Stream Macroinvertebrate Community Responses as Legacies of Forest Harvest at the H.J. Andrews Experimental Forest, Oregon

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Abstract: To evaluate long-term effects of forest harvest, we sampled benthic and emergent macroinvertebrate communities in headwater streams through young-growth and old-growth forests in the H.J. Andrews Experimental Forest, Oregon, from June, 2003 to June, 2004. Thirty to forty years after harvest, macroinvertebrate density and richness did not differ among streams through young growth and old growth. Effects of deciduous riparian vegetation, including seasonal canopy openings and litterfall, continue to influence patterns of macroinvertebrate responses to forest harvest, as shown by higher densities of shredders in young-growth sites, the timing of emergence within basin pairs, and assemblage differences in two of the pairs of basins. The paired-basin design helped in distinguishing the specific influences of forest age from natural variability of macroinvertebrate distributions within the 5th order Lookout Creek basin. Our study suggests that understanding how macroinvertebrates respond to historical disturbances is enhanced by measures sensitive to changes in life history, such as rates of emergence, and to functional composition that reflect resource availability. FOR. SCI. 53(2):281–293.

Keywords: benthic, emergence, macroinvertebrate, forest harvest, density

IN CHARACTERISTICALLY NARROW headwater streams, instream processes are intimately connected to adjacent terrestrial riparian zones. Decades of stream research suggest benthic macroinvertebrate communities are responsive to differences in resource availability in headwaters. Allochthonous resources, such as leaves, needles, and catkins, reflect riparian conditions and can sustain relatively high numbers of shredders in small streams (Anderson and Sedell 1979, Cummins and Klug 1979, Cummins et al. 1989), particularly through deciduous forests (Stout et al. 1993, Wipfli and Musselwhite 2004, Hernandez et al. 2005). More grazers occur in well lit patches (Noel et al. 1986, Stone and Wallace 1998), and gougers appear where large wood dominates instream habitat (Anderson 1978). When forest harvest, particularly clearcutting, alters riparian composition, we expect changes in physical characteristics of streams and corresponding shifts in the biota (Bilby and Bisson 1992, Fortino et al. 2004).

Because the structure and composition of riparian vegetation determine the quantity, quality, and timing of allochthonous inputs to streams (Triska et al. 1982, Cummins et al. 1989, Anderson 1992), instream biological responses to deciduous and coniferous riparian forests can be quite different. In temperate forests, riparian areas dominated by deciduous species show strong seasonality from pulses of leaves in autumn, often reflected by increased numbers of shredders during leaf fall (Murphy et al. 1981). Areas dominated by conifers have more continuous inputs throughout the year (Anderson and Sedell 1979) and less temporal variation in available light. Given the differing scenarios of allochthonous availability, patchiness of light in the canopy, and dynamics of large wood distribution, benthic community composition is likely to change with riparian composition. The potentially high diversity and multiple life history strategies of these assemblages may be represented not only by shifts in functional composition, but also by indicator organisms distinctive of particular conditions.

Immediately following riparian forest harvest, some responses of macroinvertebrate communities are predictable; abundances of benthic macroinvertebrates often increase and changes in overall taxonomic or functional feeding group community composition occur (Newbold et al. 1980, Hawkins et al. 1982, Hernandez et al. 2005). However, varied responses in taxa richness have been noted in comparisons of streams through harvested areas versus old growth: Newbold and colleagues (1980) found lower richness in streams through old-growth forests; Murphy and Hall (1981) and Stone and Wallace (1998) found higher richness; and others (Anderson 1992, Price et al. 2003, Hernandez et al. 2005) found no differences. Because of these ambiguities, Stone and Wallace (1998) suggested that neither taxa richness, which does not detect loss of species, nor diversity, which describes richness in terms of relative abundance and evenness, may be comprehensive in evaluating changes after harvest.

Although many studies have examined immediate effects

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of forest harvest and canopy removal on macroinvertebrate communities, few studies have investigated longer-term responses to forest regrowth after harvest (Stout et al. 1993, Stone and Wallace 1998, Cole et al. 2003). As riparian areas became revegetated in an eastern North American forest, macroinvertebrate community responses, coinciding with canopy closure and increases in litter inputs, included increased macroinvertebrate densities and biomass (Stone and Wallace 1998). Functional composition, represented by macroinvertebrate feeding groups such as shredders or scrapers, can also change due to differences in primary production and detrital inputs (Richardson 1992, Cole et al. 2003).

In the Pacific Northwest, riparian vegetation in undisturbed areas is generally dominated by coniferous trees (Franklin and Dyrness 1973). Deciduous trees often recolonize riparian areas after major disturbances such as forest harvest, debris flows, or major floods (Gregory et al. 1991, Harrington et al. 1994, Johnson et al. 2000). We understand little about how aquatic biota respond during the decades as the forest and riparian zone mature. Do streams flowing through second- or third-growth forests retain a signal of prior disturbance? As long-term monitoring efforts increase, particularly in comparisons of harvest and other disturbance effects to mature ecosystems, stream macroinvertebrates may be useful indicators of forest-stream dynamics and differences in biotic processes over time.

In this study, we examined whether legacies of land use activities continue to influence macroinvertebrate communities; i.e., the extent to which macroinvertebrate communities in headwater streams that have previously been harvested resemble those in streams through old-growth forests. We hypothesized:

1. Associated with differences in allochthonous inputs and canopy openings, macroinvertebrate communities in streams through young-growth forests would have higher richness and higher densities of benthic and emergent macroinvertebrates than streams through old-growth forests.

2. Shredder densities would be greater in streams through young growth than through old growth because of higher deciduous inputs into streams through young growth.

3. Based on physiological and phenological differences among taxa, benthic and emergent invertebrates would respond differently to seasonal fluctuations in allochthonous inputs and canopy openings in reaches through young-growth forests than in old-growth.

4. Indicator species of macroinvertebrates will be associated with streams through old-growth or young-growth forests.

Methods
Study Sites

H.J. Andrews Experimental Forest is located in the central Cascade Mountains of Oregon. The climate is maritime with warm, dry summers and cool to cold, wet winters. Mean annual precipitation at the lower elevations is 2,200

mm, the majority of which occurs between November and April. The topography is steep with generally shallow soils (Rothacher et al. 1967). The vegetation at the Andrews Forest is a mosaic of conifer forests including old-growth (450–550 years), mature stands (100–150 years), and early seral stages (<50 years). In the Pacific Northwest, headwater streams through old-growth forests generally have overstory riparian vegetation that is composed of Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco), Western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and Western redcedar (*Thuja plicata* Donn ex D. Don). In young-growth areas, overstory riparian vegetation typically includes red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh). Understory species in riparian areas include vine maple (*Acer circinatum* Pursh), Pacific yew (*Taxus brevifolia* Nutt.), red huckleberry (*Vaccinium parvifolium* Sm.), devil's club (*Oplopanax horridus* Miq.), and young conifers.

