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PRIMARY RESEARCH PAPER

Headwater streams and forest management: Does ecoregional context influence logging effects on benthic communities?

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Abstract Effects of forest management on stream communities have been widely documented, but the role that climate plays in the disturbance outcomes is not understood. In order to determine whether the effect of disturbance from forest management on headwater stream communities varies by climate, we evaluated benthic macroinvertebrate communities in 24 headwater streams that differed in forest management (logged-roaded vs. unlogged-unroaded, hereafter logged and unlogged) within two ecological sub-regions (wet versus dry) within the eastern Cascade Range, Washington, USA. In both ecoregions, total macroinvertebrate density was highest at logged sites ($P = 0.001$) with gathering-collectors and shredders dominating. Total taxonomic richness and diversity did not differ between ecoregions or forest management types. Shredder densities were positively correlated with total deciduous and Sitka alder (*Alnus sinuata*) riparian cover. Further, differences in shredder density between logged and unlogged sites were greater in the wet ecoregion (logging × ecoregion interaction; $P = 0.006$) suggesting that differences in post-logging forest succession between ecoregions were responsible for differences in shredder abundance. Headwater stream benthic community structure was influenced by logging and regional differences in climate. Future development of ecoregional classification models at the subbasin scale, and use of functional metrics in addition to structural metrics, may allow for more accurate assessments of anthropogenic disturbances in mountainous regions where mosaics of localized differences in climate are common.

Keywords Headwater streams · Benthic macroinvertebrates · Ecoregion · Logging · Cascade Range

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Introduction

First and second-order streams are an important component of riverine ecosystems (Gomi et al.,

2002; Haggerty et al., 2002), comprising the majority of catchment areas (Sidle et al., 2000; Meyer & Wallace, 2001) and linear riverine miles (Nadeau & Rains, 2007). These headwater streams transport invertebrates, organic matter, nutrients, and inorganic material to downstream habitats (Vannote et al., 1980; Meyer & Wallace, 2001; Wipfli et al., 2007), potentially affecting consumers in those lower elevation habitats (Wipfli & Gregovich, 2002). However, because of their small size, they can sometimes be absent from topographic maps or labeled inaccurately as intermittent. As a result, protective measures aimed at reducing disturbance effects from timber harvesting are not necessarily applied to these small streams.

Timber harvesting has been shown to alter physical and biological characteristics of streams and rivers (Murphy et al., 1986; Stout et al., 1993; Melody & Richardson, 2007). For example, forest management can influence the quality and quantity of riparian vegetation and solar radiation reaching the stream. Removal of riparian forest has been shown to initially reduce leaf litter inputs to streams and cause declines in shredder density (Stout et al., 1993; Stone & Wallace, 1998; Melody & Richardson, 2007). Increased sunlight following timber harvest can increase algal production and the abundance of macroinvertebrate scrapers (Murphy et al., 1986; Stone & Wallace, 1998; Kiffney et al., 2003). Subsequent riparian regrowth can differ from its pre-harvest composition and reduce scraper abundance through shading with a compositional shift back to shredders (Stone & Wallace, 1998).

Detecting disturbance to aquatic systems can be difficult when examining regions containing diverse topography and subregional climates (Li et al., 2001). As climate can constrain patterns of disturbance and forest vegetation types, macroclimate must be considered in regional and subregional comparisons of biological communities (Hessburg et al., 2000a; Hooper et al., 2005). For example, forest succession following fire and logging in the Pacific Northwest is thought to be under strong top-down geoclimatic control (Hessburg et al., 1999b) because annual precipitation, daytime solar radiative flux, and annual temperature can contribute significantly to the trajectory of post-disturbance succession.

Differences among ecoregions in biogeoclimatic factors such as the precipitation and temperature that influence the direction of post-logging forest succession may also affect aquatic community composition and structure (Frissell et al., 1986; Power, 1992) through top-down control of allochthonous inputs and shading. The effectiveness of protective measures (e.g., forested buffer strips) may also vary among ecoregions as these are under the influence of climate as well. Thus, macroinvertebrate responses to the combined effects of climate and logging on riparian vegetation could have significant implications for riparian corridor monitoring and management. Use of ecoregional classifications within montane subregional watersheds may improve the ability to detect biological response to disturbance.

The objectives of this study were to determine how ecoregional difference influences the extent to which headwater stream benthic communities respond to disturbance from timber harvesting in the Wenatchee River subbasin in the eastern Cascade Range, Washington, USA. Specifically, we set out to determine how logging effects, and subsequent riparian forest regeneration, influence headwater stream macroinvertebrate community composition in wet and dry ecoregions. We predicted that (1) post-logging riparian forest conversion from coniferous to deciduous species would lead to higher densities of shredding taxa, particularly in the wetter climate, and (2) scraping taxa would be favored at dry-logged sites, where lower post-logging riparian forest densities might support higher algal densities.

Methods

Study sites and sampling design

This study was conducted in the Wenatchee River subbasin in central Washington, USA (Fig. 1) where forest regeneration and timber harvesting by both commercial and private landholders has occurred over most of the twentieth century (Hessburg et al., 1999a; Rieman et al., 2000; Hessburg et al., 2000b). The river drainages within this region are heavily influenced by Pacific maritime weather patterns that extend across the Cascade Mountains and by continental air masses in interior regions east of the Cascade Range (Kovalchik, 1992). Vegetation cover, including upland forests drained by headwater streams, is heavily influenced by landscape-level characteristics that define ecoregions such as mean

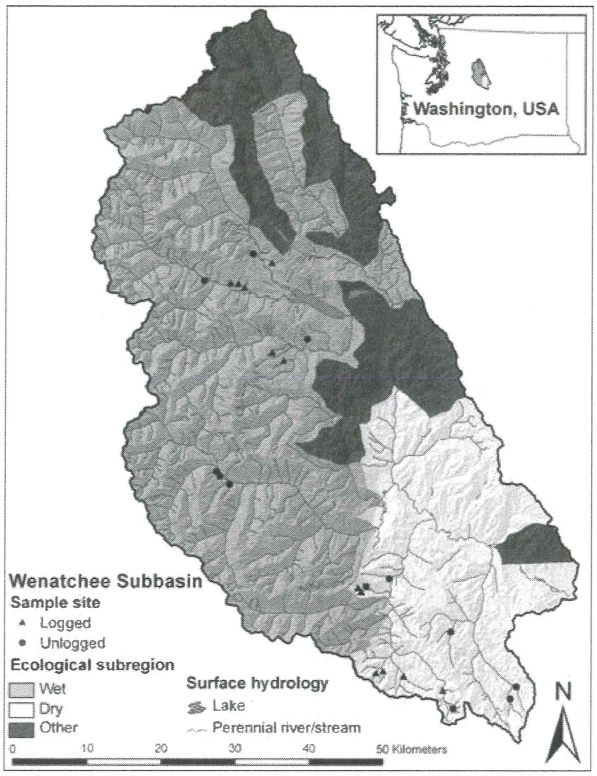

Fig. 1 Study area within the Wenatchee River subbasin of the Cascade Range in Washington state, USA. The basin is shown below with the two ecological subregions studied indicated by *green* and *yellow* and study streams pinpointed with *circular* and *triangular black dots*

precipitation, temperature, solar radiation, and underlying geology (Hessburg et al., 2000a). Eastern Cascade ecoregions are dominated by dry forest vegetation as a result of pronounced rain-shadow effects near the Cascade crest (Kovalchik, 1992).

