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SEASONAL ABUNDANCE OF GROUND-OCCURRING MACROARTHROPODS IN FOREST AND CANOPY GAPS IN THE SOUTHERN APPALACHIANS

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ABSTRACT - Arthropods compose a large proportion of biological diversity and play important ecological roles as decomposers, pollinators, predators, prey, and nutrient cyclers. We sampled ground-occurring macroarthropods in intact gaps created by wind disturbance, in salvage-logged gaps, and in closed canopy mature forest (controls) during June 199%May 1999 using drift fences with pitfall traps. Basal area of live trees, shade, and leaf litter coverage and depth were highest in controls and lowest in salvaged gaps. Coarse woody debris (CWD) cover was greater in intact gaps than in salvaged gaps or controls, but decay was more advanced and CWD had less bark in controls than gaps. We captured 2,390 grams (dry biomass) of > 28,000 macroarthropods in 21 orders and 66 identified families. Among orders, Coleoptera (36.4%), Hymenoptera (12.2 %), Orthoptera (11.7%), Araneae (7.1 %), Julida (5.9%), Spirobolida (5.7%), and Scolopendromorpha (5.5%) were numerically dominant, whereas Coleoptera (44.0%), Spirobolida (19.9%), Orthoptera (12.8%), Julida (6.8%), and Scolopendromorpha (5.0%) composed the majority of dry biomass. Total macroarthropod abundance and biomass were greater in forested controls than in intact or salvage-logged gaps, and was highest in summer, followed by fall, then spring, and lowest in winter. Differences among treatments were attributable to a higher abundance of Carabidae, Julida, Scolopendromorpha, Spirobolidae, and Araneae in forested controls than in gaps. Sclerosomatidae and Gryllidae were more abundant in salvaged gaps than in intact gaps or controls. Overall, mid-sized macroarthropods were more abundant than small (< 5 mm) or large (≥ 30 mm) macroarthropods, but those ≥ 15.0 mm were more abundant in the controls. Small macroarthropods were most abundant in fall and winter. but those ≥ 5.0 mm were most abundant in summer and fall. Important questions that remain include whether reductions in macroarthropod numbers and biomass at the levels observed are likely to adversely impact vertebrate predators, and at which scales do impacts become a conservation issue.

INTRODUCTION

Arthropods play important ecological roles as predators, prey (Hammond and Miller 1998), decomposers (Moldenke and Lattin 1990), nutrient cyclers (Asquith et al. 1990) herbivores (Wilson 1987), and pollinators (Westman 1990). They also compose a large proportion of biological diversity, and support invertebrate and vertebrate diversity by serving as an important food resource.

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Arthropod abundance is positively correlated with the density, distribution, and diversity of birds (Johnson and Sherry 2001) and salamanders (Hairston 1980). Ground-foraging birds, including neotropical migrants such as the Black and White Warbler (*Mniotilta varia* L.), Worm-eating Warbler (*Helmitheros vermivorus* Gmelin), Ovenbird (*Seiurus aurocapillus* L.), Wood Thrush (*Hylocichla mustelina* Gmelin), and Kentucky Warbler (*Oporonis formosis* Wilson) (Nicholson 1997), and gamebirds such as the Ruffed Grouse (*Bonasa umbellus* L.) and Wild Turkey (*Meleagris gallopavo* L.) rely especially on ground-occurring macroarthropods. Macroarthropod availability can affect bird productivity during the spring and summer breeding seasons (Rodenhouse and Holmes 2002), and winter survival and departure timing for spring migration (Marra and Holbertson 1998). Birds shift from insects to fruit during migration when insect prey becomes scarce (Levey and Stiles 1992). Yet, the spatial and temporal availability of macroarthropods is poorly known, and despite their importance macroarthropods are rarely considered in forest management plans (Oliveret al. 2000).

Studies suggest that different macroarthropod taxa respond differently to forest disturbance, causing changes in relative abundances within macroarthropod assemblages (Niemela et al. 1993). After clearcutting, open-habitat species may increase, whereas habitat generalists may persist, and mature forest species may decline or disappear (Niemela 1997, Niemela et al. 1993). Arthropod response also may vary according to whether they are foliage- or leaf litter-occurring taxa. Canopy and some shrub macroarthropods may increase in response to greater primary productivity in forest gaps (Blake and Hoppes 1986; Van Horne and Bader 1990). In contrast, disturbance-related reductions in leaf litter cover, depth, and moisture may affect the diversity and abundance of ground-occurring macroarthropods (Schowalter et al. 1981). Duguay et al. (2000) found fewer ground-occurring macroarthropods in harvested areas with reduced leaf litter mass. Haskell (2000) reported a reduced abundance and richness of soil macroinvertebrates along roadsides with shallow leaf litter, compared to adjacent forests in the southern Appalachians.

In the predominantly closed-canopy forests of the southern Appalachians, natural disturbance commonly creates canopy openings at scales ranging from single-tree gaps to several hectares (Greenberg and McNab 1998, Lorimer 1989, Runkle 1982). Changes within gaps that could affect arthropods may include increased light, a warmer microclimate, reduced cover and depth of the litter layer, and more coarse woody debris (CWD). Coarse woody debris is considered an important structural feature of habitat for optimizing terrestrial vertebrate diversity, partly because it attracts high densities of invertebrate prey (Harmon et al. 1986, Maser et al. 1979).

Many forest managers attempt to design silvicultural systems that mimic natural disturbance for better ecosystem management (Hansen et al. 1991). However, identification of habitat characteristics that affect macroarthropod abundance is still required (Hansen et al. 1991, Whiles and Grubaugh 1996). Without some knowledge of how macroarthropod communities respond to natural disturbance and the associated changes in habitat structure, there is no way to gauge the success or failure of management.

On October 5, 1995, the remnants of Hurricane Opal passed approximately 240 km west of Asheville, NC. Downbursts of wind created at least twenty-one 0.1–1.5 ha gaps, primarily by uprooting large trees. Gaps were irregularly shaped, and retained partial canopy cover. Tree density decreased by 19–39%, and basal area (BA) by 30–52% in measured gaps (Greenberg and McNab 1998). The uprooting of trees created pits over 1.6–4.3% of the ground surface. Several gaps were salvage-logged during 1996-1997; others were left intact, with fallen trees remaining in place. This allowed us to test experimentally whether the relative abundance, biomass, seasonal availability, and community composition (at the family level) of macroarthropods differed among intact, wind-created downburst gaps, salvage-logged gaps, and mature, closed-canopy forest having different levels of light availability, CWD, and leaf litter coverage and depth.

