

# Effects of poisoning nonindigenous slugs in a boreal forest

Steven H. Ferguson

**Abstract:** This study examined the impact of poisoning nonindigenous slugs on abundance of other soil arthropod groups occurring on the soil surface of a boreal forest. The experimental design consisted of counting soil fauna under boxes from 20 plots during weekly surveys before (year 1) and after (year 2) treatment (metaldehyde poison) with control and experimental plots. Slug abundance was negatively affected by presence of slug poison, with an 80% decrease in slug numbers following treatment. Herbaceous cover did not differ between plots (control and experimental) but the amount eaten decreased (26%–15%) with poisoning. Nonindigenous taxa, including slugs, predominated in the macrofauna at this site, accounting for a third of the individuals and a half of the biomass. Possible explanations for the observed patterns in soil arthropod community relative to invasive species are discussed.

**Résumé :** Cette étude traite de l'impact de l'empoisonnement des limaces non indigènes sur l'abondance d'autres groupes d'invertébrés du sol vivant à la surface du sol dans une forêt boréale. Le dispositif expérimental consistait en un dénombrement de la faune au sol sous des boîtes dans 20 places échantillons, au cours d'inventaires hebdomadaires avant (an 1) et après (an 2) traitement (empoisonnement au métaldéhyde) dans des places témoins et expérimentales. L'abondance des limaces était négativement affectée par la présence de poison à limaces, causant une diminution de 80 % des effectifs de limaces après traitement. Le couvert herbacé ne différait pas entre les places échantillons (témoins et expérimentales) mais la quantité mangée a diminué (26 à 15 %) avec l'empoisonnement. Les taxons non indigènes, incluant les limaces, prédominaient dans la macrofaune de ce site, comptant pour un tiers des individus et la moitié de la biomasse. Diverses explications des patrons de communautés d'invertébrés du sol sont discutées en regard des espèces envahissantes.

[Traduit par la Rédaction]

## Introduction

The community of soil animals contributes to biological processes of a forest including decomposition of organic materials, dispersal of seeds and spores, aeration and mixing of soils, and trophic energy movements (Mikola and Setälä 1998; Wardle 1999). Understanding soil food webs is limited by their great complexity (Zheng et al. 1997). Yet, knowledge of fundamental assumptions, such as the importance of keystone species and the effect of nonindigenous invaders, would considerably improve our understanding of soil processes (Kalisz and Powell 2000a). For ecosystem conservation, we need to understand the basics of distribution and abundance of soil arthropod groups under conditions of human disturbance including community changes resulting from invasive species (Scheu and Schulz 1996). The consequences of biological invasions include the evolutionary processes of invaders rapidly responding to novel abiotic and biotic conditions, while native species respond to the invasion (Sakai et al. 2001). Nonindigenous species offer the opportunity to study population biology and help to identify life history stages where forest management will be

most effective in reducing foreign invaders (Pimentel et al. 1999).

In forest soils, the macrofauna accounts for >50% of invertebrate biomass (Kalisz and Powell 2000b), and those that are detritivores play a major role in the decomposition processes and have a significant influence on ecosystem processes and trophic interactions (Anderson 1988; Schaefer 1991a, 1991b; Kajak et al. 1991; van Wensem et al. 1993). In north-temperate environments, these macrofauna include major groups of invasive species (Blair et al. 1994). For example, no native earthworms have been reported from Canada east of the Pacific Northwest, although exotic species now occur in this entire region (Hendrix and Bohlen 2002). Although situated at temperate latitudes and low human density, the community diversity of boreal forests in temperate North America is dominated by introduced species that include isopods (*Porcellio scaber* Latr.), earthworms (Lumbricidae), and slugs (*Deroceras* spp.).

It is unknown how abundant native slug populations were prior to the introduction of European slug species in the 1800s or how they might have interacted with plant species (Chichester and Getz 1969). Likely, European slugs have been present in the Thunder Bay, Ontario, study area for the past 50 years, as has been observed for nonnative earthworms (Reynolds 1977). Slugs are important pests of agricultural crops in moist temperate climates (Port and Port 1986) as well as potentially affecting seedling survival in temperate forests (Fritz et al. 2001). Damage to agriculture by slugs is sufficient to warrant substantial investment in

Received 17 February 2003. Accepted 5 September 2003.  
Published on the NRC Research Press Web site at  
<http://cjfr.nrc.ca> on 19 February 2004.

