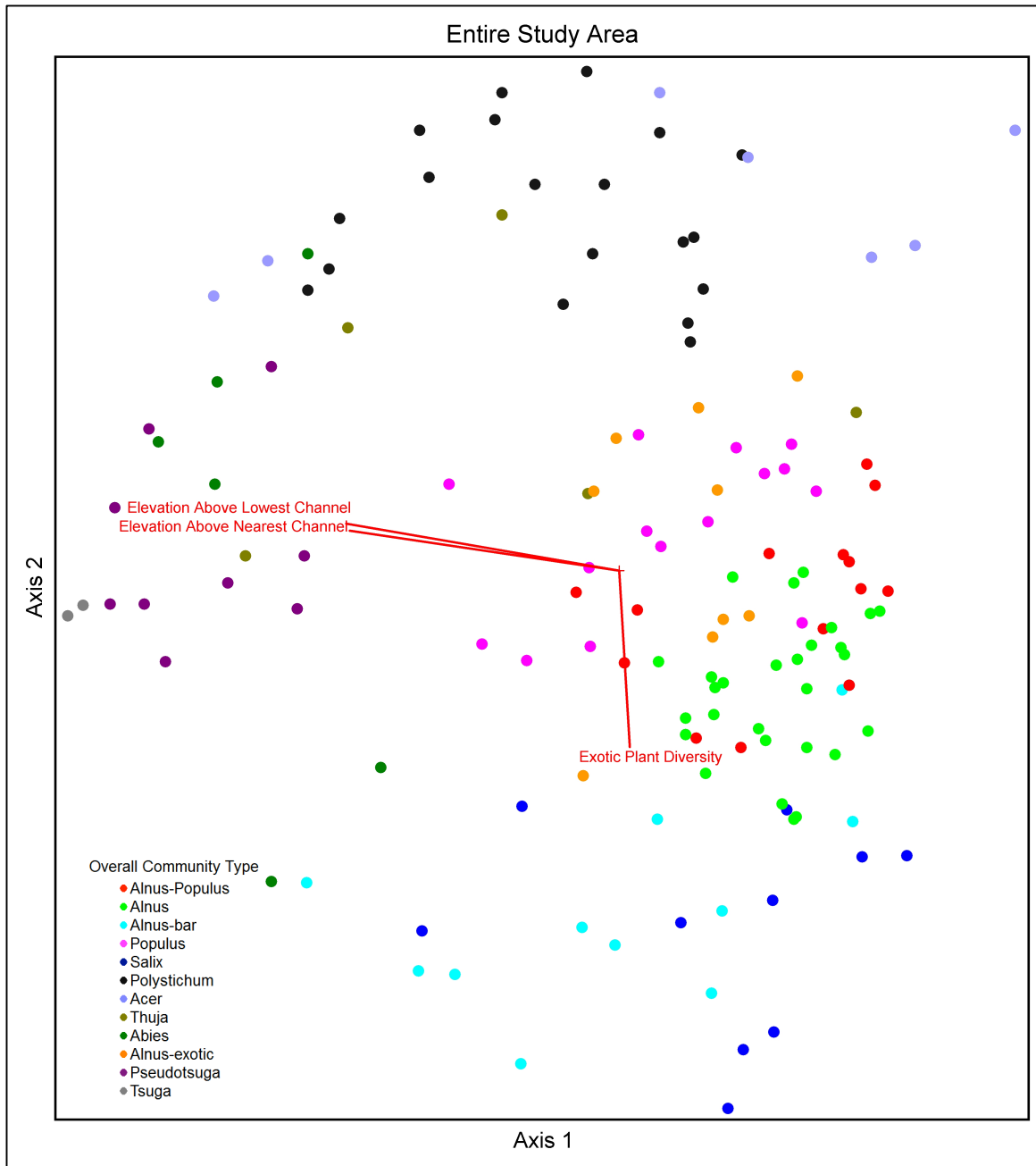
Figure 13 - NMS ordination biplot (axes 1 and 2) of entire plant community in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with $r^2>0.20$. Plots grouped by overall plant community.
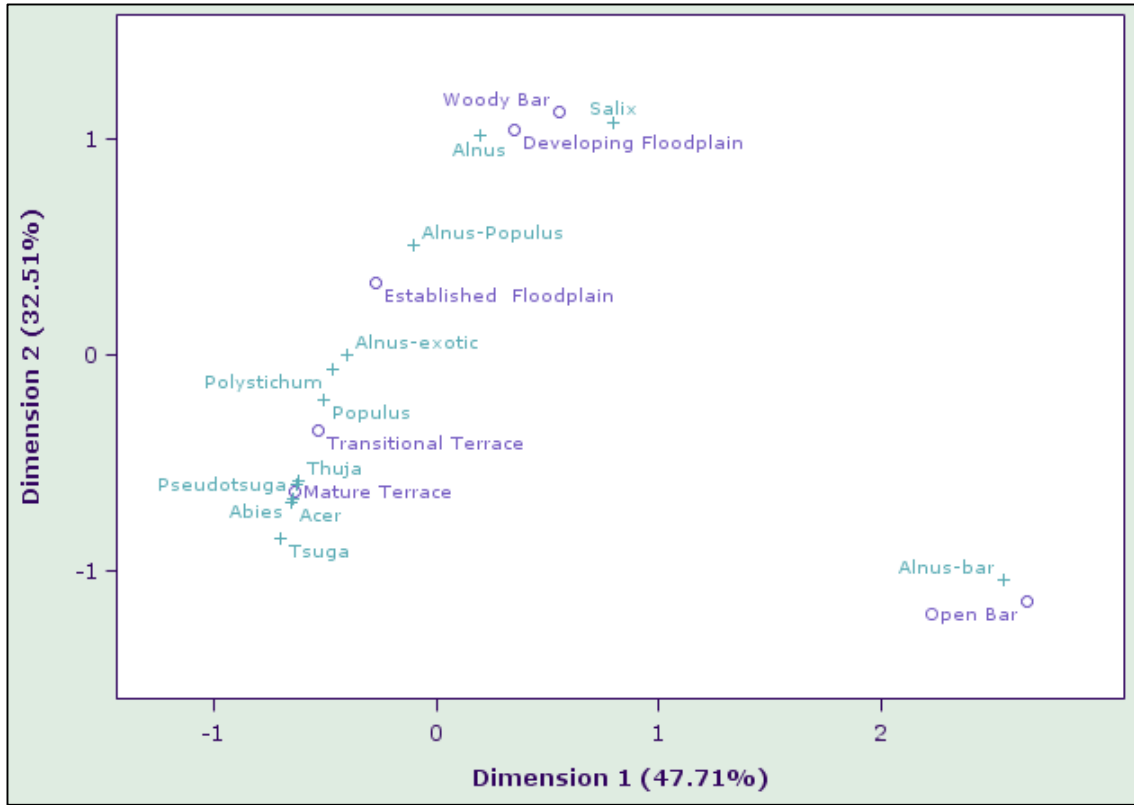
Figure 14 - Correspondence analysis showing the relationship (based on relative central tendencies between groups) between geomorphic landform and overall community group.
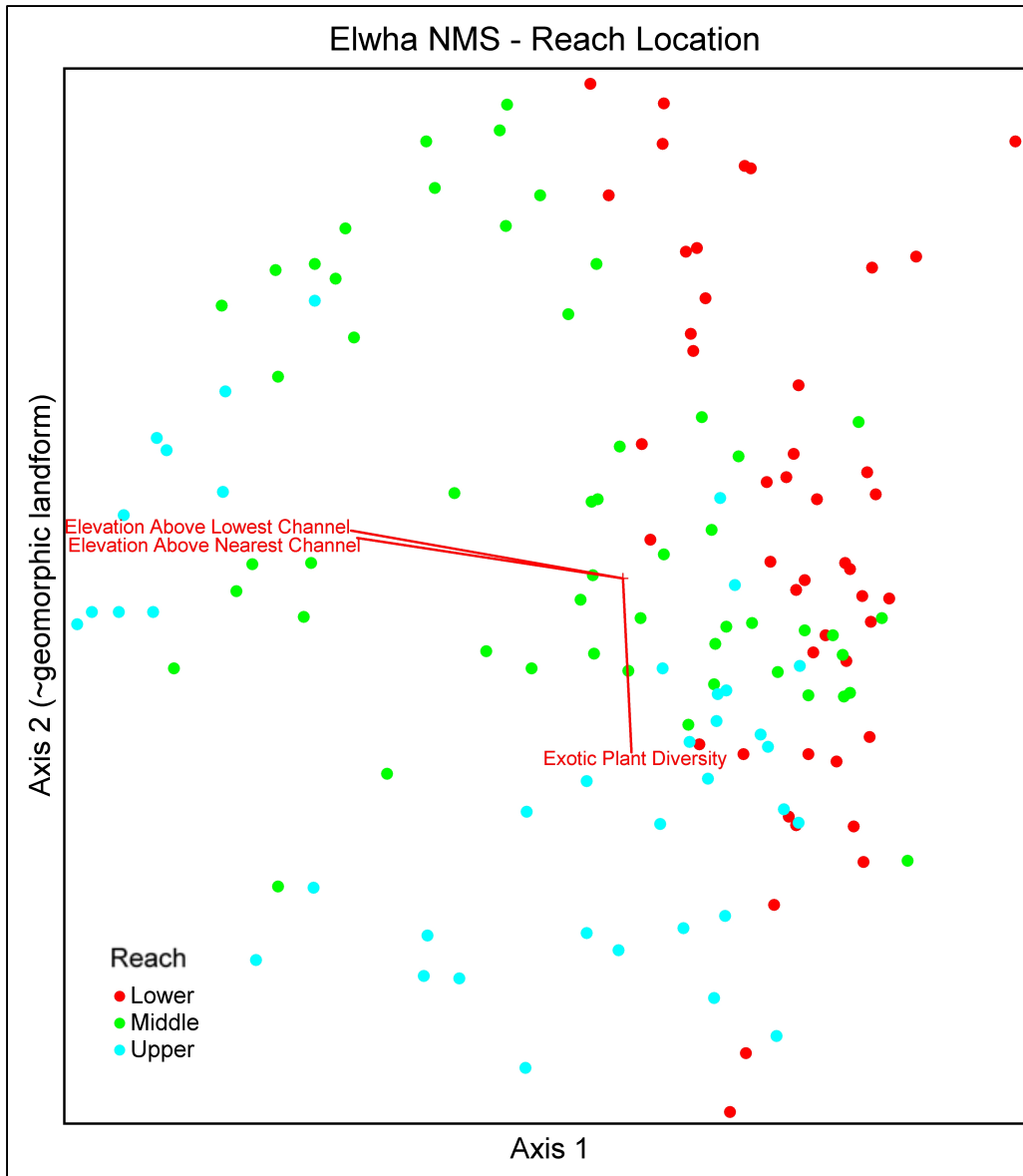
Figure 15 - NMS ordination biplot (axes 1 and 2) of entire plant community in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with $r^2>0.20$. Plots grouped by reach location.
