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Comparison of Terrestrial Invertebrate Biomass and Richness in Young Mixed Red Alder-Conifer, Young Conifer, and Old Conifer Stands of Southeast Alaska

Abstract

Coniferous stands that regenerate following clearcutting in southeast Alaska can be characterized by the amount of soil disturbance during logging. There are indications that red alder in mixed stands mitigates some of the negative effects of clearcutting. We compared invertebrate biomass in four stands each of (1) young conifers, (2) young mixed alder and conifer, and (3) old conifers to determine if alder was beneficial to invertebrates. Collembola, then Aranae taxa were most abundant but Coleoptera had the greatest invertebrate biomass on boles of red alder, Sitka spruce, or western hemlock. Diptera taxa were the most abundant in flight traps in young mixed alder and conifer stands. Psocoptera taxa were the most abundant invertebrates collected from any foliage. Some rarer invertebrate families were unique to one or another of the tree species. Crawling invertebrate species richness was greatest on red alder and in young mixed alder and conifer stands. The greatest biomass of crawling invertebrates occurred on Sitka spruce boles. Old stands had about the same invertebrate biomass as mixed alder or conifer young stands. Flying invertebrate biomass and species richness was greatest in young stands of mixed alder and conifer. Twice as many invertebrate species were found on western hemlock or Sitka spruce foliage as on red alder foliage but invertebrate species richness was greatest on red alder. Invertebrate biomass on red alder foliage was 20-100 times greater than on the equivalent weight of Sitka spruce or western hemlock foliage. Red alder significantly contributes invertebrate species richness and biomass to young forest stands of southeast Alaska.

Introduction

There is increasing interest in developing new stand management strategies to maintain or enhance biodiversity and assure long-term sustainability of forest, wildlife, and aquatic resources. Abundance of terrestrial invertebrates is closely associated with forest vegetation and some riparian plant species supply more invertebrates to streams than others (Mason and Macdonald 1982). Increased invertebrate production can increase vertebrate abundance and diversity by providing more food for birds, bats, small mammals, and fish.

Little is known about interactions among plant species composition, invertebrate abundance, and vertebrate abundance. Bird abundance has been found to be low in young stands of dense conifers (Schwab 1979, Easton and Martin 1998) and a positive association between bird abundance and the density of live deciduous trees has been found in young forests (Huff and Raley 1991, McComb 1994, Ruggiero et al. 1991) and regenerating clearcuts (Morrison 1981, Santillo et al. 1989). The role of deciduous trees and their influence on invertebrate populations is not well understood (McComb 1994), particularly in southeast Alaska. Richness of invertebrate taxa is often hard to quantify and compare between stand types because richness depends upon sample size (Gotelli and Colwell, 2001). Physical factors such as soil moisture and temperature have a large effect on invertebrate biomass and species richness; aspect and size of clear-cuts can affect the presence of soil invertebrates (Marra and Edmonds 1998). Schowalter and Ganio (1998) found that tree species and canopy height were important factors in the variation and biomass of invertebrate taxa.

In Alaska, red alder (*Alnus rubra* Bong.) is the most frequently associated deciduous tree with Sitka spruce (*Picea sitchensis* Bong. Carr.), western hemlock (*Tsuga heterophylla* Raf. Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). Red alder generally occurs near sea level as a shade intolerant tree with rapid juvenile height

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growth (Harrington 1990). It occurs as a lowland species along the northern Pacific Coast, and its range extends from southern California to southeast Alaska. Red alder grows in zones receiving from 40 to 560 cm of precipitation annually and is limited by winter temperature (Harrington et al. 1994). It grows in a wide range of soils, from well-drained gravels or sands to clays and organic soils. Red alder can tolerate poor drainage and some flooding during the growing season. The most productive alder stands are found on deep alluvial soils in river and stream flood plains. Some productive stands can be found on upland sites on residual or colluvial soils.