To assess benthic and emergent macroinvertebrate taxa richness, densities, and community composition, six perennial, headwater, fishless streams within the 6,400 ha Andrews Forest, which occupies the entire Lookout Creek Watershed, were repeatedly sampled (Figure 1). Study reaches were 50 m long and located upstream of stream gauges and access roads, except in watershed 2 (WS-2). Stage height and stream temperature were measured in the gauged basins of WS-1, -2, -7, and -8, and discharge data are available on the Andrews web pages (www.fsl.orst.edu/lter/. Last accessed Dec. 2006). Basins were paired by elevation, aspect, basin area, discharge, and geology. Each pair contained one basin that had been harvested 30 to 40 years previously (YG) and an adjacent basin with old-growth conifer forest cover (OG) (Table 1). WS-1 and WS-A were clearcut-logged in the 1960s and burned following harvest. WS-7 was harvested by overstory thinning in 1974 and 1984. Basins were replanted with Douglas-fir after harvest (Martin and Harr 1989).

Instream and Riparian Conditions

Instream and riparian attributes were measured at the time of benthic sampling. Six transects, perpendicular to streamflow, were established in study reaches, and wetted stream widths were measured at each transect. At 11 points across each transect, stream depths were measured and substrate types recorded. Substrate type was characterized by size as silt, sand, gravel, cobble, boulder, bedrock, or wood (modified from Wolman 1954). Percentage canopy cover was measured using a canopy densitometer mid-channel at each transect with the observer facing upstream, downstream, right, and left (Platts et al. 1987). For each reach, average proportion of substrate type and average percentage canopy cover were calculated. Composition of overstory and understory riparian vegetation was noted within 5 m of the stream. Allochthonous litterfall was collected continuously from July through October, 2003. At each site, six litter traps, circular baskets (0.12 m^2) with 0.6-mm mesh nets, were placed along the edges of the stream. Leaf litter was collected monthly, dried at 60°C for 24 to 36 hours, and weighed. Litter was categorized as red
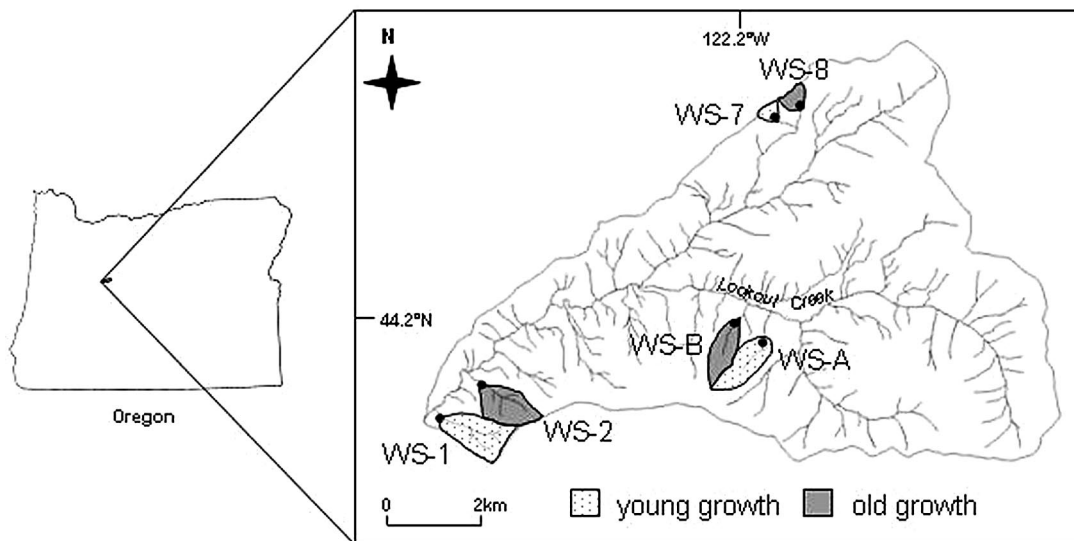
Figure 1. Locations of headwater stream study basins in the H.J. Andrews Experimental Forest, Oregon.

Table 1. Physical characteristics of headwater stream study basins in the H.J. Andrews Experimental Forest

	WS-1	WS-2*	WS-A	WS-B*	WS-7	WS-8*
Basin area (ha)	97.8	73.3	57.9	52.8	12.4	16.0
Elevation (m)	500	550	800	750	950	1,000
Aspect	NW	NW	N–NE	N–NE	S–SE	S
Forest age (years)	40	450+	38	450+	20–30	450+
Minimum streamflow (l/s)	0.06	0.54	N/A	N/A	0.03	0.03
Maximum streamflow (l/s)	707.9	353.8	N/A	N/A	55.8	94.2

Elevation was measured at the most downstream point of the basin. Streamflow summaries are for June, 2003 through June, 2004. WS-A and WS-B do not have streamflow gauges.

* Denotes streams flowing through old-growth forests.

alder leaves, other deciduous leaves, conifer needles, or miscellaneous (catkins, cones, lichens, and twigs).

Macroinvertebrate Sampling

Benthic sampling was conducted four times and during periods of relatively stable streamflow: June, 2003, November, 2003, March, 2004, and May, 2004. Emerging macroinvertebrates were collected a total of 13 times; at the time of benthic sampling, at midpoints between benthic samples in 2004, and approximately 3-week intervals during the summer and early fall 2003. Locations of benthic sampling were randomized within study reaches at each sample date; emergence sample locations were only randomized once at the start of the study. On each sampling date, six benthic samples were collected per reach. All samples were taken with a 0.25-mm mesh Surber sampler (0.093 m^2) in riffle/cascade stream units on substrates ranging from silt to cobble. Four 0.25-m^2 emergence traps, consisting of PVC frames draped with 0.6-mm mesh nets, were set over the stream bed and left in place for 6 to 8 days and then sampled. A small amount of unscented, biodegradable soap was added to the water in emergence trap collecting cups to decrease surface tension; in cold weather, rock salt was added to serve as both an antifreeze and a preservative agent. When invertebrates were collected, they were sieved through 0.25-mm mesh and stored in 95% ethanol. Emergence rates were calculated as densities of invertebrates collected in traps during each 6- to 8-day collection interval and expressed as number of individuals $\cdot$ m^{-2} day^{-1}.

All insects were identified to genus when possible (Brown 1972, McAlpine et al. 1981, Stewart and Stark 1993, Merritt and Cummins 1996, Wiggins 1996). Individuals of the family Chironomidae were identified to subfamily or tribe in benthic samples, and family level in emergence samples. Noninsects were typically identified to order (Thorp and Covich 1991). Young instar insects and individuals damaged during sampling or storage were identified to the lowest taxonomic resolution possible, typically order or family. All individuals in each sample were identified, and benthic macroinvertebrates were assigned to functional feeding groups (Merritt and Cummins 1996, Wiggins 1996).

Statistical Analyses

Benthic and emergent taxa richness were calculated as the sum of all taxa present at that site on a particular date. Benthic and shredder densities were natural log-transformed before parametric analyses. Three factor ANOVAs, with the factors being sampling date, vegetation age, and basin pair, were used to analyze benthic richness, benthic density, and shredder density (Matlab 7.2, Mathworks, Inc.). Sample size for this study was small, with only four sampling dates at six sites. Similarity was calculated using number of shared taxa for each possible pair (Colwell 2005) relative to the number of taxa in each stream of the pair.