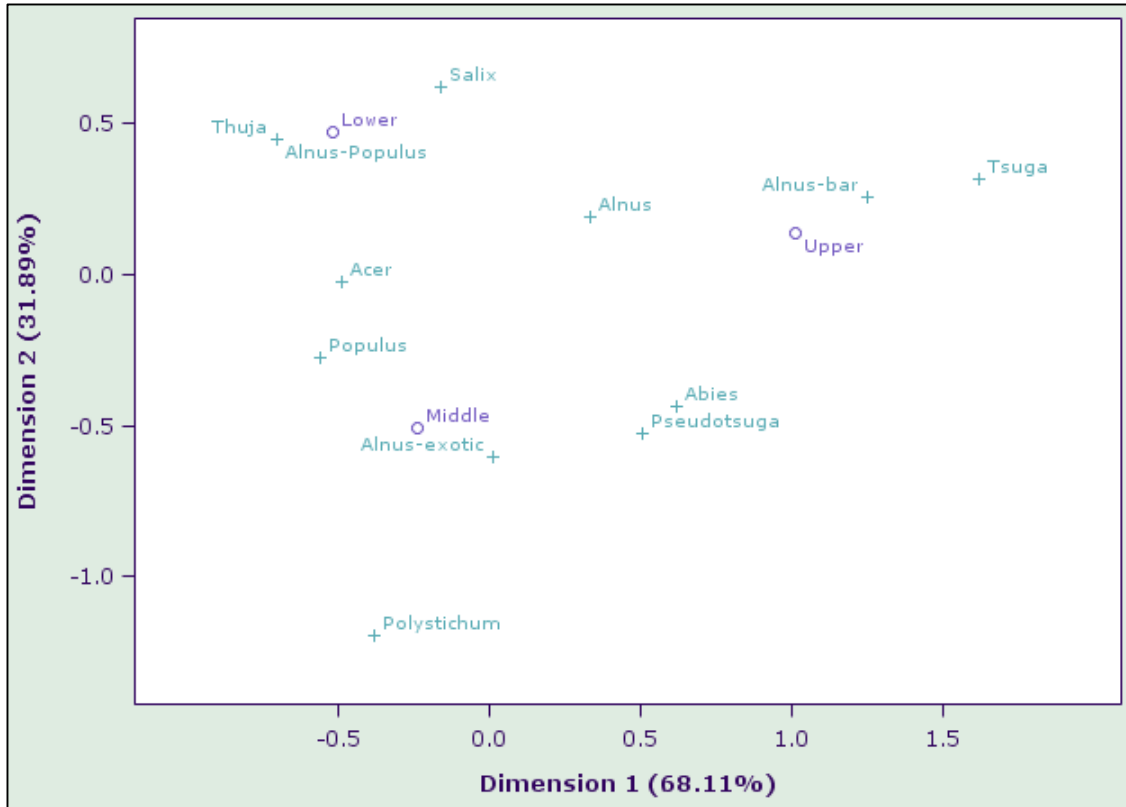
Figure 16 - Correspondence analysis showing the relationship (based on relative central tendencies between groups) between reach location and overall community group.
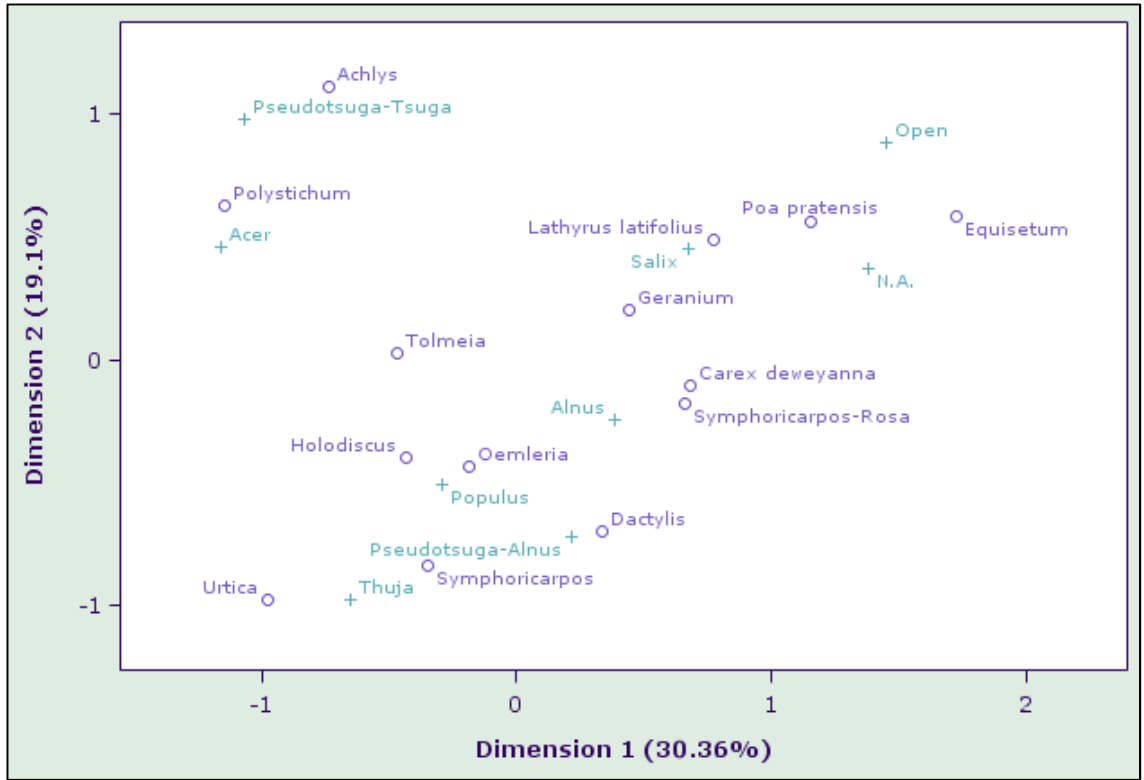
Figure 17 - Correspondence analysis showing the relationship (based on relative central tendencies between groups) between understory patch type and overstory patch type.
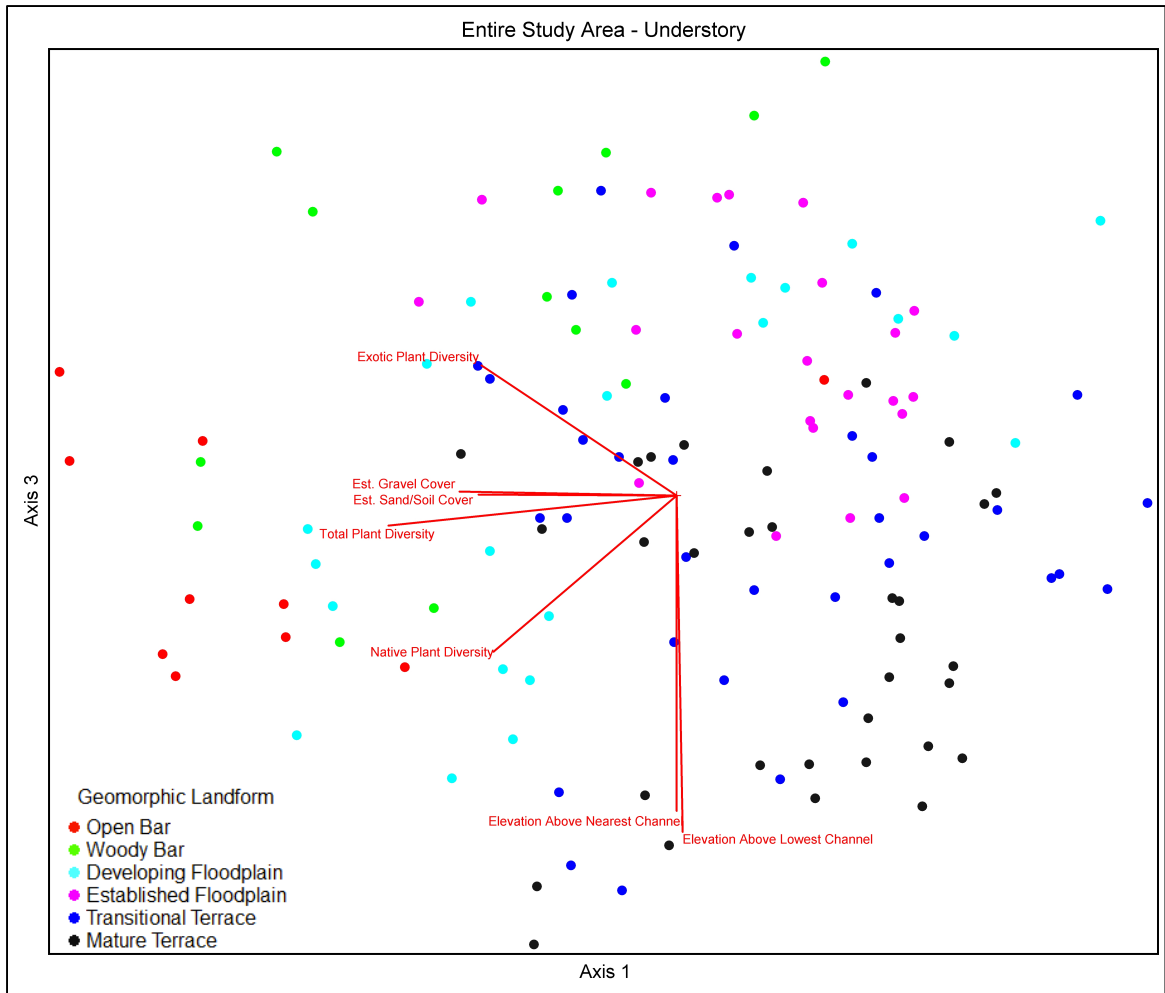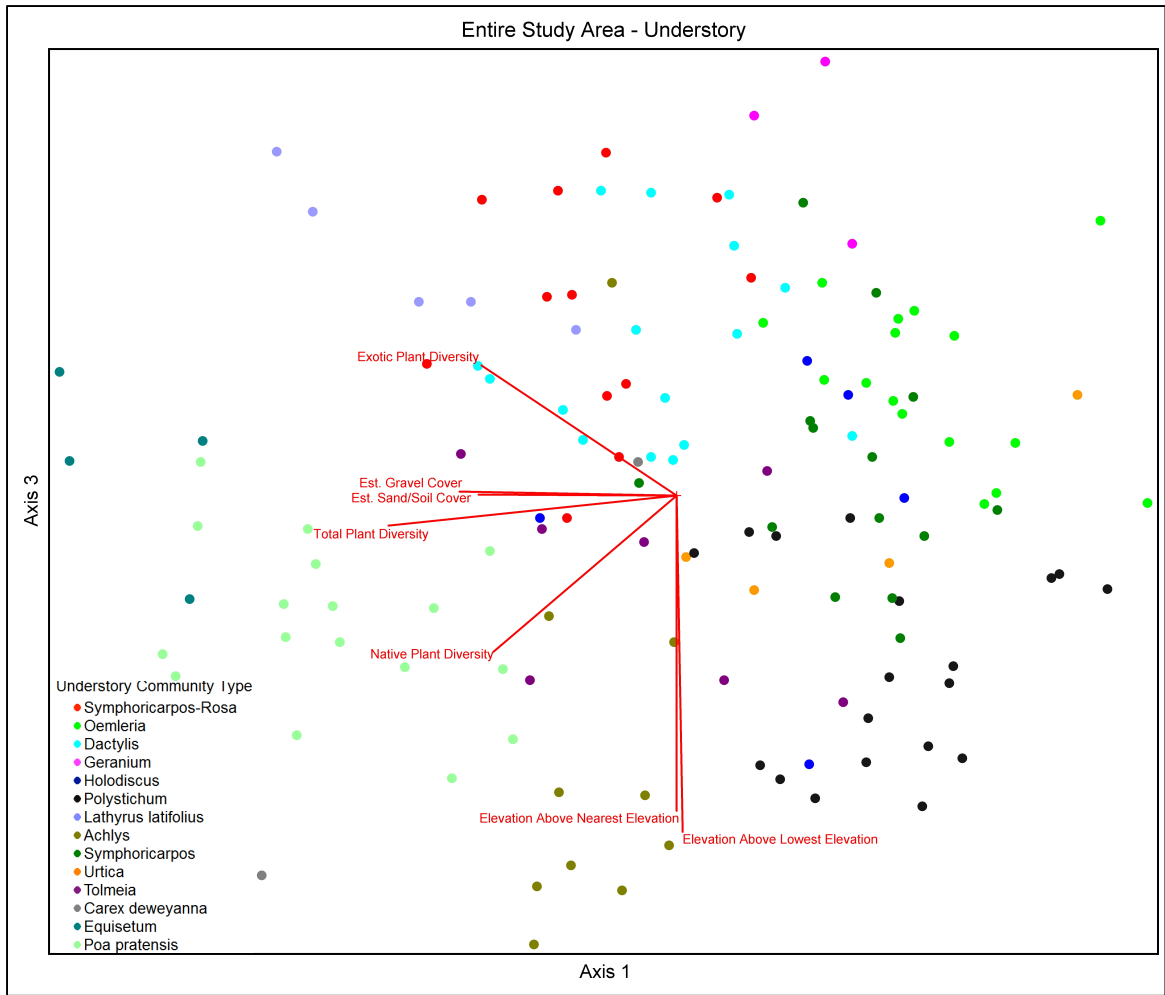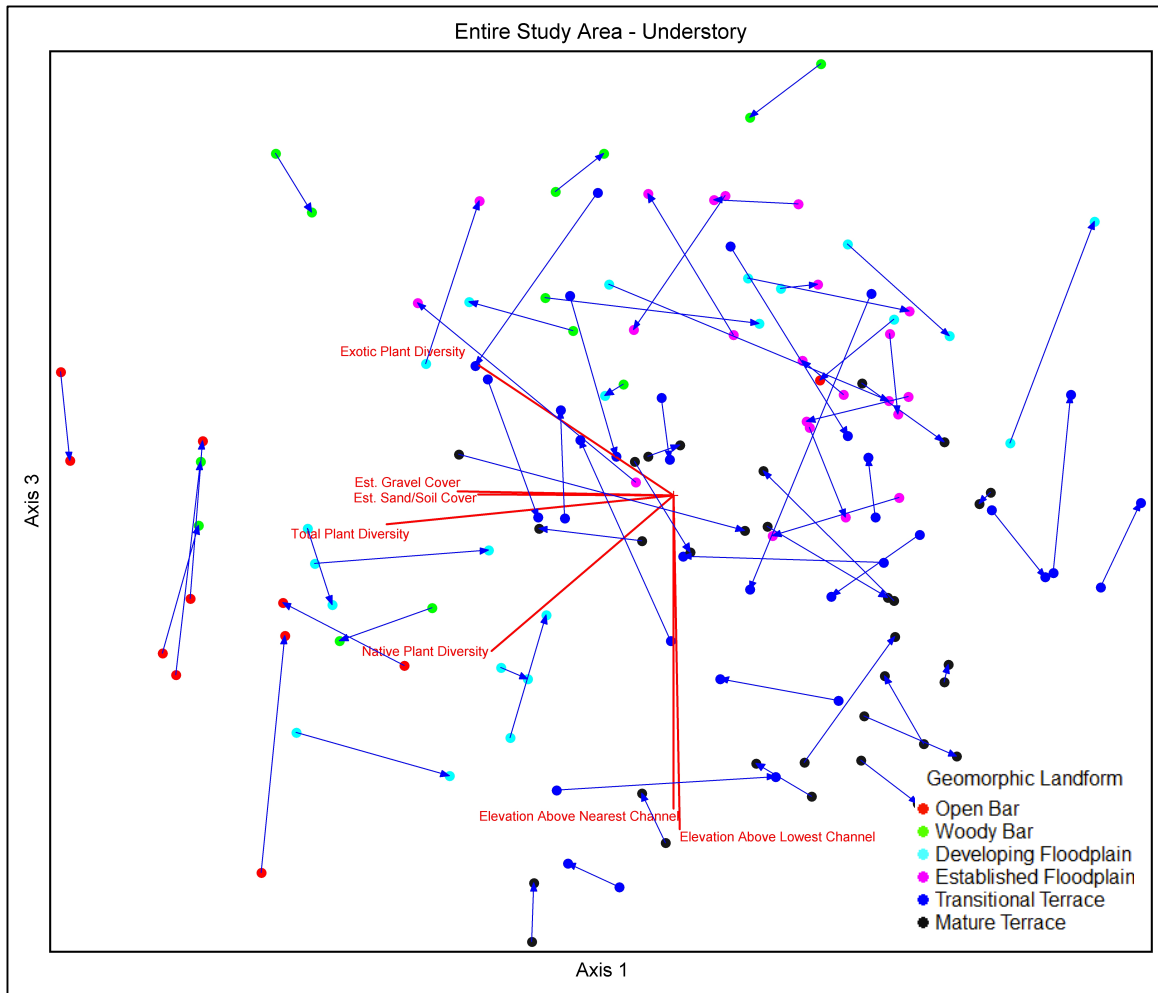
Figure 18 - NMS ordination biplot (axes 1 and 3) of understory species only in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with