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Headwater Riparian Invertebrate Communities Associated with Red Alder and Conifer Wood and Leaf Litter in Southeastern Alaska

Abstract

We examined how management of young upland forests in southeastern Alaska affect riparian invertebrate taxa richness, density, and biomass, in turn, potentially influencing food abundance for fish and wildlife. Southeastern Alaska forests are dominated by coniferous trees including Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), with mixed stands of red cedar (*Thuja plicata* Donn.). Red alder (*Alnus rubra* Bong.) is hypothesized to influence the productivity of young-growth conifer forests and through forest management may provide increased riparian invertebrate abundance. To compare and contrast invertebrate densities between coniferous and alder riparian habitats, leaf litter and wood debris (early and late decay classes) samples were collected along eleven headwater streams on Prince of Wales Island, Alaska, during the summers of 2000 and 2001. Members of Acarina and Collembola were the most abundant taxa collected in leaf litter with alder litter having significantly higher mean taxa richness than conifer litter. Members of Acarina were the most abundant group collected on wood debris and alder wood had significantly higher mean taxa richness and biomass than conifer wood. Alder wood debris in more advanced decay stages had the highest mean taxa richness and biomass, compared to other wood types, while conifer late decay wood debris had the highest densities of invertebrates. The inclusion of alder in young-growth conifer forests can benefit forest ecosystems by enhancing taxa richness and biomass of riparian forest invertebrates.

Introduction

Southeastern Alaska forests are dominated by coniferous trees, primarily Sitka spruce (*Picea sitchensis* (Bong.) Carr.)*,* western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn*)*, and Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach). Red alder (*Alnus rubra* Bong.) frequently regenerates in these stands following disturbances, such as timber harvesting or landslides. Forest management has been historically directed toward the harvest of Sitka spruce and western hemlock through clear-cutting (USDA 1997). Forest clear-cutting removes all standing timber on a section of land and can lead to the regeneration of an even-aged stand (Deal 1997). These stands become dense during forest succession and can negatively affect fish and wildlife (Wallmo and Schoen 1980, Schoen et al. 1981, 1988, Thedinga et al. 1989). Even-aged stands eventually prevent other vegetation from becoming established through canopy closure, and may completely eliminate understory vegetation for up to 100 yr (Alaback 1982, 1984, Tappeiner and Alaback 1989).

Red alder is a deciduous tree that may benefit floodplain and stream ecosystems by increasing soil nitrogen content through nitrogen fixation, and by providing greater structural diversity than homogeneous conifer stands (Deal 1997). Young-growth red alder may also benefit forest ecosystems by enhancing vegetative understory diversity (Hanley and Hoel 1996, Deal 1997), increasing habitat quality for small mammals (Hanley 1996), and increasing forage for herbivores such as deer and arthropods. Woodland floodplains may serve as temporary storage areas for leaf litter and wood detritus, before it enters streams or rivers (Cummins et al. 1989, Merritt and Lawson 1992).

Timber harvest can eliminate a potential source of large woody debris for small headwater streams. Many aquatic macroinvertebrates and fish depend on this woody debris (Dudley and Anderson 1982, Duncan and Brusven 1985, Wallace et al. 1999), which provides habitat (Hunt 1975, Sedell et al. 1975, Anderson et al. 1978, Neilsen 1992, Wipfli et al. 2003), and can enhance channel morphology

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as well as sediment and water routing (Keller and Swanson 1979, Bilby and Likens 1980). Wipfli and Gregovich (2002) reported that small headwater streams in southeastern Alaska are potentially important prey source areas for downstream salmonids. Piccolo and Wipfli (2002) documented that forest management can alter the export of invertebrates from these headwaters to downstream fishes, and Wipfli and Musselwhite (2004) reported red alder along headwater streams can increase invertebrate drift density by four-fold. Forest management techniques have included thinning red alder from riparian and upland forest stands in an effort to enhance conifer regrowth. However, the inclusion of red alder in young-growth conifer forests may increase the abundance of both riparian and aquatic invertebrate diversity and abundance (Wipfli et al. 2003), thereby providing more food for birds, bats, and downstream fish (Wipfli et al. 2002). According to Wipfli et al. (2002), information about red alder and its ecological role in southeastern Alaska is lacking, and is primarily based on research from other regions.

The overall objective of this study was to understand the role of red alder in shaping riparian invertebrate communities along headwater streams in southeastern Alaska. Specifically, we compared taxa richness, density, and biomass of riparian invertebrate communities associated with red alder and conifer leaf litter and woody debris in different decay classes (early and late) along headwater streams across a riparian alder gradient. We tested the null hypotheses that red alder and conifer leaf litter as well as woody debris and wood decay class (early vs. late) do not differ in invertebrate taxa richness, density, and biomass.

Methods

Our study was conducted in the Maybeso Experimental Forest on Prince of Wales Island, southeastern Alaska (132°67'W, 55°49'N) within the Tongass National Forest (Figure 1). Southeastern Alaska supports a temperate rainforest which has a maritime climate, moderate temperatures, and high annual precipitation (that can exceed 500 cm per year) (Harris et al. 1974). The Maybeso Experimental Forest was clear-cut during the 1950's and much of the regenerating forest contains mixed red alder-conifer stands.