STUDY AREA

The Bent Creek Experimental Forest encompasses a 2500-ha watershed in the Blue Ridge physiographic portion of the southern Appalachian Mountains of western North Carolina. Annual precipitation averages 120 cm and is evenly distributed year-round. Elevation within the watershed ranges from about 610-1070 m, and all study sites ranged from 670-730 m. Winters are short and mild, and summers are long and warm. Common tree species on xeric sites such as those found in this study include scarlet oak *(Quercus coccinea* Muenchh.), chestnut oak (Q. *prinus* L.), black oak *(Q. velutina* Lam.), blackgum (*Nyssa sylvatica* Marshall), sourwood (*Oxydendrum arboreum* (L.) DC.), and occasional shortleaf pines (*Pinus echinata* Miller). Tulip poplar (*Liriodendron tulipijera* L.) and northern red oak *(Q. rubra* L.) dominate on moist slopes and in coves. Red maple (*Acer rubrum* L.), hickory (*Carya spp.*), dogwood (*Cornus florida* L.), and white oak (Q. *alba* L.) are common throughout (McNab 1996).

METHODS

Treatments were intact gaps (remaining as they were created by wind disturbance) (n = 4), and salvage-logged gaps (n = 3). Controls were mature (80-100 years old), closed canopy forest (n = 4). Controls were adjacent to and > 25 m from intact gaps; salvage-logged gaps were ≤ 0.48 km from control-intact gap pairs. Salvage logging during 1996-l 997 removed standing and fallen trees that were killed or heavily damaged during hurricane Opal. Study gaps ranged in size from 0.1 S-l .5 ha.

Macroarthropod Sampling. Six 7.6 m long, 0.5 m high drift fences buried S-12 cm into the ground were established at random locations and orientations within each site. Two 19-liter plastic paint buckets with 2 mm holes drilled into the bottom for drainage were buried flush to the ground at both ends of each fence (12 pitfalls per site). Traps were shaded by squares of masonite pegboard. Vegetation above or immediately surrounding drift fence arrays was removed. Traps were designed to capture herpetofauna, but also captured ground-occurring macroarthropods. Our trapping methods incurred several sources of bias, including 1) macroarthropods that could climb or fly from traps were likely undersampled; 2) some consumption of macroarthropods by vertebrates likely occurred in pitfalls, but effects were likely minimal due to the relatively few vertebrate captures, and 3) a 2-week interval between collections might have permitted predation and scavenging of macroarthropods by other macroarthropods. However, we assume that these biases were consistent among treatments and hence should not affect comparisons.

We collected (by hand-scooping) macroarthropods at approximately 2-week intervals from pitfall traps that were open continuously during 2 June 1998-25 May 1999. Macroarthropods were preserved in 70% ethyl alchohol. We later sorted and counted all macroarthropods that could be seen with the naked eye by morphospecies. Morphospecies were identified by one of us (T.G. Forrest) to order or, if possible to family, genus, or species. However, because we could not consistently identify all morphospecies to genus or species we decided to report our data at the family level (or, in some cases to order). We measured the wet length and maximum width, then oven-dried and weighed 30 specimens per morphospecies. Specimens were discarded after the above information was obtained. Because our level of identification was not specific, we did not maintain permanent voucher specimens.

Habitat Measurements. We measured percent cover of bare ground, leaf litter, humic mat, shrubs, and CWD (≥12.5-cm diameter at contact point with line transect) during summer, 1998, using five randomly located 15-m line transects per site. Leaf litter and humic mat depths were measured at the beginning, middle, and end of each line transect. We measured the length of all CWD, and the diameter of each piece where it contacted the line transect. We categorized CWD bark condition as: 1 =

recently dead with 100% of bark on tree; 2 = 70% of bark on tree; 3 = 40-69% of bark on tree; 4 = 10–39% of bark on tree; 5 = < 10% of bark on tree. We subjectively categorized wood decay as: 1 = no visible decay; 2 = slight decay; 3 = moderate decay; 4 = slight fragmentation evident; 5 = heavy fragmentation; 6 = completely disintegrated but still distinguishable as CWD (modified from Maser et al. 1979).

We determined light availability (the inverse of canopy cover) using a spherical densiometer. We calculated basal area of live trees and snags from diameter at breast height (dbh) measurements of all trees > 12.5 cm dbh, measured in fixed rectangular plots that were 0.1 ha in gaps and 0.2 ha in controls. For a detailed characterization of five intact gaps, including the four that we trapped in this study, see Greenberg and McNab (1998).

Statistical Analysis. We used two-way repeated measures ANOVA (SAS Institute, Inc. 1990), using site as the replicate unit, to test for differences in the relative abundance and biomass of macroarthropod families, orders, and totals among treatments, seasons, and treatment x season interactions. Within orders larvae were treated separately from adults. We also tested for differences in macroarthropod length classes (< 5 mm, 5-14.9 mm, 1-29.9 mm, and ≥ 30 mm) among treatments, seasons, and treatment x season interactions using repeated measures ANOVA. Four seasons were defined as summer (June 2-August 29), fall (August 30-November 23), winter (November 24-March 1), and spring (March 2-May 25) based on visual inspection of the data. Because seasons did not have equal numbers of sample dates (6 sample dates in spring, summer, and fall but 7 in winter), we used the average number or biomass of macroarthropods per sample per season in our ANOVAs. We used one-way ANOVA to test for differences in the overall abundance of macroarthropods within the four length classes (treatments combined). Differences among treatments and seasons were determined using least squares means tests (SAS Institute, Inc. 1990). Data were log-transformed to reduce heterogeneity.

One-way ANOVA was used to test for differences in habitat features among treatments. Percentage data were square-root arcsine transformed prior to statistical testing. We used P < 0.10 to determine significance and to reduce Type II errors (accepting a null hypothesis when it should be rejected), which are more likely in field studies with high variability such as this one (deMaynadier and Hunter 1995). However, P values are reported so that readers can evaluate results independently.

RESULTS

Macroarthropod Response. We captured 2,390 grams (dry biomass) of > 28,000 macroarthropods in 21 orders and 66 identified families (Table 1). Among orders Coleoptera (36.4%), Hymenoptera (12.2 %),

Table 1. Proportion of total number (first line) and biomass (mg; second line) per order and per family within orders, and mean (± SE) number and dry biomass of common (> 30 specimens) arthropod orders and families captured during June 1998 – May 1999 using drift fences and pitfall traps in intact gaps (n = 4), salvage-logged gaps (n = 3), and closed canopy mature forest (controls) (n = 4) a, the Bent Creek Experimental Forest, Asheville, NC. Means are yearly totals. but P-values are from repeated measures[1] 2-way ANOVA comparing treatment (trt), season (seas), and treatment X season interactions. Different superscript letters within rows denote significant differences among treatments. Differences among seasons are denoted in the seasons column: seasons (Su = summer: F = fall: W = winter; Sp = spring) are coded sequentially based on arthropod abundance or biomass (highest to lowest). and significant differences among seasons are denoted using superscript numbers.