r²>0.20. Blue vectors indicate change in species composition from 2005 to 2010. Plots grouped by geomorphic landform.
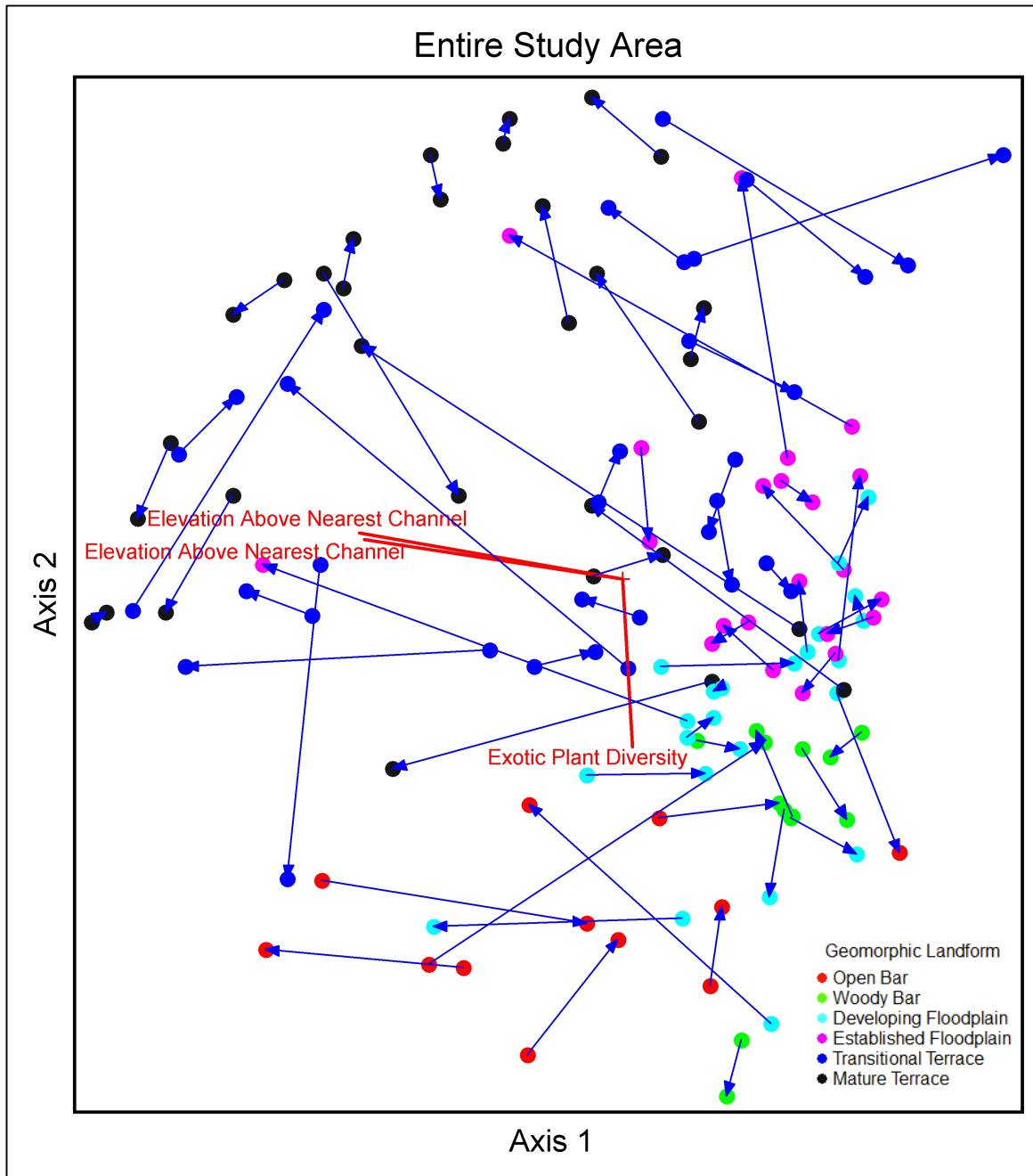
Figure 19 - NMS ordination biplot (axes 1 and 2) of entire plant community in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with $r^2>0.20$. Blue vectors indicate change in species composition from 2005 to 2010. Plots grouped by geomorphic landform.
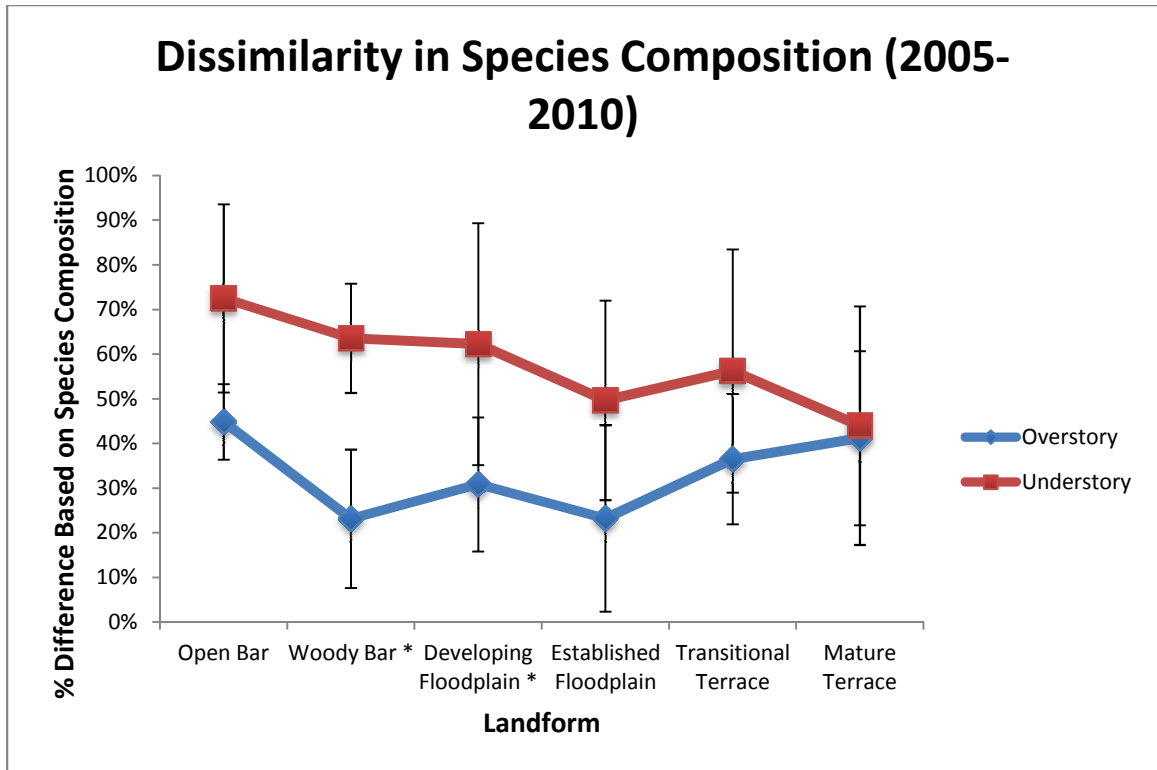
Figure 20 - Dissimilarity in species composition between successional plots in 2005 and 2010, averaged across geomorphic landform. * Indicates significant difference (p<0.05, GLM) between overstory and understory dissimilarity.