We sampled benthic invertebrates from 24 perennially flowing fishless headwater streams across four treatment categories (4 treatment categories × 6 replicates). A sampling schedule was established with collections in spring, summer, and fall of 2005 and 2006. A stratified random design was used to ensure that an equal proportion of sites from each of the four treatment categories were sampled on any given day such that temporal variability over the 2 week sampling period was evenly distributed among treatment categories.

Treatment categories were developed from two ecological subregions (hereafter, wet and dry) and two land use categories (logged-roaded and unlogged-unroaded, hereafter, logged and unlogged), and are referred to as: dry-logged, dry-unlogged, wet-logged, and wet-unlogged. Ecological subregions were defined by Hessburg et al. (2000a), grouping subwatersheds according to higher order geology, landform features, potential vegetation types, and climate attributes. The ecological subregions (ESRs) selected for this study were ESR 4—The Eastern Washington Cascades Moist & Cold Forests Subregion, and ESR 11—The Eastern Washington Cascades Dry & Warm Forests Subregion, referred to hereafter as the "wet" and "dry" ecoregions, respectively. The wet ecoregion was defined as ''warm'', "wet", with ''low solar'', and containing "moist and cold forests", however, subwatersheds included drier forests in the lowest elevations (Table 1). The dry ecoregion was defined as ''warm'', "dry" with "moderate solar'', and containing "dry and moist forests".

Evaluation of aerial photos revealed no major wildfire or debris flow disturbance in the recent past of either ecoregion. In the wet ecoregion, historical fires occurred infrequently, on average >150 years between fires, but when they occurred they were mixed and high severity fires, with stand replacement effects dominating (Hessburg et al., 2004, 2007). The dry ecoregion was quite different with more frequent fires occurring every 5–35 years. When fires occurred, they were low and mixed severity fires with surface fire effects dominating (Hessburg et al., 2007). Aerial photos revealed minor patches of recent fire, but relative to drainage size, burn area was insignificant.

For logged sites, time since harvest ranged from 8 to 35 years with a mean of 16 years along one or both banks directly adjacent to study streams. In each ecoregion, four of the six logged sites had been clear-cut across the stream reach with no buffer of uncut forest or other stream side protections present. The remaining two logged sites in each ecoregion were clear-cut on one slope to the streams edge with no buffer present and partially thinned on the other.

Unlogged watersheds showed no evidence of timber harvest activity directly adjacent to study streams for at least 100 years. Time since timber harvest was established in the field using a combination of methods including, dating tree cores, dating logging scars on surrounding trees caused by tree felling and yarding operations, and by the presence of logging roads and cut stumps. Sample locations at study streams ranged in elevation from 561 to 1,341 m. Streams were confirmed fishless through

Table 1 (a) Mean values (+SE) for site characteristics and environmental attributes within each of four ecoregion-logging classifications and (b) ranges of values defining ecological subregion classes of the Wenatchee River subbasin

(a)

Treatment category	Mean elevation (m)	Mean channel width (cm)	Mean depth (cm)	Mean stream velocity (m/s)	Mean stream discharge (l/s)	Mean annual stream temperature (°C)	Canopy cover			
							Percent conifer	Percent deciduous	Percent alder	Percent total cover
Dry-logged	1095 (51)	98.3 (17.9)	7.0 (1.6)	0.15 (0.06)	8.2 (2.0)	5.1 (0.2)	19.4 (10.8)	66.4 (6.1)	26.8 (7.5)	81.5 (6.1)
Dry-unlogged	891 (123)	83.2 (11.3)	5.6 (0.7)	0.33 (0.09)	14.7 (3.5)	5.6 (0.5)	25.2 (8.0)	51.2 (12.8)	11.6 (3.5)	81.7 (4.4)
Wet-logged	1017 (116)	101.0 (20.7)	6.0 (1.5)	0.16 (0.05)	9.1 (2.8)	5.5 (0.5)	6.6 (1.8)	81.7 (6.6)	46.1 (9.4)	90.2 (6.1)
Wet-unlogged	798 (57)	111.3 (5.0)	7.7 (0.8)	0.16 (0.03)	13.8 (3.2)	5.9 (0.3)	71.7 (4.8)	22.7 (4.6)	3.9 (2.2)	95.4 (1.5)

(b)

Ecological subregion	Mean annual air temperature (°C)	Annual average daylight incident shortwave solar radiative flux (W/m^2)	Total annual precipitation (mm/year)	Forest type
ESR 4 (wet)	5–9	200–250	1,100–3,000	Moist and cold forests
ESR 11 (dry)	5–9	250–300	150–400	Dry and moist forest

minnow trapping, electrofishing, and visual observations. Stream widths ranged from 0.6 to 1.9 m and stream depths from 3.0 to 13.1 cm (Table 1).

Macroinvertebrate sampling and physico-chemical measurements

At each sample site, a 100-m sample reach was delineated and riffle habitat identified. Six of these riffles were selected for macroinvertebrate sampling through a stratified random selection approach. Benthic macroinvertebrates were sampled from each of these six riffles with a modified 250 μm D-net sampler from a 350 cm^2 area (0.21 m^2/site) established by setting a wire boundary on the stream bottom. Substrate was dislodged directly upstream of the D-net and cleaned by hand. All six samples were combined into a single composite sample, and a standardized 20 min was spent at each sampling location removing detritus and inorganic material to reduce sample volume before preservation in 100% ethanol.