	% Total		Treatment							
Order. Family[2]	Order	Family	Intact	Salvaged	Control	P_{trt}	P_{repeat}	P_{seas}	$P_{trtXseas}$	Season
Acarina	2.0		0.0 ± 0.0	0 0 ± 0.0	143.8 ± 139.1	0221	0.072	0.116	0.216	
	0 0		0 ± 0	0 ± 0	14 ± 14	0.323	0.608	0.596	0.677	
Araneae	7.1		139.5 ± 32.0”	174.1 ± 11.2^{a,b}	235.3 ± 55.0”	0.019	0.170	0<.00I	0.082	Sp^{1} Su^{1,2} F^{2} W^{3}
	28		3946 ± 804^{a}	5480 ± 679^{a,b}	8803 ± 2658^{b}	0.01I	0.206	<0.001	0.059	Sp^{1} F^{1} Su^{2} W^{2}
Atypidae		7.4	7 0 ± 2.0	15.7 ± 5.5^{a,b}	18.5 ± 3.9^{b}	0.036	0 578	<0.00I	0.158	F^{1} Sp^{2} Su^{3} W^{3}
		11.9	378 ± 106”	845 ± 299^{a,b}	998 ± 209”	0.028	0.566	<0.001	0.161	F^{1} Sp^{2} Su^{3} W^{3}
Gnaphosidae		56.7	85.3 ± 15.3	111.0 ± 3.0	118.0 ± 27.3	0.415	0.328	0.016	0.265	Sp^{1} Su^{1} W^{1,2} F^{2}
		27 9	1401 ± 252	1824 ± 49	1939 ± 449	0.392	0231	0.004	0.238	Sp^{1} Su^{1} W^{1,2} F^{2}
Lycosidae		1.5	1.5 ± 1.0	3 0 ± 0.6	3.8 ± 2.89	0.815	0.377	0.674	0.221	
		1.9	65 ± 42	130 ± 25	163 ± 121	0.860	0 425	0.644	0.200	
Pisauridae		22.0	21.3i6.2”	30.0 ± 3.8^{a,b}	61.5 ± 27.4”	0.069	0 246	CO.001	0.345	Sp^{1} F^{1} W^{2} Su^{3}
		49.6	1597 ± 466^{a}	2255 ± 285^{a,b}	5073 ± 2061^{b}	0.037	0.197	<0.001	0.293	
Thomisidae		9.6	15.3 ± 5.9’	12.3 ± 3.5^{b}	24.3 ± 4.2’	0.003	0 607	<0.001	0.073	Sp^{1} Su^{2} F^{2} W^{3}
		5.8	307 ± 119^{a}	248 ± 71^{b}	488 ± 85^{c}	0.004	0.874	<0.001	0 123	Sp^{1} Su^{2} F^{2} W^{3}
Blattaria	2.1		53.5 ± 26.6”	41.3 ± 3.0^{a,b}	62.3 ± 16.0^{b}	0.023	0.334	<0.001	0.239	Su^{1} Sp’ ^{2} F^{2} W^{3}
	13		2082 ± 600^{a}	2468 ± 245^{a,b}	3898 ± 864”	0.037	0.269	<0.001	0.684	Su^{1} Sp^{2} F^{2} W^{3}
Blattellidae		74.3	44.8 ± 27.8	29.0 ± 1.7	42.5 ± 16.0	0.914	0.844	<0.001	0 261	Su^{1} Sp^{2} F^{2} W^{3}
		19.1	613 ± 381	397 ± 24	582 ± 220	0.946	0.653	<0.001	0.423	Su^{1} Sp’ F^{2} W^{3}
Cryptoceridae		25.1	8.8 ± 3.8	12.3 ± 1.3	19.8 ± 5.2	0.731	0.885	<0.001	0 726	Su^{1} F^{2} Sp’ W^{3}
		80.9	1469 ± 633	207 1 ± 224	3316 ± 874	0.686	0.865	<0.001	0.765	
Coleoptera (adult)	36.4		812.3 ± 109.0””	X80.0 ± 210.6”	1104.5 ± 121.8^{b}	0.018	0.234	<0.001	0.717	Su^{1} F^{2} Sp^{2} W^{3}
	44.0		75733115551	89493 ± 24845	109757 ± 13152	0.206	0.141	<0.001	0.743	Su^{1} F^{2} Sp^{2} W^{3}
Carabidae		65.6	525.3 ± 84.7^{a,b}	579.3 ± 157.4”	729.8 ± I I I .5^{b}	0.034	0.208	<0.001	0.897	Su^{1} F^{2} Sp^{2} W^{3}
		70.8	59790 ± 12956	63421 ± 19283	78583 ± 14779	0.283	0.086	<0.00I	0.902	Su^{1} F^{2} Sp^{2} W^{3}
Cicindelinae		0.4	6.0 ± 3 8	4 0 ± 2.3	1.8 ± 1.0	0.757	0.042	<0.001	0.895	Su^{1} F^{2} W^{2} Sp^{2}
		0.2	348 ± 222	232 ± 134	102 ± 60	0.750	0.047	<0.001	0.912	Su^{1} F^{2} W^{2} Sp^{2}
Cerambycidae		0.6	5.3 ± 1.1^{a,b}	7 7 ± 2.3”	3.3 ± 1.7”	0.032	0.450	<0.001	0.514	Sp^{1} Su^{1} F^{2} W^{2}
		2.4	1997 ± 1385””	2198 ± 475^{a}	2646 ± 2152^{b}	0.067	0.489	<0.00I	0.696	Sp’ Su^{1} F^{2} W^{2}
Curculionidae		1.1	7.0 ± 1.7	6 3 ± 2.3	15.8 ± 5.5	0.4I2	0.013	<0.001	0.388	Su^{1} F’ Sp^{2} W^{3}
		0.2	156 ± 69	203 ± 109	326 ± 148	0.442	0.010	<0.001	0.554	

