ANTS (HYMENOPTERA: FORMICIDAE) ASSOCIATED WITH STRIP-CLEARCUT AND DENSE SPRUCE-FIR FORESTS OF MAINE¹

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Abstract

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Four genera and 9 species of ants were collected by pitfall traps in a spruce budworm-infested forest of northern Maine. *Myrmica detritinodis* and *Camponotus herculeanus* were most abundant. In 1977, significantly more individuals and species were trapped in dense spruce-fir stands than in either uncut residual or clearcut strips. In 1978, clearcut-strip and dense-stand means were nonsignificant for individuals and species, but significantly more individuals and species were trapped in clearcut than in uncut residual strips. Ants were active during the spruce budworm's developmental stages. Diversity of ant species was generally greater in dense stands than in strip-clearcut areas. Individuals were distributed unevenly among species but more evenly in dense stands than in strip-clearcut areas (residual + clearcut strips). Coefficients of community (CC) and percentage similarity (PS) values indicated ant species and individuals shared forest conditions in common; however, the most dissimilar neighboring habitats (uncut residual and clearcut strips) had few species in common. Neither age of strip clearcut (1–6 years) nor litter depth had much influence on mean catches and mean number of species of ants/trap/week.

Résumé

Des pièges à fosse ont révélé la présence de 4 genres et 9 espèces de fourmi dans une forêt infestée par la tordeuse des bourgeons de l'épinette, située au nord du Maine, É.-U. Les espèces les mieux représentées sont *Myrmica detritinodis* et *Camponotus herculeanus*. En 1977, un nombre significativement plus élevé d'individus et d'espèces furent piégés dans un peuplement dense d'épinette et de sapin que dans des bandes à coupe rase ou des interbandes non coupées. En 1978, les nombres moyens d'individus et d'espèces ne différaient pas de façon significative entre les bandes à coupe rase et les interbandes non coupées, alors que le nombre d'individus et d'espèces piégés s'avèrait significativement plus élevé dans les bandes à coupe rase. Les fourmis demeurèrent actives durant les stades de développement de la tordeuse. La diversité en fourmi apparaît en général plus grande dans les peuplements denses que dans les zones ayant des bandes à coupe rase. Le nombre d'individus piégés varie beaucoup d'une espèce à l'autre; les différences observées restent moins grandes dans les peuplements denses. Des indices biocénotiques et de similarité indiquent que les individus et les espèces se retrouvent dans les mêmes habitats forestiers. Cependant, les habitats adjacents les plus dissemblables (bandes et interbandes) ont peu d'espèces communes. L'âge (1–6 ans) des bandes à coupe rase et l'épaisseur de la litière ont exercé peu d'influence sur la moyenne des captures et sur le nombre moyen d'espèces de fourmi capturées par piège par semaine.

Introduction

Ants are increasingly recognized as important predators of the spruce budworm, *Choristoneura fumiferana* (Clemens); however, there is little information on the species

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of ants found in spruce-fir forests of northern Maine. Wing (1939) listed 54 taxa for Maine; most were collected in southern and coastal localities. More than 30 species were recorded from various habitats on Mount Desert Island, Hancock County, Maine (Procter 1946).

In 1977 and 1978 we investigated the ant fauna of strip-clearcut and dense spruce-fir forests of northern Maine. Our objectives were to (1) determine the species of ants found in clearcut strips, uncut residual strips, and dense (control) spruce-fir stands, (2) determine their seasonal activity as related to spruce budworm development, and (3) determine if strip clearcutting influenced ant species diversity and evenness. Results of these investigations are reported herein.

Materials and Methods

Study area. Ants were studied in a dense spruce-fir forest infested with spruce budworm for 4–5 years. Portions of the forest had been strip clearcut by mechanical harvesting, which created open areas with abundant shrubs and forbs, mainly *Rubus* spp. Strip clearcutting resulted in alternating clearcut and uncut residual strips (Fig. 1). Individual study sites were located from 48 to 61 km northwest of Millinocket, Piscataquis County, Maine. The study area was sprayed with Sevin-4-oil® for spruce budworm suppression in 1976, but was not sprayed in 1977 or 1978. Budworm population estimates were 92.8 larvae–pupae/m² of balsam-fir foliage in 1977, and 100.7 larvae–pupae/m² of foliage in 1978.