In the laboratory, a minimum of 400 macroinvertebrates were sub-sampled from each composite sample using a Folsom plankton splitter (Wildco, Buffalo, NY, U.S.A.). Samples too large for the splitter were poured into a gridded sorting tray and subsamples were removed and processed until the 400 minimum was met. Sub-samples ranged from 1/32 to 1/2 of the sample with only one sample being processed in its entirety. The median sub-sample size was 1/8 of the sample. Insect taxa were identified to genus with the exception of midges identified only to family Chironomidae, and non-insect taxa were identified to order or class (Merritt & Cummins, 1996; Wiggins, 1996; Stewart & Stark, 2002).

At 10 equidistant transects within each 100-m study reach stream depth was measured and substrate particle size class (fine: <0.25 mm; sand: 0.25–2 mm; gravel: 2–16 mm; pebble: 16–64 mm; cobble: 6.4–25 cm; or boulder >25 cm) was determined by picking up and measuring the first particle encountered beneath a finger tip placed at the point of depth measure. This was performed at five equidistant points across each measured wetted width (50 points total). The presence/absence and identification of vegetation (Perish et al., 1996) directly above stream center were established at 5 m increments using a moose-horn densiometer (canopy cover estimation tool) (Garrison, 1949) once after peak leaf out in 2005. During fall base-flow conditions, the mean stream discharge was calculated from five recorded water velocities and depths measured at equidistant points across the measured wetted width of each sampled stream. Where plunge pools or culverts existed, total stream discharge was estimated directly by averaging the time it took to fill a volumetric container over three trials. Stream temperature was measured every 2 h year-round with TidBit® temperature loggers (Onset, Bourne, MA, U.S.A.).

Chlorophyll *a* concentration served as a proxy for benthic algal density. Periphyton was sampled from natural rock substrates at each of the six macroinvertebrate sampling locations; a single cobble size stone was selected from riffle habitat at random, and periphyton was removed with a toothbrush from a 26.7 cm^2 area of its upper surface. These six individual samples were combined into a composite sample and transported in darkness to the laboratory where each periphyton sample was immediately frozen. Chlorophyll *a* was extracted 4 weeks after collection using hot ethanol extraction (Sartory & Grobbelaar, 1984), and concentration was measured using spectrophotometric methods (Sartory & Grobbelaar, 1984).

Statistical analyses

Repeated measures analyses of covariance (ANCOVA) and Bonferroni corrected pair-wise comparisons were performed using SAS, version 9.1.2 (SAS Institute Inc., Cary, NC, U.S.A.) to test for differences in macroinvertebrate community assemblages among our four stream treatments. Year and sample month (our repeated measure) were included to account for temporal variation, however, as the focus of this study was to examine relationships between ecoregion and logging, their interactions with time were not included in the model. To account for developmental differences due to stream temperature, mean annual stream temperature was included as a covariate. Community response variables tested were benthic density, % Ephemeroptera, Plecoptera, Trichoptera (EPT), total taxa richness, diversity, and functional feeding group density and richness. Bonferroni corrected pair-wise comparisons were made at $\alpha = 0.0125$. Spearman correlations were also performed between functional feeding group densities and their documented food resources (Merritt & Cummins, 1996) to assess how forest management impacts may be transmitted through the food web.

Percent riparian canopy coverage was calculated for three categories (alder-deciduous, non-alder-deciduous, or coniferous) as the number of points present above the stream divided by the total number of points measured. Two factor analysis of covariance (ANCOVA) and Bonferroni corrected pair-wise comparisons were performed to test for differences in percent vegetation coverage between factors ecoregion and logging; aspect (northern or southern) was included as a covariate to account for the influence of warmer, sunnier southern aspects.

Since increased sand substrate has been shown to be detrimental to aquatic communities (Shaw & Richardson, 2001), we used analysis of variance (ANOVA) to examine percent sand among sites. Response variables were either log or arcsine square root transformed to meet model normality assumptions.

Total benthic density and functional feeding group density were extrapolated from sub-sample counts from a known area of stream bottom. Functional feeding groups could not be assigned to midges as they were only identified to family Chironomidae and thus were excluded from functional feeding group density analysis. Diversity was calculated using the Shannon–Weiner index (Hauer & Resh, 1996).

Percentage abundance EPT taxa and percent abundance of functional feeding groups was calculated as the numerical abundance of these taxa divided by the total abundance of all taxa. Regression analysis of taxonomic richness revealed that richness was correlated with the total number of macroinvertebrates identified ($P < 0.05$). Richness numbers were, therefore, rarefied (sample size of 400) (Krebs & Brzustowski, 2007) to account for differences. After rarefaction, richness values were no longer correlated with sample size.

Results

Benthic macroinvertebrate community structure

Sampling in June, August, and October 2005 was successful; however, high snowpack and spring flooding in 2006 prevented sampling from occurring until July and September of that year. Mean benthic density at individual sites ranged from 6,676 to 28,371 individuals m^{-2} and was significantly higher in logged watersheds (mean logged = 15,586 m^{-2}, unlogged = 10,452 m^{-2}; $F_{1,21.2} = 13.65$, $P = 0.001$; Table 2; Fig. 2a). No difference in density was detected between ecoregions, years, and there was no significant logging × ecoregion interaction. Mean % EPT taxa did not differ among treatment categories, but the logging × ecoregion interaction was significant ($F_{1.18.2} = 4.69$, $P = 0.044$; Fig. 2b) with lower mean % EPT taxa at dry-logged sites (mean = 36.4%) and higher % EPT taxa at wet-logged sites (mean = 41.9%). Mean % EPT was higher in 2005 than in 2006 ($F_{1,23} = 4.94$, $P = 0.036$; Table 2). No differences in taxa richness or Shannon–Wiener diversity were detected among treatment categories or between years (Table 2; Fig. 2c, d).

Riparian vegetation structure

Total riparian canopy cover ranged from 54 to 100% and was more dense in the wet ecoregion ($F_{1,19} = 4.81$, $P = 0.041$; Fig. 3a). Logging appears to have affected canopy cover in the two ecoregions differently by reducing coniferous and increasing both total deciduous and alder cover in the wet ecoregion ($P < 0.001$ for all), and having no affect in the dry ecoregion (logging × ecoregion interaction $F_{1,19} = 13.96$, $P = 0.001$; $F_{1,19} = 5.33$, $P = 0.032$; and $F_{1,19} = 4.44$, $P = 0.049$, respectively; Fig. 3b–d). When examining unlogged sites, a notable difference in coniferous composition between ecoregions was in that of Mountain Hemlock, *Tsuga mertensiana* (Bong.), absent in the dry ecoregion and composing 26% of the wet. Engelman spruce, *Picea engelmannii* (Parry) also differed greatly, composing 29% of dry conifers and only 2% of wet. Percent sand substrate did not differ among any treatment categories suggesting that either no increase in sand deposition to streams occurred following logging or no legacy effects remain.

