The effects of forest disturbance on land gastropod communities in northern New England

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We studied the gastropod communities of 16 forested sites in northern New England that had been disturbed by clear-cutting, agricultural cropping, or forest fires. There was no clear relationship between the density, species richness, or composition of the gastropod community and the time elapsed since disturbance. This result contrasts with previous studies, which reported strong correlations between the age of forested stands and the structure of gastropod communities. We suggest that gastropod communities in our study sites recovered rapidly following disturbance because of the small area of the disturbed sites, which facilitated recolonization from surrounding areas, and because of the rapid recovery of the function of the vegetation following forest disturbance in northern New England.

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Les communautés de gastropodes ont fait l'objet d'une étude en 16 stations forestières du nord de la Nouvelle-Angleterre, certaines perturbées par des cupes à blanc, d'autres par des cultures agricoles, d'autres ravagées par des feux de forêts. Il n'y a pas de relation évidente entre la densité, la richesse en espèces ou la composition d'une communauté de gastropodes et le temps écoulé depuis la perturbation. Ces résultats sont en contradiction avec les résultats obtenus au cours d'études antérieures qui concluaient qu'il y avait de fortes corrélations entre l'âge des forêts et la structure des communautés de gastropodes. Il semble que, dans les régions étudiées ici, les communautés de gastropodes aient pu récupérer rapidement après les perturbations à cause de la petite taille des territoires perturbés, ce qui a permis la recolonisation par les animaux des territoires avoisinants, et à cause aussi de la récupération rapide de la végétation après perturbation de la forêt dans le nord de la Nouvelle-Angleterre.

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Introduction

Disturbance, both natural and anthropogenic, plays an important role in determining the structure of forest vegetation in the northeastern United States (e.g., Day 1953; Bormann and Likens 1979; Canham and Loucks 1984), and likewise influences the composition of forest animal communities (e.g., Grange 1948; Odum 1950; Bendell 1974). We report here the results of a preliminary study on how three kinds of disturbance (clear-cutting, burning, and clearing land for agriculture) affect the composition of land gastropod communities in Maine and New Hampshire.

We chose to work with gastropods for several reasons. Gastropods are relatively easy to collect and identify. They also are celebrated for their lack of mobility, so they cannot easily escape a disturbance or the changed local environment that follows, and presumably are slow to recolonize disturbed sites. Thus, the gastropod fauna of a site might be expected to reflect the disturbance history of that site.

Furthermore, several species of gastropod serve as intermediate hosts for the parasitic nematode *Parelaphostrongylus tenuis* (e.g., Anderson 1963, 1972). Normally, this worm inhabits the brain of white-tailed deer, *Odocoileus virginianus*, without catastrophic results. However, when *P. tenuis* infects a moose, *Alces alces*, it causes the severe disorder known as "moose sickness," which usually leads to death of the moose. Because of the sensitivity of the moose to *P. tenuis*, populations of moose and deer rarely overlap. However, moose and deer coexist on some recently disturbed sites, and it has been suggested that such coexistence might occur because the disturbance has eliminated local gastropod populations, thereby breaking the cycle of transmission of *P. tenuis* (Irwin 1975). Because of Irwin's suggestion, we were especially interested in finding out if disturbance eliminated or severely reduced populations of gastropods and how long such reductions lasted.

The study area

We examined 16 sites in the northern hardwood forest of New Hampshire and Maine that had been either clear-cut, burned, or used for agriculture, along with two reference sites that have not been disturbed recently (Table 1). Sites within each chronosequence were matched as far as possible for important environmental characteristics.

The seven clear-cut sites, all within 50 km of one another in the White Mountains of Grafton Co., New Hampshire, include both commercial and research cuts. These are midelevation sites lying predominantly on typic Haplorthods and were studied intensively by Nodvin (1983). Five study plots are in Baxter State Park in central Maine, where forest fires burned in 1911, 1934, and 1977. General information about the vegetation and soils of Baxter State Park is given by Gleich and Gilbert (1976) and Hansen (1985).

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TABLE 1. Characteristics of the study sites

