

Research Article

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Direct and indirect drivers of instream wood in the interior Pacific Northwest, USA: decoupling climate, vegetation, disturbance, and geomorphic setting

Abstract: Instream wood is a driver of geomorphic change in low-order streams, frequently altering morphodynamic processes. Instream wood is a frequently measured component of streams, yet it is a complex metric, responding to ecological and geomorphic forcings at a variety of scales. Here we seek to disentangle the relative importance of physical and biological processes that drive wood growth and delivery to streams across broad spatial extents. In so doing, we ask two primary questions: (1) is riparian vegetation a composite variable that captures the indirect effects of climate and disturbance on instream wood dynamics? (2) What are the direct and indirect relationships between geomorphic setting, vegetation, climate, disturbance, and instream wood dynamics? We measured riparian vegetation composition and wood frequency and volume at 720 headwater reaches within the American interior Pacific Northwest. We used ordination to identify relationships between vegetation and environmental attributes, and subsequently built a structural equation model to identify how climate and disturbance directly affect vegetation composition and how vegetation and geomorphic setting directly affect instream wood volume and frequency. We found that large wood volume and frequency are *directly* driven by vegetation composition and positively correlated to wildfire, elevation, stream gradient, and channel bankfull

width. Indicator species at reaches with high volumes of wood were generally long-lived, conifer trees that persist for extended durations once delivered to stream habitats. Wood dynamics were also *indirectly* mediated by factors that shape vegetation: wildfire, precipitation, elevation, and temperature. We conclude that wood volume and frequency are driven by multiple interrelated climatic, geomorphic, and ecological variables. Vegetation composition and geomorphic setting directly mediate indirect relationships between landscape environmental processes and instream large wood. Where climate or geomorphic setting preclude tree establishment, reaches may remain naturally depauperate of instream wood unless wood is transported from elsewhere in the stream network.

Keywords: Instream wood, riparian vegetation, stream habitat, indirect effects, Columbia River, Missouri River, structural equation models.

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1 Introduction

Instream large wood is an important driver of geomorphic and biological processes within streams and rivers. Wood influences stream hydraulics that sort sediment and force pool formation. These geomorphic processes build dynamic stream habitat for fishes and other biota [1,2]. Cover provided by large wood also provides important refugia from predation for juvenile salmonids [3]. In a positive feedback loop, instream wood perpetuates the growth of riparian vegetation by regulating sediment scour and deposition that build bars and shape floodplain landforms where vegetation can colonize [4]. Vegetation that colonizes these fluvial landforms increases channel

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and floodplain roughness, furthering the positive feedback by facilitating the establishment of riparian vegetation that may eventually contribute more wood to the channel.

Given that they are less able to quickly mobilize and export instream wood, smaller, narrower streams may be influenced to a greater extent by instream wood than larger, wider channels with greater wood transport capacities [5]. These typically low-order, "wadeable" streams are also important habitats as they occupy unique hydrologic and ecological settings within stream networks [6]. In low-order streams, the volume and distribution of wood is influenced by catchment topography, forest community structure, channel geomorphology, and hydrology [1,7,8]. Additionally, biotic and physical disturbances such as livestock grazing, wildfire, and overbank flooding, among others, shape watershed ecological and hydrogeomorphic processes that (a) determine the processes by which wood is sourced to stream channels from riparian forests and (b) the factors that modulate its subsequent downstream transport. A combination of background and disturbance-related factors drive wood quantity and location in wadeable streams, making it difficult to disentangle the relative importance of intertwined physical and biological processes in shaping instream wood delivery and retention.

Because riparian vegetation responds to climate, watershed disturbance, and geomorphic setting [9–11], it can be thought of as a composite variable that responds to multiple watershed processes as well as serving as an indicator of instream habitat potential [12,13]. Riparian vegetation is clearly tied to instream wood because riparian plant communities must grow sufficiently large trees and shrubs to contribute wood to the channel. However, vegetation dynamics are not the sole predictor of instream wood dynamics. Models of instream wood based primarily on riparian vegetation size or composition may overestimate the relative influence of vegetation on instream wood dynamics while comparatively deemphasizing disturbance and geomorphic processes [14].

Most models of instream wood fail to identify the relative importance of *indirect* processes in driving *direct* processes that shape instream wood production and retention [15]. For example, riparian vegetation responds to environmental filters – processes that influence which plant communities can persist in a given area – across multiple spatial scales [16,17]. Accordingly, environmental filters that shape riparian vegetation communities, such as climate and disturbance, should be incorporated into conceptual models of wood dynamics as *indirect effects* on the amount of wood within stream channels. These

indirect effects can be contrasted with the geomorphic setting of stream reaches, which should be incorporated into conceptual models of instream wood dynamics as *direct effects* on wood contribution to and retention within channels. Stream geomorphic setting influences stream power at the reach scale, and drives localized variation in shear stress that controls sediment scour and deposition, bank erosion, and the transport of wood through channels. While there are many well-documented *direct* geomorphic effects that influence wood movement through channels, the causal relationships between processes at multiple scales are less commonly documented. By decoupling the *indirect* and *direct* effects of multiple biological and physical processes on instream wood we can create more thorough conceptual models of how physical and biotic processes affect a keystone driver of channel form and stream habitat.

To assess how geomorphology, riparian vegetation, climate, and disturbance filters influence instream wood volume and frequency within headwater streams of the Pacific Northwest, we used a structural equation modeling approach to test multiple hypotheses (Table 1; Figure 1). We generated models based on hypothesized relationships between riparian vegetation community composition and environmental factors observed in previous studies [12,18]. We built a simple conceptual model of how multiple processes *directly* and *indirectly* shape riparian vegetation and instream wood dynamics in wadeable streams (Figure 1). We used this model to identify and evaluate potential causal relationships between climate, watershed disturbance, riparian vegetation, stream geomorphic setting, and instream wood accumulation (Figure 1; Table 1).

We hypothesized that climate (elevation, precipitation, and temperature) and disturbance (percent watershed grazed and percent watershed burned) *directly* affect vegetation composition (Figure 1; Table 1; B, D), which in turn directly affects wood volume and frequency (A). Because vegetation communities are *directly* influenced by watershed disturbance (B) and regional climate (D), we considered these influences to be *indirect* drivers of wood as mediated by riparian vegetation. We also hypothesized that stream geomorphic setting (bankfull width, stream gradient, buffer slope; F) and disturbance (specifically wildfire; H) *directly* drive instream wood dynamics by shaping wood availability and the potential for reaches to transport instream wood. Because elevation, precipitation, and temperature all influence where livestock grazing and wildfire are likely to occur, we hypothesized that climate drives disturbance (C). Geomorphic setting responds to climate, which affects how much water is available for

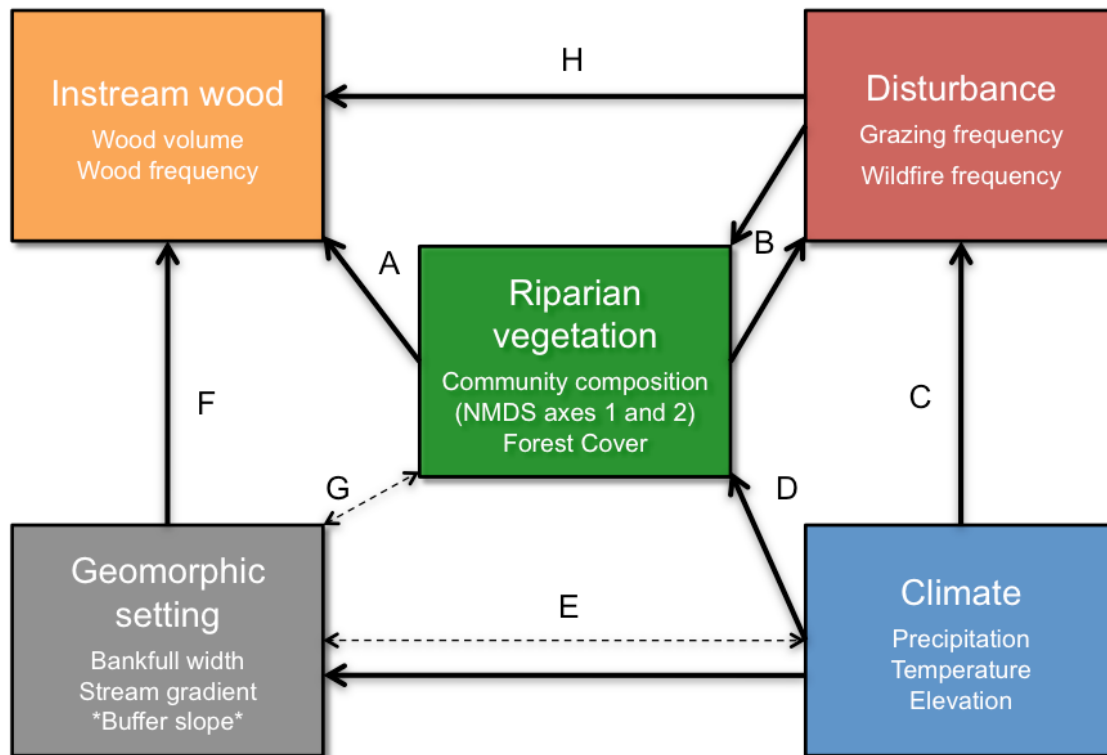


Figure 1: Initial conceptual model of how instream wood volume responds directly to vegetation and geomorphic setting and indirectly to climate and disturbance. Each box represents a conceptual set of variables considered for inclusion in structural equation models. Specific measured variables considered for use are in the subtext below. Dotted lines indicate correlated covariance relationships between variables. Variables within boxes have linked covariance structures. Pathway letters correspond to hypotheses in Table 1. Buffer slope was not included in the final model due to strong collinearity with other bankfull width and gradient.

transport within a channel, so we also tested hypotheses (E) on how precipitation indirectly drives wood by influencing bankfull width and stream gradient. Where variables were not directly related, but corresponded to the same driving variables, we built covariance relationships between variables (E, G).