Functional feeding group structure

The general pattern of relative abundance for functional feeding groups was gatherers > shredders > predators > scrapers > filterers. This pattern was the same for all treatment categories except wet-logged sites where predators exceeded shredders. Shredder abundance, dominated by the stonefly genera *Zapada* spp. and *Yoraperla* spp., tracked patterns of deciduous vegetation associated with logging and ecoregion categories. They were more abundant at logged sites,

Table 2 Mean values (+SE) for (a) composite metrics, (b) functional group density (# m^{-2}), and (c) functional group genus richness of selected community measures between sample years and among treatment categories

	Treatment categories				Sample year	
	DL	DU	WL	WU	2005	2006
(a)						
Invertebrate density (# m^{-2})	17855 (2051)^{a}	11426 (1379)^{b}	13318 (1437)^{a}	9512 (997)^{b}	13534 (1216)	12269 (906)
Rarefied taxa richness	31.0 (0.7)	32.5 (0.7)	29.8 (0.7)	31.9 (0.6)	32.0 (0.5)	30.4 (0.5)
% EPT	36.4 (2.6)	44.5 (2.0)	41.9 (2.0)	39.8 (1.8)	42.3 (1.5)^{a}	38.5 (1.5)^{b}
Shannon–Wiener diversity	2.51 (0.07)	2.67 (0.04)	2.56 (0.03)	2.62 (0.05)	2.62 (0.03)	2.55 (0.04)
(b)						
Filtering-collectors	69 (19)^{bc}	105 (23)^{ac}	129 (21)^{a}	153 (30)^{a}	116 (18)	111 (14)
Gathering-collectors	5321 (671)^{a}	3082 (351)^{b}	3552 (397)^{ab}	2593 (276)^{b}	3817 (369)	3371 (267)
Predators	703 (77)	528 (64)	616 (61)	566 (77)	644 (49)	547 (48)
Scrapers	332 (56)	213 (27)	224 (39)	190 (34)	252 (30)	222 (27)
Shredders	1168 (176)^{a}	927 (170)^{a}	1146 (160)^{a}	535 (79)^{b}	924 (113)	963 (103)
(c)						
Filtering-collectors	1.8 (0.2)^{b}	2.7 (0.2)^{a}	2.5 (0.2)^{b}	2.7 (0.2)^{a}	2.6 (0.1)	2.2 (0.2)
Gathering-collectors	12.0 (0.3)^{a}	11.7 (0.3)^{a}	11.3 (0.3)^{a}	10.7 (0.3)^{b}	11.6 (0.2)	11.1 (0.2)
Predators	8.4 (0.3)	8.1 (0.4)	8.3 (0.4)	8.1 (0.3)	8.7 (0.2)^{a}	7.6 (0.2)^{b}
Scrapers	4.6 (0.3)^{ab}	5.1 (0.2)^{a}	4.0 (0.2)^{b}	4.0 (0.3)^{b}	4.4 (0.2)	4.4 (0.2)
Shredders	6.9 (0.4)^{b}	7.5 (0.3)^{a}	6.4 (0.4)^{b}	7.3 (0.3)^{a}	7.5 (0.2)^{a}	6.3 (0.2)^{b}

Differing superscript letters indicate significantly different mean values. Absence of letters indicate no significant differences

DL dry-logged, *DU* dry-unlogged, *WL* wet-logged, *WU* wet-unlogged sites

particularly in the wet ecoregion (logging × ecoregion interaction; $F_{1,13.5} = 10.86$, $P = 0.006$; Table 2; Fig. 4a). Shredder abundance was positively correlated with the density of deciduous vegetation in August 2005 (Spearman's correlation coefficient = 0.42, $P = 0.043$), and was correlated with Sitka alder density in both August 2005 and September 2006 (Spearman's correlation coefficient = 0.53, $P = 0.007$ for both). Unlogged sites typically had one more shredder genus than logged sites ($F_{1,105} = 5.30$, $P = 0.013$); however, there were no differences between logging classifications within ecoregions (Table 2; Fig. 5a). Scraper abundance, dominated by members of the caddisfly family Glossosomatidae and mayfly family Heptageniidae did not differ among treatment categories (Table 2; Fig. 4b), however, they were the only functional group correlated with percent sand substrate; both total scraper density and the proportion of the macroinvertebrate community represented by this group were negatively correlated with percent sand (Spearman's correlation coefficient = −0.31, $P = 0.004$ and −0.29, $P = 0.003$, respectively). Scrapers and gathering-collectors both had higher genus richness in the dry ecoregion ($F_{1,105} = 10.72$, $P < 0.05$ and $F_{1,105} = 6.83$, $P < 0.05$, respectively; Table 2; Fig. 5b, c). Gathering-collector abundance did not differ among treatment categories (Fig. 4c) and was dominated primarily by three non-insect taxa Oligochaeta, Ostracoda, and Turbellaria. This was true of all treatment categories except the dry-unlogged where the mayfly genus *Baetis* was the second most abundant. In the remaining three treatment categories the genus *Paraleptophlebia* was the most abundant insect taxa. Filtering-collectors, dominated by the caddisfly genus *Ceratopsyche* spp. (Nielsen), showed higher densities in the wet ecoregion ($F_{1,17.3} = 12.36$, $P = 0.003$; Table 2; Fig. 4d). Filtering-collector genus richness was higher at unlogged sites ($F_{1,105} = 6.14$, $P = 0.024$; Table 2; Fig. 5d). Neither predator density, dominated by the caddisfly genus *Rhyacophila* spp. (Pictet), or genus richness differed among treatment categories (Table 2; Figs. 4e, 5e respectivley). Predators and shredders both had higher richness in 2005 compared with 2006 (Table 2), but no other functional group showed such temporal effects. The concentration of