Benthic macroinvertebrate communities from all seasons were compared using nonmetric multidimensional scaling (NMS) (Mather 1976) (PC-ORD 4 software, McCune and Mefford 1999). Benthic abundance estimates were log-transformed to reduce the effects of unequal weighting of zero estimates. Distance measures were calculated using Sørensen distances. Each point in the ordination represented community assemblages composed of relative abundances of member taxa. Axes were rotated to maximize variance explained by the strongest correlation with environmental variables. Monte Carlo tests were conducted to quantify if NMS axes were significant, then ordinations were evaluated by examining stress values. They were considered stable if the stress value was below 20 and the instability was <0.0001 (McCune and Grace 2002).

This study used indicator species analysis to identify taxa strongly correlated to forest type or season (Dufrene and Legendre 1997) (PC-ORD 4 software). This technique creates indicator values (from 0 to 100, 100 being a perfect indicator) for all taxa by combining values of relative abundance and relative frequency; significance of group membership was determined through 1,000 Monte Carlo simulations. Species were included for consideration of strong indicators for a forest type if they met the following conditions: (1) they were represented in at least two of three streams of a forest type, (2) they were collected during at least two seasons, and (3) at least 25 total individuals of a given taxa were collected.

Results

Instream and Riparian Conditions

In headwaters streams flowing through forests harvested 40 years ago (WS-1 and WS-A), dominant overstory riparian vegetation consisted of bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) (Table 2). In WS-7, at higher elevation, the overstory was harvested 20–30 years ago. Alder and bigleaf maple did not colonize the riparian areas of WS-7 and dominant overstory vegetation was conifer (Table 2). *Pseudotsuga menziesii* was present at all sites.

Differences in canopy cover were most apparent in November and March (Table 3). In WS-1 and WS-A, where alder dominated riparian vegetation, canopy cover in November and March was substantially lower than in the OG basin pairs. Canopy cover in WS-7 was also less in November, but not as low as along the other YG streams. We also observed seasonal lags among YG basins at different ele-

vations. In May, canopy cover at WS-1 and WS-A had returned to previous June levels, but in the high-elevation WS-7, spring cover was still lower than previous summer levels. Canopy cover coefficient of variation during the study was higher for YG than OG sites (Table 3).

Differences in litterfall between lower- and the high-elevation basins were dramatic. As would be expected, litterfall biomass was highest in October along all streams and was approximately three times greater at WS-1 and WS-A than in the OG basin pairs (Table 4). In YG basins in October, the dominant proportion of litterfall was alder leaves in WS-A, mixed alder and other leaves in WS-1, and composed of other leaves and needles in WS-7. In the OG basins, conifer needles were the dominant litterfall type in all months, except in WS-8 in September, when cones were an important component of litterfall. The pattern reversed somewhat in summer; OG basins WS-2 and WS-B had higher biomass of litter inputs in July and August than in the YG pairs.

In general, physical characteristics of study basins showed high similarity within basin pairs and high variability among pairs (Tables 1 and 3). Among pairs, as elevation increased from 550 to 1,000 m, basin areas decreased from 97.8 to 12.4 ha (Table 1). Differences in the magnitude of maximum streamflow (708–354 l/s in WS-1 and WS-2; 56–94 l/s in WS-7 and WS-8) reflected these differences in basin area (Table 1). Stream depths were similar within basin pairs and decreased as basin areas decreased (Table 3). Stream widths, however, were similar among all basins, with the narrowest widths occurring during June 2003. Gravel dominated substrates in all streams (Table 5) and composed more than 50% of total substrates in WS-2 and WS-7. Cobble was the next most common size class except in WS-8, where it was only 6.8% of total substrate composition. Sand and silt were represented in greater proportions in WS-7 than in lower-elevation streams. Wood was most abundant in WS-8, the highest-elevation OG site.

Macroinvertebrates
Benthic

Average richness of benthic macroinvertebrates through the year, over the four sampling dates, ranged from 53 to 67 taxa (Table 6). Taxa richness was slightly greater at YG streams within each basin pair but richness was not significantly different between YG and OG. Highest taxa richness was observed at mid-elevation basins (77 taxa in November and 71 in March). Across all sample times, similarity of

Table 2. Presence (+) of riparian tree species along headwater stream study reaches at the H.J. Andrews Experimental Forest

Scientific name	Common name	WS-1	WS-2*	WS-A	WS-B*	WS-7	WS-8*
Tsuga heterophylla	Western hemlock		+		+	+	+
Thuja plicata	Western red cedar		+		+	+	+
Taxus brevifolia	Pacific yew		+		+		+
Acer circinatum	Vine maple	+	+	+	+	+	
Alnus rubra	Red alder	+		+			
Acer macrophyllum	Bigleaf maple	+		+			
Populus trichocarpa	Black cottonwood	+					

Pseudotsuga menziesii (Douglas-fir) was present at all sites.
* Denotes streams flowing through old-growth forests.

Table 3. Canopy cover (%), stream width (m), and stream depth (cm) for study reaches

	WS-1	WS-2*	WS-A	WS-B*	WS-7	WS-8*
Canopy cover (%)						
June, 2003	97.5	96.6	98.3	86.5	82.6	93.4
November, 2003	44.6	85.5	45.3	77.9	63.2	89.2
March, 2004	36.8	77.5	45.6	70.6	65.0	89.2
May, 2004	95.8	95.1	92.9	86.8	59.3	83.6
CV (%)	47.3	10.1	41.2	9.6	15.3	4.5
Stream width (m)						
June, 2003	1.9	2.1	1.2	1.9	1.2	1.1
November, 2003	2.3	3.0	1.8	2.4	1.6	1.6
March, 2004	2.8	2.5	2.3	2.7	1.6	1.9
May, 2004	2.0	2.3	2.1	2.4	1.3	1.8
Stream depth (cm)						
June, 2003	7.1	8.8	4.4	4.6	2.6	2.7
November, 2003	18.4	15.3	13.6	11.0	6.0	7.1
March, 2004	19.9	16.1	10.4	12.3	4.7	7.9
May, 2004	13.6	8.2	8.5	8.3	4.3	4.7

CV% (coefficient of variation of canopy cover at sites) = (st. dev/mean) · 100.
* Denotes streams flowing through old-growth forests.