Red alder is commonly found along beaches and streams, on snow avalanche and landslide tracks, and as a pioneer species with Sitka spruce, black cottonwood (*Populus trichocarpa* Torr. and Gray) and willows (*Salix* spp.) on exposed mineral soils (Harris and Farr 1974; Ruth and Harris 1979). Logging has increased the amount of red alder in forests of southeast Alaska, particularly in upland areas with heavy soil disturbance. Young red alder grows rapidly but growth slows after the juvenile stage. Habitat quality for some small mammals in even-aged, mixed red alder and conifer stands may be equal to that of old forests (Hanley 1996). Forty year old mixed red alder and conifer stands have both species-rich and highly productive understory vegetation with biomass similar to that of old stands of the region (Hanley and Hoel 1996; Hanley and Barnard 1998). In the absence of repeated disturbance red alder is replaced by longer-lived conifers, which begin to overtop red alder within a few decades (Harrington 1990; Orlikowska et al. 2004). Canopy closure of coniferous forests generally occurs 25 to 35 years after cutting followed by a nearly complete elimination of understory vegetation for up to 100 years (Alaback 1982; Tappeiner & Alaback 1989). However, the dense, uniform, even-aged conifer stands quickly develop broadly negative consequences for wildlife and fish (Wallmo and Schoen 1980; Schoen et al. 1981; Thedinga et al. 1989; Hanley 1993; Dellasala et al. 1996). Little is known about the change in invertebrate communities as stands progress from mixed alder-conifer, to young pure conifer, to mature conifer stands.

As part of a larger study on disturbance history, stand structure, and vertebrate and invertebrate communities we compared terrestrial invertebrates in four mixed alder and conifer young stands (YA), four young conifer stands (YC), and four old conifer stands (OC). Our hypothesis was that terrestrial invertebrate biomass and richness is greater in YA than in YC or OC.

Methods

Study Area

To study the influence of red alder on invertebrate communities, we selected study areas in the Maybeso, Harris, and Polk watersheds, Prince of Wales Island, Alaska (figure 1). Maybeso and Harris watersheds were chosen because they have large areas of relatively uniform stand age and site productivity with a wide range of red alder, western hemlock, and Sitka spruce mixtures.

Polk watershed was chosen because it had older trees and stands. Mean annual temperature is 10°C and mean annual precipitation is 280 cm. The basins are U-shaped glacial valleys covered by varying thickness of glacial till (Gomi et al. 2003). Dominant forest vegetation includes western hemlock, Sitka spruce, western red cedar, and red alder; however, riparian vegetation is highly influenced by past mass movement regimes such as landslides and debris flows. Sites in the Maybeso and Harris watersheds were clearcut in the 1950's and experienced significant landslides and debris flows in 1962 and 1979. Basal area in young stands was 63-81 m^2/ha. The sites were dominated by young alder in the riparian zones of headwater streams. The Polk watershed, where the old conifer sites were located was never logged. The old stands were approximately 300-400 years old and had a basal area of 145-185 m^2/ha.

Four YA, four YC, and four OC stands were chosen. Sampling was completed from May through September, 2000 and 2001 when invertebrates were developing and active.

Crawling Invertebrates

Passive sampling of invertebrates was done on Sitka spruce, western hemlock, and red alder trees boles. One trap for each tree was installed around the bole of three trees of each tree species per site (Hanula and New 1996). Traps were located 1.5-2 meters from the ground and collected invertebrates in a detachable cup that contained 70 percent ethanol. Invertebrates, normally phototropic, crawled up