**S.H. Ferguson.** Department of Fisheries and Oceans,  
501 University Crescent, Winnipeg, MB R3T 2N6, Canada  
(e-mail: [fergusonsh@dfo-mpo.gc.ca](mailto:fergusonsh@dfo-mpo.gc.ca)).

control, mainly by pesticides (Garthwaite and Thomas 1996).

Soil surface dwelling slugs overwinter as eggs, which hatch in the spring with warming temperatures and grow to an adult length of 4–8 cm (Carrick 1942). In Ontario, adult slugs become active in the spring and peak soon after (South 1992). Slugs are active in areas that are moist and protected. Mixedwood boreal forests with hardwoods dominating are ideally suited for slug herbivory. The leaf mulch on mixedwood boreal forest floors provides a protective cover. Snails and slugs have many natural enemies, including ground beetles, pathogens, snakes, toads, and birds, but they are rarely effective enough to control abundance (Chichester and Getz 1969).

Molluscs are highly selective feeders preferring living plants to decaying plant matter (South 1992), forbs to grasses (Cates and Orisans 1975; Grime et al. 1968), and seedlings to mature plants (Barker 1989). Therefore, mollusc herbivory can act as an important selective force of the abundance and distribution of plant species (Bruehlheide and Scheidel 1999; Wilby and Brown 2001). Slugs feed primarily at night and prefer succulent foliage, including seedlings, newly expanding leaves, and herbaceous plants that are close to the ground. Slug herbivory is observed as ragged edges and (or) a ragged hole in the leaf and often results in the leaves curling up. Damaged leaves have a reduced ability to use sunlight, thereby resulting in reduced plant survival and reproduction. Slugs can also be active underground by chewing on roots below the soil surface, and roots damaged in this way are susceptible to invasion by pathogens that can decay the root. Damage to herbs occurs most commonly in the spring, although moist boreal forests are likely conducive to slug activity throughout the season.

Most field studies examining the influence of soil fauna on ecosystem processes have relied on biocides that have poor efficiency at eliminating fauna for extended periods and can have nontarget effects (Colinas et al. 1994) that confound faunal influences. The poison used in this study contains metaldehyde, which works on slugs because the most important characteristics of the environment to growth and survival of slugs are soil moisture and temperature (Young and Port 1989; Young et al. 1993; Shirley et al. 2001). Metaldehyde does not kill snails and slugs directly unless they eat a substantial amount of it; rather, it stimulates their mucus-producing cells to overproduce mucus (slime) in an attempt to detoxify the bait. The cells eventually fail and the slug dies. When it is sunny or hot, they die from desiccation, and therefore, the poison works best in low-moisture conditions where dehydrated slugs seek shelter and huddling (Cook 1981; Prior 1989). If it is cool and wet, slugs may recover if they ingest a sublethal dose. Thus, these poison products work best at night and in low-moisture conditions. Slug poison applies an additional mortality to active adult slugs; it does not necessarily mimic the effects of parasites, predators, or crop husbandry (Shirley et al. 2001).

This study examines the impact of one invasive slug species on forest functioning by significantly reducing slug numbers within a boreal forest in northeastern North America. This species, the exotic *Deroceras laeve* Muller, was the only invasive slug at this site and was introduced from Europe. I predicted that abundance of potential competitors, in-

cluding native faunal species, would increase with the reduction in slug numbers. The study design used surveys of soil fauna found under boxes placed on the forest floor (Hawkins et al. 1998; Ferguson 2001), as soil fauna are commonly found under logs (Kolstrom and Lumatjarvi 1999), where downed wood provides shelter and moisture and prevents light penetration. The goal was to determine the abundance changes of soil arthropod groups associated with removal of a significant invasive group from the forest habitat and to relate abundance changes to soil arthropod diversity. For example, changes in plant food availability may change with slug mortality and cascade through particular taxonomic groups. Thus, I also examined the effects of slug mortality on the amount of herbaceous cover damaged by slug herbivory.

