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Ecoregion and land-use influence invertebrate and detritus transport from headwater streams

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SUMMARY

1. Habitats are often connected by fluxes of energy and nutrients across their boundaries. For example, headwater streams are linked to surrounding riparian vegetation through invertebrate and leaf litter inputs, and there is evidence that consumers in downstream habitats are subsidised by resources flowing from headwater systems. However, the strength of these linkages and the manner in which potential headwater subsidies vary along climatic and disturbance gradients are unknown.

2. We quantified the downstream transport of invertebrates, organic matter and inorganic sediment from 60 fishless headwater streams in the Wenatchee River Basin located on the eastern slope of the Cascade Range in Washington, U.S.A. Streams were classified into four groups (each $n = 15$) based on their position within two ecological subregions (wet and dry) and the extent of past timber harvest and road development (logged and unlogged).

3. Time and ecoregion were significant for all response variables as transport varied across sampling periods, and dry ecoregion streams displayed significantly higher mean values. Logged sites also generally showed higher mean transport, but only inorganic sediment transport was significantly higher in logged sites. Both ecoregion and land-use interacted significantly with time depending on the response variable. Differences among stream categories were driven by relatively low levels of transport in unlogged drainages of the wet ecoregion. Interestingly, unlogged dry ecoregion streams showed comparable transport rates to logged sites in the wet ecoregion. Dominance by deciduous riparian vegetation in all but unlogged streams in the wet ecoregion is a primary hypothesised mechanism determining transport dynamics in our study streams.

4. Understanding the quantity and variation of headwater subsidies across climate and disturbance gradients is needed to appreciate the significance of ecological linkages between headwaters and associated downstream habitats. This will enable the accurate assessment of resource management impacts on stream ecosystems. Predicting the consequences of natural and anthropogenic disturbances on headwater stream transport rates will require knowledge of how both local and regional factors influence these potential subsidies. Our results suggest that resources transported from headwater streams reflect both the meso-scale land-use surrounding

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these areas and the constraints imposed by the ecoregion in which they are embedded.

Keywords: aquatic invertebrate, ecoregion, headwater stream, logging, subsidy

Introduction

Understanding the factors influencing the movement of organisms and materials across habitat boundaries and how these movements affect ecosystem dynamics have become major research directions in ecology (Hanski, 1999; Loreau & Holt, 2004; Holyoak, Leibold & Holt, 2005). This is exemplified by the concept of spatial subsidies, which holds that ecological systems are separate but open and connected by spatial flows of energy and materials (Polis, Anderson & Holt, 1997; Vanni *et al.*, 2004; Maron *et al.*, 2006; Marczak, Thompson & Richardson, 2007). Cross-habitat fluxes of energy and nutrients have been shown to strongly affect numerous ecosystems across different levels of biotic organization (Anderson & Polis, 2004; Carpenter *et al.*, 2005). Such spatial subsidies are particularly well documented in streams given the numerous tight linkages connecting the terrestrial and aquatic components of riparian ecosystems (Gregory *et al.*, 1991; Baxter, Fausch & Saunders, 2005). Thus, stream ecosystems are extensively utilised as models for quantifying the magnitude of spatial subsidies and the effects they produce (Nakano & Murakami, 2001; Sabo & Power, 2002; Power *et al.*, 2004).

The allochthonous input of terrestrial leaf litter and invertebrates into streams provides substantial energy and nutrients for numerous aquatic taxa (Richardson & Neill, 1991; Wallace *et al.*, 1997; Kiffney, Richardson & Bull, 2003). Determining the factors that influence these subsidies is a major focus of stream ecology research (Meyer, Wallace & Eggert, 1998; Webster *et al.*, 1999; Allan & Castillo, 2009) and has been complemented by research to quantify the degree to which emerging aquatic insects subsidise terrestrial consumers (Nakano & Murakami, 2001; Sabo & Power, 2002; Henschel, 2004). It is also recognised that material which flows from upstream portions of catchments influence downstream dynamics (Gomi, Sidle & Richardson, 2002; Moore & Richardson, 2003; Wipfli, Richardson & Naiman, 2007). This is a natural consequence of how stream drainage networks are arranged, with both allochthonous and autochthonous materials being transported downstream, thereby providing energy and nutrients for downstream organisms and habitats (Webster *et al.*, 1999; Wipfli & Gregovich, 2002; Wipfli *et al.*, 2007).

The magnitude of terrestrially-derived spatial subsidies and downstream transport rates could be greatest in small low-order headwater systems. Headwater streams share numerous characteristics that facilitate their capacity to transport energy and nutrients downstream (Gomi *et al.*, 2002; Wipfli *et al.*, 2007). First, their small size generates high perimeter to area ratios that greatly enhance terrestrial flux into streams (Polis *et al.*, 1997). The sheer number and abundance of headwater systems might compensate for their small size and hence transport of any individual headwater stream as they comprise 70–90% of total stream length, channel length and catchment area of larger drainage networks (Meyer & Wallace, 2001; Gomi *et al.*, 2002; Meyer *et al.*, 2007). These characteristics of headwater domains result in diverse and dynamic downstream transport that reflects variety in local conditions, including legacies of past land-use (Harding *et al.*, 1998). For example, timber harvest in southeastern Alaska was linked with increased invertebrate and organic matter transport from headwater systems by shifting the adjacent riparian vegetation from conifers to early seral nitrogen-fixing red alder, *Alnus rubra* (Piccolo & Wipfli, 2002; Wipfli & Musslewhite, 2004). Such transport has been hypothesised to subsidise downstream fish populations (Wipfli & Gregovich, 2002; Wipfli *et al.*, 2007).