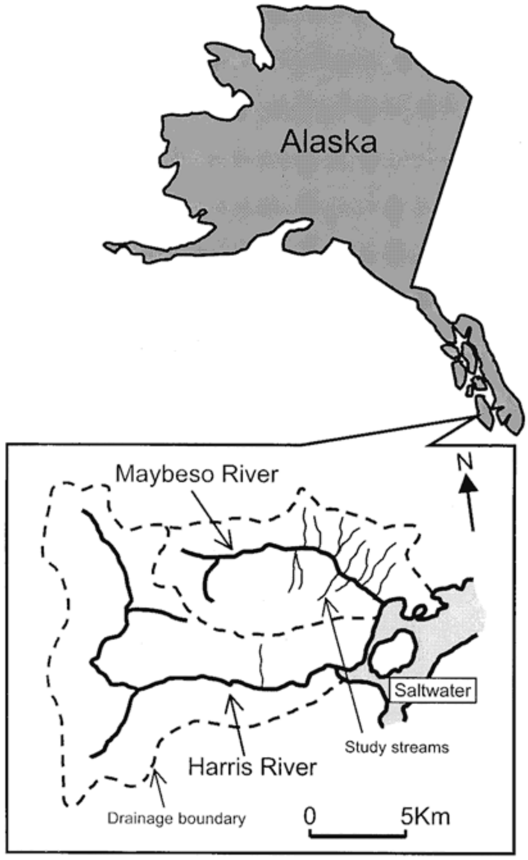

Figure 1. Study stream locations within Maybeso River and Harris River watersheds, Prince of Wales Island, southeastern Alaska.

We sampled riparian zones of 10 headwater streams in the Maybeso River catchment and one headwater stream in the adjacent Harris River catchment. This project was part of a larger, more comprehensive project where stream selection was influenced by overall project needs. Site selection involved stream segments with differing amounts of alder canopy coverage. The percent of alder along each headwater stream was measured using two methods: basal area (range 0 – 53% and mean 24%) and canopy cover (range 1 – 82% and mean 48%). Streamside vegetation methods for measuring alder basal area and percent canopy coverage were those described in Wipfli et al. (2002). Each sampling site was one 150-m transect (parallel to the stream) divided into five 30-m sections. One leaf litter sample was collected from three of the five sections randomly in 2000 and 2001. Three and four sections were randomly selected for woody debris sampling in 2000 and 2001, respectively.

Leaf Litter

Thirty-three leaf litter samples were collected within 1 m of the stream's edge during June and July of 2000 and 2001 (total of 66 samples) at randomly determined distances within each segment. Sample collection involved taking the top 0 – 5 cm layer stopping at the soil/mineral interface. A stovepipe core sampler (0.15 m diam.) was used to enclose each litter sample during collection. Samples were placed in Ziplock® bags and processed in the lab within hours of collection. Invertebrates were initially separated from the litter using a Berlese funnel, and then hand sorted under magnification to collect invertebrates not separated using the funnel. Invertebrates were preserved in 80% ethanol, their body lengths measured to the nearest millimeter (excluding antennae and cerci), counted, and identified to the lowest practical taxonomic unit (based on the author's and collaborating taxonomist's expertise and available keys) using Borror et al. (1996), Stehr (1987, 1991), Christiansen and Bellinger (1981) and McAlpine et al. (1981, 1987, 1989). Invertebrate taxa richness was expressed as mean number of taxa per sample. The area of the grab sample was estimated using the equation for a circle, and invertebrate density (#/m^2) and biomass (mg/m^2) were calculated. Invertebrate dry biomass was estimated using taxon-specific length regression equations (Rogers et al. 1977, Smock 1980, Sample et al. 1993, Hodar 1996, Benke et al. 1999). Non-animal litter components were picked and separated into alder and conifer. Each component was dried in an oven at 42°C for 24 h and weighed to quantify the dominant litter type.

Wood Debris

Wood debris samples were sorted into decay classes (early and late) and by species (alder and conifer) for a total of four classes (early alder, late alder, early conifer, and late conifer). Wood debris decay class determination was based on three criteria: amount of bark, amount of decay, and friability. Early decay wood samples were primarily bark covered, showed little evidence of decay, and were primarily solid or hard to the touch. In contrast, late decay wood samples had little or no bark coverage, decay was prevalent, and the texture was highly friable or nearly crumbling to the touch. Wood samples where decay class status was questionable were placed into the late decay class. Based on processing needs and ease of handling, wood debris size was limited to samples that would fit into a 4-L Ziplock® bag. Wood debris samples that were too large to fit into the bag were cut to fit using a handsaw, and a Ziplock® bag was placed over one end to catch any dislodged invertebrates while cutting. Invertebrates were washed from wood samples into a 20-L bucket with a pressurized backpack sprayer. Each wood piece was carefully dissected and visually inspected to remove all invertebrates that were not removed by pressure washing. A 250-µm sieve was used to separate the sample, and it was then placed into a 250 ml Whirlpak® bag, preserved with 80% ethanol, and picked under 10X magnification. Invertebrates were processed, identified, measured, and dry mass was computed in the same manner as those for leaf litter. Taxa richness was expressed as mean number of taxa per sample, regardless of wood size. Wood surface area was estimated from length (13.9– 35.0 cm range) and diameter (1.8– 9.8 cm range) using the equation for surface area of a cylinder, and invertebrate density (#/m^2) and biomass (mg/m^2) were calculated.

