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HEADWATER RIPARIAN FOREST-FLOOR INVERTEBRATE COMMUNITIES ASSOCIATED WITH ALTERNATIVE FOREST MANAGEMENT PRACTICES

Jessica J. Rykken,[1,3] Andrew R. Moldenke,[1] and Deanna H. Olson[2]

[1]*Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331 USA*
[2]*Pacific Northwest Research Station, USDA Forest Service, Corvallis, Oregon 97331 USA*

Abstract. Headwater streams and their riparian zones are a common, yet poorly understood, component of Pacific Northwest, USA, landscapes. We describe the ecological importance of headwater stream riparian zones as habitat for forest-floor invertebrate communities and assess how alternative management strategies for riparian zones may impact these communities. We compared community composition of forest-floor invertebrates at increasing distances along trans-riparian (stream edge to upslope) transects in mature forests, clearcuts, and riparian buffers of ~30-m width with upslope clearcuts. Invertebrates were collected using pitfall traps in five replicate blocks of three treatments each in the Willamette National Forest, Oregon, USA. We measured microclimate and microhabitat variables at pitfall locations. Despite strong elevation and block effects on community composition, community analyses revealed a distinct "riparian" invertebrate community within 1 m of the stream edge in mature forest treatments, which was strongly related to cool, humid microclimate conditions. Invertebrate community composition in buffer treatments was far more similar to that of mature forests than to clearcuts; a pattern mirrored by microclimate. These results suggest that, within our study sites, forest-floor invertebrate distributions are strongly associated with microclimate and that riparian buffers of ~30-m width do provide habitat for many riparian and forest species. Riparian reserves may serve as effective forest refugia and/or dispersal corridors for invertebrates and other taxa, and their incorporation into watershed management plans likely will contribute to meeting persistence and connectivity objectives.

Key words: ecotone; forest-floor invertebrate communities; forest management strategies; headwater stream; microclimate, Pacific Northwest, USA; riparian reserves.

INTRODUCTION

Riparian zones are considered to be one of the most biologically diverse and ecologically complex components of Douglas-fir forests in the Pacific Northwest, USA (Naiman et al. 1998, Pollock 1998). As ecotones between aquatic and upland terrestrial systems, riparian zones typically encompass steep environmental gradients, and are prone to frequent disturbance events such as flooding and debris flows. Consequently, riparian zones often comprise a heterogeneous mosaic of microhabitats, where species composition may be distinctive (Sabo et al. 2005) and biological diversity is assumed to be higher than in the surrounding upslope forests (Gregory et al. 1991, Naiman and Décamps 1997). Indeed, such patterns of high alpha and/or beta diversity across riparian ecotones have been documented in plants (Nilsson et al. 1989, Naiman et al. 1998, Pabst and Spies 1998), vertebrates (Doyle 1990, McComb et al. 1993, Lock and Naiman 1998), and invertebrates (Moring and Stewart 1994, Andersen 1997, LaBonte 2002). While most models of riparian diversity have been developed on mid- to high-order streams and rivers, headwater streams (i.e., first- or second-order), which comprise upwards of 70% of the lotic network within a watershed (Meyer and Wallace 2001), have received little attention (Moore 2005). Whether or not riparian zones associated with small streams exhibit similar patterns of high diversity or distinctive species composition has not been well-documented, and is an urgent research need (Richardson et al. 2005).

In the heavily harvested landscapes of Pacific Northwest forests, riparian management strategies have reflected this gap in our knowledge of headwater stream riparian ecology. Beginning in the mid-1970s, the degree of protection afforded a stream, in the form of a forested riparian "buffer," was determined by stream size and the presence of fish (e.g., salmonids). Such buffers were expected to provide benefits to the aquatic biota by shading the water and stabilizing the stream banks (Castelle et al. 1994, Gregory 1997). In contrast, non-fish-bearing headwater streams received little to no

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[3] Present address: Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138 USA.
E-mail: jrykken@oeb.harvard.edu

protection. With the growing realization that headwater conditions are linked to downstream productivity and habitat (Vannote et al. 1980, Gomi et al. 2002), and that riparian buffers not only serve to protect fish habitat but also may provide important breeding or foraging habitat and dispersal corridors for terrestrial organisms (Hagar 1999, Cockle and Richardson 2003, Hylander et al. 2004), new regulations regarding riparian buffers and reserves along streams (including non-fish-bearing headwaters) have been developed at both state and federal levels (USDA and USDI 1994, Young 2000). On United States federal lands in the western Pacific Northwest, the Aquatic Conservation Strategy specifies interim guidelines for riparian buffer widths of one site potential tree height (a minimum of ~30 m) along non-fish-bearing headwater streams, including ephemeral reaches (USDA and USDI 1994). In the region's highly dendritic landscapes, even modest riparian buffers have the potential to take a large amount of land out of timber production. For example, an interim riparian model for a small watershed in the Willamette National Forest designated up to 53% of the drainage basin area as riparian reserves (Sedell et al. 1994). Not surprisingly, the new riparian management strategies have raised concerns among forest managers.

Although riparian management strategies have been implemented for only the last 30–40 years (on larger streams), riparian buffers may now represent one of the few intact forest remnants in a rotating patchwork of clearcuts and regenerating stands. As linear forest fragments, riparian buffers may provide critical habitat or refugia for forest species (Hylander et al. 2004), or serve as connecting corridors between larger mature forest fragments (Harris 1984, Saunders et al. 1991). However, the narrow, elongate shape and high edge-to-interior ratio characteristic of riparian buffers also may make them subject to a suite of biotic and abiotic "edge effects," potentially altering their species composition and diversity. Indeed, research documenting microclimatic edge effects penetrating up to 240 m into upland forest (Chen et al. 1995), and direct biological effects as much as 100 m into the forest (Murcia 1995, Didham et al. 1998, Work 2000) suggest that riparian buffers of 30–75 m on each side of the stream (the range of widths presently implemented for non-fish-bearing streams under the federal Northwest Forest Plan) may comprise essentially all "edge" habitat. For obligate riparian or forest interior species negatively affected by edge effects such as altered microclimate, riparian buffers could theoretically represent "sink" habitats, affecting population dynamics at the landscape level (Pulliam and Danielson 1991). Likewise, fragmented riparian buffers may negatively affect populations using riparian buffers as dispersal corridors between other streams or larger forest patches (Fagan 2002).

As the region's scientists and managers work toward implementing effective and sustainable management strategies, there is clearly a need to learn more about the ecological importance of headwater stream riparian zones as habitat for forest species, and how forest diversity and function may be affected by various riparian management practices (Richardson et al. 2005). Forest-floor invertebrates are a critical group to consider in riparian systems because of their sheer diversity and abundance, as well as their functional importance in forest ecosystem processes (e.g., decomposition, nutrient recycling; Schowalter 2000). A range of mobility and sensitivity to environmental gradients (such as microclimate) among taxa also makes invertebrates ideal for studying patterns of habitat partitioning, dispersal between habitats, and community responses to human-caused disturbances such as fragmentation (Kremen et al. 1993, Niemelä et al. 1993, Didham et al. 1998). For these reasons, invertebrates have been used worldwide as biological indicators in ecological studies focused on inventory and monitoring (Kremen 1992, Pearson 1994, Rykken et al. 1997). In this study, we compared the effects of three alternative headwater riparian management strategies on the distribution of forest-floor invertebrates along a gradient from stream edge, through the riparian zone, and into the adjacent upslope forest. Focal taxa included 32 families of ground-dwelling beetles, spiders, millipedes, and gastropods, representing a broad range of functional groups and dispersal capabilities.

Specifically, we compared invertebrate community composition across three management treatments on headwater streams in western Oregon, USA: old-growth forest with an intact riparian zone; and harvested units with and without the preservation of a 30 m wide forested reserve, or buffer, on either side of the stream. Our objectives were: (1) to determine whether there is a distinctive "riparian" invertebrate community associated with headwater streams in mature (control) low- to mid-elevation forests of the western Cascade Range; and (2) to determine the necessity and/or effectiveness of 30 m wide riparian forest buffers for preserving the riparian and forest invertebrate fauna by comparing community composition and diversity in mature forest, buffer, and clearcut sites. For both objectives, we examined relationships between community composition, microclimate, and environmental variables to explain invertebrate distribution patterns, and identified individual invertebrate species as effective indicators of different habitat types.