Table 4. Average biomass of litterfall ($g\ m^{-2}\ day^{-1}$) in riparian areas along study streams July through October, 2003

	WS-1	WS-2*	WS-A	WS-B*	WS-7	WS-8*
July total	0.44	0.63	0.29	0.88	0.24	0.26
Alder leaves	0.09	0.00	0.15	0.00	0.00	0.00
Other leaves	0.03	0.00	0.00	0.00	0.02	0.02
Conifer needles	0.02	0.48	0.01	0.72	0.11	0.15
Miscellaneous	0.31	0.14	0.13	0.15	0.12	0.10
August total	0.62	1.07	0.32	0.73	0.43	0.37
Alder leaves	0.39	0.00	0.21	0.00	0.00	0.00
Other leaves	0.14	0.02	0.00	0.00	0.01	0.03
Conifer needles	0.02	0.79	0.06	0.47	0.15	0.22
Miscellaneous	0.06	0.26	0.05	0.26	0.28	0.12
September total	1.11	0.76	1.31	0.44	0.30	2.01
Alder leaves	0.93	0.00	1.20	0.00	0.04	0.00
Other leaves	0.12	0.00	0.02	0.00	0.01	0.01
Conifer needles	0.01	0.59	0.06	0.31	0.22	0.47
Miscellaneous	0.06	0.17	0.04	0.13	0.02	1.53
October total	5.27	1.78	8.91	2.97	2.61	2.59
Alder leaves	2.67	0.00	6.61	0.00	0.06	0.00
Other leaves	2.21	0.35	1.49	0.17	1.07	0.04
Conifer needles	0.20	1.27	0.43	2.25	1.38	2.43
Miscellaneous	0.20	0.16	0.37	0.55	0.10	0.13

Miscellaneous includes cones, catkins, samaras, bark, lichen, moss, twigs, and wood.
* Denotes streams flowing through old-growth forests.

Table 5. Average substrate composition of stream reaches

Substrate type	WS-1	WS-2*	WS-A	WS-B*	WS-7	WS-8*
Silt (%)	1.1	0.0	0.8	3.4	11.4	2.3
Sand (%)	12.9	4.2	15.2	10.6	13.3	15.9
Gravel (%)	37.9	53.0	39.0	37.1	51.1	42.0
Cobble (%)	30.3	26.5	33.0	22.7	15.5	6.8
Boulder (%)	9.5	11.4	7.2	6.4	4.5	2.7
Bedrock (%)	7.2	1.9	2.3	16.7	1.5	15.2
Wood (%)	1.1	3.0	2.6	3.0	2.6	15.1

* Denotes streams flowing through old-growth forests.

benthic taxa between sites within basin pairs was 65.3, 69.2, and 71.1% at low, mid, and high elevations, respectively, compared to average similarity of 67.0% among the three OG basins and 64.0% among the three YG basins.

Benthic densities across all sampling times were highly variable. YG streams had slightly greater average densities (Table 6) but benthic densities did not differ significantly between streams through YG and OG across all sampling times ($F\ stat_{veg}$ = 4.40, P = 0.051). Densities, however, were significantly different among basin pairs ($F\ stat_{basinpair}$ = 8.34, P = 0.003). The mid-elevation basin pairs had the highest average densities, including highest densities during two of the four sampling times (Table 6). In all streams but WS-2, highest densities occurred in June, 2003. The timing

Table 6. Benthic taxa richness, benthic density, and shredder density (average number of individuals m^{-2}) by stream and date

	WS-1	WS-2*	WS-A	WS-B*	WS-7	WS-8*
Benthic richness	55.8	53.3	67.0	62.5	62.5	57.5
June, 2003	63	53	65	62	65	57
November, 2003	50	65	77	63	65	59
March, 2004	55	53	59	71	56	54
May, 2004	55	42	67	54	64	60
Benthic density	4,901.0	2,958.3	8,263.5	7,140.0	5,496.8	4,324.8
June, 2003	7,188 (2,048)	2,510 (293)	10,163 (2,242)	10,961 (3,141)	8,690 (2,397)	6,444 (865)
November, 2003	2,196 (649)	5,373 (935)	8,460 (2,415)	3,905 (1,006)	5,425 (872)	4,876 (789)
March, 2004	5,791 (643)	2,045 (466)	5,453 (778)	7,965 (1,558)	4,232 (1,241)	2,506 (785)
May, 2004	4,429 (465)	1,905 (289)	8,978 (722)	5,729 (627)	3,640 (350)	3,473 (517)
Shredder density	736.5	469.5	1,383.0	664.3	1,069.0	571.3
June, 2003	866 (421)	402 (61)	2,732 (643)	1,114 (249)	1,927 (681)	626 (166)
November, 2003	395 (145)	956 (213)	1,308 (485)	434 (55)	895 (166)	640 (222)
March, 2004	967 (247)	269 (121)	369 (92)	525 (172)	805 (285)	450 (193)
May, 2004	718 (183)	251 (57)	1,123 (130)	584 (141)	649 (77)	569 (153)

Benthic richness is total number of taxa for each sampling time. Values in parentheses are standard errors.
* Denotes streams flowing through old-growth forests.

of lowest densities varied among streams; two streams had the lowest in November, two in March, and two in May. Because of the great temporal variability in density patterns, there were no significant differences in density among sampling dates (F $stat_{time}$ = 2.54, P = 0.090). The low number of stream replicates (three sites per treatment) also reduced our ability to detect differences.

Benthic shredder densities in YG streams were significantly higher than in OG streams (Table 6) (F $stat_{veg}$ = 9.80, P = 0.006). Young benthic shredders (e.g., early-instar leuctrid, nemourid, and peltoperlid stoneflies) were an abundant component of benthic densities in YG streams; on average, these taxa were 82% more abundant in YG streams than OG streams. There were not significant differences in shredders among sampling dates (F $stat_{time}$ = 2.54, P = 0.064) or among basin pairs (F $stat_{basinpair}$ = 2.28, P = 0.132). Shredder densities were generally highest in June, except in WS-2, and decreased by November. The timing of lowest shredder numbers was not consistent across streams, ebbing anytime from November through May. Benthic shredders were commonly represented in both forest types by numerous stonefly (Plecoptera) taxa including *Yoraperla* Ricker, 1952 (Peltoperlidae); early-instar Peltoperlidae, *Zapada* Ricker, 1952 (Nemouridae); early-instar Nemouridae, *Despaxia* Ricker, 1943 (Leuctridae); and *Moselia* Ricker, 1943 (Leuctridae). No benthic shredders were collected only in OG streams. Scrapers were a smaller proportion of the benthic abundance than shredders and their proportions varied greatly. In low- and mid-elevation basin pairs, scraper proportions were higher in OG than in YG, except in June in WS-A; in contrast, proportions of scrapers were greater in the stream through YG in the high-elevation basin pair.