Statistical Analysis

Density and biomass data were $\log_{10}(x + 1)$ transformed to overcome non-normal distributions. Data collected from both year's sampling events (2000 and 2001) were combined to incorporate and minimize yearly variation of macroinvertebrate communities and to increase sample size for statistical power. Multiple T-tests (litter samples) and ANOVAs (wood debris) were generated to contrast mean taxa richness, mean density, and mean biomass between litter types (alder or conifer) and among wood debris taxon-age classes (early and late decay for both alder and conifer) (SAS Institute 1996). Statistical significance was accepted at $P < 0.05$. Following a significant ANOVA, a Tukey's Studentized Range (HSD) post-hoc test was used to compare means. Correlation analyses were performed using percent alder basal area and percent alder canopy cover to test for a treatment effect of alder on litter and woody debris samples. All graphs and tables are presented using non-transformed data.

Results

Leaf Litter

A total of 47 taxa representing 15 orders and 23 families were collected from riparian leaf litter (Table 1). A similar number of invertebrate taxa were collected in alder (38) and conifer (35) leaf litter (Table 1). The majority of invertebrates collected in litter samples were collected in both types, although a few were only collected in one litter type. Because more invertebrates were associated with red alder leaf litter on average, mean taxa richness was significantly higher in alder litter compared to conifer litter (Figure 2a). Invertebrates commonly collected in leaf litter were Oligochaeta, Acarina, Collembola, Coleoptera, and Diptera (Table 2).

Invertebrate mean densities were similar for both litter types (Table 2, Figure 2b). Acarina and Collembola were the most abundant taxa collected in leaf litter, and together comprised more than 60% of the leaf litter invertebrate community (Table 2). Riparian invertebrate biomass was not significantly different between alder and conifer litter types (Figure 2c). The Oligochaeta were the dominant biomass component and contributed more than 30% for each type of litter (Table 3). Other groups contributing to leaf litter biomass included the Coleoptera, Diptera, Acarina, Chilopoda and Diplopoda.

There was no correlation in litter samples between the percent of alder basal area or percent canopy cover in any attribute (taxa richness, density, or biomass).

Wood Debris

A total of 46 taxa representing 15 orders and 27 families were collected from riparian wood debris samples (Table 1). More total invertebrate taxa were collected from conifer wood debris (38) than alder (33), and nearly all invertebrates collected on wood debris in general were associated with late decay wood (Table 1). There were more taxa associated with late decay conifer wood (36) than late decay alder wood (30), and the fewest number of taxa were associated with early decay wood (Table 1).

Even though more total riparian invertebrate taxa were associated with conifer wood, alder wood had significantly higher mean taxa richness on a per sample basis (Figure 2a). Late decay wood had significantly higher taxa richness than early decay wood (Figure 3a). Invertebrates commonly associated with riparian wood debris included Acarina, Collembola, and Diptera (Table 2).

Mean densities for late decay wood were significantly higher than for early decay wood debris (Figure 3b). Invertebrate densities were similar between late decay alder wood and conifer wood; however, conifer late decay wood had higher densities. Early decay conifer had the lowest invertebrate densities. The dominant taxon collected in all wood debris samples was Acarina, which comprised more than 50% of the total density for each wood type (Table 2). Acarina, Collembola and Diptera were the most abundant taxa collected in wood debris, and together comprised more than 90% of the invertebrate community (Table 2).

Riparian invertebrate biomass was significantly different between wood decay classes and wood types (Figures 2c and 3c). The highest invertebrate biomass was found in late decay alder wood and lowest in early decay conifer wood. Groups largely contributing to wood debris biomass included Acarina, Coleoptera and Diptera (Table 3).

There was no correlation in wood debris samples between the percent of alder basal area or percent canopy cover in any attribute (taxa richness, density, or biomass).

Discussion

Leaf Litter

In our study, we found that alder litter had greater mean taxa richness than did conifer litter. Because microbial processing of litter is often limited by nitrogen content of organic matter, and red alder has a higher nitrogen content than conifers, alder litter can likely be processed more quickly by microbes (Andersen and Sedell 1979, Motomori et al. 2001, Richardson et al. 2004). The occurrence of red alder along these young-growth conifer-dominated streams may provide an additional resource for riparian invertebrates to use. Wipfli et al. (2003) suggested that because alder detritus decays faster than conifer, it might be a more desirable food source for invertebrates. In a study conducted in some of the same headwater streams and adjacent watersheds (Prince of Wales, Alaska) as in this study, Hernandez et al. (2005) found that streams with an alder-dominated, young-growth riparian

Table 1. Invertebrates collected in riparian litter and wood debris samples in Maybeso and Harris River catchments on Prince of Wales Island, southeast Alaska