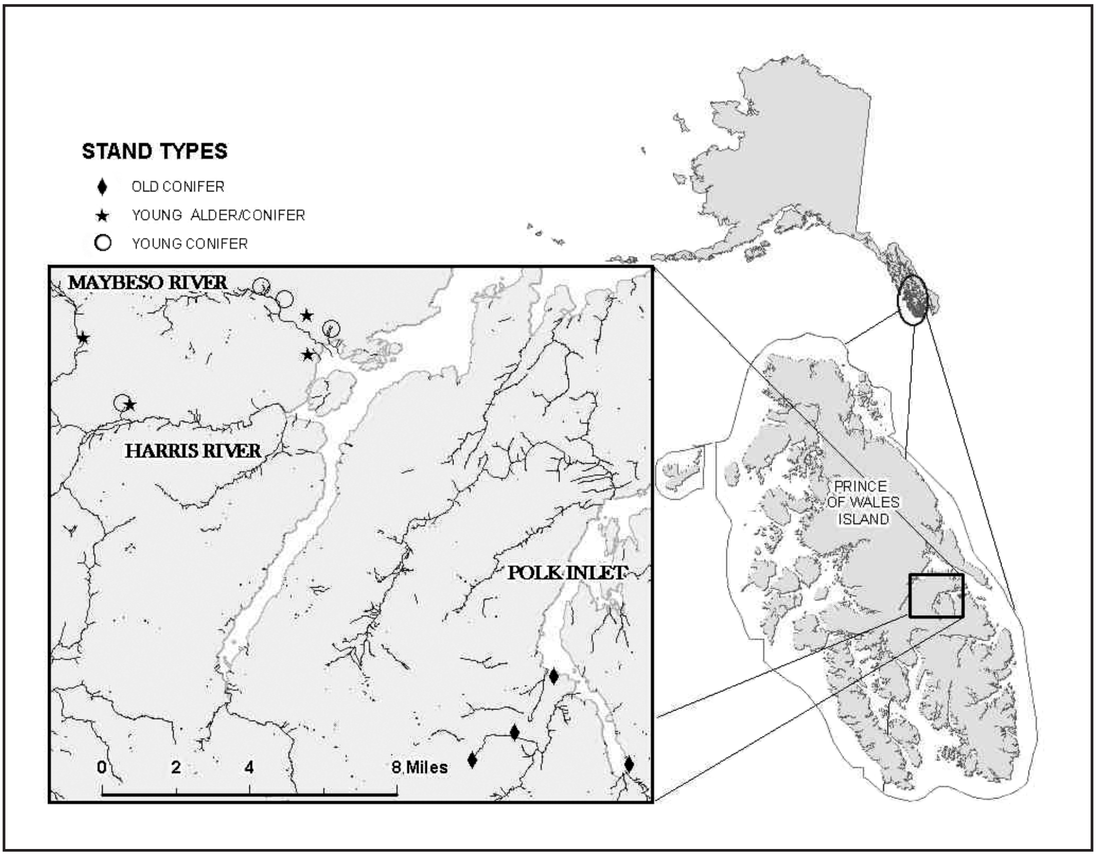

Figure 1. Location of study sites on Prince of Wales Island, southeast Alaska.

the tree into the trap and fell into the collecting cup. Invertebrates collected in traps were measured for length (Hodar 1996), and identified to species or separated into unidentified species.

In 2000, there were 14 to 15 continuous seven-day-sample periods for each of the eight young stands. The young-stand crawling-invertebrate biomass was analyzed on 704 of 845 samples. Not all stands were sampled in April, and there was bear damage to some of the traps in May and September resulting in incomplete samples. However, all 845 samples were used for species richness analyses. None of the OC stands were sampled for crawling invertebrates in 2000. In 2001, 191 YA and YC samples and 71 OC samples were used for biomass and species richness analyses.

Flying Invertebrates

Malaise traps were set up for 48 hours to collect flying and a few crawling invertebrates. Traps were located in the middle of each stand, more than 10 meters from a stream, and where there were no obstructions within 4 meters of the ground and 5 meters distance. A sample was collected after the first 24 hours and another sample after the second 24 hour period, then the traps were dismantled. Invertebrates were dry-trapped in a container at the top of each trap, and killed with a small section of Insect Guard™ (Dichlorvos; DDVP; 2,2-Dichlorovinyl dimethyl phosphate). Invertebrates were washed from the container and placed into a labeled sample container using 70 percent ethanol. There was one trap per site and each site was sampled weekly in 2000 and biweekly in 2001 beginning in May and continuing through September.

In 2000, 266 YA, YC, and OC samples were taken. In 2001, 144 samples were taken. All 400 samples from both years were used for invertebrate biomass and species richness analyses.

Foliage Invertebrates

Once a week from May through September, 2000, lower crown branch tips from three each of red alder, Sitka spruce, and western hemlock were sampled, in all YA and YC stands. No samples were taken in 2001. Approximately 50 cm of branch length was clipped from each tree. Fewer red alder branches were sampled than either Sitka spruce or western hemlock branches. OC stands were not sampled because it was hard to find lower branches that could be sampled, especially late in the sampling process. Invertebrates were shaken from branches onto a white bag so that they could be seen and collected, dispensed into a jar containing 70 percent ethanol, measured for length, and identified to the lowest taxonomic rank possible.