Five strip-clearcut stands and 5 nearby dense (control) stands were investigated in 1977; 7 strip-clearcut stands and 3 dense stands were investigated in 1978. Mean basal areas, tree heights, and stand ages in 1977 were 33.1 m²/ha, 17.3 m, and 73.7 years for uncut residual strips and 41.5 m²/ha, 15.4 m, and 73.5 years for dense stands, respectively. Most study sites had a predominately softwood component of balsam fir [*Abies balsamea* (L.) Mill.], red spruce (*Picea rubens* Sargent), white spruce [*P. glauca* (Moench) Voss], black spruce [*P. mariana* (Miller) B.S.P.], northern white cedar (*Thuja occidentalis* L.), and white pine (*Pinus strobus* L.). Common hardwood species were paper birch (*Betula papyrifera* Marshall), yellow birch (*B. alleghaniensis* Britton), and red maple (*Acer rubrum* L.).

Pitfall traps. Forty large-capacity pitfall traps (Houseweart *et al.* 1979) were used each year for collecting ants. Four traps were deployed in each strip-clearcut area, 1 each in 2 uncut residual strips and in 2 clearcut strips (Fig. 1). Correspondingly, 4 traps were placed in each nearby dense (control) stand investigated. Trap spacings in dense stands equaled spacings in strip clearcuts. In 1977, traps were installed on 26 May and their contents collected weekly for 10 weeks from 2 June to 4 August. In 1978, traps were installed 18 May and contents collected weekly for 11 weeks from 25 May to 3 August.

Captured specimens were sorted in the laboratory; all ants were removed and stored in 2-dram neoprene-stoppered vials containing 70% ethanol. Species determinations were made after Creighton (1950), except for the *Formica fusca* group (Francoeur 1973). The North American species of *Myrmica* are being revised by Francoeur; the species names used here are adjusted accordingly: *M. alaskensis* Wheeler has priority over *kuschei* Wheeler (Creighton 1950), while *M. detritinodis* Emery corresponds partly in the literature to *M. fracticornis* Emery and *M. monticola* Wheeler. Voucher specimens of all collected ant species are deposited in the U.S. National Museum of Natural History, Washington, DC, the American Museum of Natural History, New York, and in the Université du Québec à Chicoutimi, Québec.

Data analyses. Pitfall-catch data were subjected to Hartley's test for homogeneity of variance prior to statistical analyses. Natural log transformations, $\ln(X + 1)$, were used to stabilize variances. Analysis of variance (ANOVA) and Duncan's multiple range test were used to evaluate differences among pitfall catches by forest stand condition (uncut residual

FIG. 1. Schematic of pitfall-trap layout in strip-clearcut (uncut residual and clearcut strips) and nearby dense spruce-fir stands. Numbers represent placements of single traps. Strip widths: 23–50 m, uncut residuals; 19–30 m, clearcuts.

strips, clearcut strips, and dense stands). Regression analyses were used to evaluate relationships between strip-clearcut age (1–6 years) (independent variable) and mean catches of individuals and species (dependent variables) per trap per week, where R^2 = coefficient of determination. Similar analyses were used to evaluate relationships between litter depth (cm) and mean catches of individuals and species.

Because our pitfall collections represented finite populations where all individuals were counted and identified (Pielou 1966; Poole 1974), we used Brillouin's diversity formula to calculate species diversity (Pielou 1975). Brillouin's formula has been used to compare pitfall-catch diversities of spiders (Doane and Dondale 1979), of carabid beetles (Reeves *et al.* 1983), and of phalangids (Jennings *et al.* 1984). A measure of evenness was determined by the formula $J = H/H_{\max}$ where H is Brillouin's diversity and $H_{\max}$ is the maximum possible diversity. Two measures of similarity among forest conditions were made using coefficient of community (CC) and percentage similarity (PS) (Pielou 1975),

where (CC) measures similarity between species lists and (PS) measures similarity between species quantities.

Results

Numbers of individuals and species. Three genera and 9 species of ants were collected in 1977; 4 genera and 9 species were collected in 1978 (Table 1). Species composition differed among years; *Camponotus nearcticus* and *Formica impexa* were collected in 1977 but not in 1978; *Leptothorax muscorum* and *Formica podzolica* were collected in 1978 but not in 1977. For both years of trapping, *Myrmica detritinodis* and *Camponotus herculeanus* were numerically dominant, comprising 33 and 55% of the specimens in 1977 and 24 and 47% of the specimens in 1978, respectively.

Although the 40 traps were distributed unevenly among the forest conditions, about equal numbers of ants were trapped both years of study—386 in 1977 and 398 in 1978. In 1977 most of the ants were collected in dense spruce-fir stands; however, in 1978 most were collected in clearcut strips (Table 1).

In both years, more species were collected in open areas of clearcut strips than in uncut residual strips or in dense spruce-fir stands (Table 1). These differences may reflect species-specific habitat requirements. For example, *C. noveboracensis*, *F. impexa*, *F. subaenescens*, *F. podzolica*, *F. subnuda*, and *L. muscorum* were found only in clearcut strips. The first 4 of these species usually are not found in dense coniferous stands; the last 2 species can invade dense stands to some extent. *Camponotus nearcticus* was found only in a dense spruce-fir stand.