TAXA								WOOD DEBRIS			
						LEAF LITTER		Alder		Conifer	
Phylum	Class	Order	Family	Genus	Species	Alder	Conifer	Early^1	Late^2	Early^1	Late^2
Tardigrada										x	x
Annelida											
	Oligochaeta					x	x		x		x
Crustacea											
	Copepoda									x	
	Isopoda				x	x		x		x	
Arthropoda											
	Arachnida										
		Acarina				x	x	x	x	x	x
		Araneae				x	x	x	x	x	x
		Opiliones				x	x	x	x		x
		Pseudoscorpiones				x	x	x	x	x	x
	Chilopoda										
		Lithobiomorpha				x		x			
		Geophilomorpha				x	x				x
	Diplopoda										
		Polydesmida				x	x				
		Julida				x	x	x	x	x	x
	Pauropoda						x				
	Insecta										
		Collembola									
			Neanuridae			x	x		x	x	x
				Brachystomella		x	x	x	x	x	x
			Onychiuridae								
				Onychiurus		x	x		x		x
			Isotomidae			x	x	x	x	x	x
			Tomoceridae			x	x	x	x		x
			Dicyrtomidae								
				Ptenothrix	*atra*	x	x		x	x	x
		Hemiptera				x					
		Homoptera									
			Aphididae			x	x		x		x
			Coccidae			x	x		x		x
		Coleoptera									
			Carabidae								

TABLE 1, continued

TAXA								WOOD DEBRIS			
						LEAF LITTER		Alder		Conifer	
Phylum	Class	Order	Family	Genus	Species	Alder	Conifer	Early[1]	Late[2]	Early[1]	Late[2]
				Leistus	*ferruginosus*						x
			Ptiliidae								
				Actidium	*crotchianum*	x	x				
			Leiodidae								
				Agathidium		x					
			Scydmaenidae								
				Lophiodes		x				x	x
			Staphylinidae								
				Batrisodes	*albionicus*						x
				Cupila	*clavicornis*		x				x
				Lucifotychus			x				
				Megarthrus	*pictus*	x	x				
				Micropeplus	*tesserula*	x					
				Phlaeopterus					x		
				Sonoma		x					
				Stenus	*sp. 1*		x				
				Stenus	*sp. 2*		x				
				Unknown		x	x		x	x	
			Scarabaeidae								
				Aegialia	*cylindrica*	x					
			Byrrhidae								
				Exomella	*pleuralis*	x			x		
				Lioligus	*nitidus*	x					
			Elateridae								
				Ctenicera					x		x
			Cantharidae			x					x
			Cerambycidae					x			
			Curculionidae				x		x		
				Steremnius	*carinatus*		x				
				Sthereus	*horrideus*		x				
		Mecoptera									
			Boreidae								
				Caurinus					x		x
		Diptera									

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TABLE 1, continued

TAXA									WOOD DEBRIS		
						LEAF LITTER		Alder		Conifer	
Phylum	Class	Order	Family	Genus	Species	Alder	Conifer	Early[1]	Late[2]	Early[1]	Late[2]
			Tipulidae			x				x	
				Limonia		x	x		x		
				Molophilus			x				
				Pedicia		x	x		x		x
			Pachyneuridae								
				Cramptonomyia	*spenceri*			x	x		
			Mycetophilidae							x	
				Symmerus	*cogulus*			x	x		
			Sciaridae				x	x	x	x	x
			Cecidomyiidae			x	x	x	x	x	x
			Ceratopogonidae								
				Forcipomyia		x					
				Probezzia							x
			Chironomidae								
				Boreochlus							x
				Krenopelopia							x
				Metriocnemus				x	x	x	x
				Paraphaenocladius		x	x	x	x	x	x
			Xylophagidae								
				Xylophagous					x		
			Empididae					x		x	
			Platypezidae			x					
		Lepidoptera									x
		Hymenoptera									
			Diapriidae			x	x				
			Formicidae			x	x				x
Mollusca											
	Gastropoda										
			#1			x	x	x	x	x	x
			#2			x	x	x	x	x	x
Total					**65**	**38**	**35**	**19**	**30**	**18**	**36**
								Total Alder 33		**Total Conifer 38**	