## Materials and methods

### Study site

The study area consisted of a 1-km<sup>2</sup> stand of boreal forest located along the McIntyre River within the city of Thunder Bay, Ontario (48°22'N, 89°19'W). The mixed boreal forest consisted of jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.). The study site lies within the Boreal Forest Region that consists of rolling rocky uplands with coarse well-drained soils (Rowe 1972). The climate is humid continental with a mean minimum January temperature of -15 °C and a mean maximum daily temperature for July of 18 °C (Environment Canada 2001). Mean annual precipitation is approximately 700 mm, including a mean winter snowfall of 196 cm (Environment Canada 2001). For the study period (May–September), mean monthly daily temperature (1961–1990 normals) varied from 9.0 °C in May to 17.7 °C in July (annual mean = 2.4 °C) and precipitation varied from 69.3 mm in May to 88.5 mm in August (annual monthly mean = 58.6 mm) (Environment Canada 2001).

### Sampling

Twenty plots of three adjacent boxes represented sample units. Plots were randomly distributed within the forest (minimum distance between plots was 5 m). Each box consisted of two 2-L milk cartons, fitted inside the other (to create a solid box), and filled with sand (approximately 2 kg). Cardboard milk cartons had a plastic coating and were red and white in colour. Boxes depressed the leaf litter, creating a footprint-sized depression 21 cm × 9.5 cm and approximately 1 cm deep (Ferguson 2000) that became a microhabitat island for a diverse soil fauna community similar to that beneath a rock resting on the forest floor. Measured microclimate differences under the boxes relative to outside the boxes included increased humidity and decreased temperature (Ferguson 2000).

During count surveys, boxes were overturned, and the numbers and size of all soil fauna (>1 mm) directly under the box were visually counted. Individual boxes were lifted without disturbing adjacent boxes. Twenty weekly surveys

were conducted from 9 May to 24 September 2000 and 11 biweekly surveys between 3 May and 17 September 2001.

### Slug poisoning

Under every second plot, five tablets of poison (Slug Pellets) per box (total = 15 pellets per plot) were placed 5–7 days prior to the start of the 2001 count surveys. Slug pellets (Mifaslug™, Farmer Crop Chemicals, Worcester, U.K.) contained 6% metaldehyde, a molluscicide used to attract and kill slugs and snails. Of the total 20 plots that were temporally replicated during weekly (2000 before) and bi-weekly (2001 after) surveys, 10 were control and 10 were treatment replicates. Counts under all three boxes within a plot were summed to provide one measure per sample unit.

### Soil fauna identification

Soil fauna groups based on differences in size and feeding habits (Bolger et al. 2000) were used to identify individuals observed under boxes and included springtails (Collembola), spiders (Araneida), ants (Formicoidae), ant larvae, centipedes (Chilopoda), Diplura, adult flies (Diptera), phytophagous mites (Acari: Oribatida), bugs (Hemiptera and Homoptera), Pseudoscorpionida, moth and butterfly larvae (Lepidoptera), slugs and snails (Gastropoda), Isopoda (woodlouse; *Porcellio* sp.), adult and larval beetles (Coleoptera), and earthworms (Oligochaeta: Annelida). I restricted analyses to the following 11 more numerous groups: Collembola, mites, spiders, ants, beetles, bugs, centipedes, slugs, woodlouse, earthworms, and diplurans.

Species identification was limited by the nature of the live survey methodology. However, live samples of large invertebrates were taken for laboratory identification, particularly for groups with nonindigenous representatives that included earthworms, gastropods, and slugs. Three species of earthworms were identified: *Lumbricus terrestris* (Linnaeus, 1758) accounted for the majority (91%) of identified individuals (data on file), followed by *Dendrodrilus rubidus* (Savigny, 1826) and *Eisenia foetida* (Savigny, 1826). All three earthworm species are native to Europe and are thus nonindigenous to North America (Reynolds 1977). Gastropods were identified using Oughton (1948) and a key provided by R.G. Forsyth (<http://www3.bc.sympatico.ca/rforsyth/lsrc.html>). I identified only one genera of slug (*Deroceras*) and three snail genera (*Succinea*, *Euconulus*, and *Vitrina*). Numbers per square metre and size classes of invertebrate specimens were used to calculate dry mass per square metre for the various taxa using direct and typical values in regression equations (Dotson and Kalisz (1989) for Oligochaeta and Edwards (1967) and Ganihar (1997) for other groups).