METHODS

Study area

Study sites were located in the Sweet Home Ranger District of the Willamette National Forest, on the western slope of the Cascade Range in Oregon, USA (44°19′–44°33′ N, 122°09′–122°23′ W; Rykken 2004). The regional climate is broadly characterized as having wet, mild winters, with snow accumulation at higher elevations, and warm, dry summers (Franklin and Dyrness 1988). Forest canopies at mid-elevations are

TABLE 1. Characteristics of 15 riparian study sites in the Cascade Range, Oregon, USA.

Block	Treatment†	Elevation (m)	Stream aspect	Mean stream width (m)	Mean buffer width (m)‡	Harvest unit area (ha)	Harvest year(s)
2G	forest	1146	W	3.5			
2G	buffer	1146	NW	2.9	26.3	10.9	1995
2G	clearcut	1268	NW	1.2		8.5	1993
BP	forest	439	W	2.1			
BP	buffer	512	E	1.7	29.8	4.9	1994
BP	clearcut	415	W	1.5		7.3	1989
MM	forest	1097	NW	2.5			
MM	buffer	1000	N	3.8	29.8	16.2	1994
MM	clearcut	1097	SE	2.4		12.6	1978, 1995
SP	forest	1073	E	3.4			
SP	buffer	1122	NE	1.5	28.6	5.3	1994
SP	clearcut	1073	N	2.6		9.7	1986, 1999
TC	forest	610	W	3.6			
TC	buffer	561	NW	5.1	34.3	19.0	1994
TC	clearcut	561	W	1.2		14.6	1989

† Treatment labeled "forest" represents the old-growth forest control.
‡ Measurement is mean buffer width on either side of the stream.

dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and, at higher elevations, by Pacific silver fir (*Abies amabilis*; Franklin and Dyrness 1988). Shrub and herb communities within these forests vary with elevation, soils, moisture availability, and other variables, but commonly include vine maple (*Acer circinatum*), rhododendron (*Rhododendron macrophyllum*), red alder (*Alnus rubra*), Oregon-grape (*Berberis nervosa*), salal (*Gaultheria shallon*), and sword fern (*Polystichum munitum*).

Site selection

We selected 15 first- or second-order headwater stream sites in low- to mid-elevation drainages (Table 1). Five sites represented each of three treatment types: (1) old-growth forest on either side of the stream with contiguous forest upslope (control); (2) forested riparian buffer of ~30 m in width on either side of the stream with clearcut harvest upslope; and (3) clearcut harvest with minimal to no tree retention in the riparian zone. First, we identified potential riparian buffer sites (riparian forest reserves with no tree removal allowed) from aerial photos, and field checked those sites with riparian buffers along headwater streams that were ≥25 m in width (on either side of the stream) and ≥200 m long. We used five riparian buffer sites that met these criteria, each in a different subdrainage. Then, one mature forest site and one clearcut site within the same subdrainage was matched with each riparian buffer site to form a total of five replicate blocks with three treatments each. Sites within a block were located within 4 km of each other, and in four blocks, two of the three treatments were located on the same stream (separated by a minimum distance of 250 m). Three blocks were at higher elevations (1000–1268 m) and two blocks were at lower elevations (415–610 m). Because sites were not randomly selected, all inferences are limited to the 15 sites within these five blocks (Table 1). Forested control sites and forested portions of the buffer sites had never been harvested, with the exception of a very light thinning upslope in the control site of the 2G block. Clearcuts had been harvested between 5 and 22 years previously (clearcuts adjacent to riparian buffers were all 5–6 years old), were burned 0–3 years post harvest, and then replanted within a year after burning. All clearcut sites were in early stages of succession, with no developed canopy, although three of the sites (in blocks BP, TC, and SP) had a dense, narrow (2–5 m) shrub buffer of predominantly red alder and vine maple adjacent to the stream (Table 1).

Sampling design and methods

At each site, two sampling transects were located on opposite sides of the stream, perpendicular to the stream course. Transects were 70 m long in the forested control sites, and 20 m long in the clearcut and buffer sites. Transects were offset from each other by at least 10 m, and located approximately in the middle of the harvested or forested stand, a minimum of 100 m from the upstream/downstream unit boundaries. Where two sites within a block occurred on the same stream, site transects were located ≥250 m apart.

We sampled invertebrates with plastic pitfall traps (11 cm diameter at the mouth × 13.5 cm deep). Inside each trap we placed a smaller (5 cm deep) interchangeable plastic cup containing equal parts water and propylene glycol as preservative. We fit an aluminum funnel with a 2–3 cm opening at the bottom into the top of the trap to help exclude small vertebrates (i.e., small mammals, amphibians) from the traps, and to keep nimbler invertebrates inside the traps once caught. Each pitfall trap was covered with a flat aluminum roof (15 × 15 cm) supported by nails to keep out rain and organic debris, while allowing invertebrates access. Pitfall trapping has been used extensively in landscape-scale studies comparing the distributions, activity, and density of ground-dwelling arthropods (Niemelä et al. 1993, Rykken et al.

1997, Buddle et al. 2000). Although trapping efficiency can be highly variable between species, seasons, and habitats (Spence and Niemelä 1994), pitfall data gathered for two growing seasons in this study were expected to provide a measure of relative "activity-density" (Thiele 1977) within species across riparian gradients and management treatments, rather than a true estimate of diversity or abundance.

Pairs of pitfall traps were installed at each of four or five distances from the stream along each transect: 1, 5, 10, and 20 m in the buffer and clearcut sites; and also at 70 m in the forested control sites. In order to avoid depletion of more mobile species and thus potentially alter community structure (Digweed et al. 1995), we located traps within a pair ~10 m apart, and pairs were offset on either side of the transect so that every trap was located at least 10 m from all other traps.

We sampled invertebrates in six discrete events: from 16 August to 18 September 2000; from 18 May to 7 June 2001; from 17 June to 6 July 2001; from 31 July to 17 August 2001; from 13 September to 1 October 2001; and from 31 May to 5 July 2002. During each sampling event, traps were opened for ~14 days within any one block, except for the 2000 sampling event, when traps were open for 25 days in each block. All sites within a block were sampled simultaneously, and all blocks were sampled within a few days of each other, except in 2002 when higher elevation sites were accessed as soon as they were snow free (all blocks sampled within a 5-wk period). We did not sample the MM block in May–June 2001 due to snow cover. Traps were closed between sampling events by a tight-fitting lid.

Focal taxa comprised members of 9 orders and 32 families. We identified mature specimens and immature gastropods to the lowest taxonomic level possible, primarily to species level. We deposited voucher specimens of all taxa in the Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA.

In 2002, we installed one microclimate data logger (GPSE 301 203 (THT-HR) Humidity and Dual Temperature Datalogger; AR Harris GPSE, Christchurch, New Zealand) at each pair of pitfall traps 1, 10, and 20 m (and at 70 m in the forest sites) from the stream, along one randomly selected transect per site, at all 15 sites. Each data logger recorded soil temperature ~2–3 cm below the substrate surface, and ambient air temperature and percentage relative humidity ~20 cm above the substrate surface (as low to the ground as possible without creating an artificial microclimate under the inverted cup protecting the sensor). All loggers were calibrated in climate-controlled conditions and were accurate to within 0.3°C for air and soil temperature, and within 4% for relative humidity.

Microclimate parameters were sampled at two blocks (six sites) simultaneously. We sampled microclimate at all five blocks in late spring/early summer (between May 31 and July 13; average of 12 sampling days per block), and again in late summer (between August 27 and September 23; average of six sampling days per block). Although the microclimate sampling (2002) and most of the pitfall trapping (2001) were asynchronous, general microclimatic patterns among treatments were observed to be similar in a pilot study in 2001 (when just two blocks were sampled) and in 2002.