To determine invertebrate biomass per leaf biomass for red alder (124 samples) leaves were stripped from each 50 cm branch sample into a labeled paper bag, oven dried, and weighed. For Sitka spruce and western hemlock the length of all primary and secondary branches was recorded. Needles were plucked from branches, dried, and weighed. The average oven-dry weight of 5 samples of 100 needles was used to determine the mg of invertebrates per 100 g of needles. The dry weight of needles for each branch sample was determined by multiplying the average needle dry weight (6.72 mg for Sitka spruce and 1.36 mg for western hemlock) by the average number of needles per cm of twig reported by Werner (1969) (20.27 for Sitka spruce and 12.40 for western hemlock), and multiplying that product by the cm of branch length sampled to estimate foliage biomass per branch. In this way, the ratio of invertebrate biomass to foliage biomass was determined for each sample.

Data Analysis

For crawling invertebrates caught in bole traps, mean tree diameter per hectare was determined by measuring the diameter at 1.4 m height of all plot trees. Bole trap catch biomass was calculated as mg of invertebrates per cm of tree bole circumference per day. Formulas based on body length for each invertebrate taxonomic order (Hódar 1996) were used to calculate invertebrate biomass. For each invertebrate taxon a standardized biomass was estimated by multiplying biomass per cm of tree bole by average bole circumference, at 1.4m height, for each tree species. This value was multiplied by the number of boles per hectare to estimate biomass per day per hectare for each invertebrate taxon on each tree species.

Flight trap invertebrate numbers were not adjusted by stand area sampled, because there was no way to determine what area was sampled by Malaise traps. Flight trap catch was calculated as mg per day of biomass for each invertebrate taxon.

Flying and crawling invertebrate trapped biomass was averaged across collection date or across tree species and collection date. Analysis of variance (SAS®) was used to compare the invertebrate biomass of the three stand types, the three tree species, and presence of alder.

Invertebrate species richness was analyzed across tree species and stand types. Chi-square analyses of invertebrate numbers within each invertebrate taxon were used to determine differences between tree species and between all stand types.

There were too few invertebrates collected from foliage to do a statistical analysis between stand types or tree species. However, an invertebrate species richness analysis was made.

Results

Crawling Invertebrates

There was a significant difference, 2000 and 2001 data combined, in invertebrate biomass (mg/day/hectare) between YA and YC but not between YA or YC and OC (M_{YA}= 42.6,and M_{YC} = 62.4 M_{OC} = 61.2, SE_{YA} = 4.3, SE_{YC} = 8.9, SE_{OG} = 12.2,), and between Sitka spruce and western hemlock (M_{RA}=52.16, M_{SS}=63.66, M_{WH}=37.33, SE_{RA}=9.97, SE_{SS}=5.97, SE_{WH}=7.72), and between young stands with and without red alder (M_{Alder}=42.65, $M_{NoAlder}$=62.28, SE_{Alder}=4.27, $SE_{NoAlder}$=8.00). Stands without red alder had the greatest mean invertebrate biomass. Sitka spruce had the greatest mean vertebrate biomass followed by red alder and western hemlock.

In 2000 and 2001, invertebrates with the greatest aggregate biomass, all trap records combined, were insects (62%) (Coleoptera 41%), aranae (25%), Collembola (3%), and then Acari (1%). The most numerous invertebrates were Collembola (67%), Acari (18%), Insecta (12%), and then Aranae (2%). Red alder had disproportionately more crawling

Aranae and fewer Coleoptera, Collembola. and Acari; western hemlock had disproportionately more Collembola and Acari and fewer coleoptera; Sitka spruce had disproportionally more Coleoptera (Table 1). A total of 61,118 individuals were classified into 290 invertebrate taxa (Table 2) by stand type.

Red alder had more unique invertebrate species, per 100 samples, than Sitka spruce or western hemlock (Table 3). More unique families of invertebrates occurred on western hemlock tree boles, followed by Sitka spruce and red alder (19, 16, and 10 families, respectively). The Shannon-Weiner species richness index for YA stands (=0.683) was slightly greater than for YC stands (=0.649) and much greater than for OC stands (=0.093).