Stream ecologists have long recognised that large-scale processes influence local stream conditions (see Frissell *et al.*, 1986; Wiens, 2002; Allan, 2004). For example, at large spatial scales, the numerous headwater streams of a catchment can be stratified into different climatic and geological categories. However, it is not well understood how these large landscape variables may exercise spatial control or interact with local land-use to generate quantitative patterns in stream subsidies.

The objective of this study was to determine how land-use history (logged versus unlogged), geoclimatic setting within two ecoregions (wet and dry) and their potential interaction affected the downstream transport of detritus, inorganic material and invertebrates from headwater streams. We hypothesised that headwater streams draining logged catchments and those in the warmest ecoregion with the longest growing season and highest solar radiation would transport more materials downstream. Such information is timely, given the increased emphasis on understanding both the basic ecology of headwater streams and how these small and abundant streams should be managed and protected in the context of changing climatic conditions.

Methods

Study sites

Research was conducted on the eastern slope of the Cascade Mountains in Washington State, U.S.A. We stratified our sampling by two ecoregions and land-uses in a balanced design. We selected 60, first- or second-order perennial, fishless, headwater streams in the Wenatchee River sub-basin within the Wenatchee National Forest (Fig. 1). Thirty streams were in ecological subregion four (ESR 4) and 30 in ecological subregion 11 (ESR 11). These two ESR's comprise most of the land area of the Wenatchee National Forest and were delineated by Hessburg *et al.* (2000) based on differences in geology and

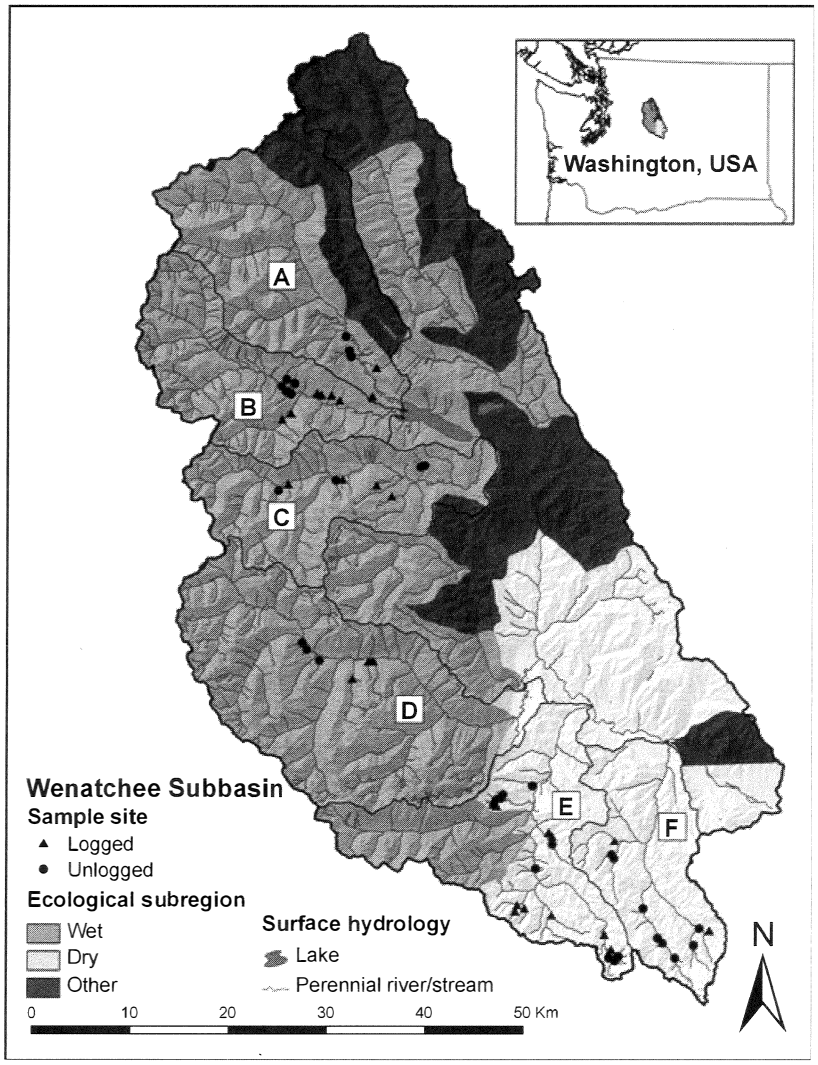

Fig. 1 Study region in Central Washington on the eastern slope of the Cascade Mountains. Sixty headwater streams were selected in the Wenatchee sub-basin of the Wenatchee Nation Forest. Streams were categorised into four groups (n = 15) based on their position within two ecological subregions (wet and dry) and extent of past timber harvest (logged and unlogged). Sampled watersheds included A. White River B. Little Wenatchee River, C. Nason Creek, D. Icicle River, E. Peshastin Creek and F. Mission Creek.

climate (Hessburg *et al.*, 2000, 2004). For simplicity, we refer to ESR 11 and 4 as the dry and wet ecoregions, respectively. Dry ecoregion streams were in the Mission and Peshastin Creek drainages, whereas wet ecoregion streams were in the Icicle Creek, Nason Creek, Little Wenatchee River and White River drainages.