We estimated percent cover of herbaceous vegetation, moss, bare mineral soil, and coniferous and hardwood leaf litter in a 1 × 1 m plot next to each pitfall trap (16 or 20 per site depending on treatment). To characterize shrub cover, we set up a 2 × 10 m sampling plot at each sampling distance on each transect (8 or 10 per site). The sampling plot was oriented parallel to the stream, and encompassed both pitfall traps at a given distance. Within each plot, we counted the number of live woody stems >1 m tall and <10 cm diameter at breast height (dbh) by species. Trees and snags were assessed in plots measuring 4 × 20 m, encompassing and extending the shrub plots described above (8 or 10 per site). We halved the plot size to 2 × 20 m for plots at 1 m from the stream because the full plot would have extended into the stream. We counted and measured the dbh of all live woody stems >10 cm dbh by species, if any part of the stem fell within the plot. We also measured the dbh of standing dead woody stems >10 cm dbh and >1 m tall (snags). All dbh measurements were converted into basal area (m^2/ha) for analyses. We used a line-intercept method to measure large woody debris (i.e., all stumps and downed wood ≥10 cm in diameter, of any length) that crossed a 10-m transect line running along the center of the shrub plot, parallel to the stream (Rykken 2004). We assigned a decay class (1–5) to each stump or piece of large woody debris, with 1 representing a recently fallen tree with bark and some limbs present, and 5 representing a tree barely discernible from the substrate (Maser and Trappe 1984).

Data analysis

Within each site, we calculated mean abundances for each invertebrate species across the four traps at a given distance from the stream over the course of a sampling period. Each of the four or five distance samples within a site was termed a "trap zone" (5 trap zones per site × 5 sites = 25 traps zones in the forest treatment; 20 trap zones each in the buffer and clearcut treatments). Trap zone mean abundances per species per sampling period were averaged with comparable abundances in all other sampling periods (six sampling periods total, but only five for the MM block).

Among environmental variables, ground cover, shrub, tree, and large woody debris plot values were averaged for each trap zone. Elevation and aspect were measured only at the site scale. We converted the measurement of aspect from degrees (1–360°) to an index of "heat load" through the following equation: heat load index = $(1 - \cos(\theta - 45))/2$ where θ is the aspect in degrees (McCune and Grace 2002). The index ranges from 0 (coolest northeast slope) to 1 (warmest southwest slope).

Microclimate data (air and soil temperature, relative humidity) were compiled in the following way: for each trap zone, we first averaged the 1500-hr value over the two hottest consecutive days of the sampling period; next, for each trap zone, we averaged these values over the two microclimate sampling seasons (early summer and late summer, 2002). These variables were meant to represent extremes in microclimate (i.e., summer afternoon high temperature and low relative humidity), which might affect the activity of some invertebrates.

We used several diversity measures to characterize invertebrate communities at each trap zone: species richness (S); the Shannon-Wiener diversity index (H; Shannon and Weaver 1949); and proportions of all species within three functional groups (predator, detritivore, herbivore), and within four taxonomic groups (beetles, gastropods, millipedes, spiders). These measures were based on the accumulated totals of species occurring in each trap zone over the five sampling periods in which all blocks were sampled.

We used multivariate community analyses (PC-ORD software; McCune and Mefford 1999) to examine patterns of association among taxa relative to distance from the stream, treatments, and environmental conditions. In order to reduce noise in the data set, we excluded species that occurred in $<5\%$ of the trap zones from all community analyses (McCune and Grace 2002). Species average abundances were log-transformed and then relativized by species maximum (thus equalizing rare and common species) in order to reduce variability among trap zones (rows) and species (columns) in the data matrix. Such transformations are well-suited to pitfall trap data where trap catches often are strongly influenced by the complexity of the surrounding substrate and species size or behavior, rather than population density. Outlier trap zones (more than two standard deviations above the mean for the average Sørenson distance [dissimilarity] between each trap zone and every other trap zone) were examined and retained because deleting them had no noticeable effect on the analyses. Environmental variables were log-transformed if the difference between minimum and maximum values was greater than one order of magnitude and/or if skewness was >1.0.

We used nonmetric multidimensional scaling (NMS; Kruskal 1964) to ordinate trap zones in species space and then to correlate community and environmental variables with axes in the ordinations. Nonmetric multidimensional scaling is a robust and effective ordination method for ecological data, which is typically non-normally distributed, and has a high proportion of zero values (Clarke 1993, McCune and Grace 2002). The method uses an iterative search for the best position of N entities (samples or species) on a reduced number of k dimensions (axes) that minimizes the "stress" of the resultant k-dimensional ordination. An ordination with low stress (<20; McCune and Grace 2002) has maximal correspondence between ranked distances in the original n-dimensional space and ranked distances in the reduced k-dimensional space. We used the quantitative version of Sørensen distance to measure dissimilarity, and used a random starting configuration for all ordinations. Forty runs with our data were performed for each ordination, and the run with the lowest stress was used for analysis. We selected three-dimensional solutions for all ordinations, as additional axes provided only small reductions in stress, but fewer dimensions increased stress to unacceptable levels (McCune and Grace 2002). We set a stability criterion of 0.00001, with the solution ending after 10 iterations within this stability (McCune and Grace 2002). We used joint plots to display the strongest correlations (Pearson's r) between quantitative community or environmental variables and the ordination axes. The proportion of variance represented by each axis in an ordination was measured by calculating the coefficient of determination (r^2) between distances in the original n-dimensional space with those in the three-dimensional ordination space.

We used blocked multiple-response permutation procedures (MRBP; Biondini et al. 1988) to test for community differences between predefined groups (i.e., distances from the stream or management treatments). This nonparametric procedure provides a measure of within-group homogeneity ($A = 1$ means that all entities within the group are identical), and a P value associated with the null hypothesis of no difference between groups. Euclidean distance was used, and medians were aligned to zero for all blocks, in order to focus the analysis on within-block differences among distances or treatments (McCune and Grace 2002).

As a complement to the MRBP, we used indicator species analysis (Dufrêne and Legendre 1997) to examine associations of individual taxa with predefined groups (i.e., distance from the stream and treatment). This method calculates an indicator value (IV, ranging from 0 to 100) for each species in each group, based on the relative abundance and frequency of the species per group (McCune and Grace 2002). A perfect indicator taxon for a group (IV = 100) would be one that occurs only in that group, and occurs in all trap zones within that group. The statistical significance of the $\mathrm{IV}_{\max}$ across groups for each species was evaluated by a Monte Carlo test using 1000 randomizations, with a null hypothesis that $\mathrm{IV}_{\max}$ is no larger than would be expected by chance alone.

Specifically, we used community analyses to address our main research questions as follows. (1) For community patterns in mature forest riparian zones, we used NMS to ordinate 25 forested trap zones (5 blocks × 1 treatment (forest) × 5 distances) in species space. We also used MRBP to look for community compositional differences between distances (1, 5, 10, 20, and 70 m from the stream; $N = 5$ trap zones for each group), and we used indicator species analysis to look for taxa strongly associated with particular distances from the stream. (2) For community patterns compared among forested, buffered, and clearcut riparian zones, we used NMS to ordinate 60 trap zones (5 blocks × 3 treatments × 4 distances) in species space. To test for community compositional differences between buffer, forest, and clearcut treatment groups, we used MRBP with sites (rather than trap zones) as within-group entities (N = 5 sites for each treatment group). Site abundances per taxon were calculated by averaging across 1-, 5-, 10-, and 20-m trap zones for each site. We used indicator species analysis to look for taxa strongly associated with forest and clearcut treatments.

Additionally, we compared diversity measures (S and H) between 1 and 20 m from the stream across all treatments, using a randomized complete block design with a repeated-measures analysis (PROC GLM in SAS, Version 8, 1999; SAS Institute, Cary, North Carolina, USA). The repeated-measures models assumed that diversity measurements made at different sites were independent, but measurements made at different distances (i.e., trap zones) within the same site were correlated. We used an unstructured model for the covariance matrix, allowing covariances for all combinations of distances to be different. Effects were considered significant at $\alpha = 0.05$.

RESULTS

Across all treatments, we captured 13 348 invertebrates in the 32 focal families, comprising 112 genera and 192 species (Appendix). The most abundant species, the wolf spider *Pardosa dorsalis*, made up 12.4% of the total catch. A few species were very abundant (nine species comprised >50% of total captures) and many species were uncommon or rare (48% of species had ≤10 captures). Invertebrate abundance varied across treatments, with clearcuts having the highest abundance per site (mean = 966 invertebrates; 95% confidence interval: 440, 1493), buffer sites having lower abundance (mean = 842; 95% confidence interval: 509, 1176), and unmanaged mature riparian forests having the fewest invertebrates (mean = 666; 95% confidence interval: 466, 866).