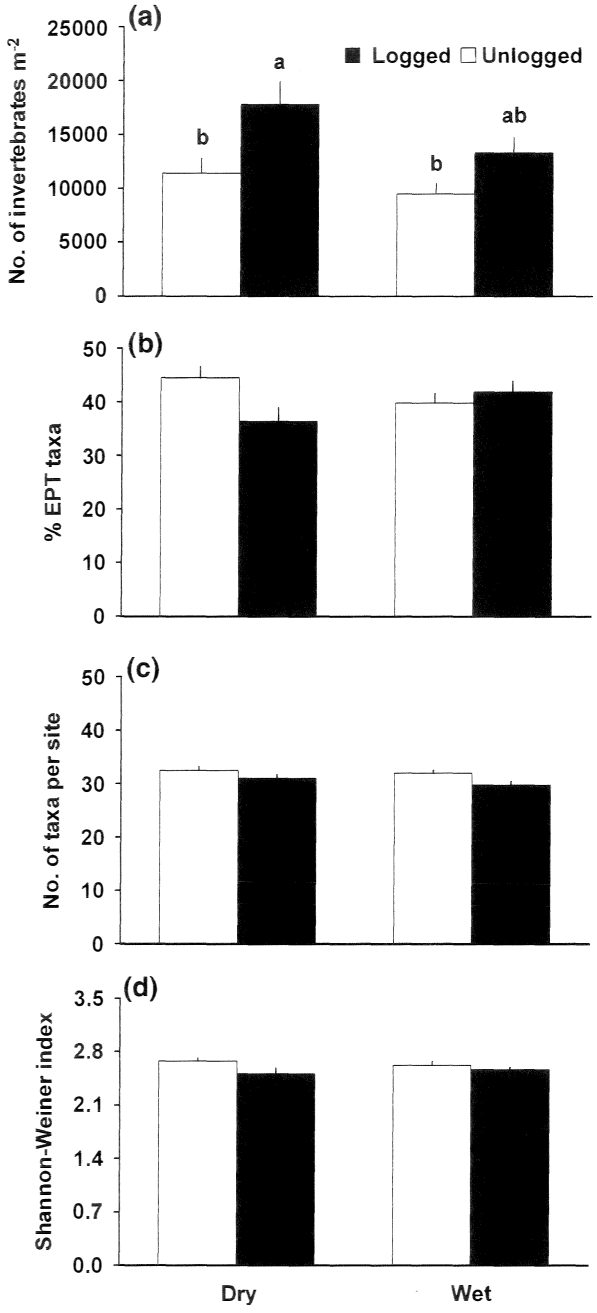

Fig. 2 Mean values (+SE) for **a** benthic density, **b** % EPT taxa, **c** taxa richness, and **d** Shannon–Weiner diversity across five sampling occasions of 24 streams divided among logged and unlogged sites, and dry and wet ecoregions. Means with the *same letter* were not statistically different based on Bonferroni's corrected *P*-values ($\alpha = 0.0125$); *absence of letters* indicate no significant differences among treatment categories

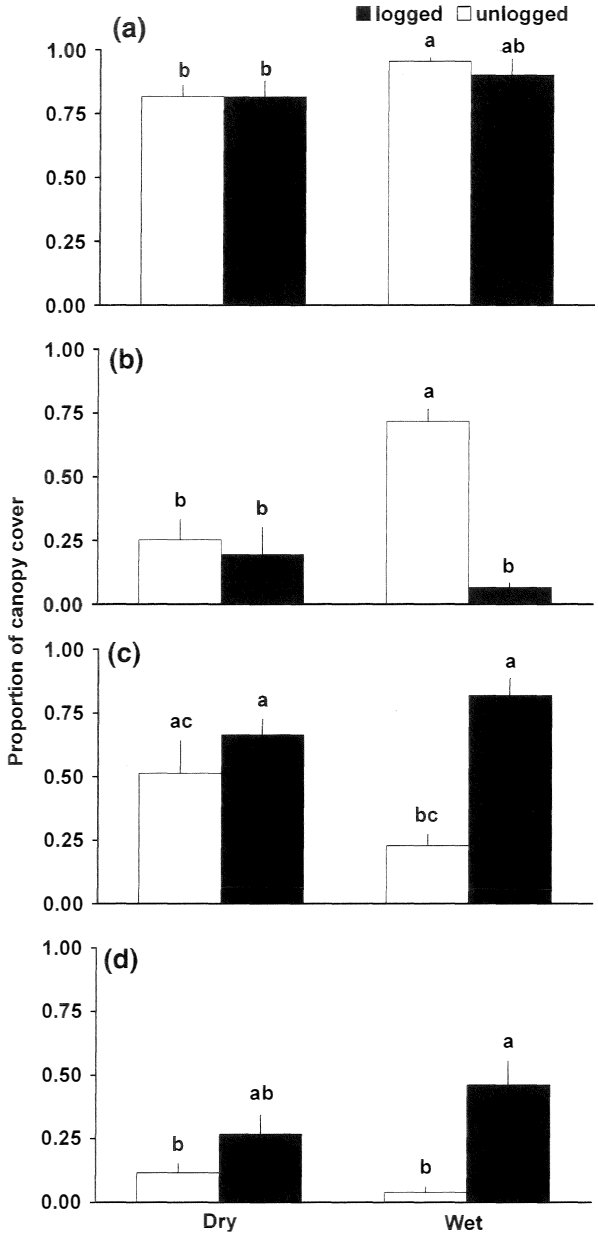

Fig. 3 Mean proportion (+SE) of riparian canopy cover for **a** total cover, **b** coniferous cover, **c** deciduous cover, and **d** alder cover for 24 sites divided among logged and unlogged sites, and dry and wet ecoregions. Means with the *same letter* were not statistically different based on Bonferroni's corrected *P*-values ($\alpha = 0.0125$); *absence of letters* indicate no significant differences among treatment categories

chlorophyll *a*, used as a proxy for periphytic algal density, did not differ among treatment categories and was negligibly correlated with scraper density.

Discussion

We proposed that both biogeoclimatic context and logging history, and their interaction, influence headwater macroinvertebrate community structure