These ecoregions are end members of a steep west–east temperature and precipitation gradient across the eastern slope of the Cascades. Wet ecoregion streams experience higher annual rainfall, lower temperatures and less solar radiation than dry ecoregion sites and reflect the rain shadow effect of the Cascade Mountains. Most of the area of the wet ecoregion has a mean annual precipitation of 1100–3000 mm year^{-1}, a mean temperature ranging from 5 to 9 °C and 200–250 W m^{-2} average annual daytime solar radiative flux. In contrast, the dry ecoregion experiences 100–400 mm year^{-1} mean annual precipitation, 10–14 °C mean annual temperature, and 250–300 W m^{-2} average annual daytime solar radiative flux (Hessburg *et al.*, 2000). These ecoregions also differ in geology, historical fire frequency/severity (Hessburg *et al.*, 2004) and late Pleistocene glacial history (Washington DNR, 2005). The dry ecoregion is dominated by friable sandstones interbedded with siltstones and shales has experienced more frequent and severe fires and was unglaciated, whereas the wet ecoregion is dominated by schists and banded gneiss and experienced extensive alpine glaciation reflected in glacial drift comprising a portion of surficial deposits.

Within ecoregions, streams were further stratified based on the extent of past road development and timber harvest (Medhurst, 2007). Logged sites were those showing evidence of prior road construction and timber harvest during the preceding 30 years compared to unlogged sites that showed no evidence of timber harvest directly adjacent to the study streams for at least 100 years. Time since timber harvest was established in the field by dating tree cores, dating logging scars on surrounding trees and by the presence of logging roads and cut stumps. Road density was not quantified but is currently being estimated from satellite imagery for another study. Our stratification resulted in a 2 × 2 design, with four categories of stream types (wet logged, wet unlogged, dry logged, dry unlogged) with 15 streams each.

Site sampling

Our sampling methods closely followed those of Wipfli & Gregovich (2002). We measured headwater stream transport of invertebrates, particulate organic matter and inorganic matter (>250-μm size). Samples were taken with 250-μm mesh nets attached to one end of a 30-cm long × 12-cm high × 12-cm deep rectangular plastic pipe frame that rested on the stream bottom. Net assemblies (one per stream) were held in place with rocks and positioned to capture the greatest surface flow but not exceeding 12 cm in depth. This allowed us to capture both suspended and bedload organic and inorganic material, and drifting invertebrates as well as those moving downstream along the stream bottom (Piccolo & Wipfli, 2002; Wipfli & Gregovich, 2002).

Streams were sampled over nine individual periods between September 2004 and September 2006 (Table 1). Only subsets of streams were sampled during the first three sampling periods as site selection was not complete, and sampling did not occur in the winter of 2006 or during flooding in May 2006 (see Table 1). We sampled over a 48-h period during September 2004 and switched thereafter to a 24-h period to successfully reduce potential net clogging.

At each sampling time and location, we measured pipe water velocities with a flow meter (Intermountain Environmental Inc., Logan, UT, U.S.A.). Pipe discharge was calculated by averaging two velocities and two depths measured within the pipe. Similarly, stream discharge was calculated from five water velocities and five depths measured at equidistant points across the wetted width. These were measured

Table 1 Sampling dates and number of samples for each stream category

Date	Total	Wet logged	Wet unlogged	Dry logged	Dry unlogged
September 2004	21	5	5	6	5
November 2004	31	8	7	9	7
January 2005	20	5	5	5	5
April 2005	60	15	15	15	15
June 2005	60	15	15	15	15
August 2005	60	15	15	15	15
October 2005	47	12	12	12	11
July 2006	60	15	15	15	15
September 2006	60	15	15	15	15
Total	419	105	104	107	103

at the start and end of each sampling bout. Stream discharge was used to estimate invertebrate density (number m^{-3} water) and invertebrate organic and inorganic mass (g m^{-3} water) transported. We corrected for changing from 48- to 24-h sampling when generating our response variables. Depending upon weather conditions, 2–3 weeks was needed to sample all 60 streams, and an equal number of streams from all four treatments were sampled during each sampling event.

We measured temperature (°C), dissolved oxygen (DO mg mL^{-1}), conductivity (mS cm^{-1}) and pH at each stream during each sampling bout with a YSI meter (Fondriest Environmental Inc., Alpha, OH, U.S.A., Table 2). We further quantified riparian vegetation crown cover and composition along each of the 60 streams once during the growing seasons of either 2004 or 2005. Crown cover sampling was conducted using a moosehorn densiometer on transects that ran directly up the middle of the stream for 200 m from our sampling locations. Riparian cover and composition were recorded at 5 m intervals along the 200 m to calculate the percentages of total, conifer, deciduous tree and shrub, and alder cover for each sampled stream (Table 2).

Sample processing

Samples were preserved in 70% ethanol, and several drops of rose bengal solution (Thermo Fisher Scientific Inc., Asheville, NC, U.S.A.) was added to each sample to stain invertebrates for later identification. Samples were first processed in the laboratory through a series of stacked sieves with screening mesh varying (top to bottom) from 4 mm to 1 mm to 250 μm. All invertebrates from the 4 and 1 mm sieves were collected, identified to family, body lengths measured and dry mass determined using published length to mass regressions. Only individuals larger than 1 mm were used to calculate invertebrate biomass transport (Wipfli & Gregovich, 2002). This ensured that we had satisfactory sampling of the largest invertebrates, which often account for most of the variation in invertebrate biomass transport. The smallest invertebrates captured on the 250-μm sieve were sorted, counted, identified and combined with counts from the larger sieves to determine invertebrate number

Table 2 Mean site characteristics for each of the four stream categories with standard error of the mean in parentheses