Community patterns in mature forest riparian zones

We identified 124 invertebrate species in the mature forest sites, and used all species for calculating diversity measures, but removed 27 rare species (occurring in only a single trap zone) from the data set for multivariate community analyses. The NMS three-dimensional solution represented a total of 91.9% of the variation in the original data (two axes shown in Fig. 1). The final solution had a stress of 8.47 (Monte Carlo test, P = 0.020), achieved after 63 iterations. We rotated the ordination to maximize the correlation of distance from the stream with axis 1; this resulted in 11.7% of the original variation being loaded onto axis 1, and 66.2% onto axis 2.

Elevation was strongly correlated with axis 2 (r = 0.943), and separated trap zones into two distinct groups of higher elevation (~1100 m) and lower elevation (~500 m) trap zones (Fig. 1). Although distance from the stream was not as strongly correlated with axis 1 (r = 0.575), four of five trap zones at 1 m from the stream clustered to the left end of the axis (solid circles; Fig. 1a, b). Trap zones between 5 and 70 m from the stream within a block clustered together in distinct groups (five ellipses, Fig. 1a), suggesting strong geographic block effects. Within three blocks, trap zones at increasing distances from the stream were ordered consecutively along axis 1. Overall, however, trap zones at 5–70 m did not cluster into distinct distance groups.

Other environmental variables that correlated strongly ($r^2 > 0.25$) with axis 2 included heat load index, percent cover of mineral soil, and percent herb cover, which all increased at lower elevations, and the density of coniferous shrubs, which increased at higher elevations (Fig. 1a, Table 2). Tree species richness showed a strong positive correlation with axis 1, and percent herb cover and heat load index were strongly negatively correlated (Fig. 1a, Table 2). Of the microclimate variables, relative humidity was very strongly negatively correlated with axis 1 (overlay on Fig. 1c, Table 2), while air temperature was strongly positively correlated with the same axis, suggesting that trap zones closest to the stream were cooler and more humid than trap zones farther from the stream. Soil temperature increased at lower elevations, perhaps related to an increased heat load index associated with aspect. The range for mean microclimate values over all trap zones was from 36.5% to 92.8% for relative humidity, from 8.9° to 30.8°C for air temperature, and from 12.0° to 22.0°C for soil temperature.

Among community diversity variables (Fig. 1b), the proportion of detritivore species (i.e., millipedes) increased at lower elevations, while the proportion of beetle and predator species increased at higher elevations. The abundances of three relatively common millipede species, *Harpaphe haydeniana haydeniana*, *Caseya dendrogona*, and *Keypolydesmus anderisus,* were strongly negatively correlated ($r < -0.500$) with axis 2 (Table 3). Abundant at higher elevations, five species of pselaphine beetles and four species of carabid beetles had strong positive associations ($r > 0.500$) with axis 2. The proportion of gastropod and herbivore species increased closer to the stream in the cool/humid microclimate, while the proportion of spider species increased in the warmer/drier microclimate. Three snail species (*Ancotrema sportella* [a predator], *Punctum randolphi*, *Striaria pugetensis*) were strongly negatively correlated with axis 1, along with the carabid beetle *Pterostichus crenicollis*. Interestingly*, Scaphinotus angulatus*, a carabid beetle that feeds on snails (Larochelle and Lariviere 2003) was strongly positively correlated with axis 1, as was the carabid *Zacotus mathewsii*.

The unique composition of the community at 1 m from the stream was supported by MRBP, which revealed a difference in species composition among distance groups (A = 0.300, P < 0.001). When the 1-m

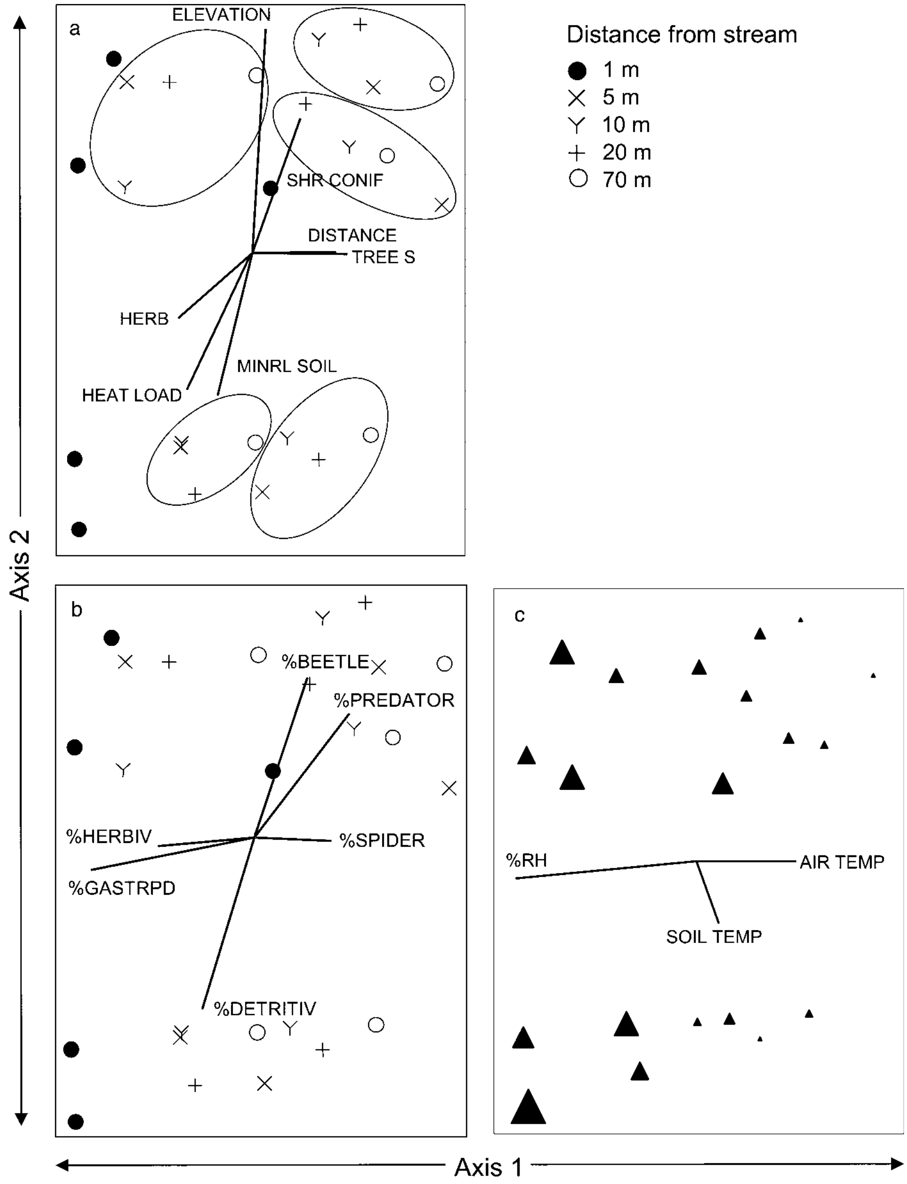

FIG. 1. Nonmetric multidimensional scaling (NMS) ordination of 25 mature forest trap zones (1–70 m from stream) in species space: only two dimensions of the three-dimensional solution are shown. (a) Vectors indicate the strength (minimum $r^2 = 0.25$) and direction of correlations between environmental variables and axis scores (variable codes are defined in Table 2). Ellipses surround trap zones at 5–70 m within the same block. (b) Community diversity variables are shown. (c) Microclimate variables are shown (no measurements taken at trap zones 5 m from the stream). The ordination is overlain with percentage relative humidity (RH) values: the size of each symbol is proportional to the magnitude of the variable (range: 36.5–92.8%).

distance group was taken out of the analysis, MRBP revealed no significant difference between the 5-, 10-, 20-, and 70-m distance groups ($A = 0.011$, $P = 0.124$).

Indicator species analysis revealed two strong indicators of the distance group 1 m from the stream: the carabid beetle *Pterostichus crenicollis* (IV = 64.0, $P = 0.001$) and the snail *Striaria pugetensis* (IV = 49.1, $P = 0.049$). For the remaining distance groups, only *Cryphoeca exlinae* (an agelenid spider) showed strong fidelity to a particular distance from the stream (20 m; IV = 51.5, $P = 0.020$).