We expected lower wood frequency and volume in high-gradient channels because higher-gradient channels have a greater capacity to transport wood [19]. Also, we expected higher wood frequency and volume in reaches surrounded by areas of steep buffer slope, which may be prone to mass movement or increased rates of tree fall toward the channel [1,15,20,21] leading to greater wood delivery to channels. Subsequently, we expect wood mobility and downstream transport to be more common in reaches with higher unit stream power (ω):

$$\omega = \rho g Q S b^{-1} \quad (1)$$

Where ρ is the fluid density, g is acceleration due to gravity, Q is a characteristic stream discharge, S is channel slope (gradient), and b is channel width (bankfull width). Thus, for a flood of the same magnitude, we would expect

greater wood mobility in narrow, steeper channels. Although unmeasured here, we note that wood mobility is also linked to the ratio of piece length to bankfull channel width [22], with larger pieces in narrow streams tending to comprise largely immobile ‘key members’ of logjams.

2 Methods

2.1 Study Area

Instream wood, stream geomorphic attributes, and riparian vegetation data were collected as a part of an ongoing habitat monitoring program within low-order streams of the interior Columbia and upper Missouri River basins between 2009 and 2011 [23]. Stream habitats within the interior Columbia and upper Missouri River basins are monitored as a part of the U.S. Forest Service’s PACFISH/INFISH Biological Opinion (PIBO; [23]). PIBO monitors stream and riparian habitat attributes that affect endangered fishes at streams within federally-owned

Table 1: Conceptual model pathways and hypotheses used during structural equation model building. Letters correspond to pathways in Figure 1.

Pathway Relationship	Hypotheses	Observation or potential mechanism
A Direct: vegetation → wood	Streams with riparian vegetation communities consisting of trees and shrubs will have more instream wood than communities dominated by herbaceous or smaller woody species.	Instream wood frequency and volume are products of the potential of riparian zones and surrounding watersheds to grow tree species that can contribute large, persistent wood to the channel [8,12]. Coniferous trees may persist in channels longer than rapidly decaying deciduous trees.
B Direct: grazing and wildfire → vegetation	Increased watershed grazing and wildfire frequency will change riparian vegetation community composition. Grazing and wildfire will occur predominantly in distinct vegetation communities.	Grazing removes vegetation and selects for species that are tolerant of herbivory and trampling [55,56]. Wildfire resets ecosystem successional trajectories by removing vegetation, propagules and organic soils.
C Direct: temperature and precipitation → grazing and wildfire	Warmer, drier watersheds experience higher grazing frequency. Wildfires are more frequent and intense in warm, dry watersheds.	Grazing frequency increases in semi-arid “badland” environments unable to support widespread forests or agriculture [48]. Wildfire occurs in watersheds with sufficiently low moisture conditions for ignition and sufficient fuels to carry the fire.
D Direct: Temperature, elevation and precipitation → vegetation	Woody vegetation is more likely to occur at reaches with moderate to low temperatures and moderate to high precipitation. High precipitation, cool temperature sites are likely to be at higher elevations.	Vegetation community composition responds to broad-scale environmental drivers that relate to climate and landscape position. Temperature, precipitation and watershed elevation broadly filter species composition based on resource availability and species/community tolerance of environmental stress [12].
E Direct: precipitation → bankfull width and gradient; Covariance: Temperature, elevation and precipitation ↔ bankfull width and gradient	Climate and stream geomorphic attributes are correlated (covariance relationship). Precipitation drives stream discharge that shapes fluvial processes related to channel form i.e. bankfull width and stream gradient.	Watershed and stream geomorphic attributes are collinear with climatic processes that change across environmental gradients such as precipitation, etc. Ex. Higher elevation watersheds are generally in steeper areas that influence stream gradient and buffer slope. Precipitation is higher at high elevations and corresponds to higher stream discharge and wider bankfull width.
F Direct: gradient and bankfull width → wood volume and frequency	Wider, low gradient streams will contain more wood than narrow, high-gradient streams.	Stream geomorphic attributes influence the riparian zone and stream potential for transport. Low-gradient meadow streams may have high water tables that preclude the establishment and survival of large coniferous tree species [57].
G Covariance: vegetation and forest cover ↔ bankfull width and gradient	Riparian vegetation, forest cover and stream geomorphic setting are correlated (covariance relationship).	The climate filters that drive riparian vegetation are also correlated to stream geomorphic setting. Ex. Higher elevation watersheds may be steeper areas that influence stream gradient. and also cooler, which influences vegetation composition.
H Wildfire → wood volume and frequency	Wildfire changes the volume of standing dead wood available for contribution to stream channels.	Jam-forming wood has been shown to be higher in burned watersheds while wood frequency may be higher or lower in burned watersheds than in unburned watersheds depending on tree species composition [57,58].

subwatersheds using a spatially-balanced, randomized sampling design [23]. Both basins contain considerable habitat for bull trout (*Salvelinus confluentus*) and steelhead trout (*Oncorhynchus mykiss*), which are threatened or endangered within portions of their native ranges. The interior Columbia and upper Missouri River basins span numerous environmental gradients across a combined 291,785 km². Much of the study area is comprised of the

Snake River Plain, Northern Basin and Range, Columbia Plateau, Blue Mountains, Northern Rockies, Idaho Batholith, and Canadian Rockies ecoregions [24]. Mean annual precipitation (1980-2010) within each sampled watershed ranges from 27 cm to 186 cm and mean watershed elevations range from 232 to 3157 m (Table 2). Mean annual temperature (1980-2010) within sampled watersheds ranged from -2.5 to 11.87 °C (Table 2).

Table 2: Summary Table of variables considered for use in the final structural equation model.

Variable	Data Source	Mean	Std. Deviation	Min.	Max.
30-year average precipitation (m)	PRISM – remote sensing	0.93	0.31	0.27	1.86
30-year average temperature (°C)	PRISM – remote sensing	3.73	1.93	-2.50	11.87
Average elevation (m)	PRISM – remote sensing	1847	473	232	3157
Watershed grazed (%)	USDA – remote sensing	48.94	46.78	0.00	100.00
Watershed burned (%)	LANDFIRE – remote sensing	10.24	25.07	0.00	100.00
Buffer forest cover (%)	LANDFIRE – remote sensing	69.89	17.59	0.78	100.00
Buffer slope (°)	USFS – field	33.98	11.09	3.00	64.95
Stream gradient (%)	USFS – field	1.97	1.20	0.01	8.64
Stream bankfull width (m)	USFS – field	6.62	3.72	0.78	23.67
Wood volume (m ³ /km)	USFS – field	97.31	144.42	0.00	1084.87
Wood frequency (pieces/km)	USFS – field	265.89	300.38	0.00	2668.09

2.2 Data Collection

We selected 720 low-gradient (mean = 2%) stream reaches for inclusion in the study (Figure 2). Reaches occurred on federal lands within subwatersheds under at least 50% upstream federal ownership and management – predominantly owned by the U.S. Bureau of Land Management (BLM) and Forest Service (USFS). Reach length at each site was based on the average of bankfull width measurements made at defined increments (~2 bankfull widths); reach length was a minimum of 20 times channel bankfull width. Field sampling occurred between June and September, coinciding with the active growing season and base-flow stream conditions.

Field and GIS-derived data were used to measure instream wood, riparian vegetation composition, watershed disturbance, stream geomorphic setting, and climate for inclusion in structural equation models. Complete data collection methods are detailed within the PIBO field sampling protocols [25,26] and summarized in Table 2. Instream large wood frequency and volume were measured at each reach. All pieces of wood within the active channel were counted. Any piece at least partially within the bankfull channel and below the bankfull elevation, with a length > 1 m and a diameter > 0.1 m at one third the distance from the base was counted [4,27]. The first ten pieces of wood that occurred at the bottom of the reach were measured for length and diameter to calculate volume. For streams with 11-100 pieces of wood, every fifth piece beyond the first ten was also measured for length and diameter. At streams with >100 pieces of wood, every tenth piece beyond the first ten was measured for length and diameter. Wood volume (V) for each individual piece was calculated based on the equation:

$$V = \pi \times r^2 \times l \quad (2)$$

where r is the radius of the piece one third the distance from its base and l is the length of the piece. For reaches with more than ten pieces, we estimated wood volume for each reach by multiplying the volume of every measured fifth (<100 pieces wood) or tenth piece (>100 pieces wood) beyond the first ten counted pieces by five or ten, respectively. Wood metrics were summarized at each reach and then standardized to wood volume in m³/km for comparison between reaches of different lengths. Wood volume and frequency were measured concurrently with stream bankfull width and water surface gradient.