Category	Elevation (m)	Width (m)	Discharge (L s^{-1})	Temperature (°C)	Conductivity (mS cm^{-1})	Dissolved oxygen (mg mL^{-1})	pH	Total cover (%)	Conifer (%)	Deciduous (%)	*Alnus* (%)
Wet logged	863 (48)	0.54 (0.05)	14.8 (2.8)	7.9 (0.26)	0.06 (0.01)	11.6 (0.09)	7.3 (0.08)	79 (6.2)	12 (6.2)	67 (6.7)	36 (6.9)
Wet unlogged	756 (30)	0.67 (0.05)	29.2 (5.3)	7.9 (0.26)	0.05 (0.01)	11.7 (0.06)	7.3 (0.05)	83 (4.6)	66 (6.9)	17 (3.9)	4 (1.5)
Dry logged	994 (59)	0.52 (0.06)	13.8 (5.6)	7.2 (0.21)	0.23 (0.04)	11.2 (0.09)	7.7 (0.07)	70 (4.8)	14 (4.7)	55 (5.8)	37 (5.4)
Dry unlogged	890 (67)	0.48 (0.06)	12.4 (3.9)	7.7 (0.45)	0.23 (0.02)	11.4 (0.15)	7.9 (0.07)	67 (4.6)	29 (4.9)	37 (6.3)	14 (3.4)

transport. The rest of the sample was oven-dried, weighed, ashed at 500 °C for 5 h and reweighed to determine organic and inorganic ash-free dry mass values.

Statistical analysis

The four primary response variables were invertebrate density m^{-3} stream water and invertebrate organic and inorganic biomass m^{-3} stream water. We used repeated measures analysis of covariance (ANCOVA) to test for the effects of sampling time (our repeated measure), ecoregion, land-use and their interactions. Although stream abiotic variables and riparian vegetation conditions were not within the set of hypotheses being tested, these can clearly affect the responses we were measuring; thus, we investigated their potential as covariates in our statistical models. Discharge was included as a potential covariate given the large differences among stream categories (Table 2); however, pH measurements were lacking during two sampling periods, and it could not be used as a covariate. To avoid multicollinearity resulting from highly correlated covariates and model overfitting because incorporating many terms in a single model (Myers, 1990), we used regression analysis to select a single covariate for each response variable. This model selection procedure examined all eight covarites as single regressors for each response variable from which we chose the variable with the highest R^2 as our covariate. Using this procedure, conifer crown cover was used as our covariate for invertebrate density, *Alnus* crown cover for invertebrate biomass and stream conductivity for both organic and inorganic transport. For significant interactions, post hoc Tukey tests determined differences among treatments. Finally, we set $\alpha = 0.10$ without bonferroni adjustment since headwater stream transport has been shown to be highly variable both within and among streams (Wipfli & Gregovich, 2002; Clarke *et al.*, 2008).

Results

Headwater transport

Time and ecoregion were significant for all response variables as headwater transport rates varied greatly across sampling periods and dry ecoregion streams displayed the highest mean values (Figs 2 & 3, Table 3). Although logged sites also generally showed higher mean values than unlogged streams, only inorganic transport was significantly higher in logged sites (Figs 2 & 3, Table 3). The ecoregion × land-use interaction was not significant for any response variable; however, both factors showed significant interactions with time depending on the response variable (Table 3).

Specifically, the number of invertebrates transported downstream was significantly higher in the dry ecoregion (8.75 ± 2.29 m^{-3} versus 5.11 ± 2.27 m^{-3} in wet, $F_{1,50} = 2.89$, $P = 0.095$), varied significantly with time ($F_{8,\ 298} = 11.48$, 13.24, $P = <0.0001$) and showed a significant ecoregion × time interaction ($F_{8,\ 298} = 2.22$, $P = 0.025$) as dry ecoregion streams transported more invertebrates than wet ecoregion sites for all time periods except during June and August 2005 (Figs 2 & 3, Table 3). Land-use did not significantly influence invertebrate transport rates ($F_{1,\ 50} = 0.51$, $P = 0.477$, Table 3); however, conifer crown coverage was significant as a covariate ($F_{1,\ 50} = 9.08$, $P = 0.004$) and associated with logging as unlogged sites had a high proportion of conifers particularly in the wet ecoregion (Fig. 4). Similarly, the biomass of invertebrates transported downstream was significantly higher in the dry ecoregion (1.94 ± 0.40 mg m^{-3} versus 1.17 ± 0.39 mg m^{-3} in wet, $F_{1,50} = 7.21$, $P = 0.009$), varied significantly with time ($F_{8,298} = 13.24$, $P = <0.0001$), was not significantly influenced by land-use ($F_{1,50} = 0.06$, $P = 0.802$), but *Alnus* crown coverage was significant as a covariate ($F_{1,50} = 4.96$, $P = 0.030$) and associated with logging as logged sites had the highest proportion of *Alnus* in the riparian zone (Figs 2–4, Table 3). These patterns were produced by unlogged streams in the wet ecoregion having the lowest values of invertebrate transport compared to the other stream groups, which were similar in their transport rates (Fig. 2).