Community patterns compared among forested, buffered, and clearcut riparian zones

We identified a total of 191 invertebrate species from all three management treatments, but removed 60 rare species that occurred in fewer than three trap zones from the data set used for multivariate community analyses. The NMS three-dimensional solution represented a total of 83.2% of the variation in the original data. The final solution had a stress of 13.55 (Monte Carlo test, $P = 0.020$), achieved after 85 iterations. The two most

Table 2. Environmental and community diversity variables and their correlation (Pearson's r) with axes 1 and 2 displayed in the nonmetric multidimensional scaling (NMS) ordinations of forest-only trap zones (Fig. 1), and of forest, buffer, and clearcut trap zones (Fig. 2).

		Forest only		All treatments	
Variable	Variable code†	Axis 1	Axis 2	Axis 1	Axis 2
Trees					
Tree species richness	TREE S	0.612	−0.074	−0.125	0.025
Live tree basal area	LIVE BA	0.345	0.225	−0.465	0.180
Conifer basal area	CONIF BA	0.338	0.248	−0.367	0.252
Hardwood basal area	HARD BA	−0.195	−0.237	−0.198	−0.337
Snag basal area	SNAG BA	−0.041	0.365	0.260	0.324
Mean live tree dbh	DBH	−0.002	−0.078	−0.226	−0.009
Shrubs					
Shrub species richness	SHRUB S	−0.243	0.287	−0.053	−0.116
Shrub total density	SHRUB TTL	−0.178	0.497	<0.001	−0.160
Conifer shrub density	SHR CONIF	0.433	0.731	0.004	0.409
Hardwood shrub density	SHR HARD	−0.315	0.337	0.032	−0.267
Ground cover (%)					
Herb cover	HERB	−0.542	−0.507	0.182	−0.402
Moss cover	MOSS	−0.289	−0.228	−0.639	−0.227
Mineral soil cover	MINRL SOIL	−0.370	−0.754	0.509	−0.035
Leaf litter cover	LITTER	0.231	−0.311	−0.562	−0.276
Large woody debris (LWD)					
LWD (decay class 1−5)	LWD TTL	−0.017	−0.132	0.001	0.198
LWD (decay class 4−5)	LWD 45	0.232	−0.141	−0.003	−0.104
Other					
Distance from stream	DISTANCE	0.575	0.058	0.447	0.092
Heat load index	HEAT LOAD	−0.502	−0.733	0.059	−0.552
Elevation	ELEVATION	0.229	0.943	0.080	0.938
Community diversity					
Invert. species richness (S)	INVERT S	−0.090	0.044	0.526	0.290
Shannon-Wiener diversity (*H*)	INVERT H	−0.246	−0.404	0.086	−0.273
Detritivore species (%)	%DETRITIV	−0.444	−0.812	−0.211	−0.646
Herbivore species (%)	%HERBIV	−0.606	−0.183	−0.395	−0.314
Predator species (%)	%PREDATOR	0.603	0.690	0.367	0.623
Beetle species (%)	%BEETLE	0.449	0.782	−0.130	0.766
Gastropod species (%)	%GASTRPD	−0.791	−0.354	−0.696	−0.398
Spider species (%)	%SPIDER	0.540	−0.117	0.778	−0.032
Microclimate					
Air temperature	AIR TEMP	0.629	−0.003	0.752	0.007
Soil temperature	SOIL TEMP	0.301	−0.501	0.756	−0.073
Relative humidity (%)	%RH	−0.822	−0.228	−0.764	−0.285

† Abbreviations used in Figs. 1 and 2.

informative axes are represented in Fig. 2. When we visually rotated the ordination to align treatment groups with axis 1, this axis represented 15.2% of the total variation, while axis 2 was loaded with 54.6% of the original variation. The third axis, which is not shown, grouped trap zones into blocks, as in the forest-only ordination (ellipses, Fig. 1a), suggesting strong block effects. Elevation, again, was strongly associated with axis 2 ($r = 0.938$), with trap zones of higher and lower elevation blocks sorting into two distinct regions of species space along the axis (Fig. 2). Most of the forest and buffer trap zones at 1-m distance from the stream clustered at the negative end of axis 1 (along with one clearcut trap zone), while clearcut trap zones at all distances from the stream clustered at the other end of axis 1 (Fig. 2a). At lower elevations, forest and buffer trap zones more than 1 m from the stream were fairly well mixed together in the middle of axis 1, while among high elevation blocks, forest and buffer trap zones were more segregated along axis 2. It should be noted that three of the buffer trap zones nearest to the clearcut end of the ordination at higher elevations represented trap zones at 5, 10, and 20 m from the stream at one site that had been subject to a severe blowdown of trees.

There were fewer environmental variables strongly associated with the axes than in the forest-only ordination (Fig. 2a, Table 2). The heat load index increased at lower elevation trap zones, a function of aspect. Moss and leaf litter cover were strongly negatively correlated with axis 1, indicating increased cover near streams and in forested conditions. Mineral soil cover was positively correlated with the clearcut-associated end of axis 1. Predictably, total tree and conifer basal area were negatively correlated with axis 1 (i.e., fewer trees in the

TABLE 3. A list of strong forest (F) and clearcut (C) indicator invertebrate species (IV > 25, $P < 0.05$) strongly correlated (Pearson's $r > |0.5|$) with axis 1 or axis 2 in the nonmetric multidimensional scaling (NMS) ordinations of forest-only trap zones (Fig. 1), and of forest, buffer, and clearcut trap zones (Fig. 2).

	Forest only		All treatments			
Species	Axis 1	Axis 2	Axis 1	Axis 2	Indicator value (P)	Group indicated
Beetles						
Actium barri				0.558		
Actium retractum		0.510				
Batrisodes albionicus		−0.508		−0.575	54.5 (0.044)	C
Cychrus tuberculatus		−0.779		−0.578		
Lophioderus similis		−0.636				
Microlestes nigrinus			0.550		55.0 (0.001)	C
Notiophilus sylvaticus		0.552		0.609		
Omus dejeani					54.7 (0.002)	C
Oropus striatus		0.629		0.507		
Otiorhynchus rugostriatus					37.1 (0.012)	C
Promecognathus crassus		−0.810		−0.625		
Pterostichus castaneus				0.520		
Pterostichus crenicollis	−0.581		−0.617			
Pterostichus herculaneus	0.551					
Pterostichus lama		−0.729		−0.536	56.2 (0.007)	C
Pterostichus lattini LaBonte		0.574				
Rhyncolus brunneus			0.516			
Scaphinotus angulatus	0.709				52.6 (0.018)	F
Scaphinotus angusticollis		0.747		0.597		
Scaphinotus marginatus		0.511		0.656		
Sonoma conifera		0.538			36.8 (0.050)	F
Sonoma hespera		0.740		0.654		
Sonoma olycalida		0.592		0.611		
Steremnius carinatus	0.604					
Sthereus horridus		0.666				
Zacotus mathewsii	0.737					
Gastropods						
Ancotrema sportella	−0.512	−0.824		−0.746		
Haplotrema vancouverense		−0.856		−0.681		
Hemphillia dromedarius		0.590			39.4 (0.013)	F
Pristiloma lansingi		−0.704				
Punctum randolphi	−0.566					
Striatura pugetensis	−0.601					
Vespericola columbianus		−0.769				
Millipedes						
Caseya dendrogona		−0.666				
Harpaphe h. haydeniana		−0.616				
Kepolydesmus anderisus		−0.795				
Nearctodesmus insulanus			−0.517			
Spiders						
Alopechosa kochii					58.8 (0.001)	C
Antrodiaetus occultus		−0.506		−0.511		
Antrodiaetus pugnax		−0.519				
Blabomma sp.1		−0.512				
Callilepis pluto			0.661		70.0 (0.001)	C
Calymmaria new sp.		−0.617		−0.622		
Cybaeus cascadius					51.8 (0.034)	F
Cybaeus multnoma		−0.661		−0.626		
Cybaeus simplex		0.535		0.579	47.7 (0.006)	C
Evarcha proszynskii					30.7 (0.040)	C
Micaria pulicaria					40.0 (0.005)	C
Pardosa californica					50.0 (0.001)	C
Pardosa dorsalis		0.554	0.548	0.596	65.7 (0.001)	C
Pardosa dorsuncata					40.0 (0.004)	C
Xysticus montanensis					58.0 (0.001)	C
Zelotes fratris			0.673		90.0 (0.001)	C
Zelotes josephine			0.529		35.0 (0.007)	C
Zelotes puritanus			0.605		60.0 (0.001)	C

Note: Indicator value (IV) and associated P value for indicator species were determined by indicator species analysis (Dufrêne and Legendre 1997).