We described reach riparian vegetation using community composition and stream buffer forest cover. Buffer forest cover was estimated in GIS (ArcGIS 9.1; ESRI, Redlands, CA) as the percent of the area in the 90 m buffer surrounding the reach that was covered by overstory tree species. We used a 90 m stream buffer because this distance is close enough to the channel that local colluvial processes may contribute wood to the channel and riparian zone [25]. Buffer pixels were designated as forested if they fell into one of the following LANDFIRE forest categories: deciduous open, evergreen closed, and evergreen open. Forest cover was verified with aerial imagery [28]. Vegetation community composition was collected within 42 to 50 Daubenmire quadrats (50 cm x 20 cm) placed along the greenline at each reach [29]. The greenline is the point on the bank adjacent to the stream at which perennial vegetation is present, and typically occurs on either the first depositional or flat, floodplain-like feature located near the channel's bankfull edge [29]. Within each quadrat vascular plant cover was measured in two layers, an upper layer of woody shrub and tree species >1 m high, and a lower layer of all vascular plant

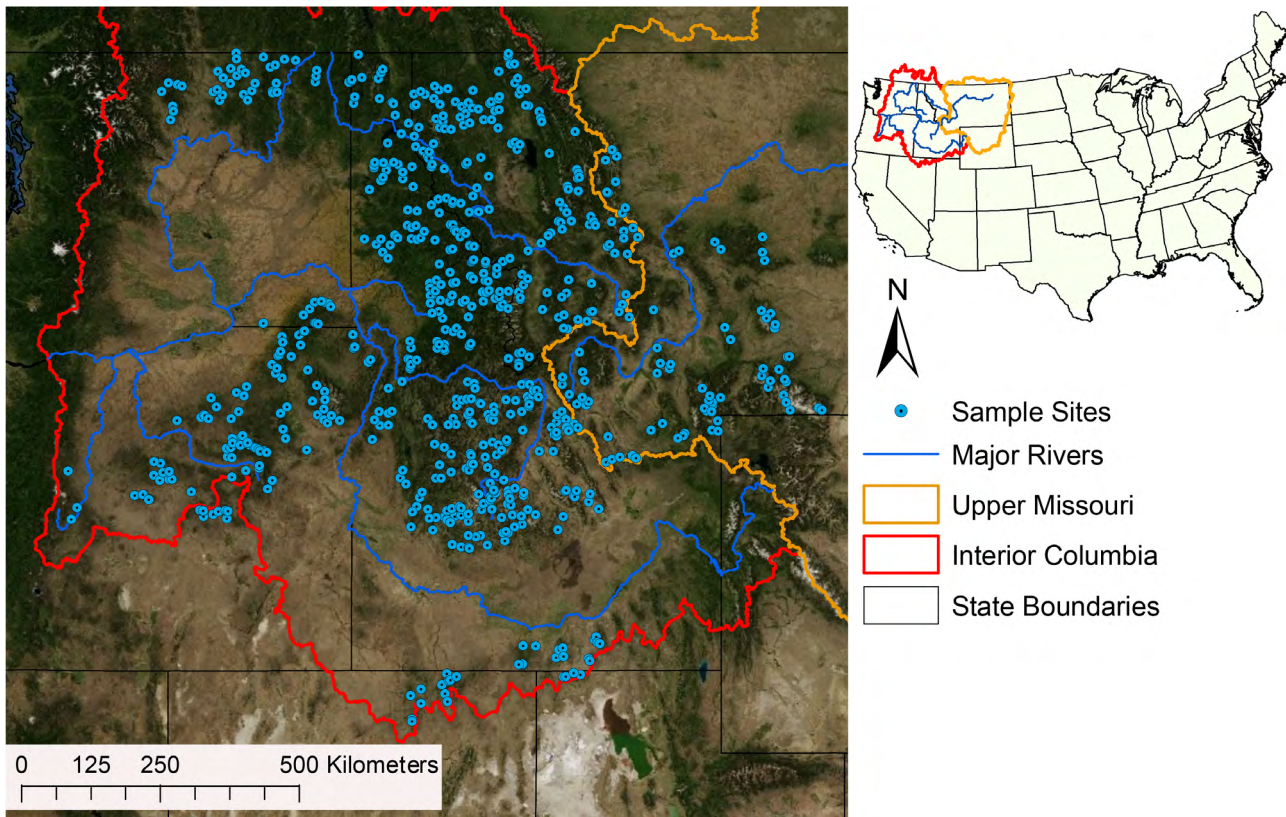


Figure 2: The 720 study reaches within the interior Columbia and upper Missouri River basins, U.S.A. Reaches occurred on federal land in watersheds predominantly under ownership and management by the U.S. Forest Service, Bureau of Land Management, and National Park Service. Base map imagery provided by Bing and licensed through ESRI.

species <1 m high. Vascular plant species whose cover exceeded 5% in either layer were classified into one of seven cover classes: 5-15%, 15-25%, 25-38%, 38-50%, 50-75%, 75-95%, or 95-100%. Cover class midpoints were taken as the relative abundance for each species within each quadrat. At each reach quadrat cover measurements for each species were summed and divided by the total number of quadrats at that reach to calculate reach-level species abundances.

Variables describing stream geomorphic setting included bankfull width, water surface gradient, and reach buffer slope. Bankfull width was estimated from the average bankfull width measured at 20 equally spaced transects throughout the reach. Gradient was estimated by surveying the difference in water surface between the top of the reach and the bottom of the reach and dividing by reach length. Reach buffer slope was estimated in GIS using the zonal mean function to estimate average slope in the 90-meter buffer polygon at each reach.

Variables describing climate included precipitation, temperature, and elevation. Precipitation and temperature were estimated using GIS to determine the weighted

average (by area) of all precipitation and temperature grids that intercepted the watershed upstream of each reach (1971 – 2000; [30]) Elevation was extracted within GIS by taking the average watershed elevation upstream of each reach from 10 m digital elevation models. Disturbance variables included the extent of grazing and wildfire within each watershed. The extent of grazing disturbance was estimated as the percent of land in the watershed upstream of each reach designated as a grazing allotment. The extent of wildfire disturbance was estimated as the proportion of the 90-meter buffer surrounding the reach that has burned in the last 15 years (Table 2).

2.3 Statistical Analyses

Our analysis consisted of three stages: (1) using ordination to visualize relationships between riparian vegetation at each reach and environmental drivers, (2) creating structural equation models that identify relationships between climate, geomorphic setting, disturbance, riparian vegetation, and instream wood volume and frequency, and (3) using multi-level pattern analysis and

permutational multivariate analysis of variance to identify what species were associated with high and low wood volumes.

We performed nonmetric multidimensional scaling (NMDS; [31]) on the riparian vegetation community using a Bray-Curtis distance matrix of the combined upper and lower layer vegetation data. Vegetation data was automatically square root transformed and Wisconsin double standardized using the metaMDS function in the R statistical environment (Version 2.14.1; [32]). We fit individual species vectors to the final NMDS configuration using the “envfit” function in R [33]. We also fit vectors onto the NMDS solution from parameters within the structural equation model (Table 2): large wood frequency, large wood volume, 30-year average temperature, 30-year average precipitation, average elevation, percent watershed grazed, percent watershed burned, buffer forest cover, buffer slope, stream bankfull width, and gradient. Individual reaches were plotted within the ordination by wood volume quartiles.

Structural equation models were generated under an iterative model building framework to assess the hypothesized relationships between the direct and indirect effects of vegetation, climate, disturbance, and stream geomorphic setting on instream wood volume and frequency (Table 1; Figure 1). Structural equation modeling is a scientific framework used to make inference by quantitatively examining scientifically-informed conceptual models between multiple interrelated variables [34]. This framework is particularly strong at identifying direct and indirect relationships between variables to infer the directional relationship between multiple causal and response variables [35]. We generated models based on the aforementioned hypothesized relationships between riparian vegetation community composition and environmental factors observed in previous studies (Figure 1; Table 1 [12,18]).

The first two NMDS ordination axes and the percent of the buffer that was forested were used as measured vegetation variables. We selected the first two axes of the NMDS solution for inclusion in the model because they were most strongly correlated to model parameters. Prior to model building we examined correlations between the hypothesized parameters within our structural equation models and plotted individual variable histograms and correlations between variables to assess normality and linear bivariate relationships between variables. Parameter variables were log or inverse square root transformed as necessary to meet assumptions of normality and linear bivariate relationships between model parameters.

We removed variables from our model that were strongly collinear with other model variables [35]. This

led to the removal of buffer slope, which was strongly correlated to stream gradient and elevation. Buffer slope was also deemed to be a less important predictor of wood than channel form (gradient) given our hypotheses. To determine whether model results supported our hypotheses (e.g. pathways; Figure 1; Table 1) regarding how each factor drives instream wood, we iteratively removed statistically non-significant pathways by weighting these paths to zero. Pathways were supported within our model if the variables describing the relationships in Table 1 showed statistically significant relationships ($\alpha = 0.05$).

To identify which riparian plant species were associated with different wood volumes, we carried out additional analyses that would validate our structural equation model results. First, we broke reaches into four quartile groups based on wood volume (Figure 3; wood quartiles: 1st: <13.8 m³/km, 2nd: 13.8 - 49.3 m³/km, 3rd: 49.3 - 123.1 m³/km, 4th: 123.1 - 1084.9 m³/km). We used PERMANOVA [36], a non-parametric distance based linear modeling technique for multivariate data, to identify if species composition differed between reaches within each of the four wood volume quartiles. We used multilevel pattern analysis [37], a form of indicator species analysis [38], to identify which species were most common within each wood volume quartile. PERMANOVA and multi-level pattern analysis between wood volume quartiles were used as confirmatory analyses to highlight differences in riparian vegetation across the range of instream wood volumes at each reach.

3 Results

The NMDS ordination converged on a three-dimensional solution after 1000 iterations with a stress of 19.91 ($p = 0.01$). Fitted environmental vectors (Table S1; Figure 4) showed strong elevation, precipitation and temperature gradients across the vegetation data (Figure 4; Table S2). Grazing pressure, a biotic disturbance, was strongly correlated to the vegetation community explained by the NMDS final solution; grazing was negatively correlated to the first ordination axis and positively correlated to the second ordination axis (Table S1). The other disturbance parameter, the proportion of each watershed burned, was weakly negatively correlated to both axes of the vegetation ordination (Figure 4). The precipitation gradient along NMDS axis one corresponded to instream wood across the study area: as precipitation increased so did the proportion of the watershed under forest cover and instream wood volume and frequency. Stream gradient was positively correlated to the first and second NMDS



Figure 3: Example reaches from each wood volume quartile illustrate multi-level-pattern analysis results that show riparian forest cover is tied to instream wood volume. Depth rods in pictures are ~1.35 meters in length. Note that streams with high wood volumes also exhibit more closed-canopy conifer forest than the first and second wood volume quartile streams. The climate and disturbance attributes correlated to these species are illustrated in Figures 4 and 5.