The dry ecoregion and logged streams also displayed a tendency of higher transport of both organic and inorganic materials (Fig. 2). The biomass of organic matter transported downstream was significantly higher in the dry ecoregion (0.08 ± 0.01 g m^{-3} versus 0.03 ± 0.01 g m^{-3} in wet, $F_{1,48} = 7.41$, $P = 0.009$), varied significantly with time ($F_{8,287} = 5.16$, $P = <0.0001$) and showed a significant land-use × time interaction ($F_{8,287} = 2.47$, $P = 0.013$) as logged streams transported more invertebrates than unlogged sites

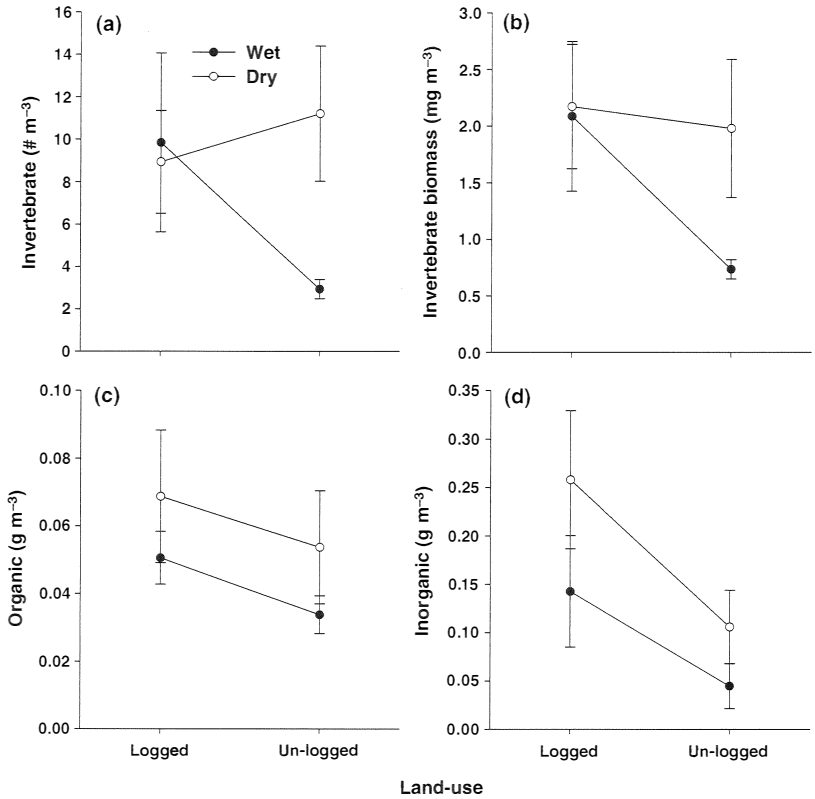

Fig. 2 Influence of ecological subregion (wet – black circle, dry – white circle) and land-use (logged, unlogged) on the headwater transport of (a) invertebrate number (b) invertebrate biomass (c) organic and (d) inorganic material.

but only during April and June 2005 (Figs 2–3, Table 3). Furthermore, stream conductivity was significant as a covariate ($F_{1,48}$ = 7.31, P = 0.009) and differed greatly among ecoregions (Table 3, Fig. 5). Similarly, the biomass of inorganic matter transported downstream was significantly higher in the dry ecoregion (0.22 ± 0.44 g m^{-3} versus 0.06 ± 0.45 g m^{-3} in wet, $F_{1,48}$ = 3.60, P = 0.063), logged streams (0.23 ± 0.04 g m^{-3} versus 0.06 ± 0.03 g m^{-3} in unlogged, $F_{1,48}$ = 9.55, P = 0.003), varied significantly with time ($F_{8,\ 287}$ = 3. 75, P = 0.0003) and showed a significant ecoregion × time interaction as dry ecoregion sites transported more sediment compared to wet ecoregion streams during April to October 2005 and September 2006 (Fig. 3).

Riparian vegetation and abiotic variables

Dry ecoregion streams had less total and conifer crown cover (Fig. 4). Logged drainages also contained more

Table 3 Repeated measures ANCOVA examining how different covariates, ecological subregion (ESR, Wet versus Dry), land-use (LU, Logged versus Unlogged), time (the repeated measure) and interactions among the main effects influenced the transport of invertebrate density, invertebrate biomass, and organic and inorganic matter. A single covariate out of nine potential was chosen for each response variable using regression model selection (see Methods, data log – transformed, α = 0.10). Bold indicates significance

	Invertebrate density (number m^{-3})	Invertebrate biomass (mg m^{-3})	Organic (g m^{-3})	Inorganic (g m^{-3})
Conifer	**0.004**	–	–	–
Alnus	–	**0.030**	–	–
Conductivity	–	–	**0.009**	–
Conductivity	–	–	–	0.243
ESR	**0.095**	**0.009**	**0.009**	**0.063**
LU	0.477	0.802	0.160	**0.003**
ESR × LU	0.636	0.434	0.759	0.849
Time	**<0.0001**	**<0.0001**	**0.0003**	**<0.0001**
ESR × Time	**0.025**	0.615	0.526	**0.025**
LU × Time	0.914	0.659	**0.013**	0.248
ESR × LU × Time	0.585	0.472	0.202	0.726