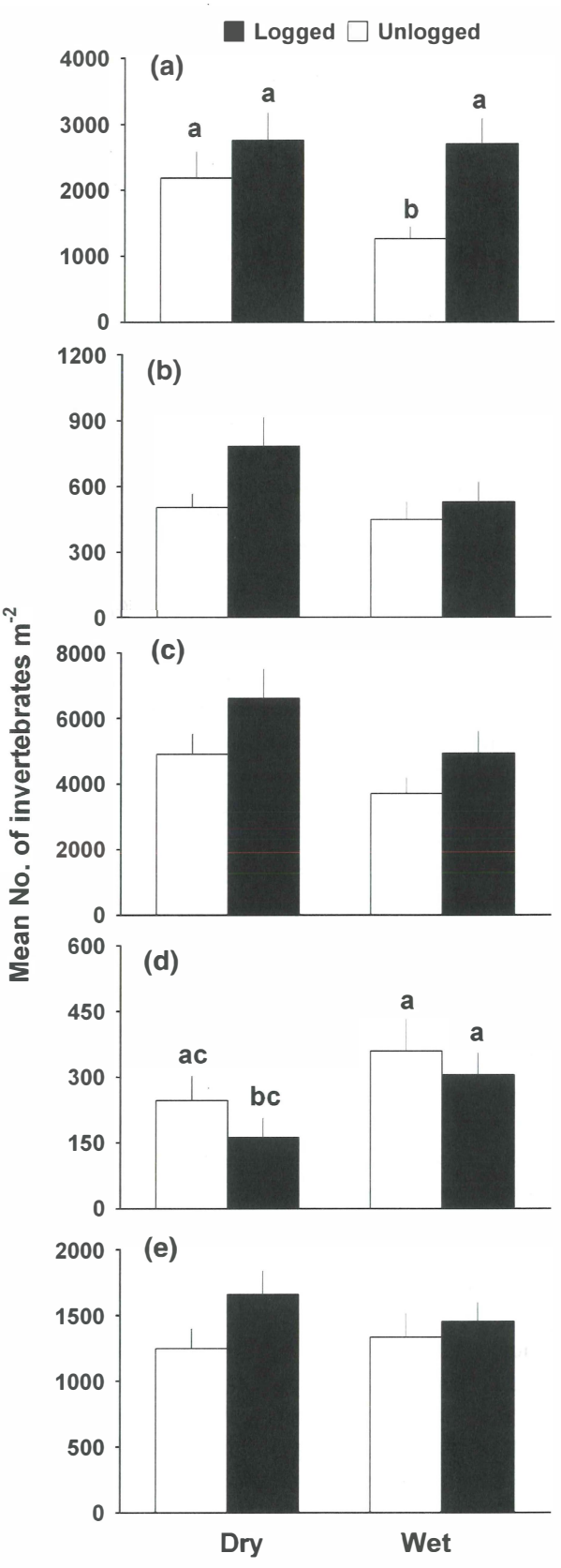

Fig. 4 Mean (+SE) density of individuals within functional feeding groups for **a** shredders, **b** scrapers, **c** gathering-collectors, **d** filtering-collectors, and **e** predators across five sampling occasions from 24 streams divided among logged and unlogged sites, and dry and wet ecoregions. Means with the *same letter* were not statistically different based on Bonferroni's corrected *P*-values ($\alpha = 0.0125$); *absence of letters* indicate no significant differences among treatment categories. Note differing scale of *Y* axes

in the eastern Cascade Range. Results supported our first prediction that post-logging riparian forest conversion from coniferous to deciduous species would lead to higher densities of shredding taxa. However, scraping taxa were not favored at dry-logged sites as expected. Riparian density was not lower at these dry-logged sites as we anticipated (Kovalchik, 1992; Wissmar, 2004) and algal densities upon which scrapers feed were not significantly different from other treatment categories. Our results also suggest that because wet-unlogged sites are dominated by conifers, once logging occurs the shift to deciduous riparian forest is more pronounced than in the dry ecoregion where dry-unlogged sites contain a higher percentage of deciduous riparian. Further, significant differences in shredder density between logged and unlogged sites occurred only in the wet ecoregion (e.g., Fig. 4) where this shift from conifer to deciduous-dominated was dramatic. Similar findings by Nislow and Lowe (2006) suggest that shredder densities are positively correlated with the extent of canopy coverage following logging. Here, the removal of conifers by logging allows for species, such as alder, to establish and dominate. Hernandez et al. (2005) found similarly higher benthic macroinvertebrate densities in streams with riparian alder in Alaska, and others showed higher densities of drifting macroinvertebrates in alder-colonized headwater systems which they postulated was a function of higher benthic densities and productivity (Piccolo & Wipfli, 2002; Wipfli & Musslewhite, 2004).

Shredder densities were similar between logged and unlogged sites in the dry ecoregion as both were dominated by deciduous vegetation in our study. Further, dry-unlogged sites had 55% more deciduous cover than wet-unlogged sites demonstrating that riparian zones in the dry ecoregion exist in a high deciduous, low coniferous state whether or not logging has occurred. This dominance of deciduous vegetation is likely due to higher temperatures and

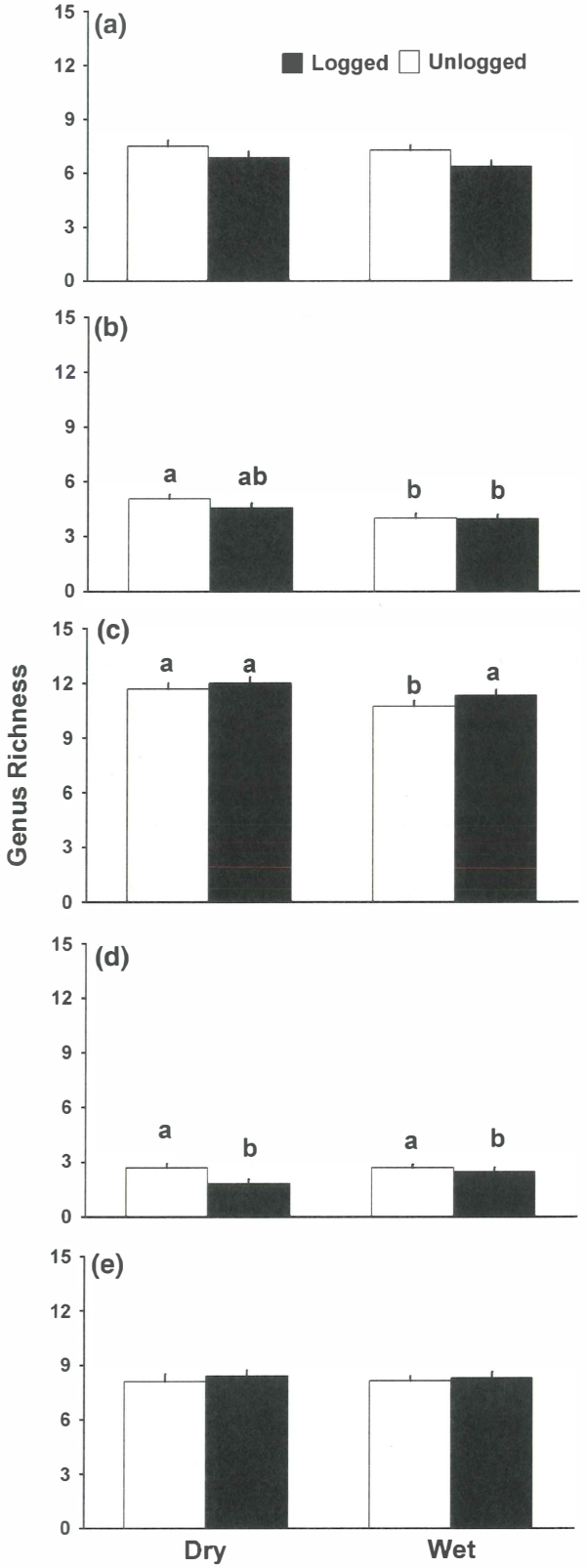

Fig. 5 Mean (+SE) genus richness for the functional groups **a** shredders, **b** scrapers, **c** gathering-collectors, **d** filtering-collectors, and **e** predators across five sampling occasions from 24 streams divided among logged and unlogged sites, and dry and wet ecoregions. Means with the *same letter* were not statistically different based on Bonferroni's corrected *P*-values ($\alpha = 0.0125$); *absence of letters* indicate no significant differences among treatment categories