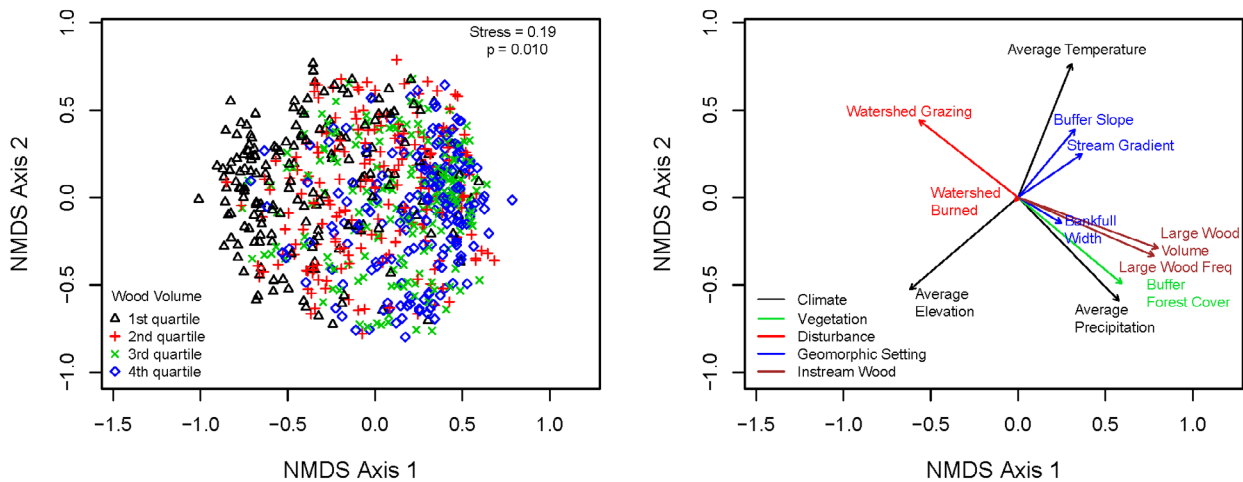


Figure 4: NMDS biplot of riparian vegetation composition, plotted by wood volume quartiles (A) and large wood volume and climate, geomorphic and disturbance attributes used in structural equation modeling (B). Note that the wood volume and frequency vectors show correlations with vegetation and environmental attributes, suggesting that vegetation-mediated environmental attributes influence instream wood dynamics.

axes. Bankfull width was positively correlated to the first axis, but negatively correlated to the second axis, and was collinear with precipitation. The vegetation community-environment relationships identified in the NMDS solution (Figure 4, Table S1) provided support for the hypotheses tested in our structural equation model.

Our final structural equation model confirmed several hypothesized *direct* and *indirect* relationships between vegetation, climate, disturbance, geomorphic setting, and instream wood volume and frequency (Figure 5; Table 4). As hypothesized, climate effects on wood were mediated through vegetation composition (pathways B, D) as evident by the relationships between temperature and precipitation and vegetation composition (ordination axes). Stream geomorphic setting *directly* influenced instream wood volume and frequency (pathways F,G), as supported by the positive relationship between both gradient and bankfull width and wood frequency and volume. Disturbance effects on instream wood were less predictable. Fire was a *direct* and *indirect* driver of wood volume and frequency (Figure 5) as it was significantly negatively correlated with NMDS axis two and weakly positively correlated to wood volume and frequency. Our model confirmed that grazing occurred more frequently in watersheds with high temperatures and low precipitation. Grazing was negatively associated with the first vegetation axis within the structural equation model, while precipitation was positively associated with the first ordination axis. These results confirm the correlations

between vegetation, climate and disturbance identified in the NMDS biplot (Figure 4) and highlight that vegetation composition drives which areas are grazed rather than grazing simply influencing vegetation composition. The second vegetation axis was not significantly affected by grazing. Precipitation was negatively correlated to the second vegetation axis while temperature was positively correlated to the same axis. Both vegetation axes were significant predictors of instream wood volume, the first axis positively and the second axis negatively. Buffer forest cover was positively correlated to precipitation and negatively correlated to temperature and elevation. Forest cover was positively correlated to NMDS axis 1 and negatively correlated to NMDS axis 2. Precipitation and catchment elevation were positively correlated to bankfull width and precipitation was negatively correlated to gradient, indicating that streams with less precipitation have lower gradients.

Riparian vegetation composition differed between reaches with different amounts of wood, with forested reaches showing the highest instream wood volumes (Figure 4; Table 3). Multi-level pattern analysis showed first quartile group (< 13.8 m³/km) and second quartile group (13.8 - 49.3 m³/km) indicator species consisted of meadow sedges like *Carex utriculata*, *Eleocharis palustris* and *Carex nebrascensis*, low-diameter willows (*Salix geyeriana*, *Salix lucida*, *Salix exigua*, *Salix wolfii*) or grasses (*Poa palustris*, *Deschampsia caespitosa*). Indicator species for the first three quartile groups (<123.1 m³/km) included

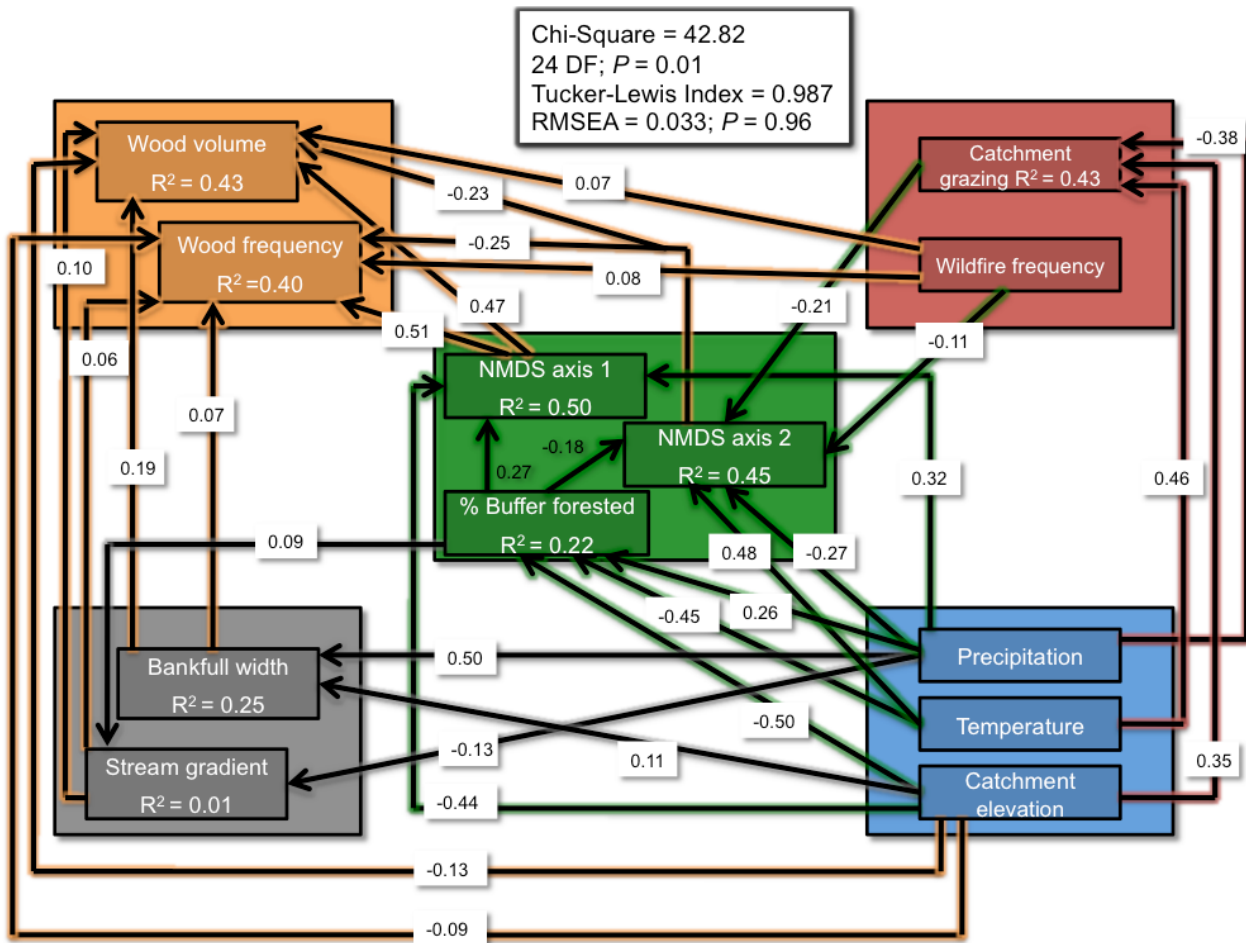


Figure 5: The final structural equation model illustrates the hypothesized relationships between geomorphic variables (bankfull width and gradient), climate (elevation, precipitation and temperature), disturbance (grazing and fire), vegetation community composition (NMDS1 and NMDS2 and buffer forest cover) and instream wood volume and frequency. Path weights are standardized coefficients. R^2 values for each predicted variable consist of effects from all direct and indirect pathways. Non-significant causal paths between variables were set to zero and not plotted here. Covariance structures between variables are not plotted here.

willows (*Salix boothii*, *Salix bebbiana*) and low-diameter deciduous trees (*Betula occidentalis*, *Crataegus douglasii*). Indicator species for the combined top three wood volume quartile groups' (13.8 - 1,084.9 m^3/km) consisted of conifer trees that grow to large diameters (*Picea engelmannii*, *Abies lasiocarpa*, *Abies grandis*, *Pseudotsuga menziesii*), and numerous shrubs and forbs that are common to interior Pacific Northwest dry conifer forests (*Rubus spp.*, *Ribes. spp.*, *Alnus viridis*, *Cornus canadensis*, *Streptopus amplexifolius*, etc. Table 3; Table S3). The two highest quartiles' (>49.3 m^3/km) indicator species included *Thuja plicata*, a long-lived conifer tree with the potential to grow several meters in diameter, and numerous mesic forbs (*Vaccinium membranaceum*, *Gymnocarpium dryopteris*, etc). These communities showed that within the study area, the potential of a site to grow large conifers that decay slowly and require higher stream power to be

evacuated [39], is paramount for reaches to maintain high instream wood volumes (Figure 4; Figure 5).