[1] Early decay wood debris

[2] Late decay wood debris

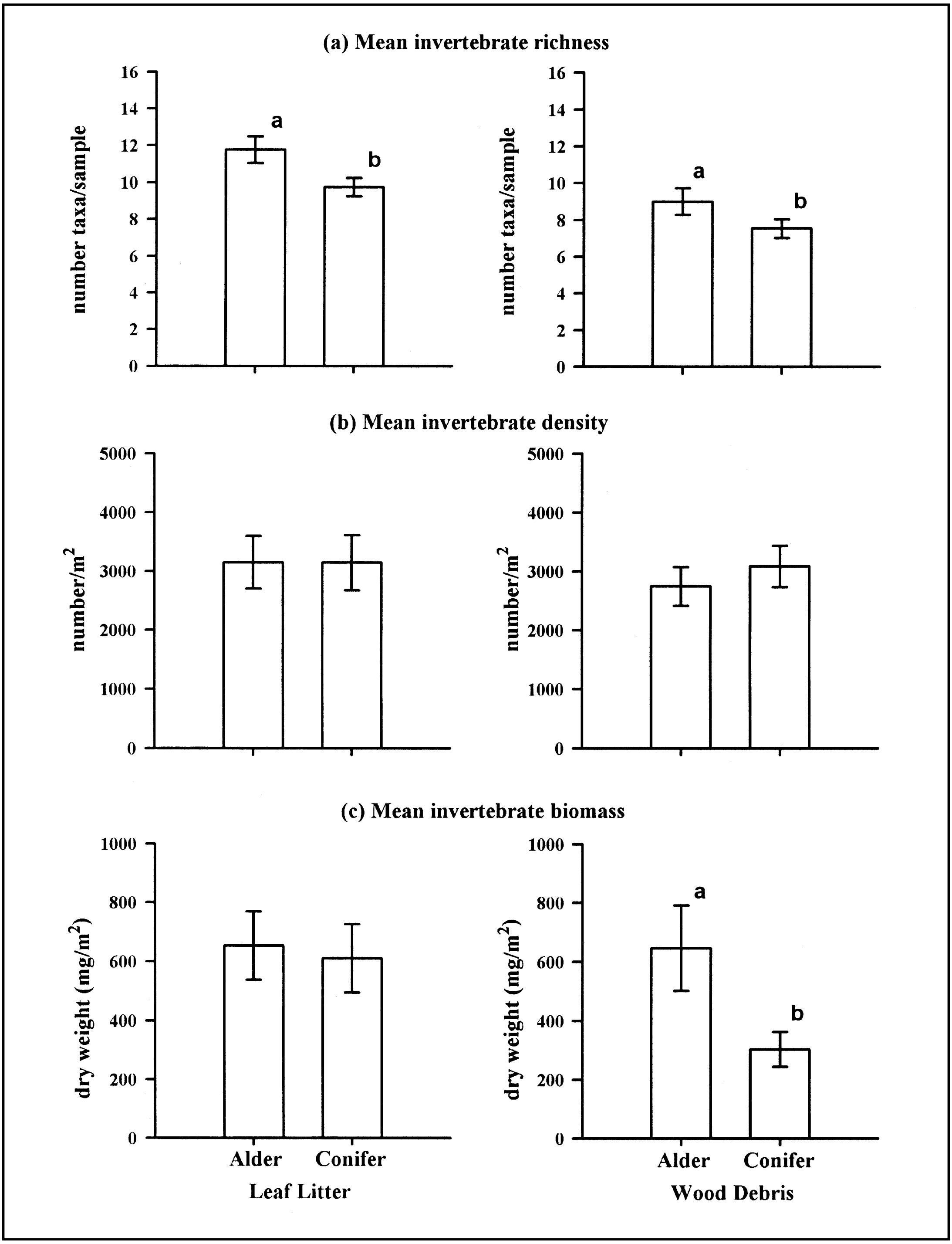

Figure 2. (a) Mean invertebrate taxa richness (number taxa/sample), (b) mean density (number/m^2), and (c) mean invertebrate biomass (dry weight mg/m^2) among leaf litter grab samples and wood debris samples (error bars = mean ± 1 SE). Total number of samples collected for each sample type: alder leaf litter (n = 26); conifer leaf litter (n = 40); alder wood debris (n = 34); and conifer wood debris (n = 43). Means with different letters are significantly different ($P < 0.05$).

TABLE 2. Mean riparian invertebrate density (#/m^2), standard error of the mean and relative percent for select taxa collected along headwater streams of Maybeso Experimental Forest and adjacent Harris River watershed Prince of Wales Island, Alaska.

							WOOD DEBRIS											
	LEAF LITTER						Alder						Conifer					
TAXA	Alder (n[1] = 26)			Conifer (n = 40)			Early Decay (n = 12)			Late Decay (n = 22)			Early Decay (n = 16)			Late Decay (n = 27)		
	(# /m^2)	sem	Rel. %	(# /m^2)	sem	Rel. %	(# /m^2)	sem	Rel. %	(# /m^2)	sem	Rel. %	(# /m^2)	sem	Rel. %	(# /m^2)	sem	Rel. %
Oligochaeta	575	± 150.6	18.2	597	± 133.0	20.3	0	± 0.0	0.0	88	± 44.9	2.5	0	± 0	0.0	18	± 9.9	0.4
Araneae	26	± 7.7	0.8	27	± 6.8	0.9	4	± 3.0	0.3	28	± 9.9	0.8	14	± 8.4	1.2	18	± 5.8	0.4
Opiliones	14	± 5.4	0.4	1	± 1.0	0.0	8	± 5.3	0.5	29	± 8.9	0.8	0	± 0	0.0	9	± 3.2	0.2
Acarina	1,050	± 249.2	33.3	1,034	± 177.1	35.1	892	± 183.0	63.8	1,930	± 341.0	55.9	707	± 177.9	59.3	2,850	± 319.7	67.7
Pseudoscorpiones	51	± 9.1	1.6	41	± 9.8	1.4	18	± 10.7	1.3	41	± 13.6	1.2	3	± 2.4	0.3	61	± 16.6	1.4
Isopoda	19	± 7.5	0.6	11	± 3.5	0.4	0	± 0.0	0.0	22	± 15.6	0.6	0	± 0	0.0	3	± 2.6	0.1
Diplopoda	14	± 0.2	0.4	9	± 4.5	0.3	7	± 4.8	0.5	17	± 5.9	0.5	2	± 1.9	0.2	2	± 1.8	0.0
Chilopoda	5	± 0.1	0.1	2	± 2.0	0.1	3	± 3.4	0.2	0	± 0	0.0	0	± 0	0.0	4	± 1.7	0.1
Collembola	942	± 8.0	29.9	1,067	± 313.1	36.3	198	± 57.8	14.1	427	± 157.8	12.4	351	± 151.6	29.4	580	± 157.3	13.8
Homoptera	8	± 0.2	0.2	6	± 3.6	0.2	0	± 0.0	0.0	7	± 6.8	0.2	0	± 0	0.0	5	± 3.9	0.1
Lepidoptera	0	± 0	0.0	0	± 0	0.0	0	± 0.0	0.0	0	± 0.0	0.0	0	± 0	0.0	2	± 1.7	0.1
Coleoptera	125	± 1.5	4.0	50	± 22.1	1.7	21	± 19.0	1.5	29	± 18.5	0.8	6	± 5.7	0.5	23	± 15.1	0.6
Hymenoptera	8	± 0.1	0.2	3	± 2.2	0.1	0	± 0.0	0.0	0	± 0	0.0	0	± 0	0.0	11	± 11.2	0.3
Diptera	260	± 3.4	8.3	239	± 91.2	7.6	241	± 171.4	17.3	782	± 267.0	22.7	100	± 42.0	8.4	597	± 327.3	14.2
Gastropoda	54	± 0.4	1.7	58	± 16.6	1.9	6	± 5.7	0.4	52	± 16.9	1.5	10	± 10.0	0.8	26	± 8.6	0.6
TOTAL	3,151		100.0	3,146		100.0	1,398		100.0	3,452		100.0	1,193		100.0	4,209		100.0