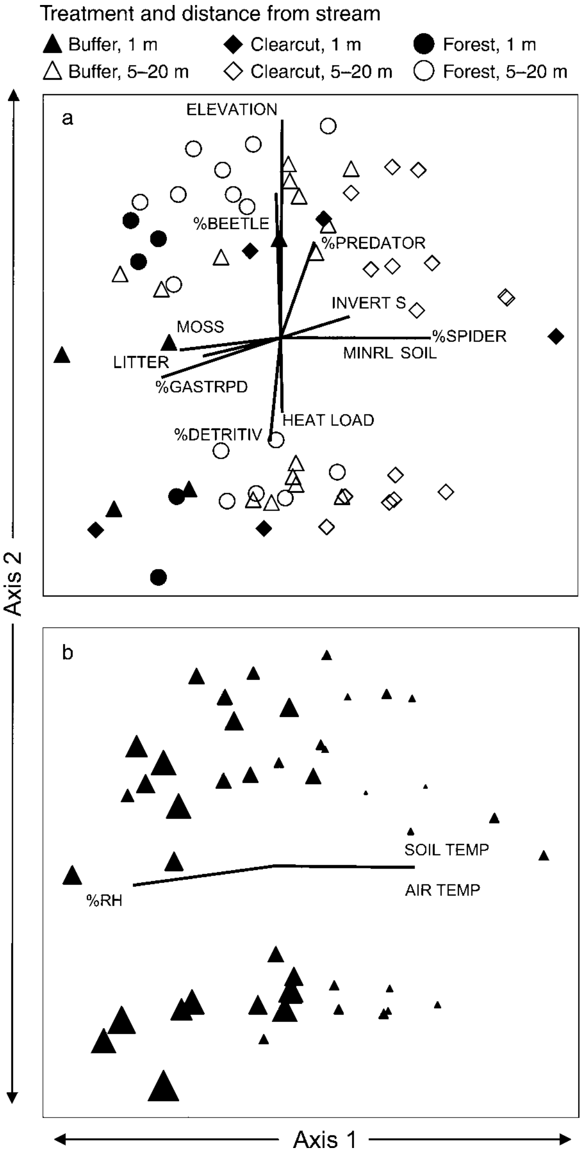

FIG. 2. Nonmetric multidimensional scaling (NMS) ordination of 60 trap zones (1–20 m from stream) from buffer, clearcut, and mature forest (control) treatments in species space: only two dimensions of the three-dimensional solution are shown. (a) Vectors indicate the strength (minimum $r^2 = 0.25$) and direction of correlations between variables and axis scores (variable codes are defined in Table 2). (b) Microclimate variables are shown (no measurements taken at trap zones 5 m from the stream). The ordination is overlain with percentage relative humidity (RH) values: the size of each symbol is proportional to the magnitude of the variable (range: 16.5–92.8%).

clearcut than in the buffer/forest), but the relative weakness of these correlations ($r = -0.465$, -0.367, respectively) is likely due to the scale at which these parameters were measured, and the presence of some large trees in several of the clearcut riparian areas.

Relative humidity showed a strong negative association with axis 1, while both air and soil temperature increased along the axis from streamside to clearcut trap zones (Fig. 2b). The range for mean relative humidity over all trap zones was from 16.5% to 92.8%, mean air temperature ranged between18.9° and 44.1°C, and mean soil temperature ranged from 12.0° to 33.4°C.

Community diversity variables showed very similar associations to those found in the forest-only ordination (Fig. 2a). The percentage of gastropod species increased with increasing relative humidity along axis 1. The percentage of detritivore species increased at lower elevations, while the percentage of beetle and predator species increased at higher elevations. Twice as many beetle species were strongly correlated with the high elevation end of axis 2, as with lower elevations (Table 3). Invertebrate species richness was positively correlated with axis 1, and the increased percentage of spider species in the clearcuts may have contributed to this overall diversity. The abundance of two lycosid spider species, one thomisid species, and three gnaphosid species were strongly positively associated with axis 1, while the carabid beetle *Pterostichus crenicollis* and a millipede, *Nearctodesmus insulanus*, were strongly associated with the streamside/forested (negative) end of axis 1 (Table 3).

MRBP revealed significant community compositional differences between the three treatment groups (buffer vs. clearcut vs. forest; within-group homogeneity $A = 0.043$; $P = 0.004$). Pairwise comparisons between treatment groups confirmed what the ordination suggested, that forest and buffer groups were not different from each other ($A = -0.006$, $P = 0.834$), while the clearcut group was different from both the forest group ($A = 0.087$, $P = 0.016$) and the buffer group ($A = 0.072$, $P = 0.016$).

Of the 134 taxa used in our community analysis, 16% were found to be significant indicator species for either the forest (4 species) or the clearcut (17 species; Table 3) treatment. A visual comparison of indicator species abundances across treatments (Appendix, species in boldface type) reveals that among forest indicators, two species (the snail-feeding carabid beetle *Scaphinotus angulatus* and a slug *Hemphillia dromedarius*) had similar abundances in the buffer and the forest treatment, and two species (the agelenid spider *Cybaeus cascadius* and the pselaphine beetle *Sonoma conifera*) had notably lower abundances in the buffer. *Scaphinotus angusticollis*, another snail-feeding carabid, was far more abundant in the forest than in the buffer sites (Appendix); however, its frequency across sites was very limited (six sites in two high-elevation blocks) and thus it did not have a high indicator value in our analysis. Clearcut indicator species included five beetles and 12 spiders. Four spider species had notably higher abundances in the buffer treatment than in the forest treatment (Appendix), including two lycosid spiders (*Pardosa dorsalis*, the most commonly captured species overall, and *Pardosa dorsuncata*), the agelenid spider

Cybaeus simplex, and a common gnaphosid spider, *Zelotes fratris*.

The two diversity indices showed similar patterns with distance from the stream but different patterns across treatments. Repeated-measures analysis of species richness (S), using univariate ANOVA tests, indicated that there was no interaction between distance and treatment ($F_{6,24} = 0.15$, $P = 0.988$). Within treatments, distance × block was not significant ($F_{12,24} = 0.96$, $P = 0.513$), and mean species richness did not differ with distance from the stream ($F_{3,24} = 1.94$, $P = 0.150$). However, when all distances were averaged, there was evidence of a treatment effect ($F_{2,8} = 5.97$, $P = 0.03$; Fig. 3); again, there were no significant block effects ($F_{4,8} = 2.69$, $P = 0.109$). Mean species richness in the clearcut (mean = 38.5 species; 95% confidence interval: 33.1, 43.9) was significantly higher than in the forest (mean = 29.7; 95% confidence interval: 24.3, 35.0); t test for difference: $t_8 = 3.35$, $P = 0.010$) and the buffer (mean = 32.2; 95% confidence interval: 26.8, 37.5; t test for difference: $t_8 = 2.40$, $P = 0.039$; Fig. 3). However, the buffer and forest were not different from each other (t test for difference: $t_8 = 0.95$, $P = 0.371$). For Shannon-Wiener diversity (H), repeated-measures analysis (based on multivariate analysis of variance for within-treatment effects) indicated no interaction between distance and treatment (Wilks' lambda = 0.36, $F_{6,12} = 1.33$, $P = 0.317$). Distance × block was also not significant (Wilks' lambda = 0.14, $F_{12,16} = 1.46$, $P = 0.236$), and there was no evidence for a difference in diversity with distance from the stream (Wilks' lambda = 0.78, $F_{3,6} = 0.55$, $P = 0.665$). Treatment effects on Shannon-Wiener diversity, averaged over all distances, also were not significant ($F_{2,8} = 0.53$, $P = 0.61$; Fig. 3), although there was weak evidence for block effects ($F_{4,8} = 3.23$, $P = 0.074$) among treatments. Of the 60 infrequently captured or "rare" species (occurring in only one or two trap zones), which were eliminated from the community analysis data set, over four times as many species occurred in the clearcut as in the forest treatment. Rare species made up >25% of all species captured in the clearcut treatment, vs. 8% of the forest species, and 11% of species captured in the buffer.