### Vegetation survey

During August before (year 1) and after (year 2) treatment, I conducted a survey of herbaceous cover. A 2-m<sup>2</sup> plot was centred on the boxes and percent herbaceous cover was estimated to the nearest 5% (excludes ground litter, moss, ferns, and grass). Also, the percent herbaceous leaves eaten (possibly by slugs) in the 2-m<sup>2</sup> plot was estimated to the nearest 5%. Major herbaceous cover was identified (Cunningham 1972).

### Statistical analysis

Soil arthropod count data, available herbaceous cover, and percent eaten data were not normally distributed (Wilk–Shapiro normality test) and transformations (e.g., log, arcsine) failed to normalize all variables. Therefore, I used nonparametric analyses by ranking data before analysis of variance (Conover and Iman 1981). I report untransformed means  $\pm$  1 SE.

Analyses were performed to determine the relationship between soil arthropod numbers (abundance) and survey (season), year (before and after), and presence of slug poison (treatment and control) using repeated measures multiple analyses of variance (Gumpertz and Brownie 1993). Ranked count data for the 11 soil arthropod groups were the multiple dependent variables. Survey was a random repeated factor. Year (before and after) and poison (treatment and control) were fixed factors.

I tested for significant effects of poison on available herbaceous cover (percentage of ground covered) and amount eaten (percent removed) while controlling for year effects using a repeated measures multiple analysis of variance test of ranked data. Sample units were the three-box groups ( $n = 20$ ) sampled every week ( $n = 20$ , year 2000) and every second week ( $n = 11$ , year 2001). Survey was the repeated measure. The multiple dependent variables were available herbaceous cover and percent eaten. The fixed factors were year (before and after) and poison (treatment and control). All statistical analyses were done using SAS (SAS Institute Inc., Cary, N.C.) statistical software for microcomputers.

### Results

Macrofauna (>2 mm) dominated the forest floor of the boreal forest study site accounting for 83.7% of individuals observed (16.3% were microarthropods: Collembola and mites). Of the macrofauna, 36.5% were represented by invasive species that included a slug species (10.8%), three earthworm species (12.7%), and a woodlouse (12.9%).

Slug abundance remained low in plots with poison, in contrast with control plots where slug numbers increased over the survey period (Fig. 1). Slug abundance over time showed a significant interaction effect between survey and treatment ( $F_{[1,20]} = 28.1$ ,  $P = 0.001$ ), indicating that slugs decreased in abundance over the summer with poison (slope =  $-0.019 \pm 0.023$ ) compared with an increase in slug number over the summer with no poison (slope =  $0.145 \pm 0.039$ ). No other soil fauna group showed a significant relationship between slopes over time on control and experimental plots.

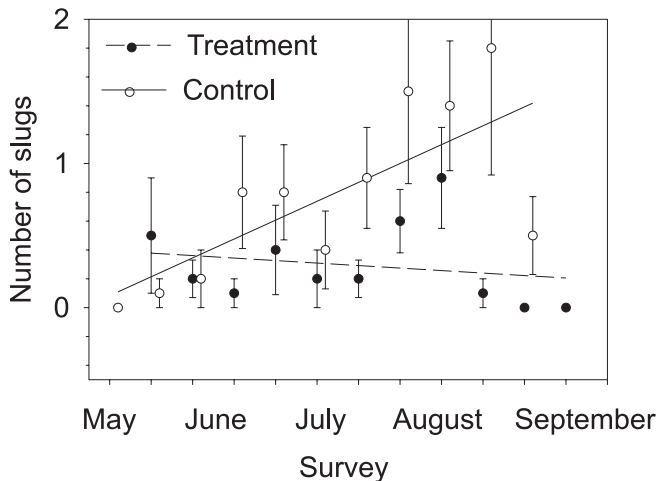
Of the 11 soil fauna groups, only slug, Collembola, mite, and isopod abundance differed with presence of slug poison (Table 1). No differences in abundance occurred for any of the arthropod groups with respect to the sites in year 2000 before poison was administered. However, in 2001 following administration of poison, four groups showed an approximate 50% decrease in abundance with the addition of slug poison relative to control sites (Fig. 2): from 3.7 to 2.2 individuals per site (41% decrease) for Collembola, from 1.00 to 0.37 (63%) for mites, from 1.5 to 0.30 (80%) for slugs, and from 3.3 to 1.5 (56% decrease) for isopods. Only centipedes differed with respect to year, showing an increase in numbers from year 2000 (0.48 individual per plot) to 2001 (0.72

**Table 1.** Results of repeated measures multiple analysis of variance to determine the effects of poison (treatment and control), survey, and year on ranked abundance of soil arthropod groups.