Flying Invertebrates

Flight traps caught different invertebrates than bole traps. When all stand types are compared there was a significant difference in biomass (mg/day) between YA and YC and between YC and OC (M_{YA} = 18.7, M_{YC} = 11.5, M_{OC} = 16.8, SE_{YA} = 1.39, SE_{YC}= 1.10, SE_{OC} = 1.62,) and a significant difference between the presence or absence of red alder (M_{Alder}=18.67, $M_{NoAlder}$=14.21, SE_{Alder}=1.39, $SE_{NoAlder}$=1.01), but not for day-of-collection (M_{Day1}=16.39, M_{Day2}=14.90, SE_{Day1}=1.20, SE_{Day2}=1.14). YA stands had the greatest mean invertebrate biomass, followed by OC stands. Stands with red alder had a greater mean invertebrate biomass than stands without red alder.

TABLE 1. Number of the most prevalent crawling invertebrates within each tree-species invertebrate-family (group) category caught in stem traps (listed when more than 100 caught) in 2000 and 2001. *Italic numbers in parenthesis are less than,* and ***bold-italic numbers more than,*** the expected number if taxa were evenly distributed among tree species (Chi-square analysis).

Class-Subclass	Order	Family (Group)	Red Alder	Sitka Spruce	Western Hemlock	Total
Number of Samples		259	594	593	1446	
Entognatha	Collembola	Sminthuridae	1413	*(6705)*	***6688***	14806
		Tomoceridae	***1371***	*(4646)*	***6338***	12355
		Entomobryidae	*(319)*	3084	***3263***	6666
		Isotomidae	***929***	2052	*(1219)*	4200
		Hypogastruridae	*(241)*	***1752***	1456	3449
	All		4,273	18,245	18,964	41,482
Arachnida	Acari	Cepheoidae	***527***	*(1924)*	***2003***	4454
		Brown type	*(330)*	1689	***1707***	3725
		Pteromorph type	***93***	242	*(180)*	515
		All	1197	4850	4804	10,851
	Aranae	Agelenidae	***47***	*(60)*	67	174
		Linyphiidae	18	63	76	157
		Pseudoscorpion	***32***	58	55	145
		Tetragnathidae	***24***	51	63	138
		All	238	537	585	1,360
	All		1435	5387	5389	12,211
Insecta	Coleoptera	Scolytidae	*(30)*	***3101***	*(124)*	3255
		Nitidulidae	*(40)*	***421***	*(167)*	628
		Rhizophagidae	22	***201***	*(58)*	281
		Staphylinidae	***51***	*(49)*	*(45)*	145
		Dermestidae	*(0)*	80	61	141
		All	191	3972	565	4,728
	Microcoryphia	All	19	767	542	1,328
	Diptera	All	146	357	343	846
	Homoptera	All	116	251	147	514
	All		518	5511	1755	7784
Total			6,283	29,255	26,432	61,970

TABLE 2: Number of stem-trap samples where each taxon occurred by stand type: young alder (YA), young conifer (YC), and old conifer (OC) (2000 and 2001 data).

Class	Subclass	Order	Family	*Genus*	Stand Type		
					YA	YC	OC
Arachnida							
	Acari						
		Brachypilina					
			Unknown				
				Liacarus	15	14	2
		Cirripedia					
			Gamasidae				
				Unknown	3	1	4
		Desmonomata					
			Unknown				
				Eupterotegaeus	308	246	21
		Unknown					
				Unknown	892	683	74
	Aranae						
		Araneomorphae					
			Agelenidae				
				Cryphoeca	32	16	1
				Wadotes	6	1	1
			Dictynidae				
				Dictyra	26	18	3
			Linyphiidae				
				Erigone	47	42	2
				Linyphantes	6	2	4
				Pimoa	3	1	2
			Theridiidae				
				Theridion	25	21	1
				Unknown	1	1	1
			Unknown				
				Unknown	141	76	42
		Pseudoscorpionidae					
				Unknown	56	59	6
Entognatha							
		Collembola					
			Entomobryidae				
				Unknown	367	317	48
			Hypogastruridae				
				Unknown	276	181	20
			Isotomidae				
Entognatha							
				Unknown	376	167	17
			Sminthuridae				
				Unknown	396	299	21
			Tomoceridae				
				Unknown	531	354	28
			Unknown				
				Unknown	1	1	2
Insecta							
		Coleoptera					
			Cantharidae				
				Unknown	16	19	2
			Cucujoidea/Nitidulidae				
				Unknown	165	167	9
			Curculionidae				
				Steremnius	1	1	1
				Unknown	35	21	7