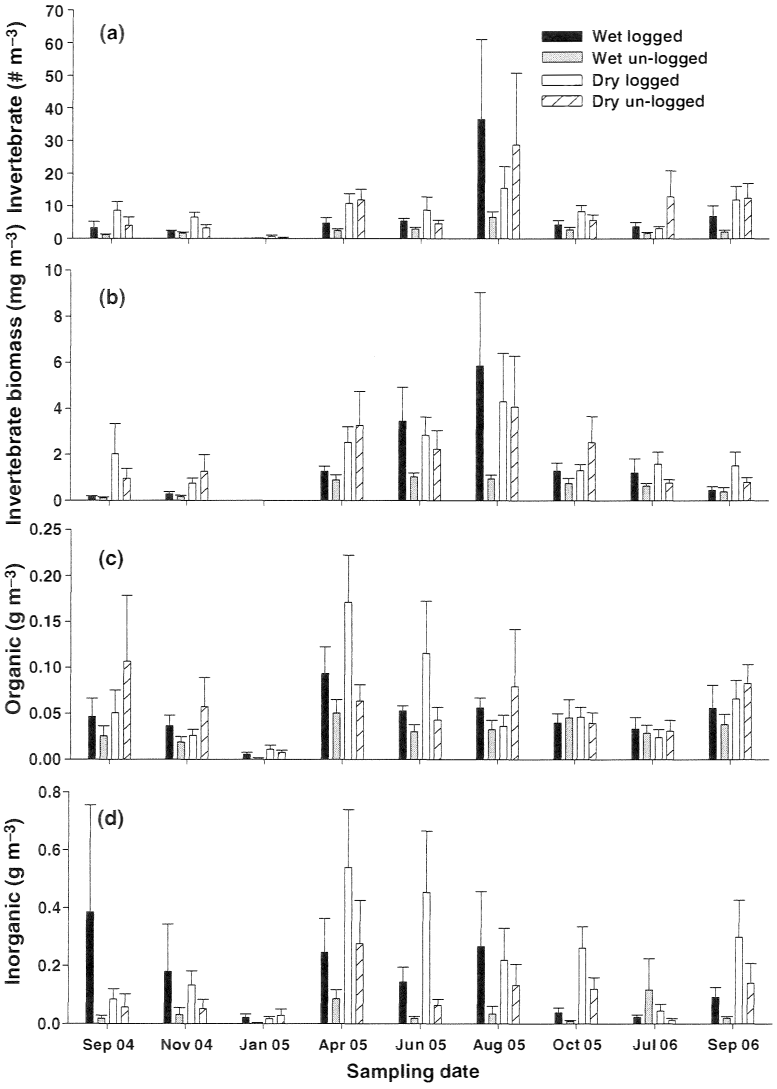

Fig. 3 Temporal results of the four stream categories (wet logged – black bars, wet unlogged – gray bars, dry logged – white bars, dry unlogged – white striped bars) on the headwater transport of (a) invertebrate number (b) invertebrate biomass (c) organic and (d) inorganic material.

deciduous trees, shrubs and *Alnus* species (Fig. 4). Stand opening caused by prior timber harvesting had likely allowed the regeneration and release of deciduous cover species in the riparian corridor. There was a pronounced shift from coniferous to deciduous crown cover with logging in the wet ecoregion. This shift was subtle in the dry ecoregion with most streams having a high proportion of deciduous and low proportion of conifer coverage (Fig. 4).

All abiotic variables varied greatly with time. Conductivity and discharge showed large differences between ecoregions with conductivity being higher in the dry ecoregion whereas discharge was higher in the wet ecoregion (Fig. 5), although discharge was not a significant covariate in the analyses that identified differences in invertebrate and organic/inorganic transport. These reflect pronounced seasonal differences in stream flow, climate and geology between ecoregions. However, the mean temperature difference among the four sampling groups was <1 °C, overall DO means were within 1 mg mL^{-1} and overall mean pH ranged <1 pH unit (Fig. 5).

Discussion

Our results demonstrated that the variability in downstream transport of invertebrates, detritus and sediment from headwater streams is a function of both their surrounding land-use (i.e., timber harvest) and the ecoregion within which they are embedded.

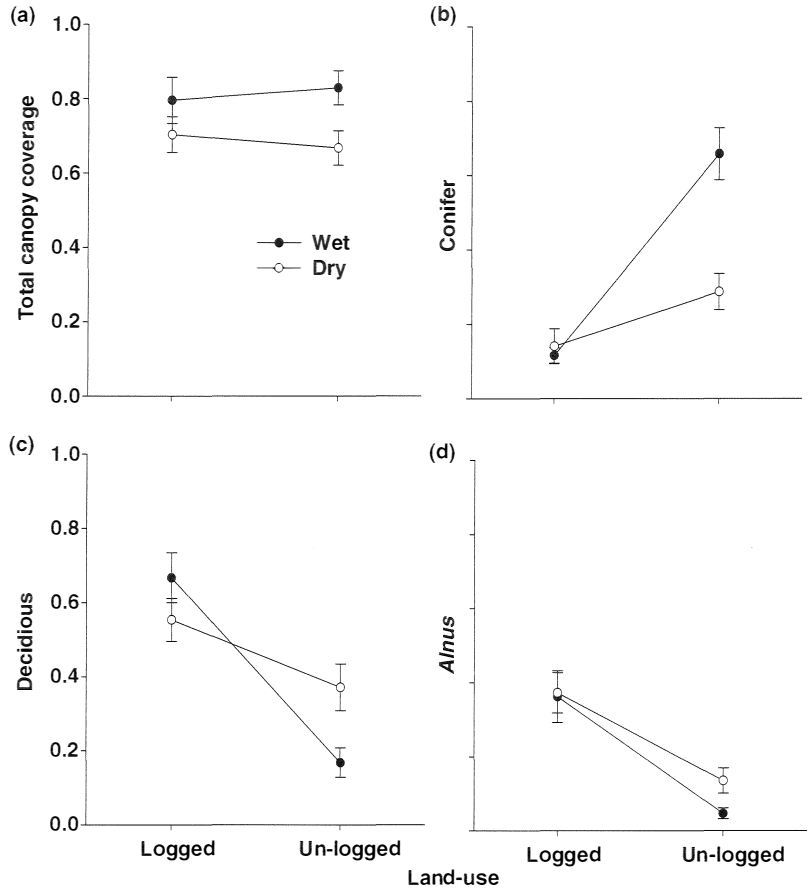

Fig. 4 Total (a), coniferous (b), deciduous (c) and *Alnus* (d) riparian canopy coverage at the study streams for each ecological subregion (wet – black circle, dry – white circle) and land-use category (logged, unlogged).