Table 1. continued

Order. Family[2]	% Total		Treatment							
	Order	Family	Intact	Salvaged	Control	P_{trt}	P_{repeat}	P_{seas}	$P_{trtXseas}$	Season
Elateridae		0.7	7.0 ± 1.5	5 7 ± 2.2	6.8 ± 1.8	0 703	0.681	<0.001	0.834	Su^1 Sp' F' W^3
		0.3	304 ± 72	250 ± 100	299 ±X9	0 760	0.550	<0.00I	0.825	Su^1 Sp^2 F^3 W^3
Histeridae		1.0	8.8±0 5	14.0 ± 8.5	7.3 ± 1.7	0 941	0 702	<0001	0 993	Su^1 F^{1}Sp^{2}W^2
		02	189 ±10	303 ± 185	157 ± 36	0981	0.886	<0.001	0.994	Su^1 F^2 Sp^3 W^3
Meloidae		0.5	4 3 ± 2.4	2.7 ± 1.5	6.0 ± 2 3	0 735	0 008	4.001	0.075	Sp^1 F^{1,2} Su^{2,3} W^3
		0.3	340 ± 189	213 ± 116	410 ± 139	0 742	0.008	<0.001	0 104	Sp^1 F^2 Su$^{2\ 3}$ W^3
Scarabaeidae		10.3	86.8 ± 7.6	71 7i24.8	124.8 ± 6.0	0 306	0.158	<0.00 I	0.110	Su^1 F^1 Sp^2 W^3
		8.7	7277 ± 537	5508 ± 2035	11556 ± 763	0 335	0.232	<0.00I	0.199	Su^1 F^1 Sp^2 W^3
Silphidae		b.3	48.5 ± 14.b	45 7 ± 12.0	79.5 ± 19.6	0 330	0.176	<0.001	0.893	Sp^1 Su^1 F^1 W^2
		6.5	5133 ± 1501	4705 ± 1 185	8528 ± 2133	0.266	0.148	<0 00 I	0.897	Su^1 F^{1,2} Sp^2 W^3
Staphylinidae		2.8	20.0 ± 9.4	25 7 ± 4.3	32.3 ± 11.7	0212	0.251	<0.001	0.003	Su^1 F^1 Sp^2 W^3
		0.9	732 ± 446	865 ± 166	920 ± 456	0.610	0 “94	<0 00 I	0.405	Su^1 F^2 Sp^3 W^4
Tenebrionidae		9.0	72 8 ± 17.9	9h 0 ± 26.6	87.8 ± 23.2	0978	0.804	<0.001	0.927	Sp^1 Su^1 F^2 W^3
		4.2	3972 ± 805	4949 ± 800	347 1 ± 868	0 99s	0.746	<0.00I	0.893	Su^1 Sp^1 F^2 W^3
Larvae	1.3		44.3 ± 6.3	3h.i ± 14 2	22.3 ± 4.2	0 460	0.406	4.001	0.390	Su^1 F$^{1\ 2}$ Sp^2 W^3
	0.3		3848 ± 1524	3166 ± 1580	2129 ± 710	0.791	0.550	<0.00 I	0.807	Su^1 F^1 Sp^2 W^3
Heteroptera	0 5		15.5 ± 6.0	I I 0 ± 5.6	8.5 ± 1.0	0871	0.762	<0.001	0.530	Sp' Su^1 F^2 W^3
	0 3		779 ± 221	523 ± 295	512 ± 83	0.705	0.559	<0.001	0.573	Sp^1 Su^1 F^2 W^3
Lygaeidae		37.2	6.5 ± 5.5	5.7 ± 2.2	1.3 ± 0.8	0 339	0.089	0.001	0.342	Sp^1 Su^{1,2} F^{2,3} W^3
		20.7	189 ± lb”	164 ± 63	h i 2 2	0 374	0.046	0.002	0.290	Sp^1 Su^{1,2} F^{2,3} W^3
Pentatomidae		38.8	6.0 ± 2.1	2.0 ± 1.2	5.0 ± 1.5	0. I25	0.602	0.036	0.709	Sp^1 Su^1 F$^{1\ 2}$ W^2
		47 I	380 ± 134	126 ± 73	318 ± 94	0 126	0.583	0.026	0.714	Sp' Su^1 F'$^{\ 2}$ W^2
Hymenoptera	12.2		220.3 ± 35.2	481 0 ± 189.1	280.8 ± 97.5	0.103	0.266	<0.001	0.111	Su^1 F^1 Sp^2 W^3
	0.7		1601 ± 320	1457 ± 70	1631 ± 290	0 938	0.985	<0.001	0.612	Su^1 F^2 Sp^2 W^3
Formicidae		96 6	206.X ± 30.0	470 0 ± 190 2”	298.8 ± 85.0‘”	0 093	0.339	<0.001	0.137	Su^1 F^1 Sp^2 W^3
		81.6	1304 ± 251	11231112	1362 ± 328	0.950	(1.987	<0.001	0.552	Su^1 F^2 Sp^2 W^3
Pompilidae		1.4	5.3 ± 2.1	5 7 ± 0.9	2 3 ± 0.9	0.649	0.226	0.025	0.196	Su^1 F^1 Sp^{1,2} W^2
		9.1	176 ± 70	190 ± 30	75 ± 32	0.581	0.228	0.016	0 161	F^1 Su^{1,2} Sp^{2,3} W^3
Julida	5.9		121.3 ± 23.6[a,b]	74 7 ± 35.5”	242.3 ± 48.9[b]	0.041	0.095	<0.001	0.159	Sp^1 Su^1 F' W^2
	6.8		11768 ± 2306.‘”	7258 ±3451”	23547 ± 4756”	0 029	0.065	<0.001	0.172	Sp' Su^1 F^1 W^2
Lepidoptera (larvae)	1.2		24.0 ± 4.6	32 3 ± 14.8	35.3 ± 8.5	0.246	0.485	<0.001	0.343	Su^1 Sp^{1,2} F^2 W^3
	0.4		725 ± 117	937 ± 96	8.53 ± 186	0.510	0.548	<0.001	0.396	Su^1 Sp^{1,2} F^2 W^3
Opiliones										
Sclerosomatidae	34		94.0 ± 13.4”	10 7 ± 23.8[b]	62.5 ± 16.8””	0.022	0.269	<0.001	<0.001	Su^1 F' W^2 Sp^2
	13		2968 ± 424[a]	34941750”	1973 ± 531[a]	0.013	0.165	<0.00 I	<0 001'	Su^1 F^2 W^3 Sp^3