Recognizable taxonomic unit	Model df = 21, 619		Poison df = 1		Survey df = 19		Year df = 1	
	F	P	F	P	F	P	F	P
Collembola	3.73	0.0001	6.70	0.013	3.63	0.0001	2.28	0.13
Mites	6.32	0.0001	7.51	0.007	6.32	0.0001	3.28	0.07
Spiders	1.40	0.11	0.09	0.67	1.13	0.11	1.92	0.17
Ants	1.48	0.08	0.05	0.73	1.56	0.06	1.17	0.27
Beetles	2.95	0.0001	2.74	0.14	2.48	0.001	0.91	0.34
Centipedes	1.34	0.15	1.48	0.25	1.06	0.38	5.4	0.02
Bugs	2.42	0.0004	1.62	0.81	2.60	0.0003	0.79	0.37
Slugs	5.33	0.0001	34.31	0.005	4.30	0.0001	4.98	0.07
Earthworms	1.76	0.02	5.06	0.13	1.52	0.074	1.14	0.29
Isopods	4.38	0.0001	13.02	0.02	4.12	0.0001	0.01	0.93
Diplurans	2.13	0.003	0.06	0.73	2.27	0.002	1.06	0.30

**Note:** Sample units were three-box plots ( $n = 20$  plots, 10 treatments and 10 controls) sampled during 20 weekly surveys during the summer of 2000 and 11 biweekly surveys during the summer of 2001. Survey was the repeated measure and year (before and after) and poison (treatment and control) were fixed effects (total  $n = 620$ ).

**Fig. 1.** Changes in slug abundance (mean of three-box plots) over time relative to poison. Solid circles represent mean slug numbers with application of slug poison on 10 treatment plots. Open circles represent mean slug numbers without poison on 10 control plots. Results presented are for 2001 and include 20 plots sampled from a boreal forest during 11 surveys (May–September). Error bars represent  $\pm 1$  SE. Lines represent linear regressions indicating increasing slug numbers over time on control plots and decreasing slug numbers on treatment plots.



individual per plot). Seven of 11 arthropod groups differed with respect to time of survey (Table 1).

Herb cover did not differ between years or between sites with and without slug poison (Table 2). However, percent herb cover eaten decreased with addition of slug poison from  $26\% \pm 2.2\%$  to  $15\% \pm 2.6\%$ . Dominant herb species included *Clintonia borealis*, *Polygonatum pubescens*, *Aralia nudicaulis*, *Cornus Canadensis*, *Cornus stolonifera*, *Trientalis borealis*, *Apocynum androsaemifolium*, *Lonicera Canadensis*, *Linnaea borealis*, *Viburnum* spp., *Sambucus Canadensis*, *Vaccinium* spp., *Solidago* spp., and *Aster* spp.