Although the influence exerted by either ecoregion or land-use shifted in importance depending on the specific response variable being measured, we showed elevated headwater transport in the dry ecoregion and in logged streams of both ecoregions. Unlogged, wet ecoregion streams consistently had the lowest transport rates, and interestingly, unlogged, dry ecoregion streams were indistinguishable from their logged, wet ecoregion counterparts for all transport variables. Across our two sampled ecoregions, unlogged and logged streams were similar in terms of their downstream transport.

High spatial and temporal variability characterised our results similar to other studies documenting transport from headwater streams (Wipfli & Gregovich, 2002; Romaniszyn, Hutchens & Wallace, 2007; Mellon, Wipfli & Li, 2008). However, the range in downstream transport of invertebrates (1–373 individuals m^{-3}), organic matter (0.01–0.95 g m^{-3}) and inorganic material (0.001–2.89 g m^{-3}) measured in this study was explained primarily by the association of streams with their ESRs, suggesting that broad landscape-scale variables are at least correlated with, if not mechanistic drivers of, productivity. Land management practices primarily influenced riparian vegetation, but interacted with ecoregions and contributed to variation in transport as well. For example, decreased deciduous vegetation in unlogged catchments of the wet ecoregion was related to lower invertebrate drift rates. Thus, we attribute some explanatory power to how factors that define ecoregions control biological production, assuming drift densities reflect productivity.

The stratification by geoclimatic setting (ecoregion) when investigating how natural and anthropogenic disturbances affect aquatic ecosystems highlighted the differences between logged and unlogged streams, which were most pronounced in the wet ecoregion. As in studies from coastal regions of the Pacific Northwest and Alaska (Piccolo & Wipfli, 2002; Wipfli & Musslewhite, 2004; Hoover, Shannon & Ackerman, 2007), logging produced obvious shifts from conifer to

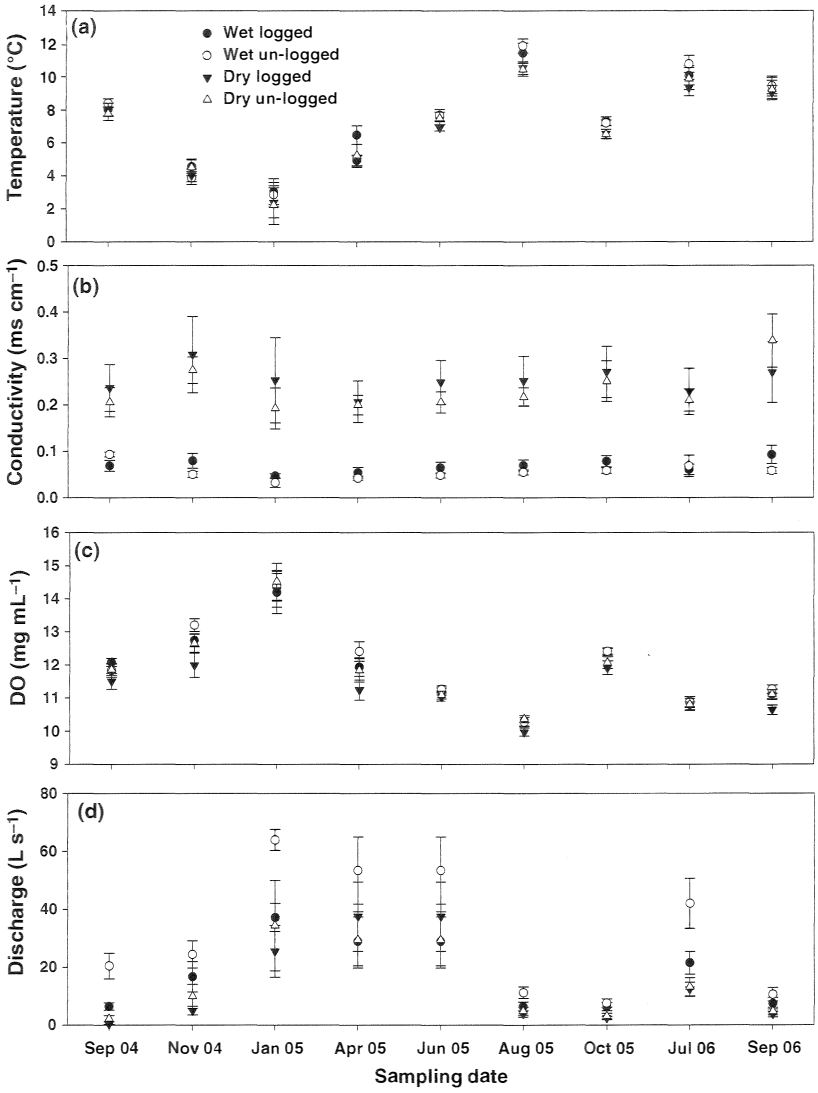

Fig. 5 Mean temperature (a), conductivity (b), dissolved oxygen (c), and discharge (d) for each ecological subregion (wet – circles, dry – triangles) and land-use category (logged – black, unlogged – white) during the nine sampling events.

deciduous riparian vegetation and increased invertebrate drift. However, within the dry ecoregion, logged and unlogged streams showed comparable drift levels suggesting local regulation of production.