Mean numbers of individuals and species. In 1977, significantly more individuals ($P \leq 0.05$) and more species ($P \leq 0.05$) of ants were caught in dense stands than in either clearcut strips or uncut residual strips (Table 2). In 1978, clearcut-strip and dense-stand means did not differ significantly for individuals or species, but significantly more individuals and species ($P \leq 0.05$) were caught in clearcut than in uncut residual strips.

Seasonal activity. Ants were active during most of the spruce budworm's developmental stages; however, seasonal activities varied considerably between study years (Fig. 2). In 1977, mean catches were greatest (A) during the budworm's late-larval, pupal, adult, and egg stages. In 1978, peaks in activity generally occurred during the early-larval stages in late May and early June (B).

For both study years, ants were active during dispersal of 1st instars of the spruce budworm, which occurs after egg hatch in July. Strip clearcutting contributes to dispersal losses of these early-stage larvae (Jennings *et al.* 1983), exposing the larvae to numerous predators, including ants.

Mean species catch rate per week was <1 for all 3 forest conditions both years (Fig. 3). This indicates that (1) ant activity varied among species, and (2) there was a sparsity of ant species regardless of forest condition.

Species diversity and evenness. For both study years, diversity of ant species in pitfall-trap catches was greater in dense stands than in strip-clearcut areas (residual + clearcut strips) (Table 3). Comparing forest conditions, individuals were distributed unevenly among species both study years. However, within strip-clearcut areas (residual + clearcut strips) and dense stands, individuals were distributed evenly both years. For unexplained reasons, both species diversity and evenness were greater in 1978 than in 1977 for pitfall catches of ants in clearcut strips.

Coefficient of community and percentage similarity. Strip-clearcut areas (residual + clearcut strips) had more ant species in common with dense stands in 1977 (CC = 71) than in 1978 (CC = 54). However, comparing catches *within* strip clearcuts (residual vs. clearcut strip) showed that fewer species shared these habitats in common in 1977 (CC = 40) than in 1978 (CC = 62).

Table 1. Species and number of ants collected in pitfall traps, 3 forest conditions, Telos Lake area, Piscataquis County, Maine, 1977-1978

Ant species	1977					1978				
	Clearcut strips (N = 10 traps)	Residual strips (N = 10 traps)	Dense stands (N = 20 traps)	Total	%	Clearcut strips (N = 14 traps)	Residual strips (N = 14 traps)	Dense stands (N = 12 traps)	Total	%
<i>Myrmica alaskensis</i> Wheeler	0	7	2	9	2.33	21	8	0	29	7.29
<i>Myrmica derritnodis</i> Emery	1	2	126	129	33.42	36	2	59	97	24.37
<i>Leptothorax muscorum</i> (Nylander)						13	0	0	13	3.27
<i>Camponotus herculeanus</i> (Linnaeus)	34	29	150	213	55.18	53	85	51	189	47.49
<i>Camponotus nearcticus</i> Emery	0	0	1	1	0.26					
<i>Camponotus novaeboracensis</i> (Fitch)	3	0	0	3	0.78	14	0	0	14	3.52
<i>Formica impexa</i> Wheeler	1	0	0	1	0.26					
<i>Formica neorufibarbis</i> Emery	1	0	10	11	2.85	28	0	2	30	7.54
<i>Formica podzolica</i> Francoeur						1	0	0	1	0.25
<i>Formica subaenescens</i> Emery	3	0	0	3	0.78	22	1	1	24	6.03
<i>Formica subnuda</i> Emery	1	0	15	16	4.14	1	0	0	1	0.25
Subtotals: Species	7	3	6	9		9	4	4	9	
Individuals	44	38	304	386		189	96	113	398	

Table 2. Mean numbers of individuals and ant species per trap per week by forest condition

Forest condition	$\bar{X}$ * number of individuals		$\bar{X}$ * number of species	
	1977	1978	1977	1978
Clearcut strips	0.44b	1.23a	0.31b	0.67a
Residual strips	0.38b	0.62b	0.29b	0.36b
Dense stands	1.52a	0.86ab	0.48a	0.46ab

*Column means followed by the same letter are not significantly different at the $P \leq 0.05$ level, Duncan's multiple range test.

FIG. 2. Mean catches of ants per trap per week; (A) week 1 = 2 June 1977; (B) week 1 = 25 May 1978.

FIG. 3. Mean species of ants per trap per week; (A) week 1 = 2 June 1977; (B) week 1 = 25 May 1978.