4 Discussion

Instream wood volume and frequency are *directly influenced* by riparian vegetation composition and stream geomorphic setting within the headwaters of the Columbia and Missouri River basins. Instream wood is *indirectly influenced* by landscape disturbance (fire) and climate attributes (temperature, precipitation, elevation) that drive vegetation community assembly. Many studies have tied either instream wood to watershed and landscape dynamics [40–42], or riparian vegetation to ecosystem function [43], but to our knowledge no study has disentangled the direct and indirect effects of climate, disturbance, geomorphic setting, and vegetation on instream wood. For example,

Table 3: The top five indicator species ($IV > 0.3$) generated using multilevel pattern analysis for each combination of wood volume quartile group. The top ten indicator species were shown for the upper quartiles (2, 3 and 4) as these quartiles had the strongest indicator species, with indicator values approaching one. Species found in the understory layer $< 1\text{m}$ in height are annotated by (u) while (o) indicates species found in the overstory layer $> 1\text{m}$ in height. P-values for each indicator species' indicator value were generated using Monte Carlo simulations (999 permutations). Growth form was categorically classified based on the USDA Plants Database.

Indicator Species	Growth Form	Large Wood Volume Quartile Groups				Indicator Value	P
(u) <i>Carex utriculata</i>	Graminoid	1				0.395	0.005
(u) <i>Salix geyeriana</i>	High shrub	1				0.364	0.005
(o) <i>Salix geyeriana</i>	High shrub	1				0.354	0.005
(u) <i>Poa palustris</i>	Graminoid	1				0.336	0.005
(u) <i>Carex nebrascensis</i>	Graminoid	1				0.301	0.005
(u) <i>Juncus balticus</i>	Graminoid	1	2			0.486	0.005
(u) <i>Phleum pratense</i>	Graminoid	1	2			0.368	0.005
(u) <i>Salix lucida</i>	High shrub	1	2			0.322	0.005
(o) <i>Salix lucida</i>	High shrub	1	2			0.306	0.005
(u) <i>Gymnocarpium dryopteris</i>	Forb			3	4	0.446	0.005
(u) <i>Linnaea borealis</i>	Forb			3	4	0.392	0.005
(u) <i>Tiarella trifoliata</i>	Forb			3	4	0.374	0.005
(u) <i>Thuja plicata</i>	Coniferous tree			3	4	0.368	0.005
(u) <i>Vaccinium membranaceum</i>	Low shrub			3	4	0.356	0.005
(u) <i>Poa pratensis</i>	Graminoid	1	2	3		0.561	0.005
(u) <i>Achillea millefolium</i>	Forb	1	2	3		0.556	0.005
(u) <i>Salix boothii</i>	High shrub	1	2	3		0.474	0.005
(o) <i>Salix boothii</i>	High shrub	1	2	3		0.473	0.005
(u) <i>Packera pseudaurea</i>	Forb	1	2	3		0.380	0.015
(o) <i>Picea engelmannii</i>	Coniferous tree		2	3	4	0.655	0.005
(u) <i>Senecio triangularis</i>	Forb		2	3	4	0.647	0.005
(u) <i>Rubus parviflorus</i>	Low shrub		2	3	4	0.618	0.005
(u) <i>Streptopus amplexifolius</i>	Forb		2	3	4	0.603	0.005
(u) <i>Athyrium filix-femina</i>	Fern		2	3	4	0.597	0.005
(u) <i>Ribes lacustre</i>	Low shrub		2	3	4	0.588	0.005
(u) <i>Ribes hudsonianum</i>	Low shrub		2	3	4	0.581	0.005
(o) <i>Acer glabrum</i>	Deciduous tree		2	3	4	0.484	0.005
(o) <i>Abies grandis</i>	Coniferous tree		2	3	4	0.483	0.005
(o) <i>Abies lasiocarpa</i>	Coniferous tree		2	3	4	0.460	0.005

numerous studies show that wood controls pool habitats [44,45], and there has been recent discussion of reciprocal interactions between vegetation and geomorphology in rivers [46,47]. Building on these studies, we have succinctly defined how vegetation community composition influences instream large wood, a major driver of stream hydraulics and geomorphic processes. By identifying vegetation as a *direct* driver of wood in streams, we can infer that the processes that drive vegetation may be *indirect* drivers of wood-forced

in-channel geomorphic units. Many controls may play a role in dictating the location of common geomorphic units, such as valley confinement, point-source sediment inputs or tributary junctions, and localized variations in bedrock and surficial geology, among others. However, in low-order wadeable streams, it has been suggested that wood may play a disproportionately large role relative to these controls in dictating the distribution of geomorphic units [22].

Table 4: The direct and indirect effects of geomorphic setting, vegetation, disturbance, and climate on large wood and volume identified in the final structural equation model.

Variable	Wood metric	Effect on wood	Which variables are indirect effects mediated through?
Vegetation composition (NMDS Axis 1)	Volume	Direct (+)	
	Frequency	Direct (+)	
Vegetation composition (NMDS Axis 2)	Volume	Direct (-)	
	Frequency	Direct (-)	
30-year average precipitation (m)	Volume	Indirect (+)	Vegetation composition - NMDS Axes 1 (+) and 2 (-); forest cover (+); bankfull width (+); stream gradient (-); grazing (-)
	Frequency	Indirect (+)	
30-year average temperature (°C)	Volume	Indirect (-)	Vegetation composition - NMDS Axes 2 (+); forest cover (-); grazing (+)
	Frequency	Indirect (-)	
Average elevation (m)	Volume	Direct (-) Indirect (+)	Bankfull width (+); grazing (+); forest cover (-); Vegetation composition - NMDS Axis 1 (-)
	Frequency	Direct (-) Indirect (+)	
Watershed grazed (%)	Volume	Indirect (-)	Vegetation composition - NMDS Axis 2 (-)
	Frequency	Indirect (-)	
Watershed burned (%)	Volume	Direct (+) Indirect (-)	Vegetation composition - NMDS Axis 2 (-)
	Frequency	Direct (+) Indirect (-)	
Buffer forest cover (%)	Volume	Indirect (+)	Stream gradient (+);Vegetation composition - NMDS Axes 1 (+) and 2 (-);
	Frequency	Indirect (+)	
Stream gradient (%)	Volume	Direct (+)	
	Frequency	Direct (+)	
Stream bankfull width (m)	Volume	Direct (+)	
	Frequency	Direct (+)	

Gradient and bankfull width were positively correlated to instream wood volume and frequency. While our initial hypothesis predicted that wider channels should contain more wood (H,F) given their decreased stream power and reduced ability to mobilize wood, the finding that steeper streams contained more wood was contradictory to our initial hypothesis (H,G). We suspect that the positive correlation found between stream gradient and instream wood volume may point to the propensity for steep-walled drainages to deliver more wood to channels than can be actively mobilized and transported downstream. The steepest channel reaches within our study often occurred in high elevation headwaters with small, confined drainages. The steeply-sloping, forested valley walls likely provide increased wood volumes to the channel resulting from hillslope mass wasting and tree fall in densely forested areas [1,20]. Combined with low discharge and relative immobility of wood pieces resulting from the high ratio of wood length to channel width in these low-order, narrow channels, it is likely that wood accumulates, rather than being exported from these locations (e.g. [22]).

We anticipated that disturbance would influence vegetation composition and serve as an indirect driver

of wood dynamics. Instead, we found that grazing disturbance is more likely to occur in hotter, drier ecotones where forest vegetation is less common [48]. Accordingly, grazing occurred in watersheds with reaches that were historically wood-poor based on landscape filters (high temperature, low precipitation) that inhibit tree establishment and growth. We saw that low temperature reaches with high precipitation were not only less likely to be in frequently grazed watersheds, but also more likely to have heavily forested stream buffers (Figure 4). Fire was a direct driver of both vegetation (NMDS axis two) and wood volume and frequency. This suggests that fire affects instream wood by killing trees that are then contributed to the channel [15] rather than just by shaping riparian vegetation composition. Without fire intensity or recurrence data, these patterns provide limited inference into how fire shapes instream wood across landscapes.

Because of the spatial extent of the Columbia and Missouri River basins, riparian plant communities assemble across large elevation and climatic gradients. These same communities are further filtered by fire disturbance and correspond to channel gradient and bankfull width that are collinear with precipitation, temperature and elevation. Environmental filters

affect how biotic communities assemble [17,49], and vegetation affects riparian landform dynamics [4,50], but we demonstrate here that *direct* environmental filters on riparian vegetation are also *indirect* filters on abiotic processes that influence stream habitat. Because tree cover corresponds to high precipitation and cool temperatures, it is likely that many hot, low-precipitation streams within the study region were historically wood poor based on their species composition alone. These meadow and shrub communities' stream habitats may form via external forcings that shape channel planform and adjacent groundwater tables. These forcings may include the location of bedrock outcrops, lithologic controls on valley form, post-glacial landforms, point source and longitudinal sediment inputs, or beaver dams that are not comprised exclusively of large wood.

Stream and riparian restoration objectives should reflect that wood is not a keystone element of all stream systems, much as forests are not ubiquitous across all riverscapes. Wood-poor reaches that are controlled by climate filters will require different approaches to restoration than heavily forested reaches whose hydraulics and geomorphology can be expected to respond to wood contributions [8]. For example, reaches where wood is naturally limited may need instream structures such as those built by North American beaver (*Castor canadensis*) to create hydraulic and planform diversity that large wood would otherwise create [51]. Reducing anthropogenic disturbances on vegetation such as grazing can change riparian vegetation dynamics, but woody plant recolonization may be impaired due to the legacy effects of disturbance [52]. These impaired sites may require short-term wood supplementation to restore hydraulic and geomorphic diversity to stream channels.

Similarly, stream restoration objectives that are tied to the life-history strategies of fishes and other aquatic biota require explicit understandings of how wood-forced pools and riffles form over time. In some cases instream wood may not be a locally sustainable restoration solution to create dynamic aquatic habitats. For example, the watershed processes required to grow and contribute wood to channels may be present, but may be outweighed by advanced transport capacities that keep reaches in a wood-poor equilibrium. Wood is unlikely to change these reaches' planform or hydraulic diversity (e.g. wood-forced pools and riffles) in the long run as these reaches (e.g. gorges) consistently evacuate wood downstream.