Contin ued

TABLE 2: Continued.

Class / Subclass / Order / Family / *Genus*	Stand Type YA	YC	OC
Monotomidae/Rhizophaginae			
Unknown	5	2	1
Scolytidae			
Hylurgops	158	155	17
Trypodendron	22	15	3
Unknown	6	10	1
Staphylinidae			
Hapalaraea	44	34	3
Diptera			
Cecidomyiidae			
Thecodiplosis	2	2	1
Unknown	22	23	14
Chironomidae			
Unknown	25	18	4
Empididae			
Unknown	1	1	1
Mycetophilidae			
Unknown	8	6	2
Phoridae			
Unknown	6	4	3
Sciaridae			
Unknown	8	4	4
Tipuloidea/Tipulidae			
Unknown	17	10	4
Insecta			
Diptera			
Unknown			
Unknown	94	73	2
Homoptera			
Aphididae			
Unknown	125	87	6
Hymenoptera			
Ichneumonidae			
Unknown	4	3	1
Mallophaga			
Ricinidae			
Unknown	16	7	1
Plecoptera			
Unknown			
Unknown	3	1	1
Archeaognatha			
Microcoryphia			
Machilidae			
Unknown	45	46	69
Malacostraca			
Malacostraca			
Unknown			
Unknown			
Unknown	6	3	1

By biomass and numbers (Table 4), the most abundant invertebrates from flight traps were Diptera (46% and 92%, respectively), Hymenoptera (27% and 3%, respectively), and then Lepidoptera (14% and 1%, respectively). YA had more invertebrate species and unique species per 100 samples than either YC or OC (Table 5). A total of 36,605 individuals were classified into 220 invertebrate taxa (Table 6, the most abundant taxa), by stand type. The Shannon-Weiner species richness index

TABLE 3. Number of crawling invertebrate species caught in stem traps in years 2000 and 2001.

	Red Alder	Sitka Spruce	Western Hemlock
On all tree species	101	101	101
On two tree species (target + 1 other)	22	54	52
Unique to a tree species	25	47	48
Total invertebrate species	148	202	201
Total (per 100 samples)	54	34	34
Unique (per 100 samples)	9.7	7.9	7.9

TABLE 5. Number of flying invertebrate species caught in Malaise traps in years 2000 and 2001.

	Young Alder/Conifer	Young Conifer	Old Conifer
In all stand types	57	57	57
In one- other stand type (target + one)	54	43	21
Unique to a stand type	44	47	12
Total	155	147	90
Total (per 100 samples)	165	138	136
Unique (per 100 samples)	47	44	18

TABLE 4. Number of flying invertebrates, within each stand, caught in Malaise traps (listed when more than 100 caught) in 2000 and 2001. *Italic numbers in parenthesis are less than,* and ***bold-italic numbers more than,*** the expected number if taxa were evenly distributed among stand types (Chi-square analysis).

Class–Subclass	Order	Family (Group)	Young Alder Stands	Young Conifer Stands	Old Conifer Stands	Total
Number of Samples			94	106	66	266
Insecta	Diptera	Chironomidae	*(4140)*	***4372***	***1960***	10472
		Cecidomyiidae	*(2360)*	***2721***	***2377***	7458
		Mycetophilidae	***2627***	*(1490)*	1347	5464
		Tipulidae	***1783***	*(159)*	*(247)*	2189
		Sciaridae	***1016***	*(447)*	392	1855
		Psychodidae	*(438)*	*(230)*	***686***	1354
		Dryomyzidae	678	421	342	1441
		Phoridae	***588***	*(253)*	272	1113
		All	14882	10923	8236	34041
	Hymenoptera	Ichneumonidae	268	*(153)*	***219***	640
		Liopteridae	76	***74***	*(24)*	174
		All	524	341	299	1164
	Coleoptera	Staphylinida /Omaliinae	249	180	98	527
	Lepidoptera					
		All	131	48	67	246
	Homoptera	Aphididae	162	*(12)*	*(3)*	177
	Homoptera					
		All	173	13	12	198
Arachnida	Acari	All	25	94	24	143
Total			16,141	11,679	8,785	36,605