lower precipitation preventing the growth of conifers and might explain why differences in shredder abundance were not observed in the dry ecoregion (Power, 1992).

Results also supported our second prediction that dry-logged sites would produce lower density riparian canopies compared to wet-logged sites. However, in both ecoregions post-logging riparian forest density was not significantly different from that of unlogged sites (e.g., Fig. 3a). As a result, the only reason dry-logged sites appear to have lower riparian densities is because they are naturally lower in the dry ecoregion whether or not logging has occurred. In addition, these lower riparian densities did not result in higher benthic algae densities as hypothesized, nor did we see higher densities of scraping taxa that rely on this food resource.

Higher macroinvertebrate density in logged versus unlogged sites suggests that logging can result in conditions that elevate the densities of some macroinvertebrates (Nislow & Lowe, 2006). Overall metrics of taxonomic diversity such as %EPT and taxonomic richness were more strongly influenced by sample year than by ecoregion or logging as both were higher in 2005 in our study. According to local stream gage readings, early season warming in May 2006 produced stream discharges that were at least twice that of any previous May since 2002 (Washington State Department of Ecology, 2009) producing flooding and channel scour in our study streams which may be responsible for observed annual differences. However, the similarity in total numerical density between years suggests that persistent taxa became more abundant. In addition, the lack of inter-annual difference in density of individuals within functional groups suggests that flooding did not disproportionately influence food availability for any specific feeding group.

Disturbance-induced changes in functional feeding group composition can persist long after densities have returned to pre-disturbance levels (Wallace et al., 1986). Our results support this with both ecoregions showing a similar pattern where unlogged sites were dominated by the shredding stonefly family Nemouridae, of which *Zapada* was the only genus, while logged sites were dominated by the shredding stonefly family Capniidae. Our study reflected post-logging time periods of 7–27 years, thus it appears these functional feeding group shifts can linger for a relatively long time.

It appears that the effects of climate and logging also affected gathering-collector species as the density of individuals within this group differed between logged and unlogged sites in the dry ecoregion only. The density of gathering-collectors and filtering-collectors was not correlated with shredder abundance suggesting that while shredders may contribute to particulate organic matter consumed by collectors, these animals were not particle limited at low shredder densities (Richardson, 1991). Taxonomic richness of functional groups was also influenced by climate and logging. For example, logged sites of the wet ecoregion exhibited higher gathering-collector richness while no such difference was detected in the dry ecoregion. In contrast, filtering-collectors had lower richness at logged sites in both ecoregions (e.g., Fig. 5c, d). However, despite differences in taxonomic richness between logged and unlogged sites, the abundance of both gathering and filtering-collectors were similar. Shredders showed a similar response to logging, with lower richness at logged sites but with higher numeric abundance (e.g., Figs. 4a, 5a). A positive correlation between shredder abundance and deciduous vegetation suggests that the increased carrying capacity of the system, facilitated by increased food availability (e.g., Fig. 3), allowed for this higher density. Scrapers showed a similar pattern with fewer taxa in the wet ecoregion and no difference in the total abundance across ecoregion and logging categories.

Although primarily correlative, our results suggest that effects of logging disturbance on the benthic food web were influenced by the specific ecoregion where logging occurred. Previous study examining patterns in aquatic macroinvertebrate community structure among ecoregions of the Pacific Northwest have compared the Willamette Valley, Columbia Basin, and high desert regions (Whittier et al., 1988; Li et al., 2001). Clear regional differences were seen among non-mountainous environments, while intra-regional differences among montane streams were more subtle (Whittier et al., 1988). Recent advances in ecological regionalization allow examination of ecoregional patterns within individual subbasins of the Cascade Range (Hessburg et al., 2000a).

Conclusion

Our results support the notion that differences in headwater stream macroinvertebrate communities within the eastern Washington Cascade Range are explained, in part, by these subbasin scale ecoregional classifications illustrating that differences in biology, geology, and climatology can exert top-down spatial control on stream biota. Expanding the use of subbasin scale ecoregional classifications to other areas could be useful for predicting how aquatic communities may respond to a wider range and types of disturbance. In this case, ecoregional classifications motivated us to examine potential shifts in macroinvertebrate community structure in terms of structural community metrics. Our results suggest that post-logging fluctuations in macroinvertebrate richness and density occur in different directions between ecoregions, with similar logging events favoring some functional groups in one ecoregion but not the other. Use of regional classifications and both structural and functional metrics appears to be a valuable tool in monitoring macroinvertebrate response to anthropogenic disturbances at multiple spatial scales.

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References

Frissell, C. A., W. J. Liss, C. E. Warren & M. D. Hurley, 1986. A hierarchical framework for stream habitat classification—viewing streams in a watershed context. Environmental Management 10: 199–214.

Garrison, G. A., 1949. Uses and modifications for the 'moosehorn' crown closure estimator. Journal of Forestry 47: 733–735.

Gomi, T., R. C. Sidle & J. S. Richardson, 2002. Understanding processes and downstream linkages of headwater systems. Bioscience 52: 905–916.

Haggerty, S. M., D. P. Batzer & C. R. Jackson, 2002. Macroinvertebrate assemblages in perennial headwater streams of the coastal mountain range of Washington, USA. Hydrobiologia 479: 143–154.

Hauer, F. R. & V. H. Resh, 1996. Benthic macroinvertebrates. In Hauer, F. R. & G. A. Lamberti (eds), Meathods in Stream Ecology. Academic Press, San Diego, CA.

Hernandez, O., R. W. Merritt & M. S. Wipfli, 2005. Benthic invertebrate community structure is influenced by forest succession after clearcut logging in southeastern Alaska. Hydrobiologia 533: 45–59.