In NMS ordinations, differences in benthic community composition between OG and YG sites were not apparent, and therefore are not presented. However, seasonal contrasts between communities were identified along axis 1, with June, 2003 samples grouping to the right (Figure 2a); March and May, 2004 samples appeared mid-axis. Canopy cover, which was highest in June, was positively correlated with axis 1, while stream widths and
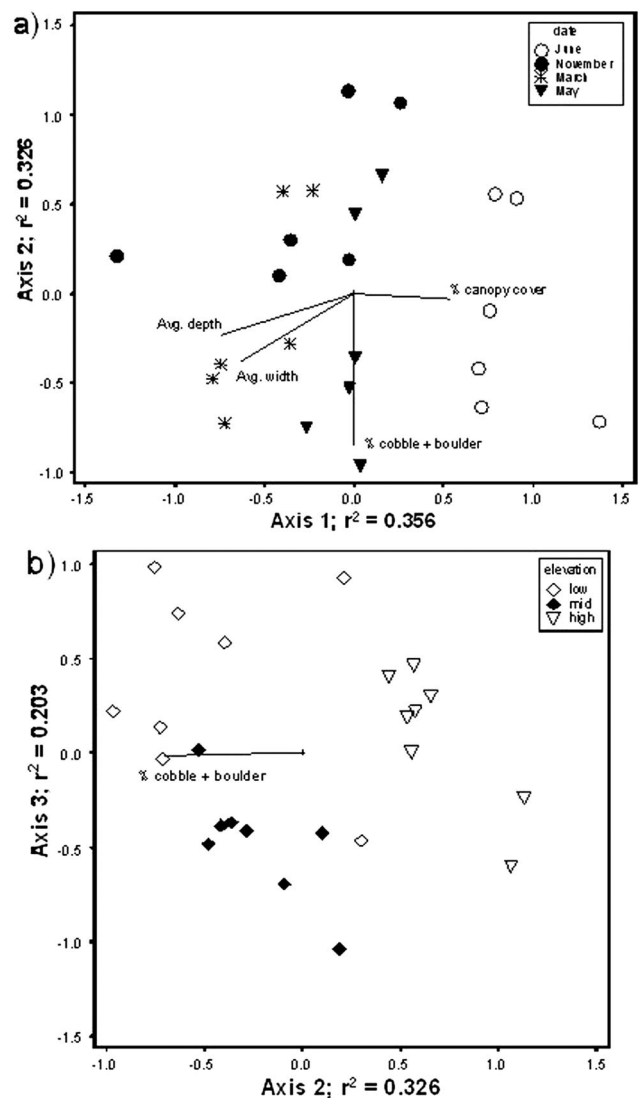

Figure 2. NMS ordinations of benthic macroinvertebrate communities across all streams and dates with samples grouped by (a) date and (b) basin pair (elevation). Each point represents the average community structure from six individual samples per stream per date.

depths, which were higher in November and March, were negatively correlated with axis 1. High-elevation sites of WS-7 and -8 separated out from the other sites along axis

2 (Figure 2b). Percentage cobble + boulder substrates correlated with axis 2 ($r = -0.75$), in association with the low- and mid-elevation basin pairs. Total variation explained by the NMS ordination was 88.4% for the three dimensions (stress level, 10.2; instability, 0.00008). When benthic communities within basin pairs were examined separately with NMS (Figure 3), we o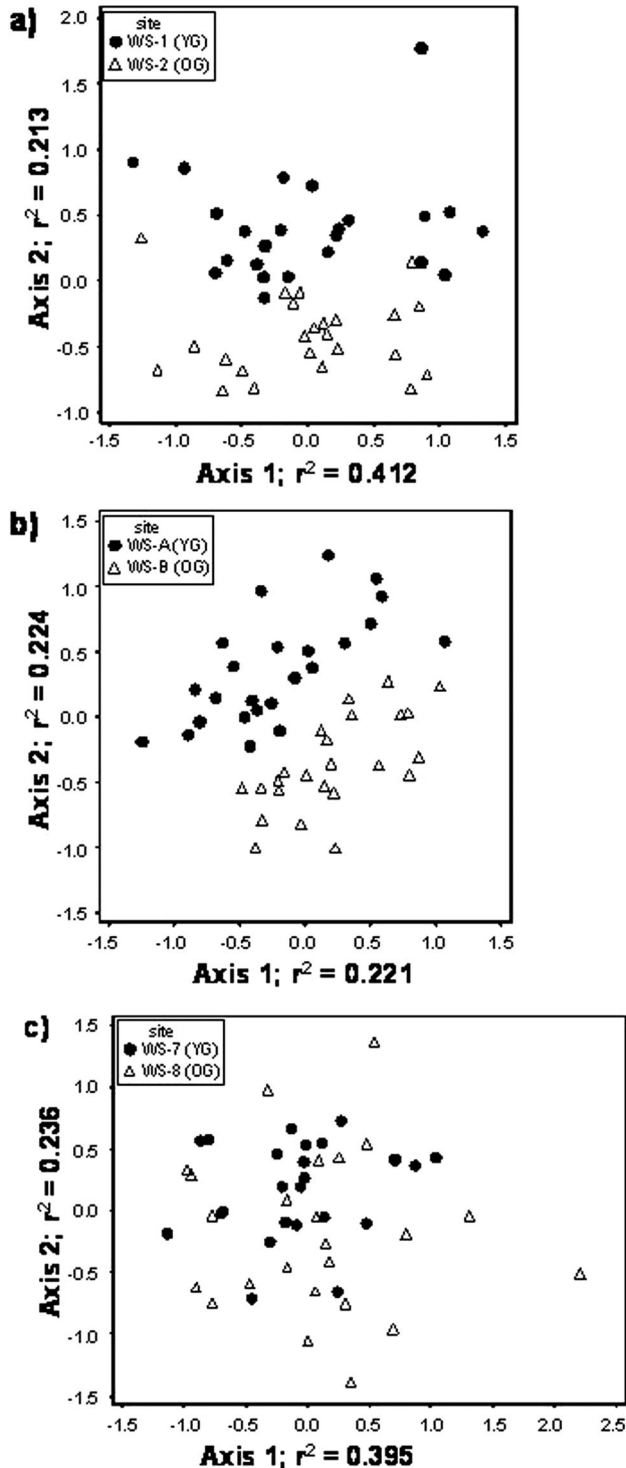bserved strong differences in benthic community structure between OG and YG sites at low and mid elevations (Figure 3a, b), but not in the high-elevation basin pair (Figure 3c). The low- and mid-elevation YG sites had abundant alder riparian cover, while no alder occurred at the high-elevation YG site.

Few benthic taxa were distinctive of YG or OG according to indicator species analysis. Only four taxa, two in YG and two in OG, were identified as significant indicators of forest type ($P \leq 0.05$). True-fly larvae of the genus *Oreogeton* Schiner, 1860 and larval caddisflies of the genus *Lepidostoma* Rambur, 1842 were found in higher abundances and more frequently in OG sites. True-fly larvae of the genus *Dixa* Meigen, 1818 were found almost exclusively in YG sites. Early-instar Perlodid stoneflies were indicators of YG sites; these nymphs were likely one or more of the genera *Caliperla* Banks, 1947, *Chernokrilus* Ricker, 1952, *Isoperla* Banks, 1906, or *Megarcys* Klapálek, 1912.

Emergence

Taxa richness of emergent taxa was similar between OG and YG (Figure 4). Greatest taxa richness occurred in June and decreased dramatically during fall and winter, when emergence rates were also low. Richness was higher in June, 2003 than June, 2004.