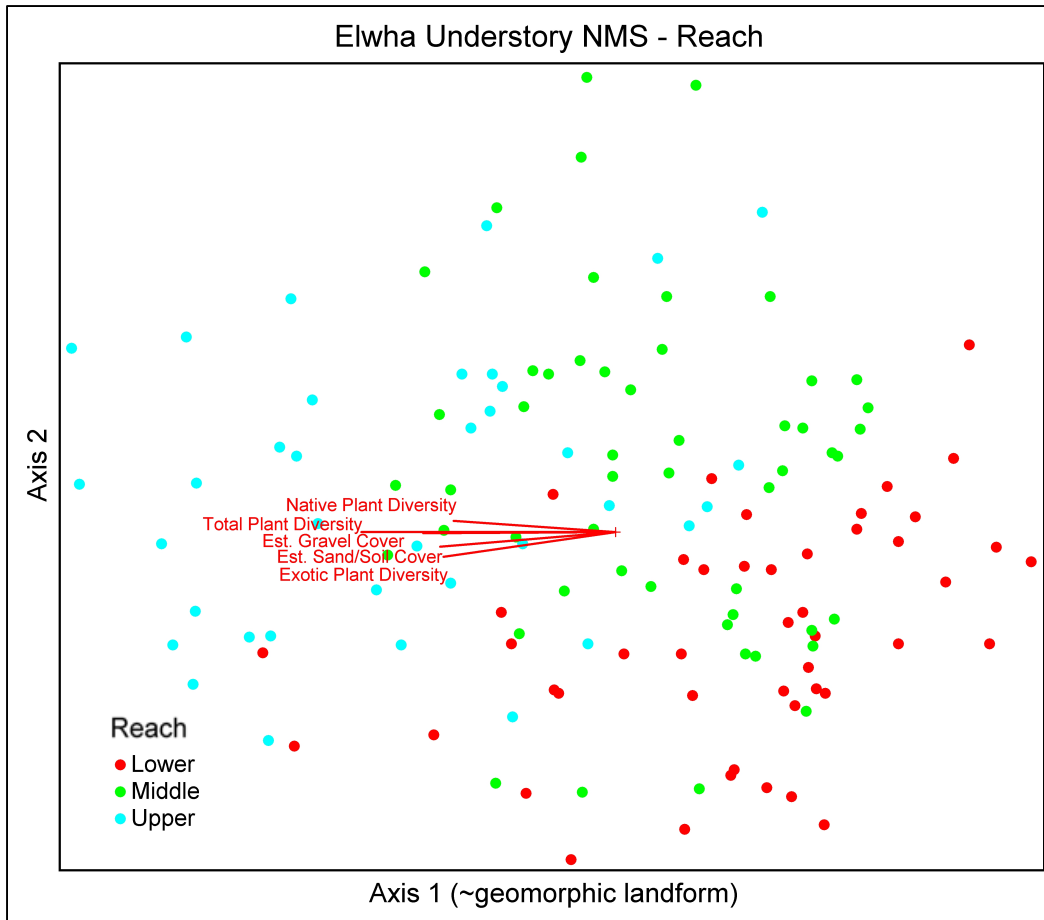

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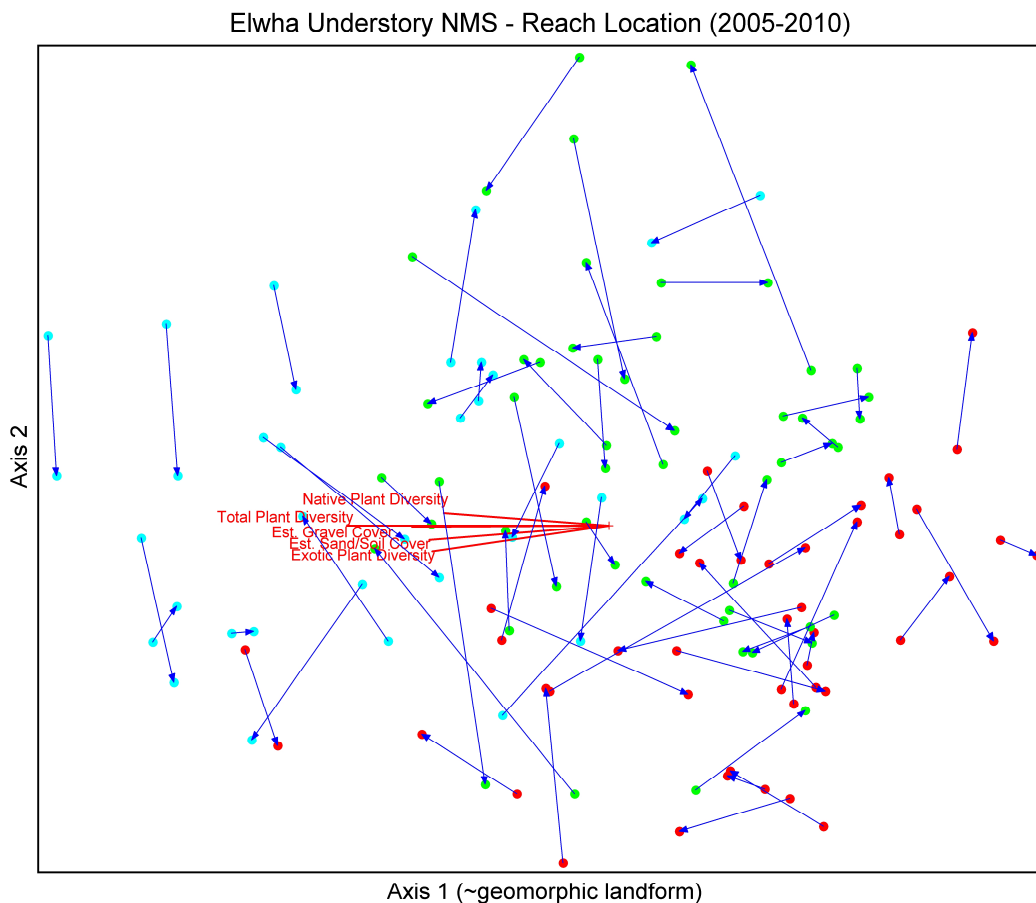
Reach
● Lower
● Middle
● Upper

Figure 21 - NMS ordination biplot (axes 1 and 2) of understory species only in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables correlated with either axis with r^2>0.20. Blue vectors indicate change in species composition from 2005 to 2010. Plots grouped by reach location.

Elwha NMS - Reach Location
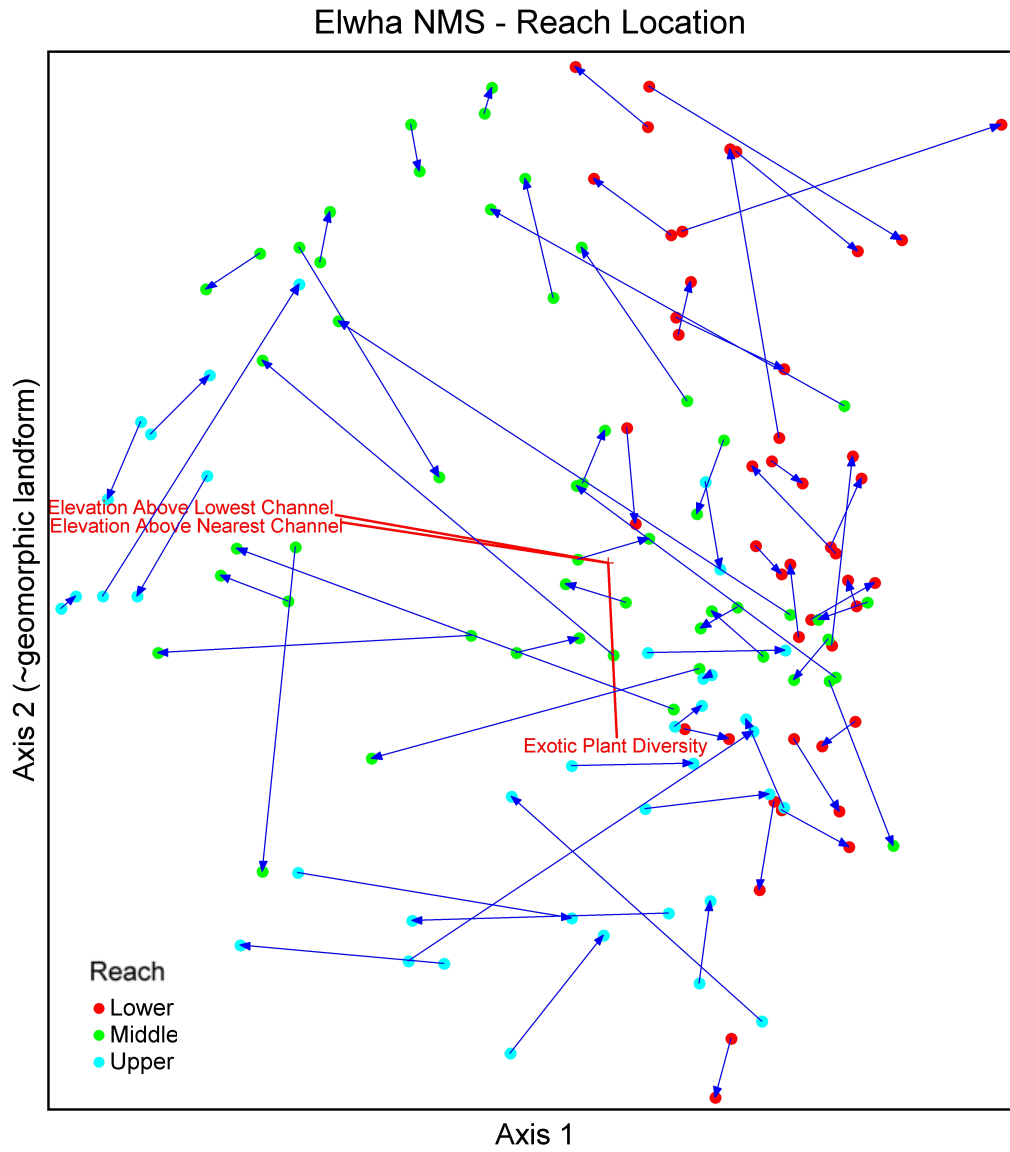
Figure 22

- NMS ordination biplot (axes 1 and 2) of entire plant community in plots along the Elwha River for 2005 and 2010 sample years. Red vectors indicate variables co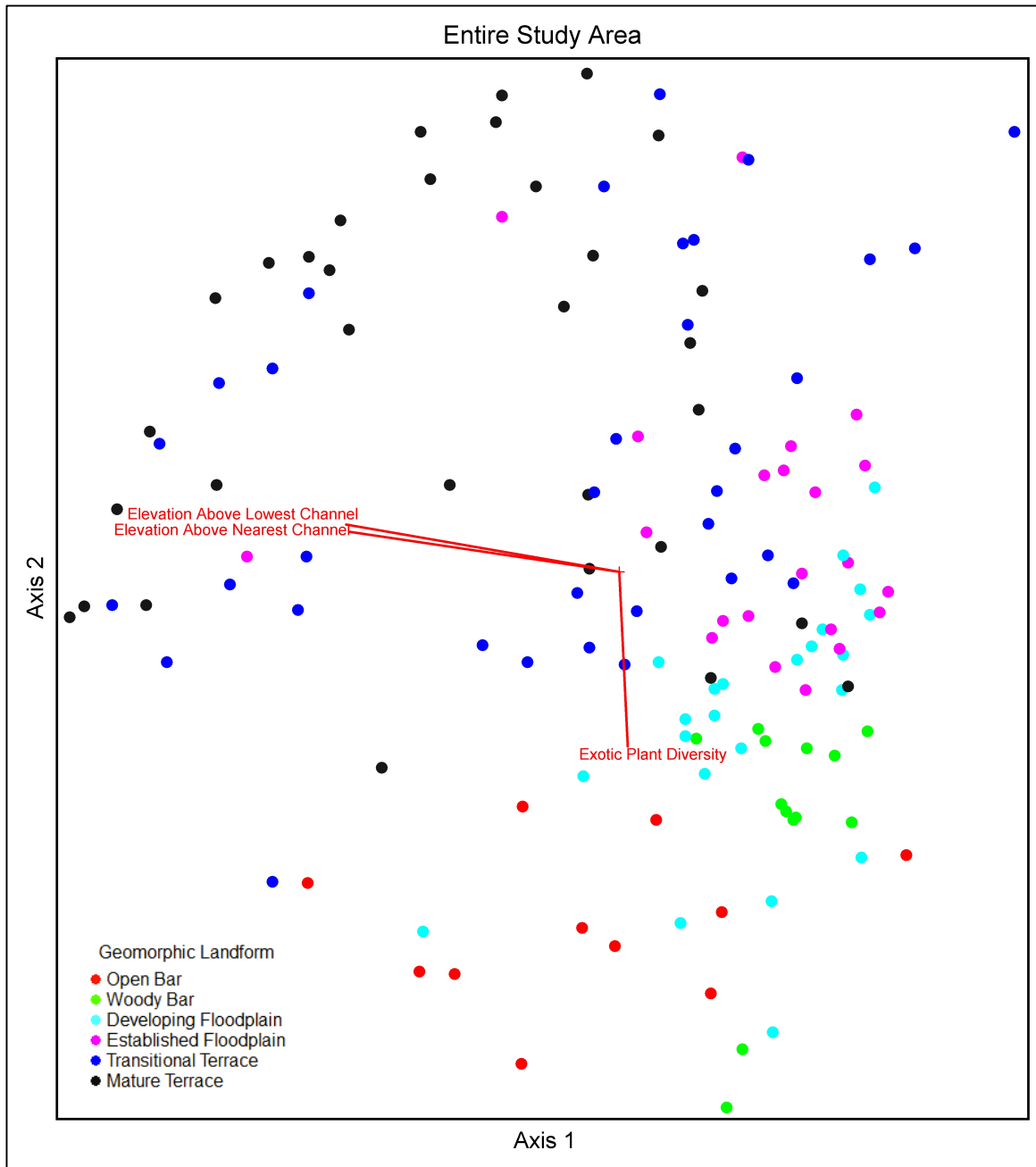rrelated with either axis with $r^2 > 0.20$. Blue vectors indicate change in species composition from 2005 to 2010. Plots grouped by reach location.