Table 3. Ant species diversity and evenness by forest condition, Brillouin's formula, 1977 and 1978

Forest condition	Diversity		Evenness	
	1977*	1978†	1977*	1978†
Residual strips	0.26	0.16	0.59	0.28
Clearcut strips	0.24	0.77	0.32	0.84
Residual + clearcut strips	0.32	0.29	0.39	0.38
Dense stands	0.43	0.32	0.56	0.56

*1977, 5 replicates each forest condition; 4 traps/replicate.

†1978, 7 replicates (residual vs. clearcut strips); 3 replicates (residual + clearcut strips vs. dense stands); 4 traps/replicate.

Percentage similarity in numbers of individuals of each ant species was less in 1977 (PS = 36) than 1978 (PS = 48) among strip-clearcut areas and dense stands. But residual and clearcut-strip habitats were less similar in numbers of each species caught in 1978 (PS = 45) than in 1977 (PS = 73).

Age of strip clearcut. Regression analyses indicated that age of strip clearcut (1–6 years) had little influence on mean catches ($R^2 = 0.28$, $P > 0.08$) and mean number of species ($R^2 = 0.17$, $P > 0.18$) of ants/trap/week.

Litter depth. Mean litter depth was significantly greater ($P \leq 0.01$) in dense stands ($\bar{X} = 11.7$ cm) than in either uncut residual ($\bar{X} = 8.5$ cm) or in clearcut strips ($\bar{X} = 8.0$ cm). Uncut residual and clearcut-strip means did not differ significantly. Regression analyses indicated that litter depth had little influence on either mean catches ($R^2 = 0.02$, $P > 0.20$) or mean species ($R^2 = 0.01$, $P > 0.57$) of ants caught/trap/week.

Discussion

Our pitfall-trapping results indicate an ant fauna typical of the boreal coniferous forest biome. Such species as *Myrmica alaskensis*, *Leptothorax muscorum*, *Camponotus herculeanus*, *Formica neorufibarbis*, and *F. subnuda* can reach the treeline or adjacent areas; they are typical of the forest tundra (Francoeur 1983). The other species, except *C. nearcticus*, also are associated with that biome but are limited to more southern districts. *Camponotus nearcticus*, which occurs as far north as southern Quebec and mainly in mixed forest, is not considered characteristic of the boreal forest.

Species represented only once, e.g. *F. impexa* and *F. podzolica*, are not significant in this sampling. These species usually prefer open forests and sandy soils (Béique and Francoeur 1966, 1968; Francoeur 1973). *Leptothorax muscorum* probably is underrepresented because it usually maintains a greater number of colonies than *C. herculeanus*. *Myrmica detritinodis* exhibits a large ecological amplitude (Francoeur, unpublished) and can invade with *C. herculeanus* rather dense, closed-canopy coniferous forests.

Our results on mean catches of individuals/trap/week indicate that the ants preferred no particular forest condition. However, detection of species-specific habitat preferences based solely on pitfall catches can be misleading because large numbers of individuals are caught when the nest is near the trap, or when scouts of larger species (*Camponotus*, *Formica*) forage far away from their home nest through different habitats.

The abundance of certain species, such as *M. detritinodis* and *C. herculeanus*, and scarcity of others, such as *F. impexa* and *F. subnuda*, no doubt contributed to low species diversity indices. Species diversity increases as species are added and as species are more evenly distributed in abundance (Price 1975).

Both measures of similarity (CC and PS) among forest conditions showed that ant species and individuals were shared in common among strip-clearcut areas and dense stands. As expected, the most dissimilar neighboring habitats (uncut residual vs. clearcut strips) had fewer species (low CC values) and fewer individuals (low PS values) in common.

Although we detected little influence of either strip-clearcut age or litter depth on mean catches of individuals and species of ants, we suspect that age and litter depth may become increasingly important during later successional stages when forest regeneration causes canopy closure.

Our results in northern Maine indicate dense stands generally support greater populations of ants than strip-clearcut areas, but not consistently. Although more species of ants were found in strip clearcuts (residual + clearcut strip) than in dense stands (Table 1), individuals were distributed unevenly (Table 3). The uneven distribution of individuals no doubt contributed to lower species diversity indices for strip clearcuts. We conclude that strip clearcutting may alter species diversity and evenness of ants. The open, cleared strips with abundant shrubs and forbs provide new and different habitats. And habitat heterogeneity enriches ant diversity (Huhta 1976; Whitford and Gentry 1981). The strip clearcuts over time (years) may induce an edge effect (ecotone) and attract species usually living in open stands (e.g. *F. impexa* and *F. podzolica*). Conversely, the uncut residual stands provide islands of "refugia" where components of the coniferous forest biome are maintained.

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