[1] (n = number of observations)

TABLE 3. Mean riparian invertebrate biomass (dry weight mg/m^2), standard error of the mean and relative percent for select taxa collected along headwater streams of Maybeso Experimental Forest and adjacent Harris River watershed Prince of Wales Island, Alaska.

TAXA	LEAF LITTER						WOOD DEBRIS											
							Alder						Conifer					
	Alder (n^1 = 26)			Conifer (n = 40)			Early Decay (n = 12)			Late Decay (n = 22)			Early Decay (n = 16)			Late Decay (n = 27)		
	(mg/m^2)	sem	Rel. %	(mg/m^2)	sem	Rel. %	(mg/m^2)	sem	Rel. %	(mg/m^2)	sem	Rel. %	(mg/m^2)	sem	Rel. %	(mg/m^2)	sem	Rel. %
Oligochaeta	265.5	± 83.9	30.5	235.2	± 50.6	39.3	0.0	± 0.0	0.0	72.4	± 48.2	8.0	0	± 0	0.0	1.7	± 0.9	0.4
Araneae	31.3	± 10.8	3.6	17.0	± 6.6	2.8	0.5	± 0.3	0.3	6.7	± 2.3	0.7	6.4	± 4.3	12.3	15.4	± 6.8	3.6
Opiliones	11.5	± 4.3	1.3	0.3	± 0.3	0.1	7.6	± 5.2	4.4	26.6	± 8.9	2.9	0	± 0	0.0	7.0	± 2.6	1.6
Acarina	43.8	± 11.1	5.0	53.2	± 9.5	8.9	43.1	± 8.6	25.1	93.8	± 15.6	10.4	28.1	± 4.6	53.6	126.0	± 15.7	29.1
Pseudoscorpiones	40.4	± 9.0	4.6	33.7	± 8.4	5.6	7.1	± 4.4	4.1	27.3	± 9.1	3.0	1.1	± 0.8	2.0	46.4	± 12.7	10.7
Isopoda	15.5	± 6.7	1.8	12.6	± 4.4	2.1	0.0	± 0.0	0.0	26.5	± 17.0	2.9	0	± 0	0.0	1.0	± 1.0	0.2
Diplopoda	23.0	± 28.9	2.6	79.6	± 50.4	13.3	2.5	± 2.2	1.4	156.3	± 129.7	17.3	3.7	± 3.7	7.0	9.4	± 9.4	2.2
Chilopoda	20.9	± 18.7	2.4	82.2	± 82.2	13.7	2.0	± 2.0	1.2	0	± 0	0.0	0	± 0	0.0	113.0	± 69.1	26.1
Collembola	26.5	± 6.9	3.0	14.4	± 6.0	2.4	1.0	± 0.6	0.6	2.8	± 1.5	0.3	1.3	± 0.6	2.4	2.3	± 0.8	0.5
Homoptera	1.8	± 1.7	0.2	5.0	± 3.6	0.8	0.0	± 0.0	0.0	1.8	± 1.8	0.2	0	± 0	0.0	2.0	± 1.8	0.5
Lepidoptera	0	± 0	0.0	0	± 0	0.0	0.0	± 0.0	0.0	0.0	± 0.0	0.0	0	± 0	0.0	3.6	± 3.5	0.8
Coleoptera	102.1	± 56.1	11.7	53.0	± 31.3	8.8	54.0	± 48.9	31.4	122.9	± 90.2	13.6	1.2	± 1.2	2.3	58.7	± 53.1	13.6
Hymenoptera	8.6	± 4.4	1.0	2.4	± 1.7	0.4	0.0	± 0.0	0.0	0	± 0	0.0	0	± 0	0.0	15.0	± 15.0	3.5
Diptera	51.5	± 33.9	5.9	20.1	± 9.7	3.3	54.1	± 44.2	31.5	366.5	± 198.7	40.5	10.6	± 8.3	20.1	30.9	± 16.2	7.1
Gastropoda	0.9	± 0.2	0.1	0.9	± 0.3	0.1	0.1	± 0.1	0.1	1.6	± 0.5	0.2	0.1	± 0.1	0.2	0.5	± 0.2	0.1
TOTAL	643.2		100.0	609.8		100.0	171.9		100.0	905.2		100.0	52.5		100.0	432.9		100.0

^{1}(n = number of observations)