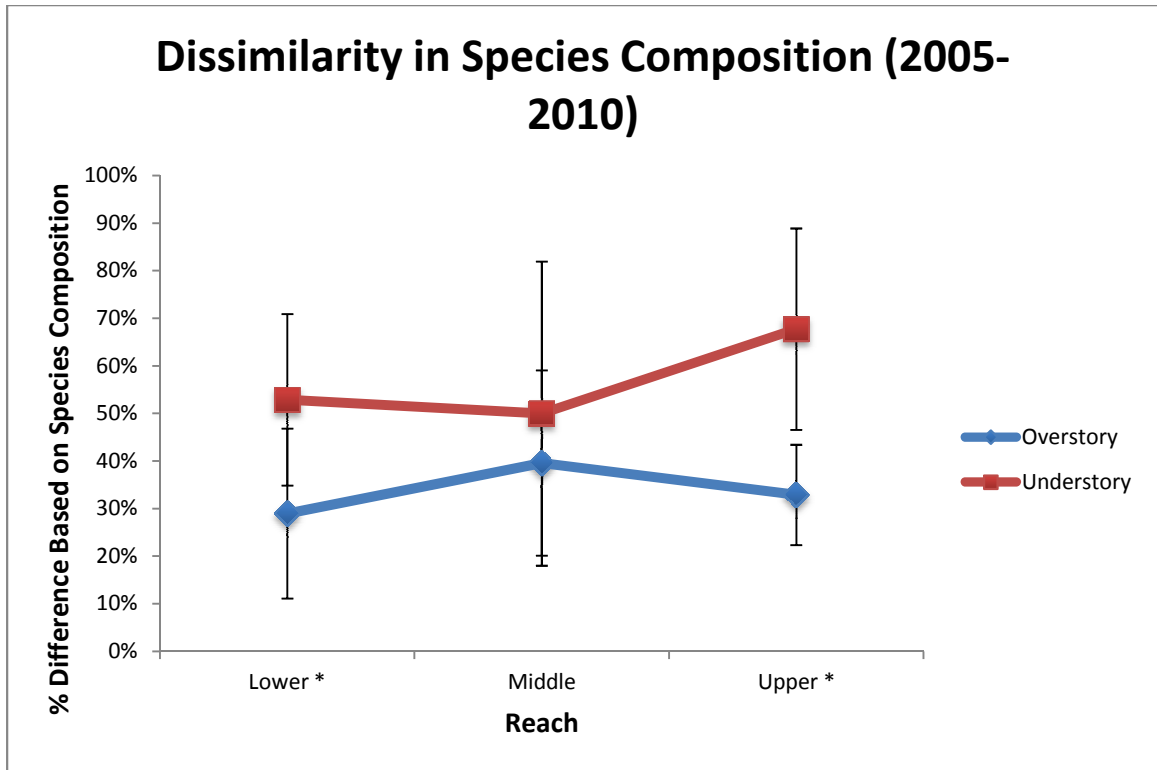
Figure 23 - Dissimilarity in species composition between successional plots in 2005 and 2010, averaged across reach location. * Indicates significant difference (p<0.05, GLM) between overstory and understory dissimilarity.
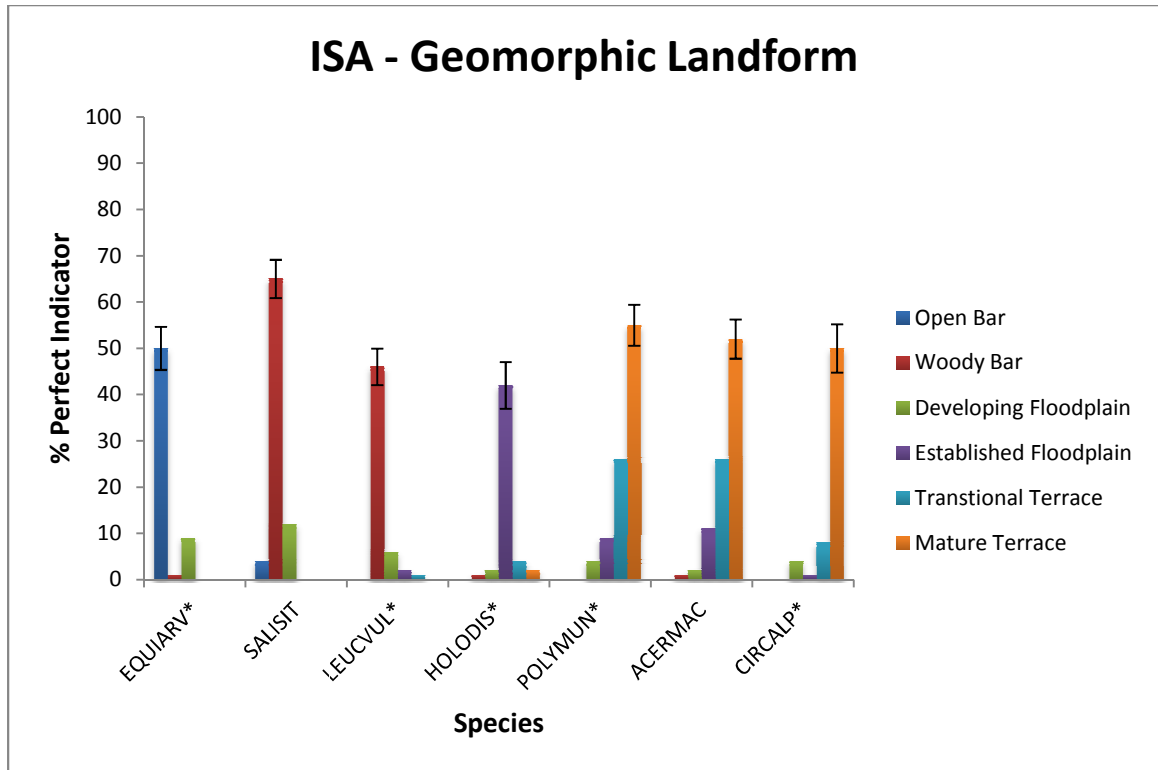
Figure 24 – Summary graph showing significant indicators of geomorphic landforms (p<0.05) from 2005 and 2010; IV represented for each species as % of perfect indication of a particular landform. * Indicates understory species.

ISA - Overall Plant Community
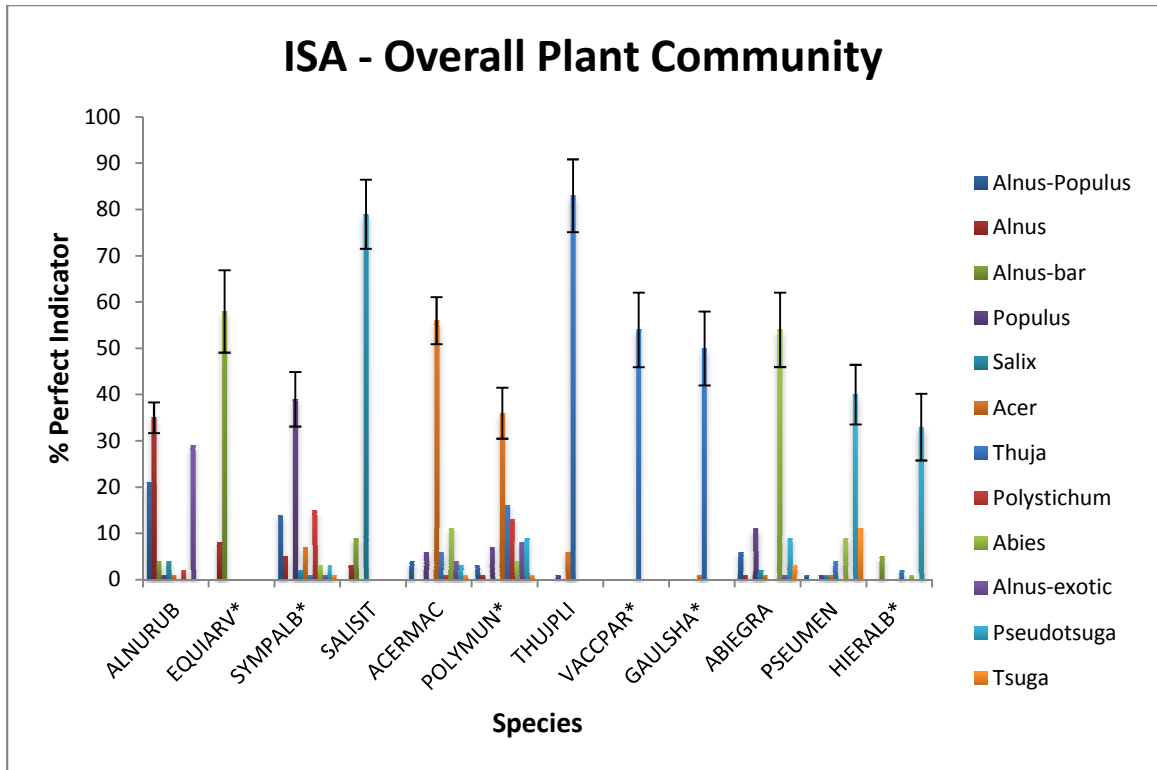
Figure 25 - Summary graph showing significant indicators of overall community groups (p<0.05) from 2005 and 2010; IV represented for each species as % of perfect indication of a particular overall plant community.   * Indicates understory species.