Table 1, continued.	% Total		Treatment							
Order, Family^{2}	Order	Family	Intact	Salvaged	Control	P_{trt}	P_{repeat}	P_{seas}	$P_{trtXseas}$	
Orthoptera	11.7		231.5 ± 12.9	273 3 ± 9x.9	391.8 ± 6.9	0.224	0.610	<0.001	0.712	Su^{1} F’ Sp^{2} W^{3}
	12.8		22570 ± 3230	20954 ± 6985	38052 ± 6900	0.189	0.87 l	<0.001	0.824	Su^{1} F^{1} Sp^{2} W^{3}
Acrididae		6.4	18.0 ± 1.7	20 0 ± 2. l	20 3 ± 4.5	0.853	(1.750	<0.001	0.378	Su^{1} F^{1} Sp^{2} W^{3}
		1.7	1840 ± 100	2070 ± 572	24x4 ± 39x	0.968	0 x77	<0.001	0.427	Su^{1} F^{1} Sp^{2} W^{3}
Gryllidae		RX.5	6 0 ± 2.4^{a,b}	40.7 ± 26.2^{a}	3.0 ± 0.7^{b}	0 004	0 037	<0.001	0.355	Su^{1} F^{1} Sp^{2} W^{3}
		86.1	408 ± 197^{a,b}	4424 ± 2670”	147 ± 67^{b}	0.002	0.067	<0 001	0.374	Su^{1} F$^{1\ 2}$ Sp^{2} W^{3}
Gryllacrididae		1.8	206 8 ± 14.0	212.3 ± 111.4	367.3 ± 7 5	0.176	0.088	<0.001	0.602	Su^{1} F^{1} Sp^{2} W^{3}
		5.1	20037 ± 2996” ^{b}	14280 ± 7348”	35013 ± 6852^{b}	0.097	0.055	<0 001	0.599	Sp^{1} Su^{2} F^{3} W^{4}
Polydesmida	1.3		so 5 ± 30.0	6 0 ± 2.9	37.x ± 8 5	0.309	0.015	<0.001	0 464	Sp^{1} Su^{1} F^{2} W^{3}
	4.3		14135 ± 8395	1680 ± 808	10566 ± 2373	0.292	0.01 l	<0.001	0.435	Sp^{1} Su^{1} F^{2} W^{3}
Scolopendromorpha	5.5		125 5 ± 17 1^{a,b}	90 7 ± 17.5^{a}	192.5 ± 39.1^{b}	0 03 l	0.070	<0.001	0.481	Su^{1} F^{2} A” Sp^{4}
	5.0		9215 ± 1945^{a,b}	6808 ± 2233’	15600 ± 4169^{n}	0.076	0.027	<0.001	0.352	Su^{1} F^{1} W^{2} Sp^{3}
Spirobolida										
Spirobolidae	5.7		145.8 ± 40.5^{a}	72 0 ± 19.0	205.3 ± 27.3^{b}	41.001	0.153	<0.001	0 626	F^{1} Sp^{2} Su^{3} W$^{2\ 3}$
	19.9		40411 ± 7348^{a,b}	26117 ± 6403^{a}	58980 ± 12204^{b}	0 00	0.180	<0.001	0.549	F’ Su$^{1\ 2}$ Sp^{2} W^{3}
TOTAL^{3}			2109.3 ± 154.6^{a}	2385.3 ± 475 6’	3175.5 ± 343.3^{b}	0.004	0.315	<0.001	0.147	Su^{1} F^{2} Sp^{3} W^{4}
			196680 ± 25955^{a}	167554 ± 26921^{a}	275573 ± 30154^{b}	0.001	0.357	<0.001	0.679	Su^{1} F^{2} Sp^{3} W^{4}

[1] P_{trt} for repeated measures ANOVA (using type III MS for gap(trt) as an error term) was used only if $P_{repeat} < 0.150$. [2]Orders or families having < 30 specimens were omitted from the table. [3]Totals include taxa with < 30 specimens that were omitted from the table.

Table 2. Mean (± SE) number of arthropods in four length classes captured during June 1998 – May 1999 using drift fences and pitfall traps in intact gaps (n = 4), salvage-logged gaps (n = 3), and closed canopy mature forest (controls) (n = 4) at the Bent Creek Experimental Forest, Asheville, NC. Means are based on totals, but P-values are from repeated measures[1] 2-way ANOVA comparing treatment, season, and treatment x season interactions. Different superscript letters within rows denote significant differences among treatments. Differences among seasons are denoted in the Seasons column; seasons are coded sequentially based on arthropod abundance (highest to lowest), and significant differences among seasons are denoted using superscript numbers (Su = summer; F = fall; W = winter; Sp = spring).

	Treatment							
Length Class	Intact	Salvaged	Control	P_{trt}	P_{repeat}	P_{seas}	$P_{trtXseas}$	Season
< 5 mm	59.8 ± 29.6	282.7 ± 115.7	237.3 ± 122.1	0.205	0.542	0.002	0.868	F^{1} W^{1} Sp^{2} Su^{2}
5.0-14.9 mm	714.8 ± 75.4	1045.7 ± 125.3	1010.8 ± 142.8	0.181	0.099	<0.001	0.077	Su^{1} F^{2} Sp^{2} W^{3}
15.0-29.9 mm	892.8 ± 97.8^{a}	777.0 ± 231.1^{a}	1268.5 ± 131.3^{b}	0.030	0.144	<0.001	0.957	Su^{1} F^{2} Sp^{3} W^{4}
≥ 30.0 mm	440.8 ± 88.3^{a,b}	278.7 ± 46.8^{a}	653.0 ± 108.9^{b}	0.016	0.090	<0.001	0.722	Su^{1} F^{1} Sp^{2} W^{3}

[1]P_{trt} for repeated measures ANOVA (using type III MS for gap(trt) as an error term) was used only if $P_{repeat} < 0.150$.

Orthoptera (11.7%), Araneae (7.1%), Julida (5.9%), Spirobolida (5.7%), and Scolopendromorpha (5.5%) were numerically dominant, whereas Coleoptera (44.0%), Spirobolida (19.9%), Orthoptera (12.8%), Julida (6.8%), and Scolopendromorpha (5.0%) comprised the majority of dry biomass.

Total macroarthropod abundance ($P = 0.004$) and biomass ($P = 0.001$) were significantly greater in forested controls than in intact or salvage-logged gaps (which did not differ) (Table 1; Fig. 1). All seasons differed significantly from one another ($P < 0.001$); macroarthropod abundance and dry biomass were highest in summer, followed by fall, then spring, and lowest in winter (Table I; Fig. 1). There was no treatment x season interaction ($P = 0.147$) (Table 1). A repeated measures effect ($P < 0.100$) was indicated for several common taxa including Julida, Scolopendromorpha, Polydesmida, and Gryllacrididae.