Type of disturbance	Time since disturbance (years)	Size of disturbance (ha)*	No. of cardboards	Dominant woody vegetation†
Agriculture‡	2–3	0.2	36	*Pt, Ar, Pv*
(cropped)	30–35	0.5	29	*As, Ps, Ar*
	45–50	1.0	36	*Pt, Ar, As, Fa, Ab*
	60–65	0.8	35	*Ar, Pru, Ab*
	63–68	0.5	36	*Pru, Ab, Bpo*
	—§	0.2	27	*Pru, As, Fa, Tc*
Burning	3	—	30	*Pp, Pt, Bpa*
	3	—	30	*Pp, Bpa, Ss, Pt*
	46	—	32	*Ps, Bpa, Pre*
	69	—	32	*Pru, Ab, Bpa*
	—‖	—	32	*Pru, Ab, Bpa*
Clear-cutting	2	<10	36	*As, Ba, Fg / Pp, Rs*¶
	4	<10	32	*As, Ba, Fg / Pp, Rs*¶
	10	10	19	*As, Ba, Fg / Pp, Rs*¶
	22	<10	35	*As, Ba, Fg / Pp, Rs*¶
	32	<10	33	*As, Ba, Fg / Pp, Rs*¶
	56	—	30	*As, Ba, Fg / Pp, Rs*¶
	63	—	35	*Ab, Pru, Ar, Vs*

*Where not given, size of disturbance is unknown.
†Key to plant species: *Ab, Abies balsamea*; *Ar, Acer rubrum*; *As, Acer saccharum*; *Ba, Betula allegeheniensis*; *Bpa, Betula papyrifera*; *Bpo, Betula populifolia*; *Fa, Fraxinus americana*; *Fg, Fagus grandifolia*; *Pp, Prunus pensylvanica*; *Pre, Pinus resinosa*; *Pru, Picea rubens*; *Ps, Pinus strobus*; *Pt, Populus tremuloides*; *Pv, Prunus virginiana*; *Rs, Rubus* spp.; *Ss, Sambucus* sp., *Tc, Tsuga canadensis*; *Vs, Vaccinium* sp.
‡In order of increasing age, these are sites 4, 3, 5, 6, 2, and 7 of Hamburg (1984).
§Reference stand, multi-aged woodlot (never farmed).
‖Reference stand, never burned within period of record.
¶Dominated by *As, Ba*, and *Fg* before logging and by *Pp* and *Rs* shortly after logging.

TABLE 2. Comparison of numbers of land snails collected under cardboard and by hand-sorting litter from twenty-five 0.1-m^2 plots at three clear-cut sites in central New Hampshire

	2-year-old stand		10-year-old stand		56-year-old stand	
	Cardboard*	Litter	Cardboard†	Litter	Cardboard‡	Litter
Discus cronkhitei	16	2	92	48	19	11
Euconulus sp.	0	1	5	12	0	0
Helicodiscus parallela	0	0	7	3	2	5
Retinella rhoadsi	0	0	8	5	0	3
Striatura exigua	2	2	25	56	2	16
Succinea sp.	1	0	2	4	1	3
Zonitoides arboreus	7	0	27	13	11	1
Immatures	7	1	56	44	10	11
Others	0	1	2	0	0	1
Total	33	7	224	185	45	51

NOTE: The species composition of the samples collected by the two different methods is different at each of the three sites, according to a χ^2 test at $p < 0.05$.
*36 sheets of cardboard.
†20 sheets of cardboard.
‡24 sheets of cardboard.

The six agricultural sites lie in a 2-km^2 area between 490 and 550 m elevation in the town of Campton, Grafton Co., New Hampshire. The presettlement forest, dominated by red spruce (*Picea rubens*) and beach (*Fagus grandifolia*), was cleared between 1790 and 1835. The sites were used for row crops and cereals in rotation with hay for the next 50 to 130 years, and then abandoned (Hamburg 1984). Soils here are typic Haplorthods.

Materials and methods

Methods used for the collection of gastropods and other soil animals must represent a compromise between speed and accuracy. We collected gastropods by putting out sheets of cardboard onto the forest floor and then collecting the gastropods that colonized the sheets. This method was used effectively by Gleich and Gilbert (1976) and Kearney and Gilbert (1978), and Boag (1982) discussed the advantages that this method offers over the traditional (and time-consuming) method of sorting litter samples to recover gastropods. We found that the cardboard sheets provided large, fairly representative samples of the gastropod community, except that the abundance of *Striatura* spp. was underestimated (Table 2).

TABLE 3. Number of gastropods (% of total) collected from 13 sites in New Hampshire and 5 sites in Maine