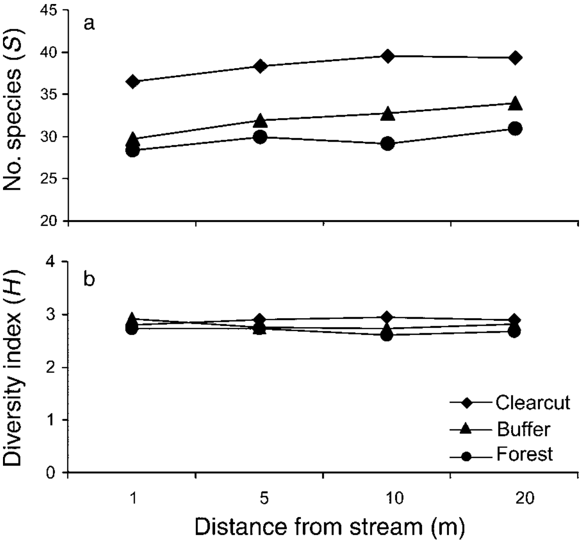

FIG. 3. Mean values for (a) invertebrate species richness (S) and (b) Shannon-Wiener diversity (H) at increasing distances from the stream across three riparian management treatments ($N = 5$). Note that the x-axis is not to scale.

DISCUSSION

Two variables, elevation and block, had substantial influence on invertebrate community composition in our study. Of the 192 species we considered, 33% were restricted to higher (1000–1200 m) and 20% were restricted to lower (400–600 m) elevation sites. While altitudinal limits for species distributions are commonly reported (Olson 1994, Reynolds and Crossley 1997), the physical or biological drivers behind these distribution patterns have been difficult to discern. Climate and its effects on vegetation composition and structure often have been proposed as factors regulating faunal distributions along elevation gradients (Thiele 1977, Olson 1994, Butterfield 1996). In our study, air temperature and relative humidity during the growing season showed little association with the axis strongly correlated with elevation in the ordinations, and thus are not likely to be controlling altitudinal distribution patterns. However, microclimate was not monitored in the winter, when conditions may be critical for overwintering invertebrates (Szujecki 1987). Higher sites were covered in snow for several months in winter, while lower sites were generally snow free. Shrub density, herb cover, mineral soil cover, and soil temperature were strongly associated with elevation in the forest-only ordination and may have influenced forest-floor invertebrate communities by varying habitat structure, food sources for herbivores, and/or affecting soil moisture. The predominantly west-facing aspect of the lower sites increased the heat load index, which also may have affected soil moisture and habitat structure. It is surprising that our five blocks, each located within a separate subdrainage but all within an area of <400 km^2, would show such distinct differences in community composition across all treatments. Whether these distribution patterns reflect environmental differences not captured by our measurements, naturally disjunct populations of invertebrate species, or are an artifact of forest management effects at a larger scale than that considered in this study cannot be determined here, but strong landscape effects have been commonly encountered in invertebrate distribution studies (Spence et al. 1996, Buddle et al. 2000, Schowalter et al. 2003). A. R. Moldenke and C. A. VerLinden (*unpublished manuscript*), working at many of the same sites as those sampled in this study, also found marked differences in the aquatic invertebrate fauna between high and low elevations, and among the five geographic blocks. In our study, despite the influential effects of elevation and block on species distributions, strong patterns emerged related to riparian and management effects.

Unique headwater riparian communities and microclimate in mature forests

At our mature forest sites, species diversity did not differ significantly with distance from the stream. The forest-floor invertebrate community composition at the stream edge (1 m) was distinct, however. This pattern reflects a "spatially compressed" headwater riparian zone, which has also been documented for amphibians (Sheridan and Olson 2003). Community analyses showed the carabid beetle *Pterostichus crenicollis* and the snail *Striaria pugetensis* to be the strongest indicators of this streamside community. Although *P. crenicollis* favors moist soils and stream edges (Kavanaugh 1992), this species is not a riparian obligate, and, in fact, has been reported in open, human-modified sites (Larochelle and Lariviere 2003). Similarly, observations of *S. pugetensis* have not been restricted to riparian habitats (Forsyth 2004). Three other carabid species found almost exclusively at 1 m from the stream at our sites (*Pterostichus campbelli*, *Pterostichus johnsoni*, and *Leistus ferruginosus*) are known to have strong associations with riparian areas (Larochelle and Lariviere 2003). Each of these species, however, occurred in only one or two of our blocks, and so was not sufficiently widespread to serve as indicator species in our community analyses. Likewise, the only documented habitat of the infrequently collected pselaphine beetle, *Abdiunguis fenderi*, is in mosses associated with streams (D. Chandler, *personal communication*), and in our study this species was found only at the stream edge (1 m) in the high elevation sites. Further, the snail *Carychium occidentale*, found only at low elevation sites in our study, and known to be strongly associated with permanently moist sites (R. Forsyth, *personal communication*), occurred predominantly within 1 m of the stream. Of the 27 "rare" species captured at only one trap zone in the forest sites, a higher proportion occurred at 1 m from the stream than at any other distance; but again, their limited distribution, although perhaps significant, precluded their inclusion in our community analyses. In sum, these results suggest that low abundance and limited distributions of riparian species may constrain our efforts to describe headwater riparian invertebrate communities with commonly used community analysis techniques, in which rare species are typically removed as "noise" in the data set (McCune and Grace 2002). Additionally, the more widely distributed species that served as "riparian indicators" in our study are not known to be riparian obligates in other parts of their range. Nevertheless, our findings suggest headwater riparian areas at our sites may support critical life history functions of these taxa.

The stream edge riparian community associated with headwater streams at our sites may be less distinctive from upslope communities than comparable communities on larger streams. Research on larger streams has documented a discrete riparian fauna associated with alluvial microhabitats such as gravel bars, floodplains, and other habitats close to the water's edge. Some carabid beetle species are known to specialize on aquatically derived prey (Hering and Plachter 1997); other carabids have shown adaptations to periodic flooding events (Bonn 2000). Habitat partitioning by carabid and lycosid assemblages alongside rivers and in floodplain forests has been well-documented (Moring and Stewart 1994, Andersen 1997, Antvogel and Bonn 2001). Brenner (2000), working just 30 km south of our study sites, found twice as many individuals and a higher diversity of beetles in the riparian zone of a third-order stream than in the adjacent upslope forest habitat. It appears that habitat diversity (i.e., gravel bars and floodplain forests) contributes to riparian invertebrate diversity, and as smaller streams typically have little floodplain development, the uniqueness of the riparian community is correspondingly less than on larger streams.

Our ordination results suggested that patterns of invertebrate distribution through the riparian ecotone were more strongly associated with microclimatic gradients than with distance from the stream, and it seems likely that streamside "riparian" species in these forests were responding to the cool, humid microclimate associated with headwater streams (i.e., the "stream effect"; Rykken et al. 2007) rather than to any particular riparian microhabitats. The spatial extent of this microclimatic stream effect will vary from site to site, depending on riparian topography, and the degree of channel constraint (Richardson et al. 2005). While headwater stream margins are not the only places providing cool temperature and high humidity in these forests during the dry summer months, they are an important resource along with seeps and other damp, shaded areas. Affinity of some species for a cool, humid microclimate has been reported among carabid beetles (Thiele 1977, Andersen 1985) and lycosid spiders (Moring and Stewart 1994, Wenninger and Fagan 2000). Soil moisture, which we did not measure directly but often observed to be higher next to the stream, also is known to be important for determining invertebrate distributions (Andersen 1997, Antvogel and Bonn 2001).

Functional and taxonomic diversity also varied with microclimate. Herbivores, especially gastropods, increased in proportion in cooler, humid trap zones closer to the stream, corresponding with an increased cover of herbaceous vegetation. One very common predaceous snail, *Ancotrema sportella*, also increased in abundance in the cooler, humid trap zones, perhaps because its prey source (other snails) was more abundant here. However, none of the four snail-feeding carabids in the tribe Cychrini showed notably higher abundances in the cool, humid sites. The proportion of spider species increased in the warmer, drier trap zones. This may have been influenced by the occurrences of species such as *Zelotes* *fratris* and *Pardosa dorsalis*; both are mobile predators typically associated with open habitats such as clearcuts (McIver et al. 1992, Buddle et al. 2000).