Differences among treatments were attributable to a few common macroarthropod taxa. Generally, carabid beetles ($P = 0.034$) (predominantly Calosoma externum Say, Dicaelus spp., Eumalops spp., and Pasimachus spp.), Julida ($P = 0.041$), Scolopendromorpha ($P = 0.031$), Spirobolidae ($P < 0.001$) and Araneae ($P = 0.019$) were more abundant in forested controls than gaps. In some cases numbers were similar in controls and intact gaps but Araneae abundance was similar in controls and salvaged gaps (Table 1). In contrast, Sclerosomatidae ($P = 0.022$) was more abundant in salvaged gaps than in intact gaps (controls were similar to other treatments) and Gryllidae ($P = 0.004$) was more abundant in salvaged gaps than in controls (intact gaps were similar to other treatments). Generally, dry biomass followed similar trends as numbers (Table 1). Seasonal differences in overall macroarthropod abundance and biomass also were due to seasonal fluctuations within common families; most taxa were more abundant in summer and fall than in spring, and lowest in winter (Table I; Fig. 2).

Overall (treatments combined), mid-sized macroarthropods (5-29.9 mm) were more abundant than small (< 5 mm) or large ones (≥ 30 mm) ($P < 0.001$). However, their abundance in different length-classes varied among treatments and seasons (Table 2). Macroarthropods < 5 mm were similarly abundant among treatments ($P = 0.205$), but were more abundant in fall and winter than in spring and summer ($P = 0.002$); macroarthropods 5.0-14.9 mm were similarly abundant among gap treatments and forested controls ($P = 0.18$ I), and were most abundant in summer, followed by fall and spring (no difference), and least in winter ($P < 0.001$). Macroarthropods 15.0–29.9 mm were most abundant in summer, followed by fall, spring, and winter (all seasons differed) ($P < 0.001$), and were more abundant in forested controls than in intact or salvaged gaps ($P = 0.030$). The largest macroarthropod length class ($\geq$ 30 mm) was most abundant in forested controls and least abundant in salvage-logged gaps (intact gaps did not differ from salvaged gaps or controls) (P = 0.016); large macroarthropods were most abundant in summer and fall, followed by spring and then winter (P = 0.001) (Table 2). Smaller taxa such as ants and flies probably were undersampled by our trapping methods, but this bias should be consistent among the treatments.

Habitat Characteristics. Live tree BA was significantly higher in controls (27.X ± 1.9 m^2/ha) than in intact (9.8 ± 1.6 m^2/ha) or salvaged

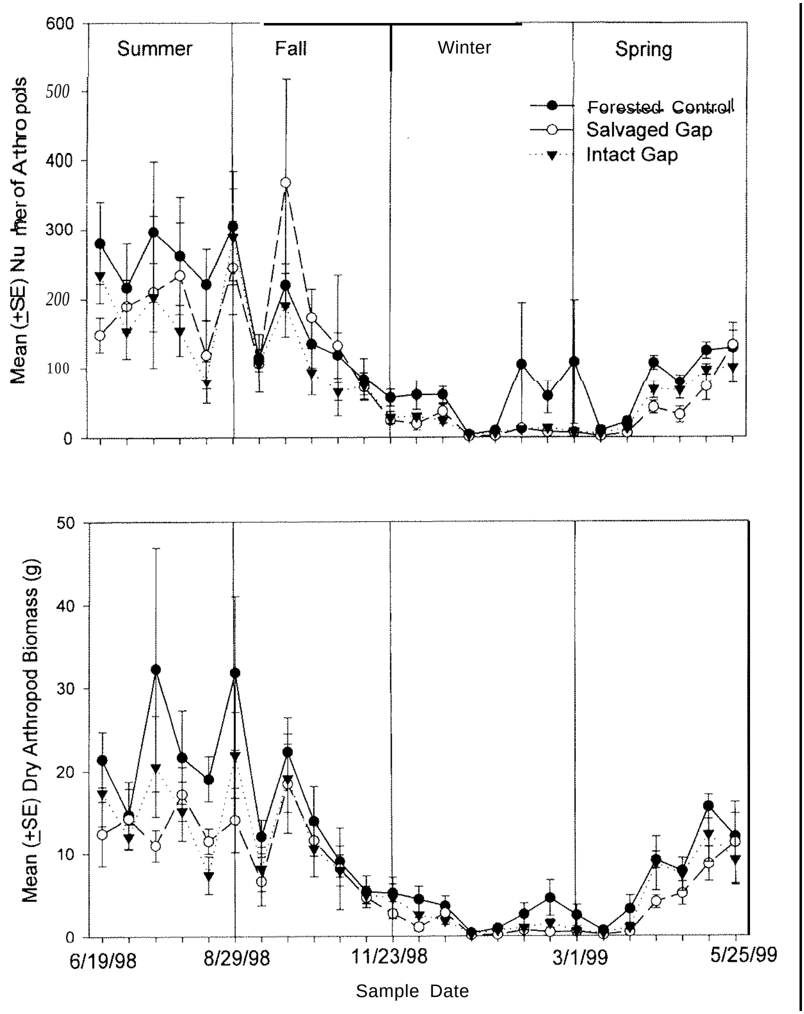

Figure 1. Mean (±SE) number and dry biomass of arthropods captured during June 199%May 1999 using drift fences and pitfall traps in intact gaps, salvage-logged gaps, and closed-canopy mature forest (controls) at the Bent Creek Experimental Forest, Asheville, NC.

gaps (9.0 ± 1.0 m^2/ha), and standing dead tree BA was significantly lower in salvaged gaps (0.6 ± 0.5 m^2/ha) than in intact gaps (3.2 ± 0.3 m^2/ha) or controls (2.6 ± 2.8 m^2/ha) ($P = 0.042$). Percent light differed significantly among both gap treatments and controls ($P = 0.001$), with highest light levels in salvaged gaps (50.5 ± 3.3) followed by intact gaps (29.1 ± 2.3), and lowest in controls (3.3 ± 0.5). Leaf litter cover was highest in controls and lowest in salvaged gaps ($P = 0.001$) (Fig. 3). Litter depth was significantly lower in salvaged gaps than in controls