Emergence rates of adult aquatic insects were not consistently related to vegetation age (Figures 5 and 6). Diptera composed a substantial proportion of emergence, but Ephemeroptera, Plecoptera, and Trichoptera were also important. High rates of emergence were observed in one YG stream, WS-1, in early May and late June, 2004 (Figure 5a). At its paired OG stream (WS-2), emergence rates rose in June but not to the same levels. In the mid-elevation basins, the OG stream had higher rates of emergence than the YG stream (Figure 5b); the highest rates in WS-B occurred in June, 2004. In OG streams in late fall 2003, a small pulse of emergence occurred at both low and mid elevations (Figure 5). Emergence rates from high-elevation streams were lagged and followed a unimodal pattern (Figure 5c). The highest rates in high-elevation basin pairs occurred in late June, 2003. In June, 2004, however, the rates were lower, likely influenced by climatic differences between years and lower cumulative
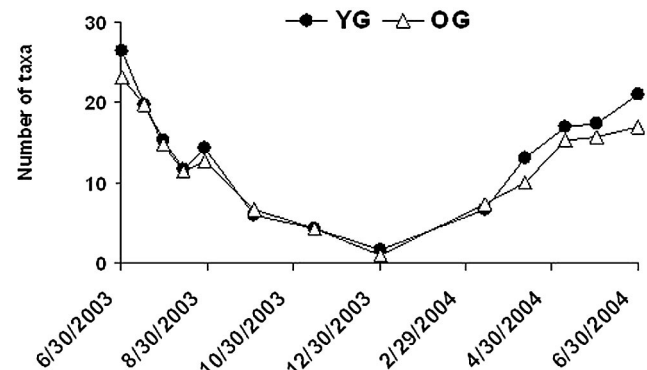

Figure 3. NMS ordinations of benthic macroinvertebrate communities across all dates for (a) low-elevation basin pair, (b) mid-elevation basin pair, and (c) high-elevation basin pair. Each point represents an individual benthic sample from each stream per date.

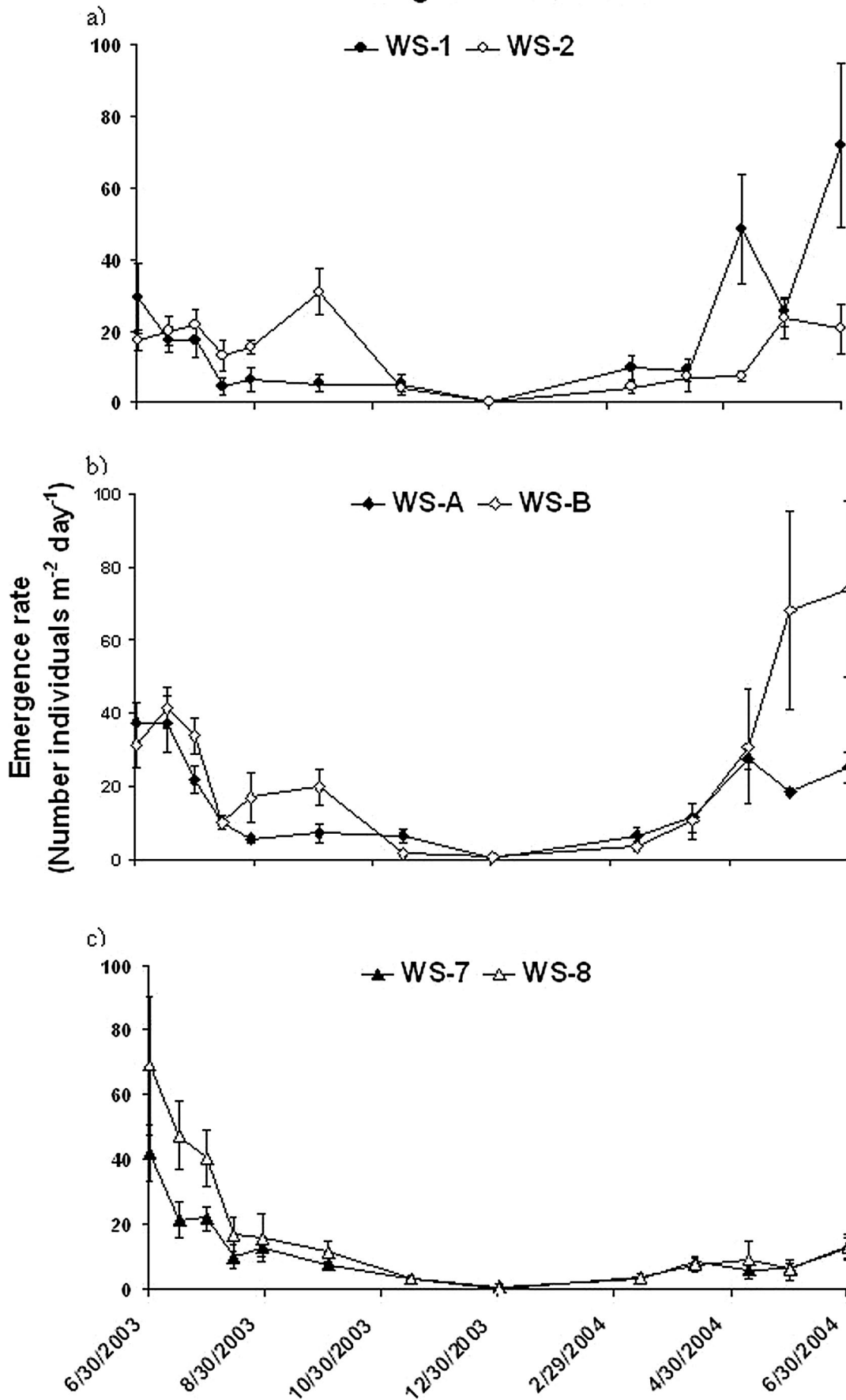Figure 4. Average taxa richness for emergence samples. Solid symbols are YG, open symbols are OG.