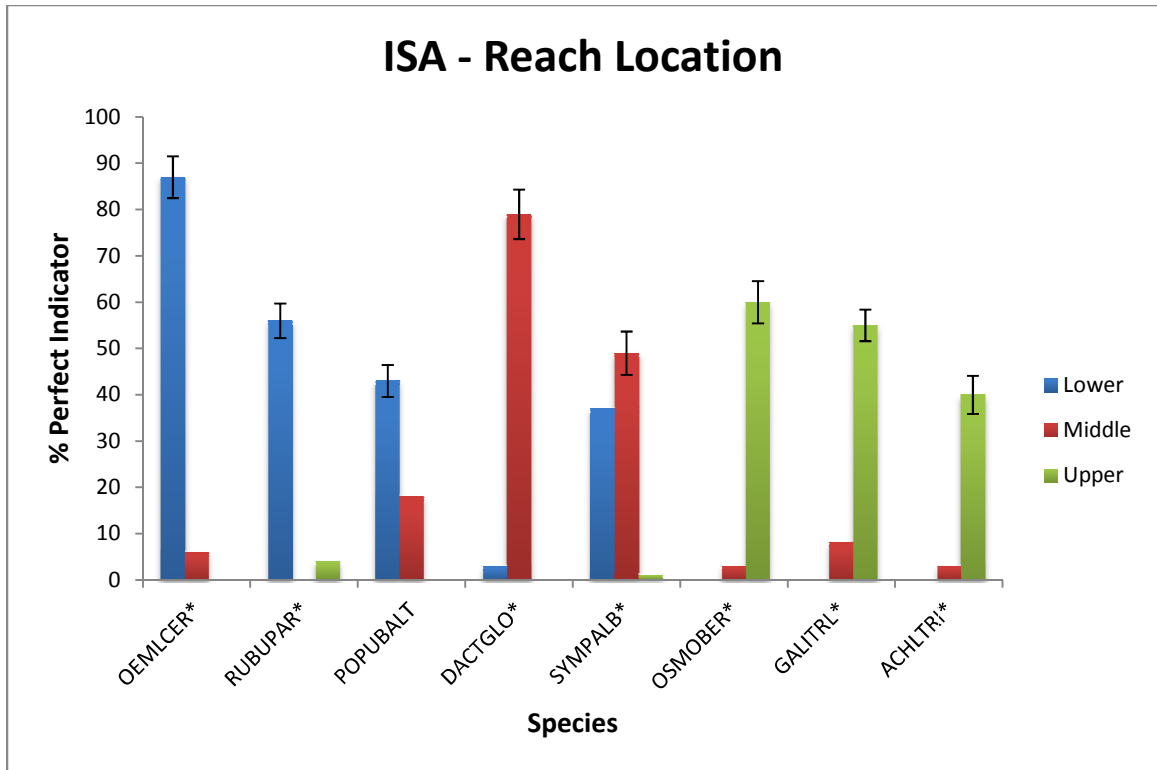
Figure 26 - Summary graph showing significant indicators of reach location (p<0.05) from 2005 and 2010; IV represented for each species as % of perfect indication of a particular reach location. * Indicates understory species.
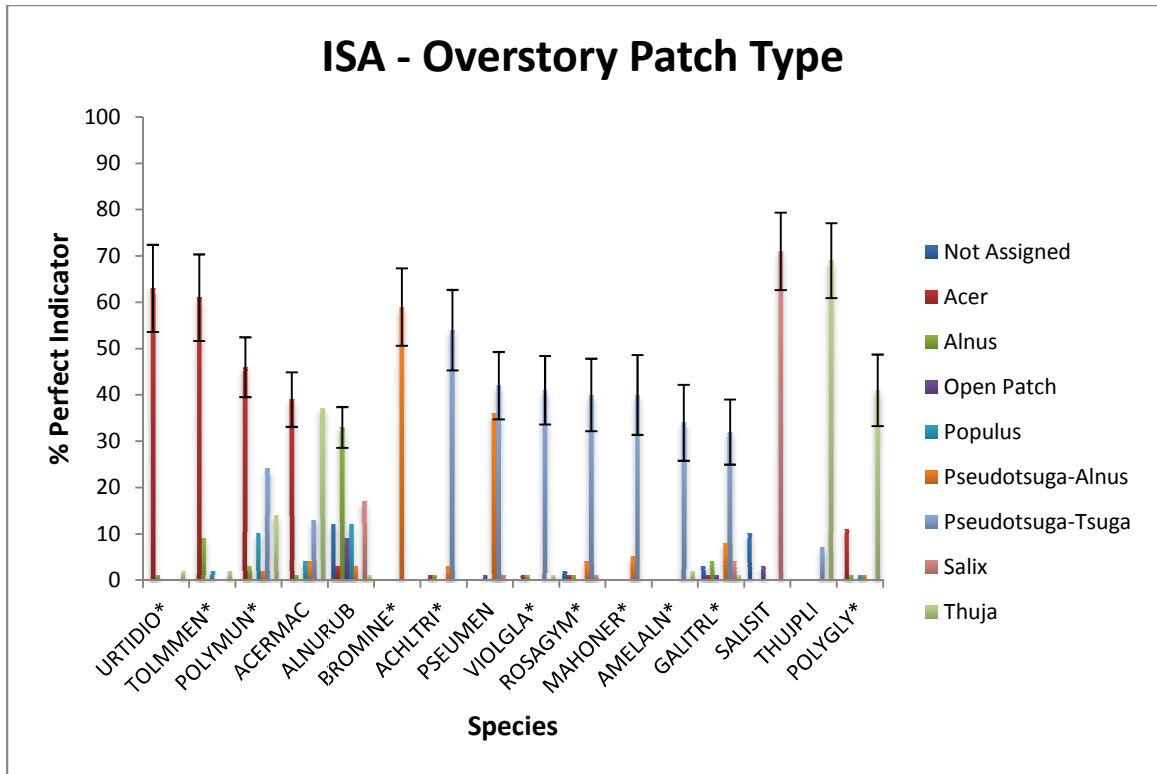
Figure 27 - Summary graph showing significant indicators of overstory patch type (p<0.05) from 2005 and 2010; IV represented for each species as % of perfect indication of a particular reach location. * Indicates understory species.
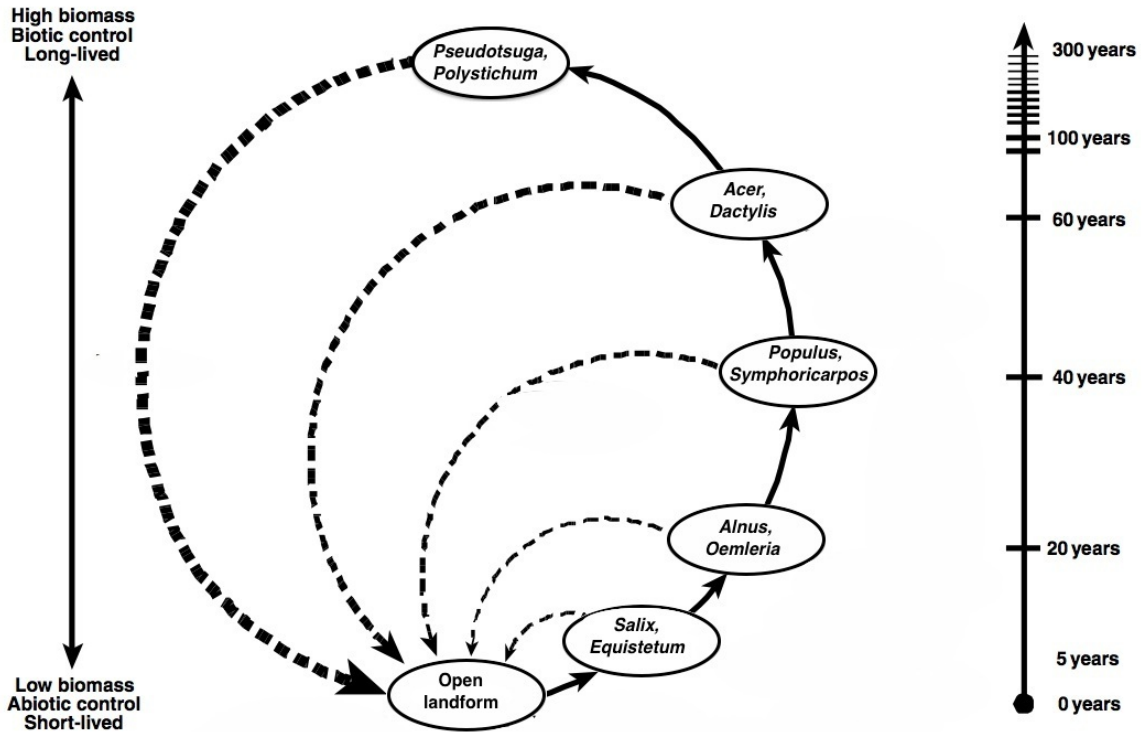
Figure 28 – Simplified illustration of potential community succession/turnover in the Elwha River riparian zone, modified from Latterell *et al.* (2006). Each stage is shown with overstory/understory community commonly associated with particular landform age; presence of communities in similar age-classes does not imply correlation. Solid arrows indicate succession in absence of flood disturbance, dashed arrows indicate disturbance re-initiating succession. Modifications replaced landform with community groups from the Elwha, with permission from Joshua J. Latterell.

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Appendix I - Table listing scientific and common names of all vascular plant species observed in this study, their native status, and their 7-character species codes.