	New Hampshire	Maine
Discus cronkhitei	865(30.8%)	71(26.9%)
Zonitoides arboreus	544(19.4%)	80(30.3%)
Arion subfuscus	348(12.4%)	24(9.1%)
Pallifera dorsalis	215(7.7%)	0
Striatura exigua	196(7.0%)	15(5.7%)
Succinea sp.	108(3.8%)	8(3.0%)
Deroceras laeve	103(3.7%)	19(7.2%)
Retinella rhoadsi	83(3.0%)	0
Helicodiscus parallela	58(2.1%)	5(1.9%)
Euconulus sp.	51(1.8%)	10(3.8%)
Arion fasciatus complex	37(1.3%)	4(1.5%)
Zoogenetes harpa	14(0.5%)	0
Philomycus carolinianus	12(0.4%)	4(1.5%)
Striatura ferrea / milium	7(0.2%)	0
Triodopsis albolabris	6(0.2%)	0
Vertigo sp.	6(0.2%)	0
Triodopsis tridentata	4(0.1%)	0
Mesodon sayanus	3(0.1%)	0
Strobilops labyrinthica	3(0.1%)	0
Oxychilus cellarius	2(0.1%)	0
Stenotrema fraternum	2(0.1%)	1(0.4%)
Cionella lubrica	2(0.1%)	0
Deroceras reticulatum	1(<0.1%)	0
Anguispira alternata	1(<0.1%)	0
Retinella indentata	0	15(5.7%)
Pallifera ohioensis	0	5(1.9%)
Unidentifiable immatures	137(4.9%)	3(1.1%)
Total	2808	264

Twenty to 36 sheets of cardboard (75×75 cm) were set out systematically in each of our study stands in late June 1980, in a roughly rectangular grid usually well within the boundaries of the stand. We returned to these sites after approximately 1 month (32–44 days) and again after approximately 2 months (26–33 days after the first collection) and collected all living gastropods from beneath the cardboard. Each collection period was completed within 7 days (usually 3 days) of stable weather conditions to minimize any possible effects of weather on gastropod behaviour. Data presented here are the means of the July and August collections, except for species richness, for which we used the pooled collections. Gastropods were identified using Burch (1962) and Pilsbry (1939–1948). Although voucher specimens were collected, they were unfortunately lost.

We used a mathematical ordination technique, detrended correspondance analysis (DECORANA), to summarize patterns of faunal composition. DECORANA provides a summary of faunal differences among sites that can be compared with differences in environmental conditions among sites. DECORANA uses only information on the presence or absence of species at each site to construct its ordination; no environmental data are used (Hill and Gauch 1980; Gauch 1982).

Results

We collected 3072 gastropods, representing 26 species. The fauna was dominated by slugs and small zonitid and endodontid snails (Table 3), and is similar to those reported previously from cool acid woodlands elsewhere in northeastern North America (e.g., Baker 1942; Getz 1962; Gleich and Gilbert 1976; Kearney and Gilbert 1978). Our collections from Maine contain *Pallifera ohioensis* and *Retinella indentata* in the place of *Pallifera dorsalis* and *Retinella rhoadsi*, but otherwise are similar to the New Hampshire collections.

There are only weak indications that the distribution and

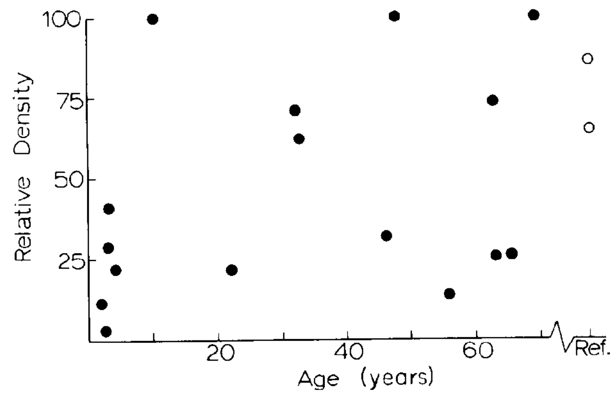

FIG. 1. Relative density of gastropods as a function of stand age. Relative density is the absolute density at a site as a percentage of the density of gastropods found at the site with the highest density in its chronosequence. Reference sites are shown as open circles. $r = 0.24$, $p > 0.2$.

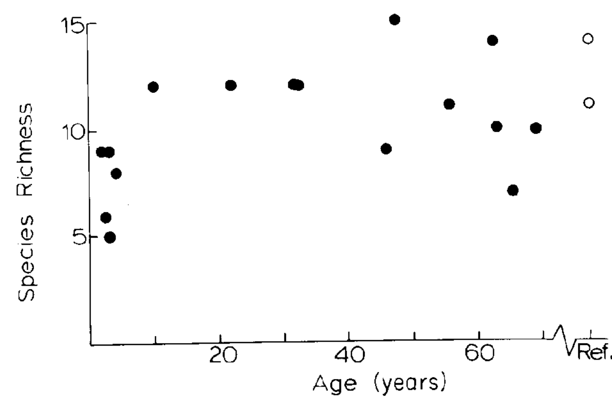

FIG. 2. Species richness of gastropods as a function of stand age. Reference sites are shown as open circles. $r = 0.31$, $p > 0.2$.

abundance of gastropods is related to stand age in the study area. Total density of gastropods is uncorrelated with stand age ($r = -0.03$, $p > 0.5$). However, variation in gastropod density among chronosequences (mean number of gastropods/cardboard was 3.9 in the clear-cut stands, 3.4 in the old-field stands, and 0.8 in the burned stands) may have obscured any age-related patterns, so we normalized the gastropod densities within each chronosequence. However, even these normalized densities are not linearly correlated with stand age (Fig. 1). The data in Fig. 1 suggest that there may be a curvilinear relationship between stand age and gastropod density, with depressed densities in very young (<5 years old) stands, and somewhat higher but very variable densities in older stands. Species richness also is not linearly correlated with stand age (Fig. 2), but again may be described by a curvilinear function with lower species richness in very young stands.