In contrast, disturbances like fire may transition forest vegetation toward early-seral species that cannot contribute wood to channels in the short-term [53]. In heavily forested watersheds where riparian trees are

ubiquitous and instream wood is abundant, disturbance may drive wood contributions to the channel, but may not specifically control vegetation composition. Complex synergies exist between climate, disturbance, vegetation, hydrology, geomorphology, and instream habitat. Predicting trajectories of instream wood across broad spatial extents requires understanding how vegetation responds to watershed processes that interact with larger climatic and physiographic gradients.

5 Conclusions

Because wood is a strong driver of channel form and aquatic habitat dynamism, any process that impacts the direct and indirect drivers of wood has the potential reduce the resilience of riparian zones and wood-forced instream physical habitat. The direct relationships between disturbance and vegetation and between vegetation and instream wood illustrate that watersheds must maintain sufficient riparian vegetation to facilitate wood-mediated processes within key watersheds that provide habitat for endangered fishes.

While watershed disturbance and riparian vegetation interact directly, the interactions between climate, disturbance, riparian zones, stream channels, and instream wood may become more difficult to predict as global change – invasive species, altered climate, human development and resource extraction – intensifies. For example, the timing, intensity and frequency of individual snowfall, rain, snowmelt and runoff events may become more novel under climate change [54]. Novel hydrology may lead to reduced base flows that cause some riparian communities to decline from reduced hydrologic connectivity, even in the absence of watershed disturbance. Similarly, more intense overbank flooding may change sediment erosion and deposition patterns that lead to transitions in riparian vegetation from large-long-lived conifer trees to early-successional shrubs and graminoids that cannot contribute large wood to channels. Wood mobility may be altered under novel hydrologic regimes, given that alterations in flood magnitude and frequency have the potential to alter stream power and channel geometry. Interactions between climate and fire disturbance on vegetation and the direct effects that vegetation have on patterns of instream wood must be considered when accounting for the habitat potential of low-order streams in the future. Any disturbance or climate impact that affects vegetation or stream hydrology will likely also affect instream wood, and the potential for small streams to form dynamic aquatic habitat.

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Statement of author contributions: NH-S and CM formulated the project. NH-S formatted and analyzed data, and created figures and tables. NH-S, AK, CM, and BBR wrote the manuscript.

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Supplementary Materials

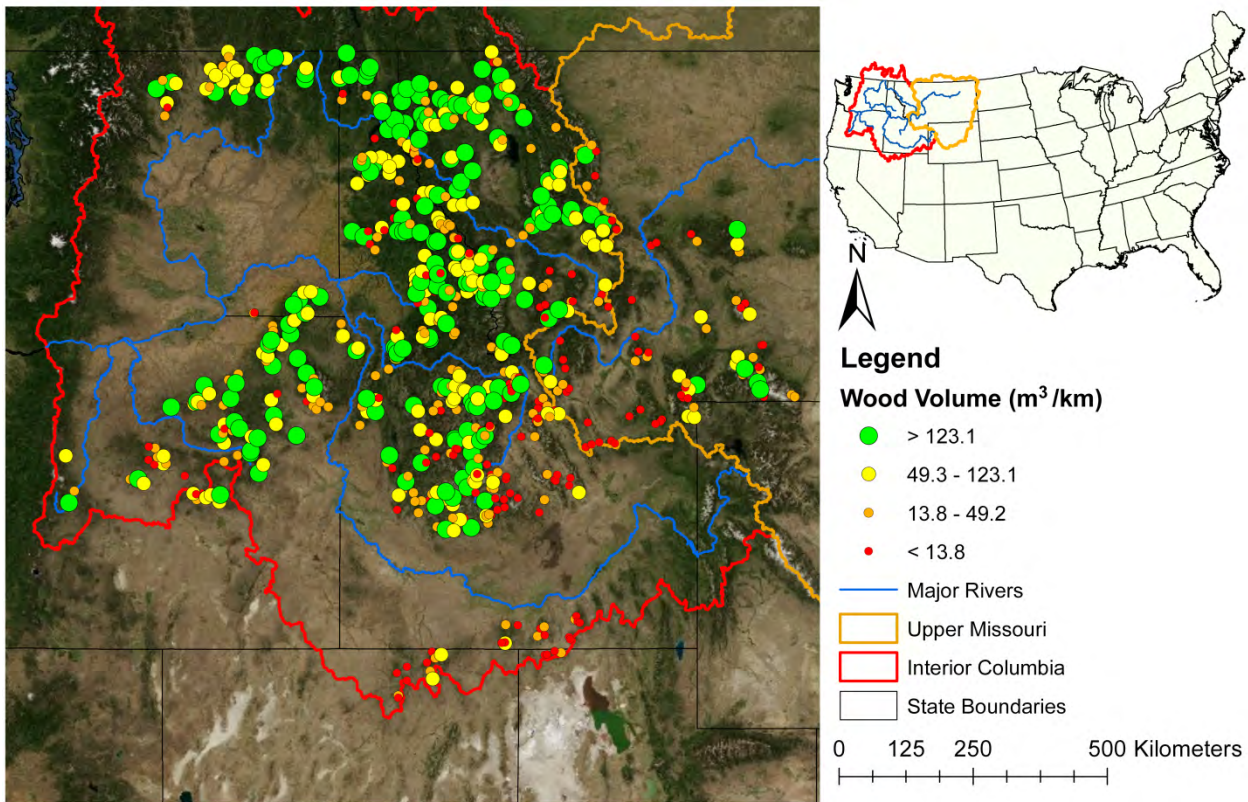


Figure S1: Sampled reaches within the Columbia and Missouri River basins by wood volume quartiles. Wood volume was related to patterns in climate and vegetation quantified using ordination (Figure 4) and the structural equation model illustrated in (Figure 4). Basemap imagery provided by Bing and licensed through ESRI.

Table S1: Model fits between environmental variables used during structural equation model building and the 3-dimensional NMDS solution. Variables were fit to the ordination solution using the envfit function in the vegan package in R [32,33].

Variable	NMDS1	NMDS2	NMDS3	R ²	P
Average precipitation	0.697997	-0.715578	0.027374	0.3725	0.001
Average temperature	0.325508	0.81086	0.486365	0.4840	0.001
Average elevation	-0.642378	-0.547302	-0.53648	0.5041	0.001
Watershed grazing	-0.787134	0.612947	0.068674	0.2816	0.001
Watershed burned	-0.071607	-0.090875	-0.993285	0.0316	0.001
Buffer forest cover	0.769508	-0.637994	0.028654	0.3247	0.001
Buffer slope	0.52837	0.631668	-0.567292	0.2069	0.001
Stream gradient	0.825652	0.560239	-0.066576	0.1062	0.001
Bankfull width	0.820272	-0.484047	-0.304718	0.0494	0.001
Wood frequency	0.918526	-0.394932	0.01839	0.3903	0.001
Wood volume	0.934655	-0.339021	0.107165	0.3996	0.001

Table S2: Alphabetical list of overstory and understory species and their Pearson correlations with the 3-dimensional NMDS solution. Species were fit to the ordination solution using the `envfit` function in the `vegan` package in R [32,33]. Species found in the understory layer < 1m in height are annotated by (u) while (o) indicates species found in the overstory layer > 1m in height.