for YA stands (=0.658) was greater than for YC stands (=0.487) or OC stands (=0.398).

Foliage Invertebrates

About one invertebrate was found on every third red alder branches sampled (Table 7), and an average of three invertebrates were found per four Sitka spruce or western hemlock branches sampled. The collections of invertebrates in June and September, 2000 were about three invertebrates per sample compared to four and five per sample in July and August. Forty-five percent of the total catch was Psocoptera, 19% Aranae, 13 % Diptera, and 5% Homoptera:Aphidoidea. Coleoptera, Lepidoptera, and Hymenoptera were only 6 % of the catch.

The biomass of invertebrates caught on red alder was a 20 to 100 times greater than that caught on Sitka spruce or western hemlock. About one-half of the dipterans collected from Sitka spruce or western hemlock foliage was also collected

TABLE 6. Number of Malaise-trap samples where each taxon occurred by stand type: young alder (YG-A), young conifer (YG-C), and old conifer (OG-C) (2000 and 2001 data).

Class	Subclass	Order	Family	Genus	Stand Type YA	Stand Type YC	Stand Type OC
Arachnida							
	Acari						
		Unknown					
				Unknown	10	11	8
Entognatha							
		Collembola					
			Isotomidae				
				Unknown	4	3	1
Insecta							
		Coleoptera					
			Cantharidae				
				Unknown	5	6	1
		Chrysomelidae					
				Unknown	4		1
		Staphylinidae					
				Hapalaraea	39	34	19
		Diptera					
			Anisopodidae				
				Sylvicola	2	4	7
				Unknown	2		3
			Anthomyiidae				
				Acridomyia	2	1	
				Unknown	45	44	22
			Anthomyzidae				
				Unknown	3	5	6
			Bibonidae				
				Unknown	2	1	2
			Cecidomyiidae				
				Contarinia	3	5	
				Corinthomyia	5	1	1
				Unknown	61	68	46
			Ceratopogonidae				
				Psilokempia	2		
				Unknown	34	21	16
			Chironomidae				
				Chironomis	2	3	1
				Micropsectra	2	4	1
				Orthocladius	3	5	1
				Rheotanytarsus	2	7	
				Unknown	69	79	47
			Dixidae				
				Unknown	2		1
			Dolichopodidae				
				Unknown	9	3	4
			Dryomyzidae				
				Dryomyza	2	4	
				Oedoparena	4	2	
				Unknown	42	36	29
			Empididae				
				Anthalia	2		
				Hilaria	2	1	
				Unknown	52	44	36
			Heleomyzidae				
				Unknown	24	14	15

Continued

TABLE 6. Continued.

Class	Subclass	Order	Family	Genus	Stand Type YA	YC	OC
			Lauxaniidae				
				Unknown	2		
			Muscidae				
				Unknown	17	9	13
			Mycetophilidae				
				Exechia	4	5	
				Mycetophila	3	2	2
				Unknown	67	73	45
			Pelecorhynchidae				
				Unknown	3		
			Phoridae				
				Lecanocerus	3	4	
				Pericyclocera	3	4	1
				Unknown	58	48	36
			Psychodidae				
				Pericoma	3	5	1
				Unknown	54	50	43
			Sciaridae				
				Unknown	63	67	44
			Sciomyzidae				
				Unknown	2		
				Sphaeroceridae			
				Unknown	9	5	7
			Syrphidae				
				Unknown	5	2	7
			Tabanidae				
				Unknown	3		
			Tipuloidea/Limoniidae				
				Molophilus	3		
			Tipuloidea/Tipulidae				
				Unknown	53	41	33
			Trichoceridae				
				Trichocera	2	3	
				Unknown	20	25	14
			Unknown				
				Unknown	28	15	4
			Xylophagidae				
				Unknown	3		
		Homoptera					
			Aphididae				
				Unknown	33	7	3
			Unknown				
				Unknown	5	3	
		Hymenoptera					
			Braconidae				
				Unknown	12	9	5
			Braconidae/Alysinnae				
				Unknown	2		
			Charipidae				
				Unknown	5	2	2
			Diapriidae				
				Unknown	17	10	9

Continued

TABLE 6. Continued.