There is no evidence at all for shifts in species composition following disturbance. The ordination axes, which summarize compositional variation, are uncorrelated with stand age (axis 1: $r = 0.30$, $p > 0.2$; axis 2: $r = 0.16$, $p > 0.5$), and there is no apparent age-related pattern in the scatter of stands in ordination space (Fig. 3). Furthermore, we found no correlations between the stand age and the abundance of any single gastropod species ($p > 0.05$ for each of the 13 most common species).

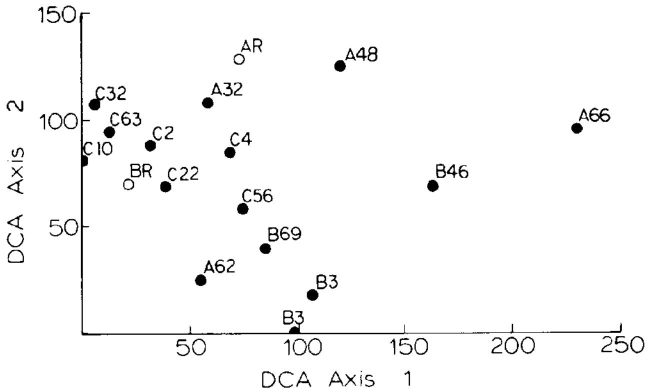

FIG. 3. DECORANA ordination of study sites according to their gastropod faunas. The proximity of two sites in this figure reflects the degree of similarity of their gastropod faunas. Each study site is labelled by the type of disturbance (A, agriculture; B, burning; C, clear-cutting) and the time since disturbance, in years. Reference sites (R) are shown as open circles. This ordination does not include the 2- to 3-year-old agricultural site, since we collected only 17 specimens at that site and initial ordinations showed that it was an outlier (cf. Gauch 1982).

Discussion

Our results suggest that disturbance may reduce population densities of gastropods in northeastern forests, resulting in the local extinction of some species, but that site to site variation in gastropod communities is so large that it almost masks any pattern. Furthermore, it appears that any reduction in density or species richness of the gastropod community is ephemeral and the gastropod community recovers rapidly from forest disturbance. It does not appear likely that the kinds of disturbance that we studied reduce gastropod populations enough to break the transmission cycle of *Parelaphostrongylus tenuis*, although a definitive answer to this question would of course require additional information about the transmission dynamics of *P. tenuis*, and the microhabitat use and behavior of gastropods, moose, and deer.

It is perhaps surprising that stand age was so poorly correlated with gastropod community structure in our study, since work elsewhere has shown age to be an important correlate of gastropod community structure. Reinink (1979) found a strong correlation between species richness of gastropods and the age of forest plantations on reclaimed polders in the Netherlands. Cameron et al. (1980) studied the gastropod faunas of British hedges and reported that hedges of 20th century origin contained many fewer species of gastropods than did the older hedgerows.

The difference between our results and those of these prior studies are probably due to the different nature of the habitats investigated. Reinink's (1979) study sites were isolated woodlands planted on reclaimed polders, and many of the hedges studied by Cameron et al. (1980) were planted between fields and are remote from woodlands. In these situations, we might expect environmental conditions in the litter layer of the newly planted hedgerow or forest to be very different from those presented by old woodlands or hedges. Furthermore, the isolation of these habitats would make colonization difficult for gastropods.

In contrast, the disturbed sites that we studied are relatively small and are part of a mosaic of patches of different ages. Our study sites should therefore be relatively accessible to colonists. Also, although there are great differences in vegetational composition between newly disturbed sites and old stands in northern New England, productivity, leaf area index, microbial communities, and microenvironmental conditions on the forest floor recover rapidly following disturbance (Bormann and Likens 1979; Nodvin 1983; Thorne and Hamburg 1985). Since vegetation apparently influences gastropod communities indirectly by altering local environmental conditions rather than by forming specific plant–snail associations (Burch 1956; Beyer and Saari 1977), it seems likely that the rapid recovery of the function of the plant community provides a hospitable environment for gastropods within a few years of the disturbances of the kind that we studied. It is thus not possible to generalize about the influence of stand age on gastropod communities without knowing more about the size and nature of the disturbance that initiated the stand.

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