The majority of material exported from the streams in our study (organic and inorganic; see also Kiffney, Richardson & Feller, 2000; Richardson, Bilby & Bondar, 2005) appears also to be controlled by both ecoregion and local land-use with the greatest differences occurring between logged dry ecoregion sites and unlogged streams of the wet ecoregion. Inorganic material constituted the largest fraction of transport measured in this study and was highest with logging, particularly in the dry ecoregion (Fig. 2d). The impact of inorganic transport rates on downstream consumers is unknown, but given that sedimentation has documented detrimental effects (Shaw & Richardson, 2001; Kaller & Hartman, 2004; Suttle *et al.*, 2004), and increased invertebrate transport is hypothesised to be positive (Wipfli & Gregovich, 2002), the possibility exists for offsetting influences between inorganic and invertebrate transport. Logging is notorious for increasing sedimentation (Gomi, Sidle & Swanston, 2004; Kreutzweiser, Capell & Good, 2005; Houser, Mulholland & Maloney, 2006) and detritus export from headwater streams (Piccolo & Wipfli, 2002; Wipfli & Musslewhite, 2004). We suggest that predicting how contemporary logging events are transmitted across the terrestrial–aquatic ecotone, and transported by headwaters downstream, requires

an understanding of regional differences in climate, geology and legacies of past disturbances.

Significant time and time × treatment interactions suggested that headwater subsidies are temporally pulsed in the Wenatchee sub-basin. Such pulses are common in stream (Webster *et al.*, 1999; Kiffney *et al.*, 2000; Richardson *et al.*, 2005) and other ecosystems (Stapp & Polis, 2003). However, we could find no clear explanation for the pattern in temporal variation. Streams from the four ecoregion/land-use classifications oscillated back and forth regarding which had the highest transport with no apparent seasonality (Fig. 3). Whether this was the result of stochastic variation in time or the dominance of other biogeoclimatic factors across seasons requires further study.

Dominance by deciduous species in all but wet, unlogged streams and how these are modified by larger-scale processes that differentiate ecoregions is our primary hypothesised mechanism influencing transport dynamics in our study streams. The ecoregions studied here differ significantly in climate, geological setting, and the frequency and intensity of past disturbance (Hessburg *et al.*, 2000, 2004). Longer growing seasons, more solar radiation (see Kiffney *et al.*, 2003; Kiffney, Richardson & Bull, 2004) and higher air temperature associated with the dry ecoregion may enhance overall stream productivity and the transport of invertebrates downstream. Furthermore, past disturbances (e.g., fire, see Hessburg *et al.*, 2004 or older timber harvest, see Hessburg & Agee, 2003) may still be affecting contemporary headwater stream dynamics by altering the quantity and quality of riparian vegetation and abiotic characteristics (Kiffney *et al.*, 2003, 2004; Piccolo & Wipfli, 2002; Wipfli & Musslewhite, 2004; Wipfli *et al.*, 2007; Medhurst, 2007). Following disturbance, rapid shifts from coniferous to deciduous dominance of riparian vegetation can provide more resources for stream invertebrates as deciduous inputs break down faster (Webster *et al.*, 1999). A pronounced shift from conifers to deciduous species exists in the wet ecoregion where unlogged streams had the highest proportion of conifers and lowest proportion of deciduous species, including nitrogen-fixing *Alnus* (*A. sinuata*, *A. incana*) that are more common in the other stream categories. Forest patches adjacent to streams in the dry ecoregion have been repeatedly harvested by selective cutting over the last 100 years. As a result, riparian cover is currently dominated by deciduous species and is significantly lower under both land-use scenarios.

There has been a growing interest concerning the ecological importance of headwater streams and how to protect and manage them best within a landscape context (Meyer *et al.*, 2007; Richardson & Danehy, 2007; Wipfli *et al.*, 2007; Clarke *et al.*, 2008). Their small size and high density tightly couples these streams to surrounding terrestrial environments and their associated local disturbances. Materials that are products of legacies of past land-use practices are exported downstream by many headwater systems, which at larger spatial scales can be clustered into ecoregions. Information regarding how physical and biotic processes occurring at different spatial and temporal scales influence headwater stream transport is lacking but critical for predicting the magnitude and variability of headwater stream subsidies and how they impact downstream communities. Of particular interest is how headwater streams might facilitate the production of species that are of conservation or wildlife interest, such as some salmonids, by providing direct energy sources via invertebrate drift (see Wipfli & Gregovich, 2002; Romaniszyn *et al.*, 2007; Wipfli *et al.*, 2007). The contribution of any single headwater stream might be minor, but the sheer number of headwater streams and their numerous connections to fish-bearing reaches indicates their importance as providers of energy and materials (Richardson & Danehy, 2007). This study suggests that a full understanding of how disturbances affect headwater stream transport, and hence downstream dynamics, will depend on the geoclimatic context of the streams and surrounding land-use.

Understanding how headwater subsidies vary along gradients of climate and disturbance is needed to accurately predict their impact on downstream consumers and habitats. Headwater streams and their associated riparian forests can greatly influence material flow from headwater catchments to downstream environments. Materials originating from headwaters likely affect food webs inhabited by fish and other consumers at the broader catchment scale (Vannote *et al.*, 1980; Gomi *et al.*, 2002; Wipfli *et al.*, 2007). Ecological connections between headwaters and downstream habitats support the notion that headwaters and transport processes in stream ecosystems affect overall catchment productivity. How riparian forests and associated riparian

vegetation are managed influences sediment, detritus, and prey inputs and their delivery to consumers. In food-limited systems, management actions that affect these food resources will undoubtedly affect upper-level consumers.

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