Figure 5. Emergence rates of insects (±SE) from June, 2003 to June, 2004. Solid symbols are YG, open symbols are OG. (a) Low-elevation basin pair; (b) mid-elevation pair; (c) high-elevation pair.
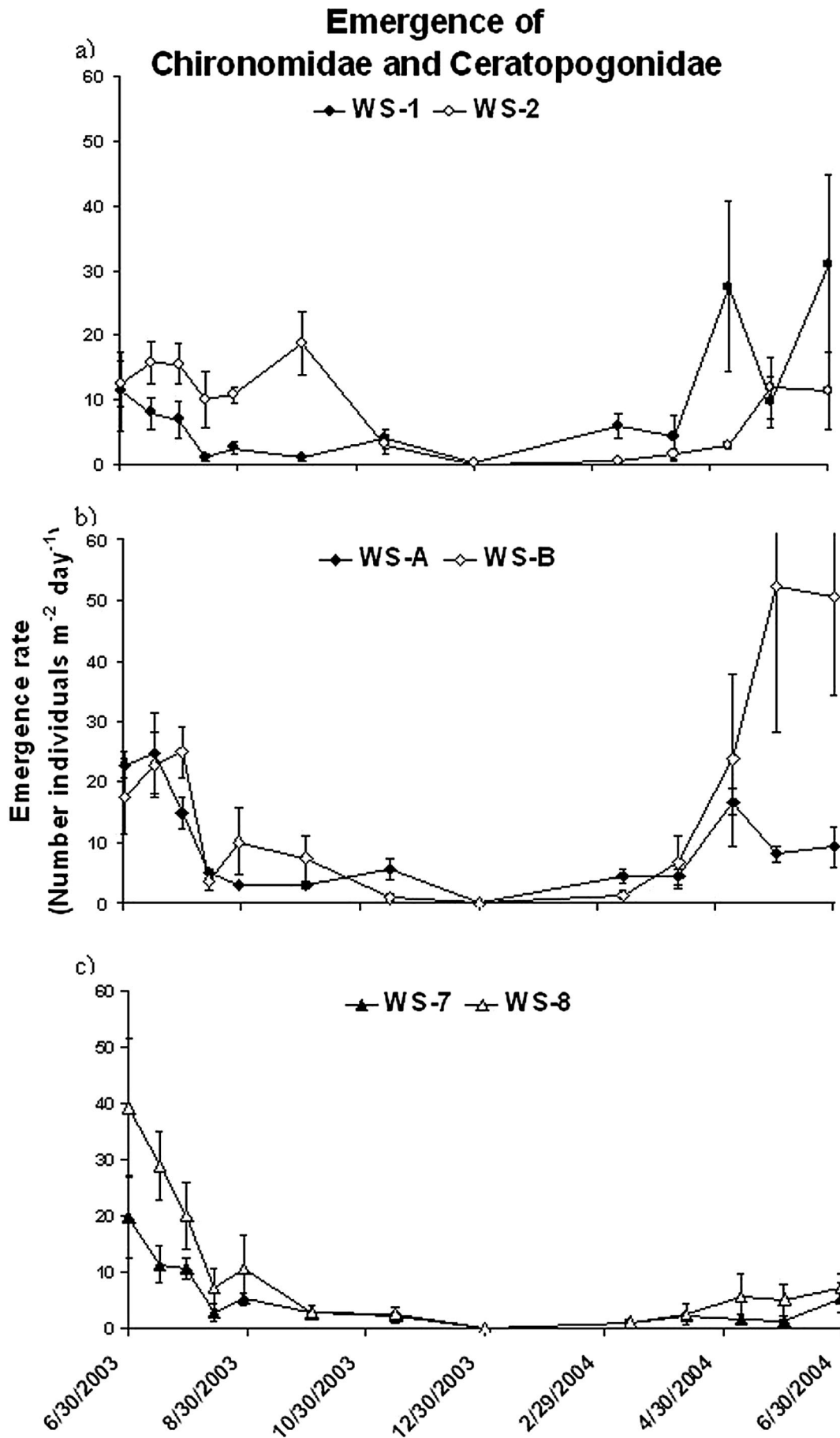
Figure 6. Emergency rates of only Chironomidae and Ceratopogonidae (±SE) from June, 2003 to June, 2004. Solid symbols are YG, open symbols are OG. (a) Low-elevation basin pair; (b) mid-elevation pair; (c) high-elevation pair.

degree day temperatures in June, 2004 than in 2003 (Frady 2006). Chironomidae and Ceratopogonidae contributed to the high rates of emergence in both OG and YG basins (Figure 6).

A comparison of emergence patterns with cumulative stream temperatures suggests an association between this life history phenomenon and temperature (Figure 7). Cumulative degree-days in 2004 (calculated as the sum of daily average stream temperature in gauged basins beginning January 1) showed greater accumulation of temperature in the lower-elevation basins than in the high-elevation basins (Figure 7, top). Within basin pairs, YG sites gradually accumulated more cumulative temperature by late June than their OG counterparts. Cumulative emergence was greatest in WS-1, a YG site (Figure 7, bottom). In WS-7 and WS-8, the high-elevation basin pair, cumulative emergences were equivalent, possibly related to climatic lags in emergence rates observed in those basins during the study. Although temperature data from the mid-elevation streams were not available, the slightly more open riparian canopy in May in WS-B (87%) compared to WS-A (93%) might have contributed to potential differences in temperature and higher emergence rates from WS-B.
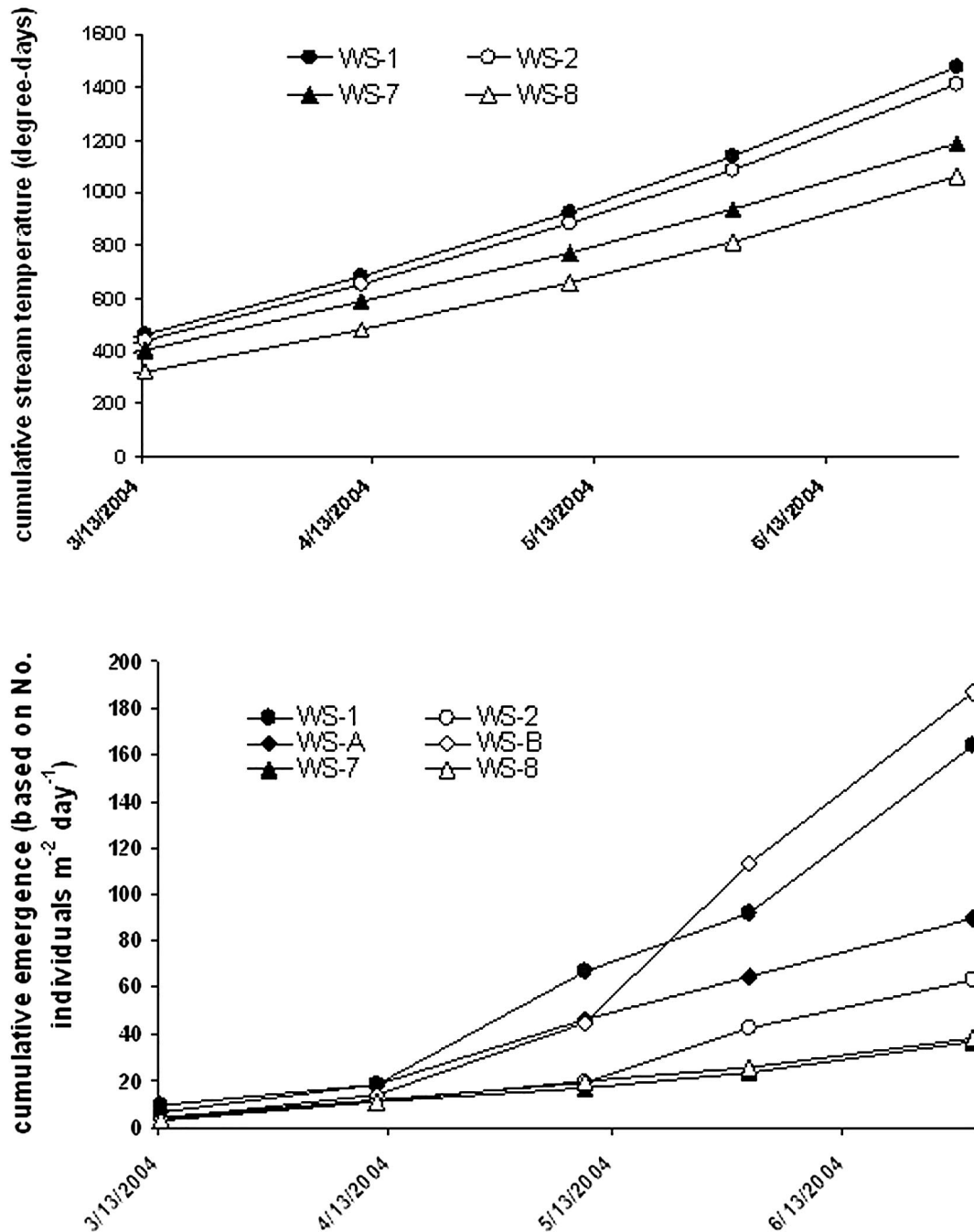

Figure 7. (Top) Cumulative stream temperature (degree-days) calculated beginning January, 2004. (Bottom) Cumulative rate of emergence calculated from samples collected from March, 2004 through June, 2004. WS-1 and -2 are low-elevation, WS-A and -B are mid-elevation, and WS-7 and -8 are high-elevation basin pairs. Solid symbols are YG, open symbols are OG.