Class / Subclass / Order / Family / *Genus*	Stand Type YA	YC	OC
Ichneumonidae			
Unknown	51	45	26
Liopteridae			
Unknown	20	19	10
Platygastridae			
Unknown	2		
Proctotrupidae			
Unknown	9	3	
Sclerogibbidae			
Unknown	14	10	9
Unknown			
Unknown	8	10	2
Lepidoptera			
Unknown			
Unknown	27	22	18
Neuroptera			
Unknown			
Unknown	2	1	
Plecoptera			
Nemouridae			
Unknown	3	1	
Unknown			
Unknown	9	6	3
Psocoptera			
Psocidae			
Unknown	2	1	
Unknown			
Unknown	9	15	5

TABLE 7. Invertebrate data for red alder, Sitka spruce, and western hemlock foliage.

	Red Alder	Sitka Spruce	Western Hemlock
Branches Examined	124	332	355
Percent of Branch Samples with Invertebrates	34	79	75
Number of Invertebrates per meter of branch*	67	131	90
New Species per 100 meters of branch length*	34	6.3	4.2
Average biomass(mg) per 100g Foliage	192.4	1.7	9.9

* based on an average of 0.7, 3.0, and 4.7 meters of primary and secondary branch length for red alder, Sitka spruce, and western hemlock, respectively.

from red alder foliage. Sitka spruce and western hemlock had about the same number of unique invertebrate taxa; red alder had about one-third as many.

Species richness, however, was greater for red alder than for Sitka spruce or western hemlock. Ten different species for every 16 invertebrates were collected from red alder foliage, compared to 10 different species for every 60 and 63 invertebrates from Sitka spruce and western hemlock, respectively.

Discussion

Red alder was an important source of invertebrate diversity in the conifer stands examined in this study. Although biomass of crawling invertebrates was greater in stands without red alder, biomass of flying insects was greater in stands with red alder, and red alder trees had more unique species of both crawling and flying invertebrates per 100 samples that did either western hemlock or Sitka spruce. Stands with red alder also had the highest Shannon-Wiener species richness index for flying insects. In addition to the more complex forest structure found in stands with red alder (Deal et al. 2004), our results suggest that red alder may harbor an important source of invertebrate food for birds. Old 300-400 year old stands in this study did not offer more food to insectivorous birds than 35-40 year old young stands.

Relative species richness of invertebrates in southeast Alaska forested ecosystems is complex and cannot be attributed to a single factor. In the Pacific-Northwest, Schowalter and Ganto (1998) found that arthropod communities were associated quite closely with tree species. Diversity goes beyond tree species and might reside more in the site factors. Progar and Schowalter (2002) found that tree age was a factor of Shannon-Wiener diversity in Douglas-fir arthropod catches and precipitation was a factor of invertebrate biomass and diversity. Cole et al. (2003) determined that species richness of stream macro-invertebrates was not associated with stand age, perhaps due to inadequate sampling of headwater streams. Peck and Niwa (2004) determined that biomass and species richness of Aranae, but not Carabidae, was greater in thinned than in unthinned 16-41 year old mixed conifer stands in western Washington. Dunn (2004) found that vertebrate and invertebrate species richness completely recovered in second growth stands 39 years after deforestation, compared to what existed in its former old-age condition.

We found that old stands had a lower Shannon-Weiner species richness number for both crawling and flying invertebrates than young stands with or without red alder.

Managing forests in southeast Alaska for diversity of wildlife requires careful consideration of maintaining diverse sources of food. While old forests might offer unique assemblages of invertebrates, maximizing diversity requires maintenance of other forest types as well, including young stands of conifers mixed with a red alder component.

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