Species	NMDS1	NMDS2	NMDS3	R ²	P
(u) <i>Abies lasiocarpa</i>	0.202585	-0.9768877	0.0681884	0.1411	0.001
(u) <i>Acer glabrum</i>	0.8408795	0.5343674	0.0858668	0.1089	0.001
(u) <i>Achillea millefolium</i>	-0.9849766	0.1602284	-0.0644051	0.2110	0.001
(u) <i>Aconitum columbianum</i>	0.6589498	-0.7012472	-0.2720985	0.0349	0.001
(u) <i>Actaea rubra</i>	0.9525271	-0.3021303	-0.0375429	0.0416	0.001
(u) <i>Agrostis stolonifera</i>	-0.4037587	0.834704	-0.3744971	0.0573	0.001
(u) <i>Alnus incana</i>	0.4700143	0.5781867	-0.6669233	0.3035	0.001
(u) <i>Alnus viridis</i>	0.5022738	-0.8646895	-0.0057511	0.1650	0.001
(u) <i>Amelanchier alnifolia</i>	0.9291986	0.3676305	-0.0379167	0.0391	0.001
(u) <i>Anaphalis margaritacea</i>	0.5353059	-0.0678195	-0.8419312	0.0167	0.005
(u) <i>Angelica arguta</i>	0.5638687	-0.0380896	-0.8249856	0.1149	0.001
(u) <i>Arnica cordifolia</i>	0.6707937	-0.6878065	0.277413	0.0259	0.001
(u) <i>Artemisia ludoviciana</i>	-0.9167641	0.348275	-0.1955715	0.0255	0.002
(u) <i>Athyrium filix-femina</i>	0.9253848	0.0949988	0.3669308	0.3385	0.001
(u) <i>Boykinia major</i>	0.7822782	-0.6015968	0.1616235	0.1467	0.001
(u) <i>Calamagrostis canadensis</i>	-0.1607194	-0.8753198	-0.4560533	0.1234	0.001
(u) <i>Canadanthus modestus</i>	0.1685333	-0.2814346	-0.9446645	0.1197	0.001
(u) <i>Carex aquatilis</i>	-0.8714598	-0.4785715	-0.1073646	0.0993	0.001
(u) <i>Carex lenticularis</i>	0.5914018	0.2316227	-0.7723955	0.0019	0.71
(u) <i>Carex microptera</i>	-0.8955466	0.0412243	-0.4430539	0.0701	0.001
(u) <i>Carex nebrascensis</i>	-0.8941898	0.313362	0.3197325	0.0926	0.001
(u) <i>Carex utriculata</i>	-0.8811906	-0.0529278	-0.469789	0.1276	0.001
(u) <i>Chamerion angustifolium</i>	0.0113538	-0.0579867	-0.9982528	0.1304	0.001
(u) <i>Cinna latifolia</i>	0.8510226	-0.1067378	-0.5141669	0.021	0.004
(u) <i>Circaea alpina</i>	0.8671368	0.3465635	0.3577256	0.0853	0.001
(u) <i>Cirsium arvense</i>	-0.5143466	0.8575797	0.0021647	0.0338	0.001
(u) <i>Claytonia cordifolia</i>	0.8797327	0.3906441	0.2710488	0.0722	0.001
(u) <i>Cornus canadensis</i>	0.987367	-0.0481059	0.1509712	0.0463	0.001
(u) <i>Cornus sericea</i>	0.6723408	0.5123524	-0.5342778	0.3653	0.001
(u) <i>Dasiphora floribunda</i>	-0.8725796	-0.3951995	-0.2870927	0.1069	0.001
(u) <i>Deschampsia caespitosa</i>	-0.9445396	-0.2147005	-0.2484926	0.0528	0.001
(u) <i>Eleocharis palustris</i>	-0.6586327	0.7455681	0.1016423	0.0879	0.001
(u) <i>Elymus glaucus</i>	0.5795981	0.6473061	-0.4950362	0.0796	0.001
(u) <i>Epilobium ciliatum</i>	0.0537979	0.8121611	-0.5809477	0.045	0.001
(u) <i>Equisetum arvense</i>	-0.0267231	0.167666	-0.9854816	0.1048	0.001
(u) <i>Equisetum hyemale</i>	0.3024286	0.6089121	-0.7333233	0.0809	0.001
(u) <i>Fragaria vesca</i>	0.6134273	0.3277576	0.7185276	0.0067	0.188
(u) <i>Fragaria virginiana</i>	-0.8483497	-0.4070156	-0.3385869	0.1706	0.001
(u) <i>Galium boreale</i>	-0.5708853	0.8195882	0.0486332	0.0105	0.061
(u) <i>Galium triflorum</i>	0.7838079	0.6016827	0.1536983	0.1071	0.001
(u) <i>Geum macrophyllum</i>	-0.2456383	0.8289522	-0.5024939	0.0373	0.001
(u) <i>Glyceria striata</i>	0.0187244	0.8598294	-0.510238	0.0344	0.001
(u) <i>Gymnocarpium dryopteris</i>	0.9229241	-0.0268739	0.3840429	0.1506	0.001
(u) <i>Juncus balticus</i>	-0.8990635	0.3834873	0.2112398	0.2692	0.001
(u) <i>Juncus ensifolius</i>	-0.7722778	0.1908263	-0.6059475	0.0304	0.001

Species	NMDS1	NMDS2	NMDS3	R ²	P
(u) <i>Ligusticum canbyi</i>	0.7308406	-0.6782984	0.0760485	0.1092	0.001
(u) <i>Linnaea borealis</i>	0.9155747	-0.2069762	0.3447953	0.0467	0.001
(u) <i>Lonicera involucrata</i>	0.4221571	-0.4310873	-0.7974629	0.2149	0.001
(u) <i>Lupinus polyphyllus</i>	-0.2823496	-0.9514054	0.1229086	0.0545	0.001
(u) <i>Luzula parviflora</i>	-0.2973863	-0.7515192	-0.5888806	0.0334	0.001
(u) <i>Maianthemum stellatum</i>	0.3250828	0.9292542	0.1755213	0.0274	0.001
(u) <i>Mentha arvensis</i>	-0.2236227	0.9247264	-0.3080163	0.1492	0.001
(u) <i>Menziesia ferruginea</i>	0.4087711	-0.8259375	0.3882441	0.2057	0.001
(u) <i>Mertensia ciliata</i>	-0.204573	-0.799984	-0.5640705	0.0194	0.002
(u) <i>Mertensia paniculata</i>	0.5510259	-0.805745	0.21713	0.036	0.001
(u) <i>Mimulus guttatus</i>	-0.7912644	0.5945637	0.1428098	0.0133	0.023
(u) <i>Mimulus lewisii</i>	0.0449893	-0.5024227	-0.8634509	0.0561	0.001
(u) <i>Mitella pentandra</i>	0.7199952	-0.6912895	-0.0610394	0.0412	0.001
(u) <i>Packera pseud aurea</i>	-0.5753764	-0.5122149	-0.6376346	0.0317	0.001
(u) <i>Parnassia fimbriata</i>	-0.0775174	-0.9048792	-0.4185506	0.1081	0.001
(u) <i>Pedicularis groenlandica</i>	-0.4784885	-0.7884461	-0.3865249	0.0923	0.001
(u) <i>Phalaris arundinacea</i>	0.2286287	0.9153514	0.3314524	0.0586	0.001
(u) <i>Philadelphus lewisii</i>	0.4302948	0.8949068	0.1182718	0.1384	0.001
(u) <i>Phleum pratense</i>	-0.7972956	0.5908848	-0.123186	0.0788	0.001
(u) <i>Picea engelmannii</i>	0.2161196	-0.9590715	-0.1829598	0.1854	0.001
(u) <i>Pinus contorta</i>	-0.5520738	-0.8065241	-0.2115027	0.0639	0.001
(u) <i>Poa palustris</i>	-0.7436523	0.2284526	-0.6283237	0.0847	0.001
(u) <i>Poa pratensis</i>	-0.7981379	0.5966773	0.0833792	0.2537	0.001
(u) <i>Polemonium occidentale</i>	-0.9022966	-0.0690061	-0.4255574	0.053	0.001
(u) <i>Populus balsamifera</i>	0.1934841	0.9768037	0.091752	0.0475	0.001
(u) <i>Potentilla gracilis</i>	-0.9446096	0.2393249	0.2245802	0.0769	0.001
(u) <i>Prenanthes sagittata</i>	0.6638667	-0.6519831	-0.3663318	0.0716	0.001
(u) <i>Prunella vulgaris</i>	0.1941451	0.8332964	0.5176145	0.0366	0.001
(u) <i>Pseudotsuga menziesii</i>	0.8806174	0.3626474	-0.3049587	0.0026	0.585
(u) <i>Rhamnus alnifolia</i>	0.5718908	-0.0615127	-0.8180202	0.0171	0.003
(u) <i>Ribes hudsonianum</i>	0.2849088	-0.0150183	-0.958437	0.1147	0.001
(u) <i>Ribes inerme</i>	-0.2719783	-0.1653813	-0.9479856	0.0869	0.001
(u) <i>Ribes lacustre</i>	0.7282796	-0.5316359	-0.4324027	0.1202	0.001
(u) <i>Rosa acicularis</i>	0.4083678	0.8539952	-0.3223786	0.0024	0.646
(u) <i>Rosa nutkana</i>	0.8869723	0.4156279	-0.2013296	0.0094	0.077
(u) <i>Rosa woodsii</i>	-0.3496673	0.9213016	-0.1701062	0.0814	0.001
(u) <i>Rubus idaeus</i>	0.5594725	0.5152144	-0.6492647	0.078	0.001
(u) <i>Rubus parviflorus</i>	0.9586964	0.268658	-0.0934027	0.3395	0.001
(u) <i>Rudbeckia occidentalis</i>	0.6904426	0.2084717	-0.6926966	0.0148	0.013
(u) <i>Rumex crispus</i>	0.0698132	0.9821335	0.1747564	0.0521	0.001
(u) <i>Salix bebbiana</i>	-0.3408	0.0128974	-0.9400474	0.0103	0.057
(u) <i>Salix boothii</i>	-0.6693679	-0.061556	-0.7403766	0.3055	0.001
(u) <i>Salix drummondiana</i>	-0.3215064	-0.3792858	-0.8676266	0.3447	0.001
(u) <i>Salix exigua</i>	-0.282018	0.5733372	-0.769253	0.0288	0.001
(u) <i>Salix geyeriana</i>	-0.9195339	0.0942707	-0.381537	0.0761	0.001
(u) <i>Salix lucida</i>	-0.4381773	0.5409683	-0.7178816	0.0931	0.001
(u) <i>Salix melanopsis</i>	-0.2007421	-0.0709143	-0.9770741	0.0557	0.001
(u) <i>Salix sitchensis</i>	0.9197458	-0.292138	-0.262151	0.0441	0.001
(u) <i>Salix wolfii</i>	-0.7706382	-0.6275265	0.1110283	0.1314	0.001