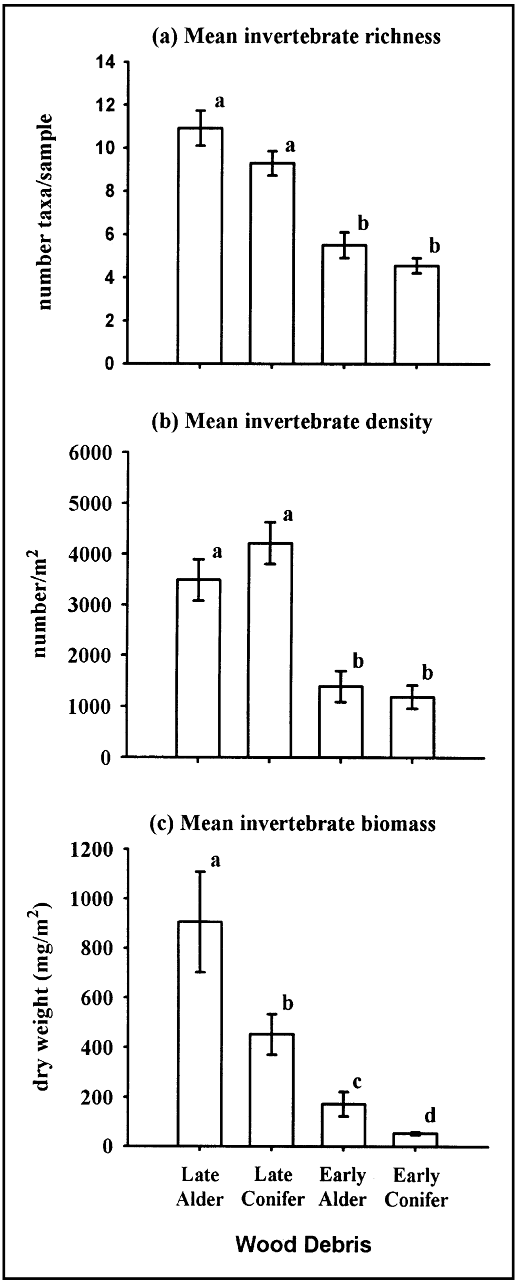

Figure 3. (a) Mean invertebrate taxa richness (number taxa/sample), (b) mean density (number/m^2), and (c) mean invertebrate biomass (dry weight mg/m^2) among wood debris samples (error bars = mean ± 1 SE). Total number of samples collected for each of the different wood decay types: late alder (n = 22); late conifer (n = 27); early alder (n = 12); and early conifer (n = 16). Means with different letters are significantly different ($P < 0.05$).

vegetation had a richer, more diverse fauna with higher macroinvertebrate densities. Even though mean taxa richness in riparian alder litter was significantly higher in our study, we did not find the same relationship with respect to mean densities, which were not different between litter types. Therefore, although density and biomass did not differ between litter types, alder litter was associated with higher invertebrate richness which may be important for maintaining rare taxa in these riparian habitats.

Acarina and Collembolans are usually the most abundant soil arthropods of forest litter (Wallwork 1976). Members of these groups are important secondary decomposers and fungivores of organic matter, and their activities may increase the rate of litter decomposition (Kaczmarek 1977). Both groups were highly abundant in our litter samples (Table 2). Hutchens and Wallace (2002) compared invertebrate assemblages and leaf litter breakdown in streams, banks, and uplands along two southern Appalachian headwater streams. They found that Acarina were the dominant non-insect group in bank and upland habitats, and Collembola were the dominant insect group in these two habitats. Kaczmarek (1977) studied the role of Collembola in different habitats of two forest types (43-year-old pine forest and deciduous forest) and found their numbers and biomass were higher in the deciduous forest than the pine forest. In our study, when Acarina and Collembola were combined they were relatively more abundant in both conifer litter and both age classes of wood debris compared to alder.

Oligochaeta, which are important decomposers, were common in riparian leaf litter samples as well. We found that both litter types had high densities of these worms which have been estimated to consume up to 94% of the total annual leaf fall on a Michigan woodland floodplain (Knollenberg et al. 1985). The Oligochaeta were the dominant biomass component in this study, due primarily to their size, and contributed nearly 40% for each litter substrate. Other groups contributing to leaf litter biomass included the Coleoptera, Diptera, Acarina, Chilopoda and Diplopoda. The Coleoptera (17) and Diptera (10) represented the highest diversity of invertebrates collected from riparian litter, similar to Merritt and Lawson's (1981) findings in a Michigan woodland floodplain.

Wood Debris

The process of wood decay or deterioration can be driven by the presence of fungi. Wood decay caused by fungi involves the enzymatic breakdown of the constituents of wood into cellulose and lignin (Wipfli et al. 2002). Fungal wood decay can be classified as either brown rot or white rot (Boyce 1961). In brown rot cellulose is degraded, while in white rot both cellulose and lignin are degraded (Cowling 1961, Blanchette 1980). Hennon (2000) reported that both processes lead to greatly reduced strength and formation of different wood debris structures, and therefore, each plays a different role in ecosystem function. Brown rot reduces wood strength (with little effect on volume) and biomass, while leaving a residue of partially modified lignin which plays an important role in soil formation (Wifpli et al. 2002). In contrast, white rot can result in total wood consumption. Both types of rot can occur on each wood type, but in our study most rot encountered on red alder appeared to be white rot, and brown rot was typically associated with conifer wood debris. The differences in rot type may have influenced habitat or even food availability, which in turn, may have influenced invertebrate colonization and composition. Brown rot may result in more prolonged wood debris habitat (e.g., colonizable surface area) than white rot, providing food and space for a higher number of invertebrates.