Evaluating management alternatives for headwater stream riparian zones

Community analyses indicated that overall differences in forest-floor invertebrate community composition were most pronounced between our mature forest and clearcut treatments. In general, invertebrate communities in riparian buffers of 30 m were far more similar to those in intact riparian forests than to communities in clearcut riparian zones. At lower elevations especially, there was little difference in community composition along axis 1 between the buffer and forest treatments. At higher elevations, three of the buffer trap zones most similar in species composition to the clearcut trap zones were from a buffer site where many trees had blown down due to wind. Invertebrate communities at 1 m from the stream in all of the forest sites, four of five buffer sites, and at one low elevation clearcut site (block BP, with a dense shrub canopy along the stream) shared a similar riparian fauna. This suggests that these riparian buffers were effective at preserving some component of the forest riparian fauna, and that even a clearcut with dense shrub cover along the stream may have provided adequate habitat for invertebrate species associated with the stream edge. For instance, the riparian indicator *Pterostichus crenicollis* was abundant in both of the low elevation clearcut sites (blocks BP and TC) at 1 m from the stream. *Pterostichus johnsoni*, a carabid known primarily from stream edges (Larochelle and Lariviere 2003), occurred in only one block (SP), in both the forest and clearcut sites at 1 m from the stream. Clearcut sites in blocks BP, SP, and TC all had dense shrub buffers alongside the stream. However, not all streamside trap zones in the clearcut treatment comprised a "typical" riparian fauna. Buffer and clearcut trap zones in one high elevation block (MM) defined opposite ends of axis 1 (Fig. 2). The clearcut in this block was southeast facing and the stream banks were sandy and very erosive, with little herbaceous ground cover. Species serving as strong indicators for the clearcut treatment, such as the wolf spider *Pardosa dorsalis* and the ground spider *Zelotes josephine*, were very abundant at the stream edge in this site. Again, microclimate explained much of the variation associated with treatment differences, with a gradient of cool, humid conditions at the stream edge, to intermediate conditions at further distances from the stream in forest and buffer treatments, to the warmest, driest microclimate in the upslope clearcut treatment. Comparably strong associations of invertebrate distributions and microclimatic variables were observed across a forest–grassland transect by Magura et al. (2001).

Over four times as many species served as indicators for the clearcut treatment as for the forest treatment (17 vs. 4 species). Forest indicators included a jumping-slug (*Hemphillia dromedarius*), which is listed as threatened in Canada. On Vancouver Island, British Columbia, this species is known only from forests with old-growth characteristics (COSEWIC 2004). While the low number of forest indicators in our study is supported by Niemelä's (1997) estimation that old-growth specialists make up only 10% of the forest-floor arthropod fauna, the contrast in abundance of forest and clearcut indicators also may be, in part, because the majority of clearcut indicators were spiders, and many of these had widespread distributions at all elevations (with the exception of the lycosid wolf spiders), their high frequency across blocks contributing to a high indicator value. Three carabids described as "old-growth arthropods of conservation value" in the Pacific Northwest by Lattin (1993), *Cychrus tuberculatus*, *Promecognathus crassus*, and *Zacotus mathewsii*, showed no strong association with forest sites in our study, and two of these species were found exclusively at low elevation. Block or elevational effects did not appear to be as strong for diversity measurements as for species composition. Overall species richness was higher in the clearcut treatments; hence more indicators may be expected, although persistent "legacy" forest species also contributed to this increase in diversity (McIver et al. 1992, Niemelä 1997). Over 25% of the clearcut species were rare or incidental (i.e., occurring at only one or two trap zones across all treatments), and this resulted in the diversity index, which incorporates species evenness, being very similar among treatments.

A biological edge effect in riparian buffers, as measured by the absence of forest indicator species, and the presence of clearcut indicator species, was apparent in a few cases. Notably, the abundance in buffer sites of the forest-associated agelenid spider, *Cybaeus cascadius*, was almost as low as in clearcut sites. Of the four clearcut-associated spiders with a notable presence in the buffer sites, *Pardosa dorsalis* was the most "invasive" and generally was found at all distances from the stream in the buffer.

Riparian buffer functions and implications for watershed management

In order to assess the ecological value of riparian buffers as part of a headwater riparian management strategy, it is critical to have a clear understanding of what functions the buffers are intended to serve. For instance, a primary aim may be to protect aquatic resources (such as headwater stream salamanders or downstream salmonids) by providing shade and erosion control for the headwaters. An additional management goal may be to protect the unique terrestrial riparian fauna associated with headwater streams. Results from our study suggest that the zone harboring a distinctive "riparian" invertebrate fauna along headwater streams may be <5 m wide, and that, at our sites, a forested buffer of 30-m width on either side of the stream provided adequate habitat for some riparian populations, at least for the short term (i.e., five years or less). In one case, a 5 m wide dense shrub canopy within a clearcut also appeared to provide adequate habitat for the riparian invertebrate community. However, if riparian buffers are intended to provide long-term refugia or dispersal corridors for not only riparian, but also forest specialists, then the buffers should be evaluated as forest fragments, and characteristics such as size, shape, connectivity, and physical/biological edge effects should be considered.

While the elongate, narrow shape and resulting high edge-to-interior ratio of riparian buffers makes them vulnerable to physical edge effects, their position in the landscape (adjacent to a stream and often in steep topography) may afford some protection from these effects. Brosofske et al. (1997), working in relatively small forested streams in the Pacific Northwest, found that the stream exerted microclimatic gradients that extended 30–60 m from the stream, where they reached upland forest interior values. This microclimatic "stream effect" that provides cool, humid conditions some distance upslope, may mitigate the opposing warm, dry conditions contributed by the clearcut-influenced "edge effect" in a riparian buffer, especially a buffer that is only 30 m wide. Indeed, microclimatic measurements from our study sites indicated no detectable difference for any microclimatic variables between 1 and 20 m from the stream between the buffer and forest (Rykken et al. 2007). If our findings are typical, then relatively narrow riparian buffers may provide cooler, moister habitat for both riparian and forest specialists than comparably shaped upland forest fragments. However, biological edge effects, such as the invasion of clearcut-associated species into forest fragments (often mobile species well-adapted to colonizing new habitats), were documented at our buffer sites and could have long-term negative consequences for riparian and forest communities by introducing intraguild interference (Lang 2003). Susceptibility of narrow buffers to disturbances such as blowdowns (toppling of trees due to wind) also remains problematic.

For less mobile forest species not readily able to recolonize regenerating habitat, or riparian species that rely on unfragmented habitat for dispersal (Collinge et al. 2001), the connectivity of riparian buffers also may be significant for life history functions (Fagan 2002, Richardson et al. 2005). In this study, riparian buffers were approximately five years old, and thus some invertebrates within them may have persisted from the pre-harvest stand, representing forest "remnants," especially those species with limited dispersal potential or high affinity to the near-stream zone (e.g., snails [Hylander et al. 2004]; carabids [Halme and Niemelä 1993, Lattin 1993, Rykken 2004]). Even if riparian buffers do not provide viable breeding habitat for some riparian/forest specialists, they may serve an important function as corridors for dispersal between larger forest fragments upstream and downstream.

An effective riparian management strategy will encompass a range of ecological functions, and balance the needs of invertebrate, vertebrate, and plant taxa at all positions in the watershed. Riparian buffers of various widths and thinning densities have been proposed for breeding and dispersing populations of vertebrates (Hagar 1999, Vesely and McComb 2002, Cockle and Richardson 2003), and an examination of invertebrate groups other than those included in this study will likely provide additional considerations for buffer design. Flexibility in the configuration of riparian reserves at a landscape scale, according to local conditions and management goals, will be a key factor for success. Fixed-width buffers may represent one effective management tool; however, alternative strategies, such as the preservation of larger patch reserves at the confluences of small streams (e.g., Cissel et al. 1998), may complement traditional approaches and deserve further study.

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APPENDIX

Functional role, overall abundance, frequency, and mean abundance of invertebrates between 1 and 20 m from the stream in three management treatments (*Ecological Archives* A017-042-A1).