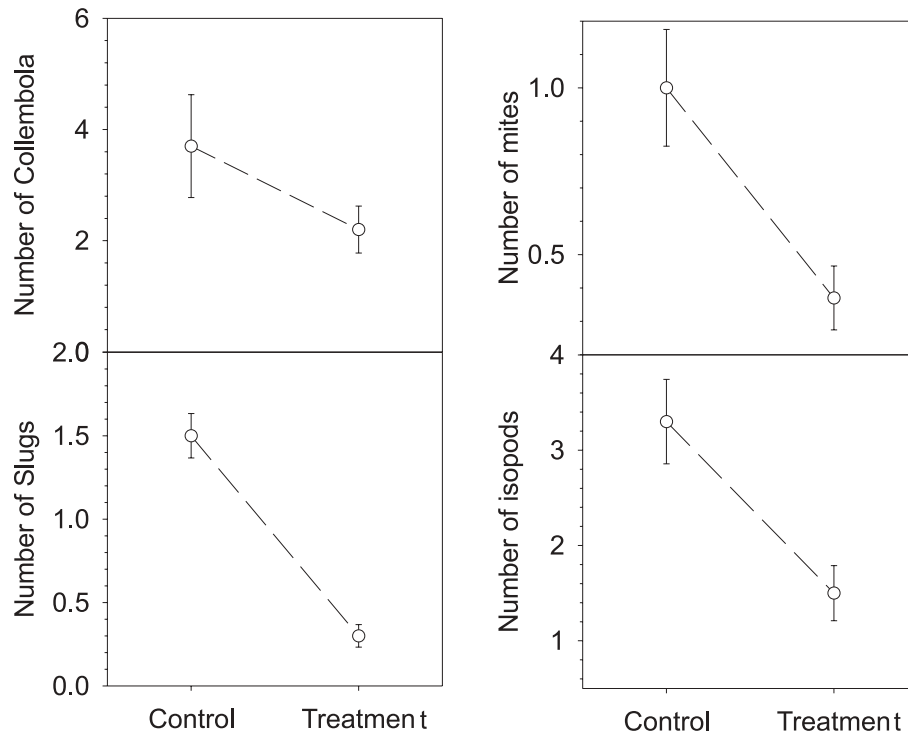
## Discussion

In this study, nonindigenous taxa predominated in the macrofauna, accounting for a third of the individuals and a half of the biomass. This result supports conclusions of soil invertebrate researchers in North America that forests north of the glacial limits are impoverished in native soil invertebrate fauna and that considerable invasive species now predominate (Blair et al. 1994; Kalisz and Dotson 1989; Hendrix et al. 1992). Dominance of macrofauna by non-native groups has also been reported south of the glacial limits in areas associated with greater edge and fragmented habitat (Bolger et al. 2000). In this study area, considerable forest fragmentation and disturbance had occurred with human development, and significant removal of one of these invasive groups, slugs, resulted in a decline in abundance of three other arthropod groups, Collembola, mites, and non-indigenous isopods. Reasons for these changes were not obvious. The large numbers of nonnative soil fauna may exist as an alternative food web that does not relate directly to the native community. Such a functional group redundancy, if it exists, may have affected the results.

The effect of poisoning slugs on predator abundance was not obvious. Slugs are a major part of the diet of carabid beetles (Digweed 1993; Symondson et al. 2002). Generalist carabids are known to be voracious feeders consuming at least their own body mass daily (Thiele 1977; Kromp 1999) and up to three times their body mass per day (Thiele 1977). Although, not significant once time was incorporated into the general linear models, beetles decreased in abundance from 0.63 individual per plot in control plots to 0.25 in treatment plots (76% decrease). More detailed taxonomic and diet analyses will be necessary to further evaluate the effect of removing slugs on carabid beetle abundance.

The only nonnative group affected by slug removal was isopods that declined in abundance. Isopods consume mostly litter from forbs (Rushton and Hassall 1983). Perhaps, removal of slugs reduced litter from damaged herbs eaten by slugs and thereby reduced potential food for isopods. Slugs

**Fig. 2.** Effect of slug poison on soil fauna abundance for a boreal forest in northwestern Ontario, Canada. Mean number  $\pm$  1 SE for 10 treatment plots (poison added) versus mean number of soil fauna for 10 control plots averaged over 11 surveys in 2001. The broken line indicates significant decline in numbers. Soil fauna groups that are not shown because they were not statistically affected by slug poison include spiders, ants, beetles, centipedes, bugs, earthworms, and diplurans.



**Table 2.** Results of multiple analysis of variance to determine the effects of poison and year on herbaceous vegetation cover and percent herbaceous cover eaten.

	Model df = 2, 39		Poison df = 1		Year df = 1	
	F	P	F	P	F	P
Herb cover	1.06	0.36	0.27	0.61	1.85	0.19
% eaten	8.64	0.0008	12.53	0.001	4.75	0.036

**Note:** Sample units were 20 plots (10 treatments and 10 controls) sampled in August 2000 and 2001. Year (before and after) and poison (treatment and control) were fixed effects (total  $n = 40$ ). Ranked values of percent herbaceous cover available and eaten were the multiple response variables.

are known to preferentially select herbaceous forage (Grime et al. 1968), and isopods reproduce more successfully on this litter (Zimmer and Topp 2000) following microbial colonization of leaf litter (Zimmer and Topp 1997), as microbiota are digested by isopods (Gunnarsson and Tunlid 1986).