Wood provides a relatively stable habitat, and in most cases, a food resource for a wide range of organisms. We observed differences in invertebrate communities associated with alder and conifer wood. Alder wood had higher mean total numbers of taxa for both early and late decay wood compared to conifer wood of the same decay classes, although these differences were not significantly different. Coniferous species such as Sitka spruce and western hemlock have been found to decay in about 8 to 13 years (Eslyn et al. 1985), while red alder often decays in less than seven years. Due to red alder's faster decay rate, invertebrates may be selecting it as a response to habitat or food availability. Late decay wood had significantly higher invertebrate mean taxa richness than early decay wood, which was expected as wood deteriorated leaving more surface area available for colonization. Braccia and Batzer (2001) also reported an increase in invertebrate richness as wood decayed along streams in South Carolina.

Late decay wood had significantly higher invertebrate densities than early decay wood. This may be a response to a higher number of cracks, crevices, and interstitial spaces associated with decay processes, providing increased refugia for invertebrates (Wipfli et al. 2003), or possibly due to greater food availability as the decay process progressed. Also, the activity of wood-boring invertebrates may provide access for other organisms such as Collembola, Acarina, Diplopoda, and Oligocheata. These latter organisms have been reported to accelerate the communitive processes as well as inoculate the interior of the wood with fungi and bacteria (Swift 1977). Channelizing invertebrates have been recognized as essential rate regulators of the wood decomposition process (Ausmus 1977). As invertebrate densities increase the decay rate increases, creating more habitat and food resources for more invertebrate colonization. Therefore, invertebrates play a substantial role in both nutrient and energy cycling of riparian wood and leaf litter debris, and this could influence connected habitats such as in-stream food webs and trophic structure.

Acarina and Collembola were the most abundant groups found colonizing conifer wood debris in this study, similar to Abbott and Crossley (1982) who observed that these two groups were the dominant taxa of decaying wood in North Carolina. However, Diptera were relatively more abundant than Collembola for both alder wood decay types in our study. The higher density of Diptera may be due to the prevalence of white rot in red alder wood debris. White rot was determined to be the dominant rot type in red alder wood debris, and since white rot causes loss of cellulose and lignin (Cowling 1961, Blanchette 1980), the remaining softer substrate may benefit Dipterans that can penetrate and colonize the decayed wood.

In our study, the prevalence of Diptera larvae was associated with significantly higher invertebrate mean biomass between wood and decay types. Diptera were the dominant component in biomass for both alder decay types comprising 31% for early decay and 40% for late decay, but Diptera biomass was much less in both conifer wood types (20% for early and 7% for late decay). Dipterans collected in our wood debris samples were much larger than most the other invertebrates, and their larger sizes may be more beneficial to downstream fishes as food than the smaller invertebrates. The substantially greater dipteran biomass associated with red alder leaf litter and wood debris may be important to both in-stream and riparian food dynamics. In conifer wood debris, the biomass dominant shifted to Acarina and other invertebrates. Thus, the type of dominant riparian invertebrates that are potential food items in aquatic and riparian habitats was dependent on the type and decay stage of leaf litter and woody debris.

Previous studies have documented that invertebrate density and diversity increase in upland forest woody debris as it decays (Abbott and Crossley 1982, Irmler et al. 1996). We also found this relationship to be true in riparian wood debris samples. Riparian late decay wood had significantly higher invertebrate mean taxa richness, mean densities, and mean biomass than early decay wood, regardless of type. In terms of taxa richness, the orders Diptera (14) and Coleoptera (9) were the most common in riparian wood debris in southeast Alaska, similar to the findings of Braccia and Batzer (2001) in South Carolina.

Conclusion

This study showed that riparian red alder provided a richer, more diverse invertebrate community with higher standing crop biomass than riparian zones without an alder component. Headwater streams are an abundant feature of the landscape throughout southeastern Alaska and these forested streams form a drainage network influenced by riparian vegetative cover that in turn influence ecosystem processes downstream (Piccolo and Wipfli 2002, Wipfli and Gregovich 2002). Headwater forest landscapes can influence stream allochthonous inputs as well as provide critical habitat for terrestrial invertebrates which are important prey items for stream fishes, particularly juvenile salmonids (Wipfli 1997).

Our findings support the forest management practice of encouraging some red alder in regenerating young-growth conifer forests in southeastern Alaska, and perhaps in other areas of the Pacific Northwest. Increasing or promoting red alder should benefit riparian invertebrate richness, diversity, and biomass through the colonization of riparian wood and litter, and lead to a potential increased prey supply (i.e., terrestrial invertebrates) for downstream salmonids. Piccolo and Wipfli (2002) indicated that the biomass of flying insects may increase in stream drift as the percent basal area of red alder increases along riparian zones. Although this study did not find the same positive relationship between increased litter and wood invertebrates and increases in percent of basal alder, it did demonstrate that the mere presence of riparian alder can increase riparian invertebrate richness, diversity and biomass that could contribute to increased production, potentially affecting higher trophic levels and subsidizing downstream riverine ecosystems.

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