Code	Scientific Name	Common Name	Native Status
ABIEAMA	Abies amabilis (Dougl. ex Loud.) Dougl. ex Forbes	Pacific silver fir	Native
ABIEGRA	Abies grandis (Dougl. ex D. Don) Lindl.	grand fir	Native
ACERCIR	Acer circinatum Pursh	vine maple	Native
ACERMAC	Acer macrophyllum Pursh	bigleaf maple	Native
ACHIMIL	Achillea millefolium L.	common yarrow	Native
ACHLTRI	Achlys triphylla (Sm.) DC.	sweet after death	Native
ACTARUB	Actaea rubra (Ait.) Willd.	red baneberry	Native
ADENBIC	Adenocaulon bicolor Hook.	American trailplant	Native
AGOSGRA	Agoseris grandiflora (Nutt.) Greene	bigflower agoseris	Native
AGROCAP	Agrostis capillaris L.	colonial bentgrass	Exotic
AGROEXA	Agrostis exarata Trin.	spike bentgrass	Native
AGROGIG	Agrostis gigantea Roth	redtop	Exotic
AGROSTO	Agrostis stolonifera L.	creeping bentgrass	Exotic
AIRACAR	Aira caryophyllea L.	silver hairgrass	Exotic
AIRAPRA	Aira praecox L.	yellow hairgrass	Exotic
ALISTRI	Alisma triviale Pursh	northern water plantain	Native
ALLOVIR	Allotropa virgata Torr. & Gray ex Gray	sugarstick	Native
ALNURUB	Alnus rubra Bong.	red alder	Native
AMELALN	Amelanchier alnifolia (Nutt.) Nutt. ex M. Roemer	Saskatoon serviceberry	Native
ANAPMAR	Anaphalis margaritacea (L.) Benth.	western pearly everlasting	Native
AQUIFOR	Aquilegia formosa Fisch. ex DC.	western columbine	Native
ARBUMEN	Arbutus menziesii Pursh	Pacific madrone	Native
ARCTMIN	Arctium minus Bernh.	lesser burrdock	Exotic
ARCTUVA	Arctostaphylos uva-ursi (L.) Spreng.	kinnikinnick	Native
ARRHELA	Arrhenatherum elatius (L.) Beauv. ex J.& K. Presl	tall oatgrass	Exotic
ARTELUD	Artemisia ludoviciana Nutt.	white sagebrush	Native
ARTELUDC	Artemisia ludoviciana Nutt. ssp. candicans (Rydb.) Keck	white sagebrush	Native
ARTESUK	Artemisia suksdorfii Piper	coastal wormwood	Native
ARTETIL	Artemisia tilesii Ledeb.	Tilesius' wormwood	Native
ARUNDIO	Aruncus dioicus (Walt.) Fern.	bride's feathers	Native
ASARCAU	Asarum caudatum Lindl.	British Columbia wildginger	Native
ASPLTRI	Asplenium trichomanes L.	maidenhair spleenwort	Native
ATHYFIL	Athyrium filix-femina (L.) Roth	common ladyfern	Native
BARBVUL	Barbarea vulgaris Ait. f.	garden yellowrocket	Exotic
BROMCOM	Bromus commutatus Schrad.	meadow brome	Exotic
BROMINE	Bromus inermis Leyss. ssp. inermis	smooth brome	Exotic
BROMPAC	Bromus pacificus Shear	Pacific brome	Native
BROMSIT	Bromus sitchensis Trin.	Alaska brome	Native
BROMVUL	Bromus vulgaris (Hook.) Shear	Columbia brome	Native
CAMPSCO	Campanula scouleri Hook. ex A. DC.	pale bellflower	Native
CARDOCC	Cardamine occidentalis (S. Wats. ex B.L. Robins.) T.J. Howell	big western bittercress	Native
CARDOLI	Cardamine oligosperma Nutt.	little western bittercress	Native
CARDPEN	Cardamine pensylvanica Muhl. ex Willd.	Pennsylvania bittercress	Native
CARECUS	Carex cusickii Mackenzie ex Piper & Beattie	Cusick's sedge	Native
CAREDEW	Carex deweyana Schwein.	Dewey sedge	Native
CAREHEN	Carex hendersonii Bailey	Henderson's sedge	Native
CARELENP	Carex lenticularis Michx. var. lipocarpa (Holm) L.A. Standley	Kellogg's sedge	Native
CARELIM	Carex limnophila F.J. Herm.	carex microptera	Native
CAREMER	Carex mertensii Prescott ex Bong.	Mertens' sedge	Native
CAREOBT	Carex obtusata Lilj.	obtuse sedge	Native
CAREPAC	Carex pachystachya Cham. ex Steud.	chamisso sedge	Native
CAREPRA	Carex praticola Rydb.	meadow sedge	Native
CENTMON	Centaurea montana L.	perennial cornflower	Exotic
CERAFON	Cerastium fontanum Baumg. ssp. vulgare (Hartman) Greuter & Burdet	big chickweed	Exotic
CERAGLO	Cerastium glomeratum Thuill.	sticky chickweed	Exotic
CERASEM	Cerastium semidecandrum	fivestamen chickweed	Exotic
CHAMANG	Chamerion angustifolium (L.) Holub	fireweed	Native
CHAMLAT	Chamerion latifolium (L.) Holub	dwarf fireweed	Native
CHIMMEN	Chimaphila menziesii (R. Br. ex D. Don) Spreng.	little prince's pine	Native
CHIMUMB	Chimaphila umbellata (L.) W. Bart.	pipsissewa	Native
CINNLAT	Cinna latifolia (Trev. ex Goepp.) Griseb.	drooping woodreed	Native
CIRCALP	Circaea alpina L.	small enchanter's nightshade	Native
CIRSARV	Cirsium arvense (L.) Scop.	Canada thistle	Exotic
CIRSEDU	Cirsium edule Nutt.	edible thistle	Native
CIRSVUL	Cirsium vulgare (Savi) Ten.	bull thistle	Exotic
CLAYPER	Claytonia perfoliata Donn ex Willd.	miner's lettuce	Native
CLAYSIB	Claytonia sibirica L.	Siberian springbeauty	Native
CLEMLIG	Clematis ligusticifolia Nutt.	western white clematis	Native
COLLGRA	Collomia grandiflora Dougl. ex Lindl.	grand collomia	Native

COLLHET	Collomia heterophylla Dougl. ex Hook.	variableleaf collomia	Native
CRATDOU	Crataegus douglasii Lindl.	black hawthorn	Native
CRATMON	Crataegus monogyna Jacq.	oneseed hawthorn	Exotic
CREPCAP	Crepis capillaris (L.) Wallr.	smooth hawksbeard	Exotic
CREPOCC	Crepis occidentalis Nutt.	largeflower hawksbeard	Native
CYNOCRI	Cynosurus cristatus L.	crested dogstail grass	Exotic
CYTISCO	Cytisus scoparius (L.) Link	scotsbroom	Exotic
DACTGLO	Dactylis glomerata L.	orchardgrass	Exotic
DANTCAL	Danthonia californica Boland.	California oatgrass	Native
DAUCCAR	Daucus carota L.	wild carrot	Exotic
DESC1S1	Deschampsia Beauvois	hair grass	Native
DESCCAE	Deschampsia caespitosa (L.) Beauv.	tufted hairgrass	Native
DESCELO	Deschampsia elongata (Hook.) Munro	slender hairgrass	Native
DICEFOR	Dicentra formosa (Haw.) Walp.	Pacific bleeding heart	Native
DIGIPUR	Digitalis purpurea L.	purple foxglove	Exotic
DISTSPI	Distichlis spicata (L.) Greene	inland saltgrass	Native
DRYOARG	Dryopteris Adans.	woodfern	Native
DRYOAUS	Dryopteris austriaca (Jacq.) Woynar ex Schinz & Thellung	spiny shield fern	Native
DRYOEXP	Dryopteris expansa (K. Presl) Fraser-Jenkins & Jermy	spreading woodfern	Native
DRYOFIL	Dryopteris filix-mas (L.) Schott	male fern	Native
ELYMGLAG	Elymus glaucus Buckl. ssp. glaucus	blue wildrye	Native
ELYMHIR	Elymus hirsutus J. Presl	northern ryegrass	Native
ELYMREP	Elymus repens (L.) Gould	quackgrass	Exotic
EPILBRA	Epilobium brachycarpum K. Presl	tall annual willowherb	Native
EPILCIL	Epilobium ciliatum Raf.	fringed willowherb	Native
EPILCILG	Epilobium ciliatum Raf. ssp. glandulosum (Lehm.) Hoch & Raven	fringed willowherb	Native
EPILGLFA	Epilobium glaberrimum Barbey ssp. fastigiatum (Nutt.) Hoch & Raven	glaucus willowherb	Native
EPILMIN	Epilobium minutum Lindl. ex Lehm.	chaparral willowherb	Native
EPIPGIG	Epipactis gigantea Dougl. ex Hook.	stream orchid	Native
EQUIARV	Equisetum arvense L.	field horsetail	Native
EQUISYL	Equisetum sylvaticum L.	woodland horsetail	Native
ERIGPHI	Erigeron philadelphicus L.	Philadelphia fleabane	Native
ERIOLANL	Eriophyllum lanatum (Pursh) Forbes var. lanatum	common woolly sunflower	Native
FALLJAPJ	Fallopia japonica (Houtt.) Dcne.	Japanese knotweed	Exotic
FESTOCC	Festuca occidentalis Hook.	western fescue	Native
FESTRUB	Festuca rubra L. ssp. rubra	red fescue	Native
FESTSAX	Festuca saximontana Rydb.	Rocky Mountain fescue	Native
FESTSUF	Festuca subuliflora Scribn.	crinkleawn fescue	Native
FESTSUT	Festuca subulata Trin.	bearded fescue	Native
FRAGCRI	Fragaria crinita Rydb.	Pacific strawberry	Native
FRAGVES	Fragaria vesca L.	woodland strawberry	Native
FRAGVIR	Fragaria virginiana Duchesne	Virginia strawberry	Native
FRAXLAT	Fraxinus latifolia Benth.	Oregon ash	Native
GALIAPA	Galium aparine L.	stickywilly	Native
GALIBIF	Galium bifolium S. Wats.	twinleaf bedstraw	Native
GALIKAM	Galium kamtschaticum Steller ex J.A. & J.H. Schultes	boreal bedstraw	Native
GALIORE	Galium oreganum Britt.	Oregon bedstraw	Native
GALITRF	Galium triflorum Michx.	fragrant bedstraw	Native
GALITRL	Galium trifidum L.	threepetal bedstraw	Native
GAULSHA	Gaultheria shallon Pursh	salal	Native
GERAMOL	Geranium molle L.	dovefoot geranium	Exotic
GERAROB	Geranium robertianum L.	Robert geranium	Exotic
GEUMMAC	Geum macrophyllum Willd.	largeleaf avens	Native
GOODOBL	Goodyera oblongifolia Raf.	western rattlesnake plantain	Native
HEDEHEL	Hedera helix L.	English ivy	Exotic
HERASPH	Heracleum sphondylium L. ssp. montanum (Schleich. ex Gaudin) Briq.	Heracleum maximum	Native
HIERALB	Hieracium albiflorum Hook.	white hawkweed	Native
HOLCLAN	Holcus lanatus L.	common velvetgrass	Exotic
HOLODIS	Holodiscus discolor (Pursh) Maxim.	oceanspray	Native
HORDBRA	Hordeum brachyantherum Nevski	meadow barley	Native
HYDRFEN	Hydrophyllum fendleri (Gray) Heller	Fendler's waterleaf	Native
HYDRTEN	Hydrophyllum tenuipes Heller	Pacific waterleaf	Native
HYPEPER	Hypericum perforatum L.	common St. Johnswort	Exotic
HYPORAD	Hypochaeris radicata L.	hairy catsear	Exotic
IMPAECA	Impatiens ecalcarata Blank.	spurless touch-me-not	Native
JUNCEFF	Juncus effusus L. var. effusus	common rush	Native
JUNCENS	Juncus ensifolius Wikstr.	swordleaf rush	Native
JUNCMER	Juncus mertensianus Bong.	Mertens' rush	Native
LAPSCOM	Lapsana communis L.	common nipplewort	Exotic
LATHLAT	Lathyrus latifolius L.	perennial pea	Exotic
LATHNEV	Lathyrus nevadensis S. Wats.	Sierra pea	Native