Species	NMDS1	NMDS2	NMDS3	R ²	P
(u) <i>Saxifraga odontoloma</i>	-0.1032663	-0.8427373	-0.5283274	0.0669	0.001
(u) <i>Scirpus microcarpus</i>	-0.1069405	0.9883733	0.108083	0.0749	0.001
(u) <i>Senecio triangularis</i>	0.5656151	-0.8106707	-0.1513028	0.2946	0.001
(u) <i>Solidago canadensis</i>	-0.0395316	0.7200182	-0.6928283	0.0545	0.001
(u) <i>Spiraea betulifolia</i>	0.9429398	-0.2794013	-0.1811061	0.0504	0.001
(u) <i>Spiraea douglasii</i>	0.084396	0.3860272	-0.9186187	0.0224	0.001
(u) <i>Streptopus amplexifolius</i>	0.9427506	-0.3333898	-0.008519	0.2331	0.001
(u) <i>Symphoricarpos albus</i>	0.5538611	0.789028	0.2658433	0.3246	0.001
(u) <i>Symphyotrichum foliaceum</i>	-0.39776	-0.4930469	-0.7737517	0.0657	0.001
(u) <i>Symphyotrichum sp</i>	-0.9419711	-0.1443818	-0.3030582	0.0967	0.001
(u) <i>Taraxacum officinale</i>	-0.859803	0.3973445	-0.3207119	0.1927	0.001
(u) <i>Thalictrum occidentale</i>	0.4724116	-0.5247155	-0.7081673	0.0605	0.001
(u) <i>Thuja plicata</i>	0.7525419	0.1256666	0.646443	0.1049	0.001
(u) <i>Tiarella trifoliata</i>	0.8230319	-0.0237766	0.5674973	0.0698	0.001
(u) <i>Trautvetteria carolinensis</i>	0.9035437	-0.3053998	0.3005658	0.0752	0.001
(u) <i>Trifolium longipes</i>	-0.8739655	-0.4689319	-0.1276215	0.1046	0.001
(u) <i>Urtica dioica</i>	0.0524069	0.9966688	0.0624885	0.048	0.001
(u) <i>Vaccinium membranaceum</i>	0.4793823	-0.8458548	0.2339279	0.1668	0.001
(o) <i>Abies grandis</i>	0.8418226	0.1843699	0.5072894	0.1685	0.001
(o) <i>Abies lasiocarpa</i>	0.3690822	-0.9257052	0.0827532	0.196	0.001
(o) <i>Acer glabrum</i>	0.8286708	0.5274192	0.1874395	0.2381	0.001
(o) <i>Alnus incana</i>	0.536029	0.6402736	-0.5502024	0.3962	0.001
(o) <i>Alnus viridis</i>	0.5821709	-0.8119272	0.043027	0.2071	0.001
(o) <i>Amelanchier alnifolia</i>	0.8336904	0.5490078	-0.0595882	0.08	0.001
(o) <i>Betula occidentalis</i>	-0.0439294	0.9885897	0.1440856	0.063	0.001
(o) <i>Cornus sericea</i>	0.6573742	0.5834373	-0.4769278	0.3861	0.001
(o) <i>Crataegus douglasii</i>	0.2446043	0.9643498	0.1009862	0.075	0.001
(o) <i>Lonicera involucrata</i>	0.3007627	-0.2998696	-0.9053287	0.0927	0.001
(o) <i>Philadelphus lewisii</i>	0.3939347	0.9152188	0.0847933	0.1404	0.001
(o) <i>Picea engelmannii</i>	0.3741648	-0.9265099	0.0397505	0.3217	0.001
(o) <i>Pinus contorta</i>	-0.5903351	-0.7840081	-0.1919264	0.1622	0.001
(o) <i>Pinus ponderosa</i>	-0.1975631	0.8238652	0.5312391	0.0823	0.001
(o) <i>Populus balsamifera</i>	0.3431037	0.9051867	-0.2508323	0.0401	0.001
(o) <i>Pseudotsuga menziesii</i>	0.68945	0.5714793	-0.4450507	0.0385	0.001
(o) <i>Ribes hudsonianum</i>	0.4458408	0.2998877	-0.8433821	0.0667	0.001
(o) <i>Ribes lacustre</i>	0.8850824	-0.3683148	-0.2845582	0.0498	0.001
(o) <i>Rosa woodsii</i>	-0.286646	0.8732114	-0.3941268	0.0915	0.001
(o) <i>Rubus parviflorus</i>	0.8924912	0.4388118	-0.1044201	0.1322	0.001
(o) <i>Salix bebbiana</i>	0.0478305	0.3461841	-0.9369465	0.0223	0.001
(o) <i>Salix boothii</i>	-0.6321926	0.0279502	-0.7743069	0.324	0.001
(o) <i>Salix drummondiana</i>	-0.2471062	-0.2577209	-0.934087	0.3162	0.001
(o) <i>Salix exigua</i>	-0.2884391	0.8397223	-0.4600754	0.0215	0.002
(o) <i>Salix geyeriana</i>	-0.8845744	0.2741948	-0.3772868	0.1242	0.001
(o) <i>Salix lucida</i>	-0.4630401	0.5886002	-0.6626792	0.0912	0.001
(o) <i>Salix melanopsis</i>	-0.0332019	-0.0262084	-0.999105	0.0544	0.001
(o) <i>Salix sitchensis</i>	0.723764	-0.5030942	-0.4722943	0.0427	0.001
(o) <i>Symphoricarpos albus</i>	0.5458193	0.8007753	0.246658	0.2029	0.001

Table S3: Indicator species generated using multilevel pattern analysis for each combination of wood volume quartile group. Species found in the understory layer < 1m in height are annotated by (u) while (o) indicates species found in the overstory layer > 1m in height. P values for each indicator species were generated using 999 permutations.

Indicator Species	Large Wood Volume Quartile Groups				Indicator Value	P
(u) <i>Carex utriculata</i>	1				0.395	0.005
(u) <i>Salix geeyeriana</i>	1				0.364	0.005
(o) <i>Salix geeyeriana</i>	1				0.354	0.005
(u) <i>Poa palustris</i>	1				0.336	0.005
(u) <i>Carex nebrascensis</i>	1				0.301	0.005
(u) <i>Eleocharis palustris</i>	1				0.291	0.005
(u) <i>Salix wolfii</i>	1				0.289	0.005
(u) <i>Juncus balticus</i>	1	2			0.486	0.005
(u) <i>Phleum pratense</i>	1	2			0.368	0.005
(u) <i>Salix lucida</i>	1	2			0.322	0.005
(o) <i>Salix lucida</i>	1	2			0.306	0.005
(u) <i>Dasiphora floribunda</i>	1	2			0.292	0.005
(u) <i>Trifolium longipes</i>	1	2			0.288	0.015
(u) <i>Deschampsia caespitosa</i>	1	2			0.251	0.005
(o) <i>Salix exigua</i>	1	2			0.251	0.01
(u) <i>Artemisia ludoviciana</i>	1	2			0.235	0.015
(u) <i>Gymnocarpium dryopteris</i>			3	4	0.446	0.005
(u) <i>Linnaea borealis</i>			3	4	0.392	0.005
(u) <i>Tiarella trifoliata</i>			3	4	0.374	0.005
(u) <i>Thuja plicata</i>			3	4	0.368	0.005
(u) <i>Vaccinium membranaceum</i>			3	4	0.356	0.005
(u) <i>Trautvetteria caroliniensis</i>			3	4	0.343	0.005
(o) <i>Ribes lacustre</i>			3	4	0.298	0.005
(u) <i>Salix sitchensis</i>			3	4	0.284	0.035
(u) <i>Cinna latifolia</i>			3	4	0.26	0.01
(u) <i>Poa pratensis</i>	1	2	3		0.561	0.005
(u) <i>Achillea millefolium</i>	1	2	3		0.556	0.005
(u) <i>Salix boothii</i>	1	2	3		0.474	0.005
(o) <i>Salix boothii</i>	1	2	3		0.473	0.005
(u) <i>Packera pseudoaurea</i>	1	2	3		0.38	0.015
(o) <i>Rosa woodsii</i>	1	2	3		0.318	0.035
(o) <i>Crataegus douglasii</i>	1	2	3		0.283	0.025
(o) <i>Salix bebbiana</i>	1	2	3		0.277	0.025
(u) <i>Salix bebbiana</i>	1	2	3		0.277	0.01
(u) <i>Salix exigua</i>	1	2	3		0.275	0.01
(o) <i>Betula occidentalis</i>	1	2	3		0.256	0.035
(u) <i>Potentilla gracilis</i>	1	2	3		0.249	0.045
(o) <i>Picea engelmannii</i>		2	3	4	0.655	0.005
(u) <i>Senecio triangularis</i>		2	3	4	0.647	0.005
(u) <i>Rubus parviflorus</i>		2	3	4	0.618	0.005
(u) <i>Streptopus amplexifolius</i>		2	3	4	0.603	0.005
(u) <i>Athyrium filix-femina</i>		2	3	4	0.597	0.005
(u) <i>Ribes lacustre</i>		2	3	4	0.588	0.005
(u) <i>Ribes hudsonianum</i>		2	3	4	0.581	0.005
(o) <i>Acer glabrum</i>		2	3	4	0.484	0.005

Indicator Species	Large Wood Volume Quartile Groups			Indicator Value	P
(o) <i>Abies grandis</i>	2	3	4	0.483	0.005
(o) <i>Abies lasiocarpa</i>	2	3	4	0.46	0.005
(u) <i>Rubus idaeus</i>	2	3	4	0.446	0.005
(o) <i>Pseudotsuga menziesii</i>	2	3	4	0.433	0.005
(o) <i>Alnus viridis</i>	2	3	4	0.38	0.005
(u) <i>Alnus viridis</i>	2	3	4	0.378	0.005
(o) <i>Amelanchier alnifolia</i>	2	3	4	0.378	0.005
(u) <i>Aconitum columbianum</i>	2	3	4	0.376	0.005
(u) <i>Circaea alpina</i>	2	3	4	0.371	0.005
(o) <i>Rubus parviflorus</i>	2	3	4	0.369	0.005
(u) <i>Claytonia cordifolia</i>	2	3	4	0.363	0.005
(u) <i>Arnica cordifolia</i>	2	3	4	0.363	0.005
(u) <i>Amelanchier alnifolia</i>	2	3	4	0.357	0.005
(u) <i>Boykinia major</i>	2	3	4	0.357	0.005
(o) <i>Ribes hudsonianum</i>	2	3	4	0.352	0.005
(u) <i>Spiraea betulifolia</i>	2	3	4	0.35	0.01
(u) <i>Acer glabrum</i>	2	3	4	0.347	0.005
(u) <i>Cornus canadensis</i>	2	3	4	0.331	0.005
(u) <i>Menziesia ferruginea</i>	2	3	4	0.326	0.005
(u) <i>Elymus glaucus</i>	2	3	4	0.326	0.005
(u) <i>Mertensia paniculata</i>	2	3	4	0.312	0.035
(u) <i>Prenanthes sagittata</i>	2	3	4	0.296	0.005
(u) <i>Philadelphus lewisii</i>	2	3	4	0.292	0.015
(u) <i>Actaea rubra</i>	2	3	4	0.28	0.005
(o) <i>Philadelphus lewisii</i>	2	3	4	0.277	0.01
(u) <i>Rhamnus alnifolia</i>	2	3	4	0.274	0.03