Discussion

Previous studies at the H. J. Andrews Experimental Forest described the importance of canopy openings shortly after timber harvest to macroinvertebrate communities (Murphy et al. 1981, Hawkins et al. 1982). Two to four decades postharvest, streams through YG have similar densities and taxa richness of benthic and emergent macroinvertebrates as streams through OG. However, effects of deciduous riparian vegetation including seasonal canopy openings and litterfall continue to influence patterns of macroinvertebrate responses to forest harvest over longer time spans, as shown by higher densities of shredders in YG sites, timing of emergence within basin pairs, and assemblage differences within two of the basin pairs.

Results from our study and others following forest harvest suggest higher shredder densities may be a continuing legacy of prior disturbance many years after harvest. Soon after harvest, increased light levels and subsequent availability of algal resources have been shown to lead to increased numbers of scrapers (Murphy et al. 1981, Wallace et al. 1988). Over time, with reestablishment of overstory canopy in harvested riparian areas, shredder taxa are likely to become more abundant in association with increased autumnal leaf litter inputs (Cummins et al. 1989). In a study of streams that flow through hardwood riparian forests of Georgia, scraper abundances declined 5 years postharvest while numbers of collectors increased (Wallace et al. 1988); after 16 years, shredders had also increased (Stone and Wallace 1998). Likewise, in a study of 40 Oregon Coast Range headwater streams, Cole et al. (2003) observed dominance by shredders and detritivorous taxa, not scrapers, in streams through young-growth riparian forests. Thirty to forty years after forest harvest, we found higher shredder densities in streams through YG and no scraper taxa that were indicators of or uniquely represented in YG sites.

As observed in other studies (Triska et al. 1982, Stone and Wallace 1998), we found differences in the kinds of allochthonous litter and in timing of inputs from riparian forests with differing vegetation, yet there was no net difference in annual biomass of litter into our YG and OG streams. Deciduous vegetation, such as red alder and vine maple observed in riparian areas of YG study sites, can be a highly nutritious resource for stream macroinvertebrates (Petersen and Cummins 1974, Cummins and Klug 1979, Cummins et al. 1989). In eastern hardwood forested streams (Stone and Wallace 1998), benthic invertebrate abundances were three times greater and biomass was double in streams through deciduous forests. Several recent studies have found increased drift rates associated with alder sites (Piccolo and Wipfli 2002, Wipfli and Musselwhite 2004). Although we detected differences in shredder densities, there were none in either macroinvertebrate density or richness, traditional metrics used to evaluate responses to disturbances and associated with variations in riparian vegetation through YG or OG.

Immediately following disturbances in headwaters, such as clearcuts (Banks et al. 2007) or fires (Mellon 2006), distinctive instream invertebrate taxa and assemblages were associated with disturbed sites. In our study, which occurred decades after harvest, instream and physical differences between previously harvested and OG sites were more subtle, and identifying indicator taxa for streams in each riparian type was difficult. We had predicted that we would find taxa representative of streams through OG or YG forests, but our low sample size limited the replication and statistical power of our study. The study design was constrained by the number of streams of appropriate forest age, size, and pairing, as well as by time necessary for macroinvertebrate identification.

Evaluating similarities and differences among streams is complicated by the variability or patchiness of invertebrate distributions (Li et al. 2001). In part due to the natural variability among sites, even within an area of the size of Lookout Creek Watershed, multivariate ordinations of overall community composition did not segregate sites as OG or YG. Taxonomic similarities between and among our study streams suggest conditions for successful dispersal between streams overcame riparian differences, resulting in high benthic and emergent taxa richness. In regional summer studies, median benthic richness was 41 taxa in headwaters in western Oregon and a mean of 45 in the Oregon Coast range (Herlihy et al. 2005). In our study, taxa richness was consistently higher than in the regional studies during summer and high throughout the year. These levels of richness suggest healthy larval growth and successful adult dispersal were supported by suitable upland forest, riparian, and instream habitats.

Headwater streams can exhibit a wide range of variability of physical parameters. Recent experiments in British Columbia demonstrated that similarities in hydraulic and food resource availability can greatly influence the microdistribution of detritivores (Negishi and Richardson 2006). In our study, multivariate ordinations of overall community composition showed that macroinvertebrate communities in the high-elevation basins were different from those in other basin pairs; macroinvertebrates probably responded not only to temperatures associated with elevational differences, but also to lower discharge, deeper soils, and finer substrates (Williams et al. 2002, Cole et al. 2003, Herlihy et al. 2005). We expected that basin pairs, where adjacent streams were matched by basin size, aspect, elevation, microclimatic influences, geology, and stream substrates, would have been most likely to reveal differences between YG and OG sites due to macroinvertebrate behavioral affinities for similar habitat conditions. Only in comparisons within basin pairs were we able to detect assemblage-level differences associated with alder domination of YG riparian vegetation.

Our study benefited from multiple approaches to assessing long-term effects of disturbance, as recommended by Resh et al. (1988). By complimenting benthic with emergence sampling, we examined potential temporal responses related to seasonal differences in canopy cover between YG and OG streams. Stream insects often emerge in response to cues from photoperiod (Marten and Zwick 1989, Dieterich and Anderson 1995), temperature (Anderson and Cummins 1979, Short and Ward 1981, Sweeney and Vannote 1986), or streamflow (Steedman and Anderson 1985, Lytle and Poff 2004). Cumulative temperatures at low elevations in

our study increased more quickly than at higher elevation, and emergence peaks at low-elevation YG occurred much earlier than at the corresponding cooler OG site, likely facilitated by canopy opening during spring.

Conclusions

Whether there is a legacy of effects of forest harvest depends in part on the metric used to evaluate macroinvertebrate responses. Standard metrics of abundance and richness suggested these YG sites did not differ from OG. However, higher densities of shredders in YG sites, in combination with temporal differences in emergence patterns, revealed these instream communities were not entirely similar to their OG counterparts. Analysis of basin pairs, which controlled for variability of physical conditions among headwater streams, highlighted subtle differences in community composition in those streams where alder had regenerated in riparian areas after forest harvest. As forests reach the age of re-harvest (e.g., after 40 years in the Pacific Northwest), monitoring macroinvertebrate communities for effects of past or future harvest may require not only traditional measures of abundance, but would best include metrics responsive to changes in life history and resource availability.

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