LEPIHET	Lepidium heterophyllum	purpleanther field pepperweed	Exotic
LEUCVUL	Leucanthemum vulgare Lam.	oxeye daisy	Exotic
LINNBOR	Linnaea borealis L.	twinflower	Native

LONICIL	Lonicera ciliosa (Pursh) Poir. ex DC.	orange honeysuckle	Native
LONIINV	Lonicera involucrata Banks ex Spreng.	twinberry honeysuckle	Native
LUZUCON	Luzula congesta (Thuill.) Lej.	Heath woodruse, spike woodrush	Exotic
LUZUHIT	Luzula hitchcockii Hämet-Ahti	Hitchcock's smooth woodrush	Native
LUZUMUL	Luzula multiflora (Ehrh.) Lej.	common woodrush	Native
LUZUPAR	Luzula parviflora (Ehrh.) Desv.	smallflowered woodrush	Native
LUZUPIP	Luzula piperi (Coville) M.E. Jones	Piper's woodrush	Native
LYCHCOR	Lychnis coronaria (L.) Desr.	rose campion	Exotic
MADIGRA	Madia gracilis (Sm.) Keck & J. Clausen ex Applegate	grassy tarweed	Native
MAHONER	Mahonia nervosa (Pursh) Nutt.	Cascade barberry	Native
MAIARAC	Maianthemum racemosum (L.) Link	feathery false lily of the vally	Native
MAIASTE	Maianthemum stellatum (L.) Link	starry false lily of the vally	Native
MALUFUS	Malus fusca (Raf.) Schneid.	Oregon crabapple	Native
MEDILUP	Medicago lupulina L.	black medick	Exotic
MEDISAT	Medicago sativa	alfalfa	Exotic
MELIOFF	Melilotus officinalis (L.) Lam.	yellow sweetclover	Exotic
MICRDOU	Micromeria douglasii (Benth.) Kuntze	yerba buena	Native
MICRGRA	Microsteris gracilis (Hook.) Greene	slender phlox	Native
MIMUGUT	Mimulus guttatus DC.	seep monkeyflower	Native
MIMULEW	Mimulus lewisii Pursh	purple monkeyflower	Native
MIMUMOS	Mimulus moschatus Dougl. ex Lindl.	muskflower	Native
MOEHMAC	Moehringia macrophylla (Hook.) Fenzl	largeleaf sandwort	Native
MONOHYP	Monotropa hypopithys L.	pinesap	Native
MONOUNI	Monotropa uniflora L.	Indianpipe	Native
MONTLIN	Montia lamprosperma Cham.	annual water minerslettuce	Native
MONTPARP	Montia parvifolia (Moc. ex DC.) Greene ssp. parvifolia	littleleaf minerslettuce	Native
MYCEMUR	Mycelis muralis (L.) Dumort.	wall-lettuce	Exotic
MYOSSCO	Myosotis scorpioides L.	true forget-me-not	Exotic
MYOSSYL	Myosotis sylvatica Ehrh. ex Hoffmann	woodland forget-me-not	Exotic
NEMOPAR	Nemophila parviflora Dougl. ex Benth.	smallflower nemophila	Native
OEMLCER	Oemleria cerasiformis (Torr. & Gray ex Hook. & Arn.) Landon	Indian plum	Native
OSMOBER	Osmorhiza berteroi DC.	sweetcicely	Native
PETAFRP	Petasites frigidus (L.) Fries var. palmatus (Ait.) Cronq.	arctic sweet coltsfoot	Native
PHACLEP	Phacelia leptosepala Rydb.	narrowsepal phacelia	Native
PHACNEM	Phacelia nemoralis Greene	shade phacelia	Native
PHALARU	Phalaris arundinacea L.	reed canarygrass	Exotic
PHLEALP	Phleum alpinum L.	alpine timothy	Native
PHLEPRA	Phleum pratense L.	timothy	Exotic
PICESIT	Picea sitchensis (Bong.) Carr.	Sitka spruce	Native
PIPEELE	Piperia elegans (Lindl.) Rydb. ssp. elegans	elegant piperia	Native
PIPEUNA	Piperia unalascensis (Spreng.) Rydb.	slender-spire orchid	Native
PLANLAN	Plantago lanceolata L.	narrowleaf plantain	Exotic
POA_COM	Poa compressa L.	Canada bluegrass	Exotic
POA_PAL	Poa palustris L.	fowl bluegrass	Exotic
POA_PRA	Poa pratensis L.	Kentucky bluegrass	Exotic
POA_TRV	Poa trivialis L.	rough bluegrass	Exotic
POLYGLY	Polypodium glycyrrhiza D.C. Eat.	licorice fern	Native
POLYMIN	Polygonum minimum S. Wats.	broadleaf knotweed	Native
POLYMUN	Polystichum munitum (Kaulfuss) K. Presl	western swordfern	Native
POPUBALT	Populus balsamifera L. ssp. trichocarpa (Torr. & Gray ex Hook.) Brayshaw	black cottonwood	Native
PROSHOO	Prosartes hookeri	drops of gold	Native
PROSSMI	Prosartes smithii	largeflower fairybells	Native
PRUNAVI	Prunus avium (L.) L.	sweet cherry	Exotic
PRUNEMA	Prunus emarginata (Dougl. ex Hook.) D. Dietr.	bitter cherry	Native
PRUNVUL	Prunella vulgaris L.	common selfheal	Native
PSEUMEN	Pseudotsuga menziesii (Mirbel) Franco	Douglas-fir	Native
PTERAQU	Pteridium aquilinum (L.) Kuhn	western brackenfern	Native
RANUREP	Ranunculus repens L.	creeping buttercup	Exotic
RANUUNC	Ranunculus uncinatus D. Don ex G. Don	woodland buttercup	Native
RHAMPUR	Rhamnus purshiana DC.	Frangula purshiana	Native
RIBEBRA	Ribes bracteosum Dougl. ex Hook.	stink currant	Native
RIBEDIV	Ribes divaricatum Dougl.	spreading gooseberry	Native
RIBELAC	Ribes lacustre (Pers.) Poir.	prickly currant	Native
ROSAGYM	Rosa gymnocarpa Nutt.	dwarf rose	Native
ROSANUT	Rosa nutkana K. Presl	Nootka rose	Native
ROSAPIS	Rosa pisocarpa Gray	cluster rose	Native
RUBULEU	Rubus leucodermis Dougl. ex Torr. & Gray	whitebark raspberry	Native
RUBUPAR	Rubus parviflorus Nutt.	thimbleberry	Native
RUBUSPE	Rubus spectabilis Pursh	salmonberry	Native
RUBUULM	Rubus ulmifolius Schott.	elmleaf blackberry	Exotic
RUBUURS	Rubus ursinus Cham. & Schlecht.	California blackberry	Native
RUMEACE	Rumex acetosella L.	common sheep sorrel	Exotic
RUMECRI	Rumex crispus L.	curly dock	Exotic
RUMEOBT	Rumex obtusifolius L.	bitter dock	Exotic

SALILUC	Salix lucida Muhl.	shining willow	Native
SALISIT	Salix sitchensis Sanson ex Bong.	Sitka willow	Native
SAMBNIG	Sambucus nigra L.	European black elderberry	Native
SAMBRAC	Sambucus racemosa L.	red elderberry	Native
SANICRTR	Sanicula crassicaulis Poepp. ex DC. var. tripartita (Suksdorf) H. Wolff	Pacific blacksnakeroot	Native
SANIGRA	Sanicula graveolens Poepp. ex DC.	northern sanicle	Native
SCHEPRA	Schedonorus pratensis (Huds.) P. Beauv	festuca pratensis	Exotic
SEDUSPA	Sedum spathulifolium Hook.	broadleaf stonecrop	Native
SENEJAC	Senecio jacobaea L.	stinking willie	Exotic
SENESYL	Senecio sylvaticus L.	woodland ragwort	Exotic
SENEVUL	Senecio vulgaris L.	old-man-in-the-Spring	Exotic
SOLADUL	Solanum dulcamara L.	bittersweet	Exotic
SOLICAN	Solidago canadensis L.	Canada goldenrod	Native
SONCARV	Sonchus arvensis L.	field sowthistle	Exotic
SONCASP	Sonchus asper (L.) Hill	spiny sowthistle	Exotic
SONCOLE	Sonchus oleraceus L.	common sowthistle	Exotic
SORBSCO	Sorbus scopulina Greene	Greene's mountain ash	Native
STACCHA	Stachys chamissonis Benth.	coastal hedgenettle	Native
STACMEX	Stachys mexicana Benth.	Mexican hedgenettle	Native
STELBORS	Stellaria borealis Bigelow ssp. sitchana (Steud.) Piper	Sitka starwort	Native
STELCAL	Stellaria calycantha (Ledeb.) Bong.	northern starwort	Native
STELCRI	Stellaria crispa Cham. & Schlecht.	curled starwort	Native
STELGRA	Stellaria graminea L.	grasslike starwort	Exotic
STELMED	Stellaria media (L.) Vill.	common chickweed	Exotic
SYMPALB	Symphoricarpos albus (L.) Blake	common snowberry	Native
TARAOFF	Taraxacum officinale G.H. Weber ex Wiggers	common dandelion	Native
TAXUBRE	Taxus brevifolia Nutt.	Pacific yew	Native
TELLGRA	Tellima grandiflora (Pursh) Dougl. ex Lindl.	bigflower tellima	Native
THALOCC	Thalictrum occidentale Gray	western meadow-rue	Native
THUJPLI	Thuja plicata Donn ex D. Don	western red cedar	Native
TIARTRI	Tiarella trifoliata L.	threeleaf foamflower	Native
TOLMMEN	Tolmiea menziesii (Pursh) Torr. & Gray	youth on age	Native
TRIELAT	Trientalis latifolia Hook.	broadleaf starflower	Native
TRIFCAM	Trifolium campestre Schreb.	field clover	Exotic
TRIFHYB	Trifolium hybridum L.	alsike clover	Exotic
TRIFPRA	Trifolium pratense L.	red clover	Exotic
TRIFREP	Trifolium repens L.	white clover	Exotic
TRILOVA	Trillium ovatum Pursh	Pacific trillium	Native
TRISCERC	Trisetum cernuum Trin. var. canescens (Buckl.) Beal	tall trisetum	Native
TSUGHET	Tsuga heterophylla (Raf.) Sarg.	western hemlock	Native
URTIDIO	Urtica dioica L.	stinging nettle	Native
VACCALA	Vaccinium alaskense T.J. Howell	Alaska blueberry	Native
VACCOVT	Vaccinium ovatum Pursh	California huckleberry	Native
VACCPAR	Vaccinium parvifolium Sm.	red huckleberry	Native
VEROAME	Veronica americana Schwein. ex Benth.	American speedwell	Native
VEROARV	Veronica arvensis L.	corn speedwell	Exotic
VEROCUS	Veronica cusickii Gray	Cusick's speedwell	Native
VEROOFF	Veronica officinalis L.	common gypsyweed	Exotic
VEROPRS	Veronica persica Poir.	birdeye speedwell	Exotic
VEROSER	Veronica serpyllifolia L.	thymeleaf speedwell	Native
VICIAME	Vicia americana Muhl. ex Willd.	American vetch	Native
VICIHIR	Vicia hirsuta (L.) S.F. Gray	tiny vetch	Exotic
VICINIG	Vicia nigricans Hook. & Arn.	giant vetch	Native
VICISAT	Vicia sativa L.	garden vetch	Exotic
VIOLGLA	Viola glabella Nutt.	pioneer violet	Native
VIOLPAL	Viola palustris L.	marsh violet	Native
VIOLSEM	Viola sempervirens Greene	evergreen violet	Native
VULPBRO	Vulpia bromoides (L.) S.F. Gray	brome fescue	Exotic
VULPMYU	Vulpia myuros (L.) K.C. Gmel.	rat-tail fescue	Exotic

Appendix II - Variance explained (as r[2] values) by the axes in each of the NMS ordinations. Total variance explained by each ordination can be found in the cumulative column.

NMS – Understory Species Only			
Ordination:	Axis:	Increment:	Cumulative:
Entire Study Area	1	0.263	0.263
	2	0.143	0.406
	3	0.184	0.590

NMS – Entire Plant Community			
Ordination:	Axis:	Increment:	Cumulative:
Entire Study Area	1	0.207	0.207
	2	0.29	0.497
	3	0.257	0.754