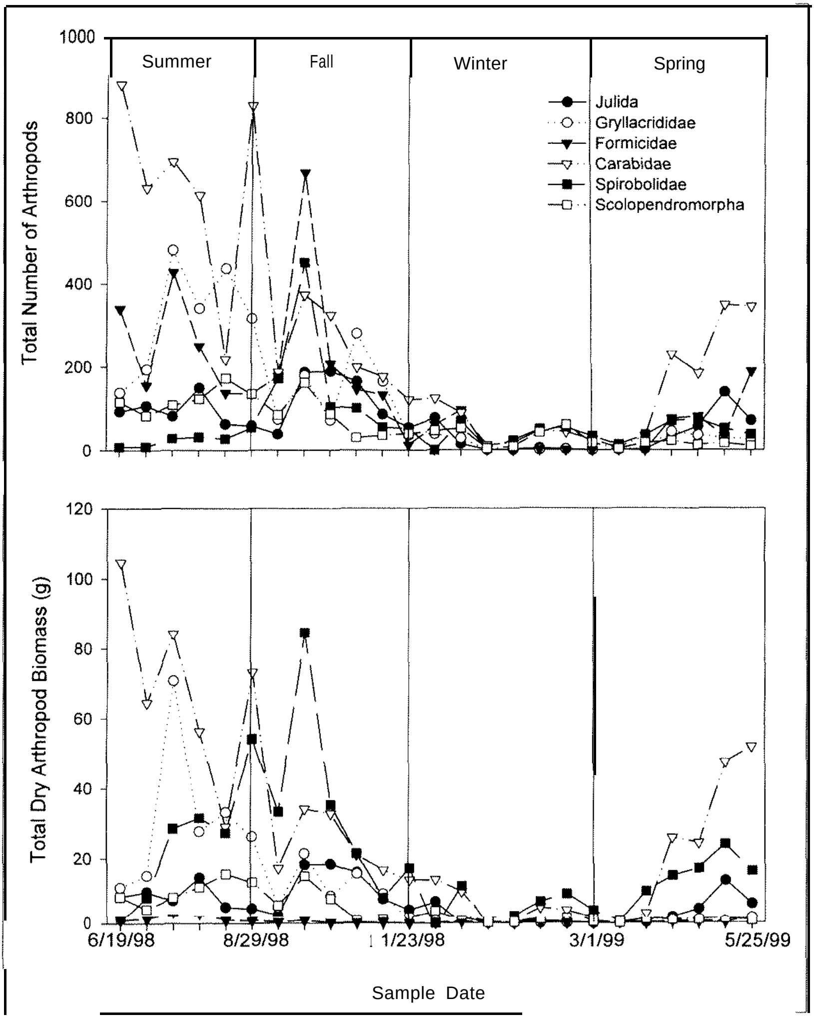

Figure 2. Mean total (treatments combined) number and dry biomass of common arthropod taxa captured during June 199%May 1999 using drift fences and pitfall traps in intact gaps, salvage-logged gaps, and closed canopy mature forest (controls) at the Bent Creek Experimental Forest, Asheville, NC.

(and lower than intact gaps; P = 0.064). Percent cover of humic mat was significantly lower (P = 0.003), and depth was (marginally) significantly less (P = 0.091) in salvaged gaps than in intact gaps or controls. Salvaged gaps had the most bare ground, and controls had the least (bare ground in intact gaps did not significantly differ from salvaged gaps or controls) (P = 0.023). Percent cover of CWD was significantly higher in intact gaps than in salvaged gaps or controls (P = 0.007) (Fig. 3). Coarse woody debris within control sites had significantly less bark (< 10%, on average) than in intact gaps or salvaged gaps (P = 0.005), and wood decay also was significantly lower in intact gaps than in salvaged gaps, and highest in controls (P < 0.001) (Greenberg 2001).

DISCUSSION

Our results show that several taxa of ground-occurring macroarthropods are more abundant and contribute more dry biomass in mature, closed canopy forest than in intact or salvage-logged gaps. Differences among treatments could be due to the greater canopy cover that provided more shade and a cooler, moister microclimate in controls than in gaps. Greater cover and depth of leaf litter within the forested control sites also likely contributed to more favorable conditions for ground-occurring invertebrates. Other studies also indicated that litter

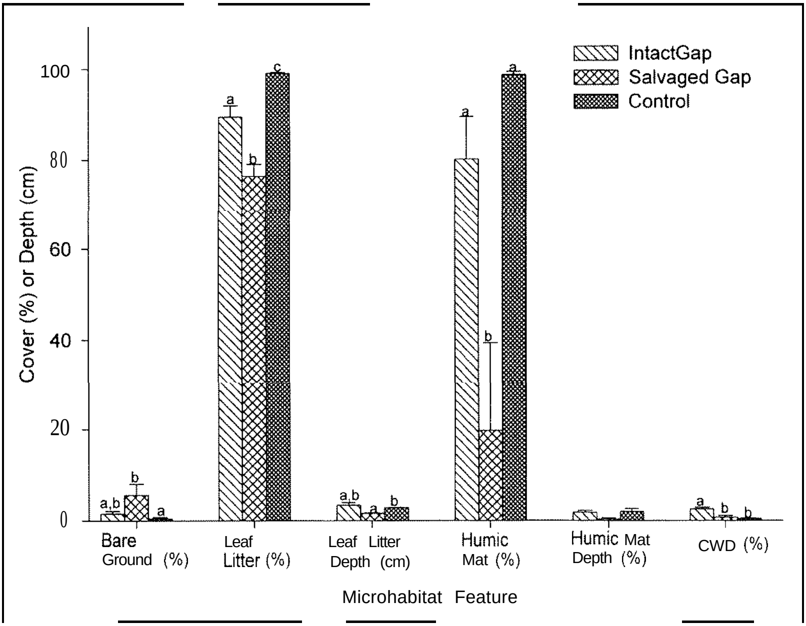

Figure 3. Characteristics (mean I-SE) of select microhabitat features in intact and salvage-logged gaps created in 1995 by hurricane-related wind disturbance, and forested controls at the Bent Creek Experimental Forest, Asheville, NC.

depth affects the abundance of ground-occurring macroarthropods. Harper et al. (2001) reported higher density and biomass of invertebrates in forests of several age-classes than in managed or unmanaged openings, and both density and biomass were correlated with leaf litter weight (but not depth). Duguay et al. (2000) found more litter-occurring invertebrates in unharvested forest than in clearcuts during summer in West Virginia. Hollifield and Dimmick (1995) reported more macroarthropods in mature forest with herbaceous groundcover, and on logging roads that were planted with clover (*Trifolium spp.*) or orchardgrass (*Dactylis glomerata* L.) than in unplanted logging roads or in three post-clearcutting age-classes in the southern Appalachians. In contrast, Healy (1985) reported more invertebrates in clearings than in forests. Similarly, Van Horne and Bader (1990) found more ground-occurring macroarthropods, including Coleoptera and Araneae, in clearcuts than in forests. Harper et al. (2001) suggested that contrasting results among studies is partly due to different sampling methods, and that the leaf-litter macroarthropod component is frequently underestimated by sweep nets.