Hessburg, P. F., B. G. Smith & R. B. Salter, 1999a. Detecting change in forest spatial patterns from reference conditions. Ecological Applications 9: 1232–1252.

Hessburg, P. F., B. G. Smith & R. B. Salter, 1999b. Using estimates of natural variation to detect ecologically important change in forest spatial patterns: a case study, cascade range, eastern Washington. USDA Forest Service Pacific Northwest Research Station Research Paper.

Hessburg, P. F., R. B. Salter, M. B. Richmond & B. G. Smith, 2000a. Ecological subregions of the interior Columbia basin, USA. Applied Vegetation Science 3: 163–180.

Hessburg, P. F., B. G. Smith, R. B. Salter, R. D. Ottmar & E. Alvarado, 2000b. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. Forest Ecology and Management 136: 53–83.

Hessburg, P. F., K. M. Reynolds, R. B. Salter & M. B. Richmond, 2004. Using a decision support system to estimate departures of present forest landscape patterns from historical conditions: an example from the Inland Northwest Region of the United States. In Perera, A. H., L. J. Buse & M. G. Weber (eds), Emulating Natural Forest Landscape Disturbances: Concepts and Applications. Columbia University Press, New York: 158–175.

Hessburg, P. F., K. M. James & R. B. Salter, 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecology 22(1): 5–24.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer & D. A. Wardle, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75: 3–35.

Kiffney, P. M., J. S. Richardson & J. P. Bull, 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. Journal of Applied Ecology 40: 1060–1076.

Kovalchik, B. L., 1992. Riparian zone associations on national forests of eastern Washington. U.S. Department of Agriculture, Forest Service, Colville National Forest, Colville, WA.

Krebs, C. J. & J. Brzustowski, 2007. Rarefaction calculator program. http://www2.biology.ualberta.ca/jbrzusto/rarefact.php#Calculator. Accessed January 2007.

Li, J., A. Herlihy, W. Gerth, P. Kaufmann, S. Gregory, S. Urquhart & D. P. Larsen, 2001. Variability in stream macroinvertebrates at multiple spatial scales. Freshwater Biology 46: 87–97.

Melody, K. J. & J. S. Richardson, 2007. Riparian forest harvesting and its influence on benthic communities of small streams of sub-boreal British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 37: 907–918.

Merritt, R. W., K. W. Cummins (eds), 1996. An introduction to the aquatic insects of North America, 3rd ed. Kendall/Hunt, Dubuque, Iowa.

Meyer, J. L. & J. B. Wallace, 2001. Lost linkages and lotic ecology: rediscovering small streams. In Press, M., N. Huntly & S. Levin (eds), Ecology: Achievement and Challenge. Blackwell Science, Oxford, UK: 295–317.

Murphy, M. L., J. Heifetz, S. W. Johnson, K. V. Koski & J. F. Thedinga, 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 43: 1521–1533.

Nadeau, T. L. & M. C. Rains, 2007. Hydrological connectivity between headwater streams and downstream waters: how science can inform policy. Journal of the American Water Resources Association 43: 118–133.

Nislow, K. H. & W. H. Lowe, 2006. Influences of logging history and riparian forest characteristics on macroinvertebrates and brook trout (*Salvelinus fontinalis*) in headwater streams (New Hampshire, USA). Freshwater Biology 51: 388–397.

Perish, R., D. Lloyd & R. Coupe, 1996. Plants of Southern Interior British Columbia and the Inland Northwest. Lone Pine Publishing, Auburn, WA.

Piccolo, J. J. & M. S. Wipfli, 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? Canadian Journal of Fisheries and Aquatic Sciences 59: 503–513.

Power, M. E., 1992. Top-down and bottom-up forces in food webs—do plants have primacy. Ecology 73: 733–746.

Richardson, J. S., 1991. Seasonal food limitation of detritivores in a montane stream—an experimental test. Ecology 72: 873–887.

Rieman, B. E., D. C. Lee, R. F. Thurow, P. F. Hessburg & J. R. Sedell, 2000. Toward an integrated classification of ecosystems: defining opportunities for managing fish and forest health. Environmental Management 25: 425–444.

Sartory, D. P. & J. U. Grobbelaar, 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114: 177–187.

Shaw, E. A. & J. S. Richardson, 2001. Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*)

growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 58: 2213–2221.

Sidle, R. C., Y. Tsuboyama, S. Noguchi, I. Hosoda, M. Fujieda & T. Shimizu, 2000. Stormflow generation in steep forested headwaters: a linked hydrogeomorphic paradigm. Hydrological Processes 14: 369–385.

Stewart, K. W. & W. P. Stark, 2002. Nymphs of North America Stonefly Genera (Plecoptera), 2nd ed. The Caddis Press, Columbus, OH.

Stone, M. K. & J. B. Wallace, 1998. Long-term recovery of a mountain stream from clearcut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biology 39: 151–169.

Stout, B. M., E. F. Benfield & J. R. Webster, 1993. Effects of a forest disturbance on shredder production in southern Appalachian headwater streams. Freshwater Biology 29: 59–69.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Wallace, J. B., D. S. Vogel & T. F. Cuffney, 1986. Recovery of a headwater stream from insecticide-induced community disturbance. Journal of the North American Benthological Society 5: 115–126.

Washington State Department of Ecology, 2009. Stream flow monitoring station Nason Cr. https://fortress.wa.gov/ecy/wrx/wrx/flows/station.asp?sta=45J070. Accessed June 20, 2009.

Whittier, T. R., R. M. Hughes & D. P. Larsen, 1988. Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. Canadian Journal of Fisheries and Aquatic Sciences 45: 1264–1278.

Wiggins, G. B., 1996. Larvae of the North American Caddisfly Genera (Trichoptera), 2nd ed. University of Toronto Press Inc, Toronto, Canada.

Wipfli, M. S. & D. P. Gregovich, 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47: 957–969.

Wipfli, M. S. & J. Musslewhite, 2004. Density of red alder (*Alnus rubra*) in headwater influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. Hydrobiologia 520: 153–163.

Wipfli, M. S., J. S. Richardson & R. J. Naiman, 2007. Ecological linkages between headwaters and downstream ecosystems: transport of organic matter, invertebrates, and wood down headwater channels. Journal of the American Water Resources Association 43: 72–85.

Wissmar, R. C., 2004. Riparian corridors of eastern Oregon and Washington: functions and sustainability along lowland-arid to mountain gradients. Aquatic Sciences 66: 373–387.