Microarthropods (Collembola and mites) decreased in abundance with the removal of slugs. Soil microarthropod communities are among the most diverse components of terrestrial ecosystems (Giller 1996; Petersen and Luxton 1982). Perhaps, as a result of this diversity, microarthropod communities generally recover quickly after disturbance (Liiri et al. 2002). This was not the case in this study, which found a consistent decline of approximately half of the abundance of microarthropods with the experimental poisoning of slugs. A possible explanation for the observed pattern of decreased abundance of microarthropods is reduced food for these groups from decreased slug activity. Fewer slugs meant less

fragmented dead plant material falling to the forest floor. Also, Collembola feed on slime and slug defecation (e.g., Salmon 2001), which would have been reduced with slug poisoning. Without further experimentation, metal poisons may have been toxic to these invertebrates.

There are limitations of the sampling methodology used in this study, and therefore, interpretations of the results should be tempered by recognition of the coarseness of the taxonomic analysis and the general lack of knowledge of the diets of local invertebrates. Changes in the abundance of particular species, genera, or families of soil fauna may be more important than arthropod group abundance in understanding changes associated with removal of slugs. The study of trophic cascades associated with removal of a major soil arthropod group is illustrative of potential problems that are related to the adequacy of sampling methodologies (André et al. 2002). An alternative technique to assess faunal influences on ecosystem process in the field is the use of intact soil cores wrapped in meshes of various sizes and planted in the field (Kampichler et al. 1995).

There is increasing evidence that soils and their communities are negatively influenced by human activities (Ingham et al. 1989; Parmelee et al. 1993; Haimi and Siira-Pietikinen 1996; Wall 1999) and that invasive species threaten world biodiversity (Lovel 1997). Concerns about the effects of the widespread loss of biodiversity through anthropogenic changes have prompted many recent studies investigating the relationship among soil fauna as indicators of these changes (Andersen 1990; Symstad et al. 2000; Andersen et al. 2002). Monitoring soil arthropod biodiversity will provide a means to assess changes in forest environments with climate warm-

ing and forest management practices that include silvicultural intervention to maintain forest health (Strayer et al. 1986; Prezio et al. 1999; S.H. Ferguson and D.K.A. Berube, unpublished data). Experimental removal of one group of soil fauna, particularly a nonnative one, provides the means to investigate the effects of trophic dynamics and invasive species on biodiversity. Experimental removal of the slug functional group, using slug poison, may help uncover the mechanisms of trophic cascades associated with anthropogenic changes.

## Acknowledgements

Earlier drafts of this manuscript were improved by the constructive comments of three anonymous reviewers. Post-doctoral funding from the Natural Sciences and Engineering Research Council of Canada and Bowater Pulp and Paper Inc., Thunder Bay Woodlands Division, provided financial support.