Lower overall macroarthropod abundance and dry biomass in intact and salvage-logged gaps than in forested controls were apparently driven by the response of a few common taxa. For example, Spirobolida and Julida, which together composed 11.6% of total macroarthropods and 26.7% of total dry biomass, are common in damp places such as under leaves (Borror et al.1976), and likely declined in response to higher light and reduced leaf litter in gaps. Gryllacrididae, which composed 4.8% of total macroarthropods and 5.1% of total dry biomass, also are most common in dark, moist places. Many Coleoptera also are sensitive to soil moisture (Niemela et al. 1992) and litter depth (Michaels and McQuillen 1995). Carabid beetles, which contributed the majority of coleopteran numbers and dry biomass and which mostly prey on other invertebrates, may also have responded to an abundance of invertebrate prey in forested controls relative to both gap treatments. Jennings et al. (1986) found more individuals and species of carabid beetles in uncut residual strips of forest than in clearcut strips or in dense stands. Niemela et al. (1993) found that carabid beetles that were forest generalists, mature forest species, and open-habitat species responded differently to clearcut harvesting. Coleoptera, Hymenoptera, Orthoptera, and Diplopoda also were the most abundant taxa captured in pitfall traps in South Carolina (Hanula and Franzreb 1998). The abundance and biomass of most taxa did not differ among treatments, but they also represented a small proportion of total macroarthropod numbers or dry biomass.

Niemela et al. (1996) emphasized the importance of small-scale habitat heterogeneity to increase diversity of forest-floor invertebrates.

Although several common taxa occurring in our study showed a decline in response to conditions created by natural disturbance, a few were more abundant in gaps. This suggests that forest gaps provide optimal conditions for some taxa, such as Opiliones and Gryllidae.

Pitfall trapping portrays only a limited view of the total macroarthropod community (Haskell 2000), and likely undersamples small invertebrates, especially climbing and flying taxa. Hanula and Franzreb (1998) reported only a 10% similarity in macroarthropod composition between pitfall trap and flight-intercept trap captures. However, similarity of assemblages collected in pitfalls and crawl traps on tree boles was high (58%), suggesting that some taxa of ground-occurring macroarthropods also use other strata and substrates. Macroarthropods inhabiting other strata may show different response patterns to natural disturbance. For example, Duguay et al. (2000) reported higher numbers of macroarthropods that hide under bark in clearcuts, and Scholwalter et al. (1981) reported increases in canopy macroarthropods after clearcutting. Although our study cannot generalize results to all invertebrates, ground-occurring macroarthropods are an important component of the invertebrate community, and are critical for ground-foraging reptiles, amphibians, small mammals, and birds (Haskell 2000).

Macroarthropod size may have important implications on availability and attractiveness to predators, because predators likely select prey that will maximize their energy intake given their mouth gape limitations (e.g., Schoener 197 1). We found no differences among treatments in the abundance of macroarthropods < 5.0 mm in length. However, macroarthropods 15.0-29.9 mm were more abundant in forested controls and the abundance of macroarthropods ≥ 30 mm was similar in forested controls and intact gaps. Again, this largely was due to greater abundance of common, large macroarthropod taxa in forested controls, such as Carabidae, Scolopendromorpha, and Spirobolida.

Higher numbers of some taxa, such as the millipede orders Julida and Spirobolida, do not necessarily indicate higher prey availability, because some species may be toxic (Borror et al. 1976). Further, ground-occurring macroarthropod abundance may not be a limiting factor that determines abundance patterns of vertebrate predators. For example, Greenberg and Miller (in review), using the same study sites, found that the abundance of five shrew species was similar among intact gaps, salvage-logged gaps, and forested controls (a sixth species was most abundant in salvaged gaps). Greenberg (2001), using the same study sites as in the current study, found that amphibian abundance did not differ among treatments, but some reptile species were more abundant in both gap treatments than in forested controls. Greenberg and Lanham (2001) found that overall bird density was higher in intact gaps than in forested controls (salvage-logged gaps were omitted from this study); however, ground-foraging Ovenbirds were more abundant in controls. Clearly, ground-occurring macroarthropod abundance does not have a predictable influence on the local distribution of most vertebrate taxa.

Peak abundance of ground-occurring macroarthropods was not synchronous with peak breeding season for many bird species. Ground-occurring macroarthropod abundance was highest during summer in all treatments (no treatment x season interaction effects), although increases were apparent by April or May. Greenberg and McGrane (1996) also found that macroarthropod abundance was still relatively low during early breeding season for many bird species in Florida. In this study, macroarthropod abundance also was relatively high during fall and spring, when many bird species migrate. Increased frugivory by birds during fall migration (Levey and Stiles 1992) does not appear to correspond with a paucity of ground-occurring macroarthropods in the southern Appalachians. Our study indicated that ground-occurring macroarthropod abundance was lowest in winter. However, Hanula and Franzreb (1998) reported that macroarthropod biomass on longleaf pine (*Pinus palustris* Miller) bark in South Carolina was highest in fall and winter, suggesting that bark is an overwintering place for some species. The abundance of each macroarthropod taxon varied temporally, but abundance patterns also varied among taxa, likely due to differences in seasonal activity or juvenile recruitment. Temporal differences in abundance both within and among taxa caused seasonal shifts in size classes, and in the abundance of taxa relative to others.

A repeated measures effect was detected for some abundant taxa (e.g., Julida, Polydesmida, Scolopendromorpha), suggesting that a decline in abundance from summer through winter could be due to the removal of specimens from study sites. However, most taxa also showed their greatest abundance in spring, which was the last trapping season. A significantly greater abundance in spring despite a potentially negative removal effect suggests that the actual response by those taxa might have been even greater than observed had specimens not been removed.

Canopy gaps created by windthrow are common, and historically have been a primary natural disturbance type in the southern Appalachians (Greenberg and McNab 1998) that created habitat heterogeneity. At the small scale of canopy gaps, declines in some common macroarthropod taxa would be unlikely to have far-reaching, population-level effects on vertebrate predators. Forest management practices that reduce canopy cover and leaf litter (Ash 1995) at a larger scale, such as clear-cutting, likely would result in declines of common ground-occurring macroarthropods similar to or greater than what we found. However, this effect could potentially be offset by increases in foliageoccurring macroarthropods, which we did not address. Important forest management questions that remain include whether reductions in macroarthropod numbers and biomass at the levels observed are likely to adversely impact vertebrate predators, whether the taxa that declined are important prey resources, and at which scales do impacts become a conservation issue.

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