## References

- Andersen, A.N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proc. Ecol. Soc. Aust.* **16**: 347–357.
- Andersen, A.N., Hoffmann, B.D., Muller, W.J., and Griffiths, A.D. 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. *J. Appl. Ecol.* **39**: 8–17.
- Anderson, J.M. 1988. Spatiotemporal effects of invertebrates on soil processes. *Biol. Fertil. Soils*, **6**: 216–227.
- André, H.M., Ducarme, X., and Lebrun, P. 2002. Soil biodiversity: myth, reality or conning? *Oikos* **96**: 3–24.
- Barker, G.M. 1989. Slug problems in New Zealand pastoral agriculture. Slugs and snails in world agriculture. British Crop Protection Council, Guilford, U.K. *Br. Crop Prot. Council. Monogr.* **41**. pp. 59–68.
- Blair, J.M., Parmelee, R.W., and Wyman, R.L. 1994. A comparison of the forest floor invertebrate communities of four forest types in the northeastern U.S. *Pedobiologia*, **38**: 146–160.
- Bolger, D.T., Suarez, A.V., Crooks, K.R., Morrison, S.A., and Case, T.J. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecol. Appl.* **10**: 1230–1248.
- Bruelheide, H., and Scheidel, U. 1999. Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *J. Ecol.* **87**: 839–848.
- Carrick, R. 1942. The grey field slug, *Agriolimax agrestis* L., and its environment. *Ann. Appl. Biol.* **29**: 43–55.
- Cates, R.G., and Orisans, G.H. 1975. Successional status and the palatability of plants to generalized herbivores. *Ecology*, **56**: 410–418.
- Chichester, L.F., and Getz, L.L. 1969. The zoogeography and ecology of Arionid and Limacid slugs introduced into North America. *Malacologia*, **7**: 313–346.
- Colinas, C., Ingham, E., and Molina, R. 1994. Population responses of target and non-target forest soil organisms to selected biocides. *Soil Biol. Biochem.* **26**: 41–47.
- Conover, W., and Iman, R. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* **35**: 124–129.
- Cook, A. 1981. Huddling and the control of water loss by the slug *Limax pseudoflavus* Evans. *Anim. Behav.* **29**: 289–298.
- Cunningham, G.C. 1972. Forest flora of Canada. Department of Northern Affairs and National Resources, Forestry Branch, Ottawa, Ont. Bull. 121.
- Digweed, S.C. 1993. Selection of terrestrial gastropod prey by Cydrine and Pterostichine ground beetles (Coleoptera: Carabidae). *Can. Entomol.* **125**: 463–472.
- Dotson, D.B., and Kalisz, P.J. 1989. Characteristics and ecological relationships of earthworm assemblages in undisturbed forest soils in the southern Appalachians of Kentucky, USA. *Pedobiologia*, **33**: 211–220.
- Edwards, C.A. 1967. Relationships between weights, volumes and numbers of soil animals. *In Progress in soil biology. Edited by O. Graff and J.E. Satchell.* North-Holland Publishing Company, Amsterdam, Netherlands. pp. 585–594.
- Environment Canada. 2001. Canadian climate normals 1961–1990. Environment Canada, Downsview, Ont. Available from [http://www.msc-smc.ec.gc.ca/climate/climate\\_normals\\_1990/show\\_normals\\_e.cfm?station\\_id=1001&prov=ON](http://www.msc-smc.ec.gc.ca/climate/climate_normals_1990/show_normals_e.cfm?station_id=1001&prov=ON) [cited 10 December 2001].
- Ferguson, S.H. 2000. Predator size and distance to edge: is bigger better? *Can. J. Zool.* **78**: 713–720.
- Ferguson, S.H. 2001. Changes in trophic abundance of soil arthropods along a grass–shrub–forest gradient. *Can. J. Zool.* **79**: 457–464.
- Fritz, R.S., Hochwender, C.G., Lewkiewicz, D.A., Bothwell, S., and Orians, C.M. 2001. Seedling herbivory by slugs in a willow hybrid system: developmental changes in damage, chemical defense, and plant performance. *Oecologia*, **129**: 87–97.
- Ganihar, S.R. 1997. Biomass estimates of terrestrial arthropods based on body length. *J. Biosci.* **22**: 219–224.
- Garthwaite, D.G., and Thomas, M.R. 1996. The usage of molluscicides in agriculture and horticulture in Great Britain over the last 30 years. *In Slug and snail pests in agriculture.* British Crop Protection Council, Canterbury, U.K. *Br. Crop Prot. Council. Monogr.* **66**. pp. 271–280.
- Giller, P.S. 1996. The diversity of soil communities, the ‘poor man’s tropical rainforest’. *Biodivers. Conserv.* **5**: 135–168.
- Grime, J.P., MacPherson-Stewart, S.H., and Dearman, R.S. 1968. An investigation of leaf palatability using the snail *Cepea nemoralis* L. *J. Ecol.* **56**: 405–420.
- Gumpertz, M.L., and Brownie, C. 1993. Repeated measures in randomized block and split-plot experiments. *Can. J. For. Res.* **23**: 625–639.
- Gunnarsson, T., and Tunlid, A. 1986. Recycling of fecal pellets in isopods: micro-organisms and nitrogen compounds as potential food for *Oniscus asellus* L. *Soil Biol. Biochem.* **18**: 595–600.
- Haimi, J., and Siira-Pietikäinen, A. 1996. Decomposer animal communities in forest soil along heavy metal pollution gradient. *Fresenius’ J. Anal. Chem.* **354**: 672–675.
- Hawkins, J.W., Lankester, M.W., and Nelson, R.A. 1998. Sampling terrestrial gastropods using corrugated cardboard sheets. *Malacologia*, **39**: 1–9.
- Hendrix, P.F., and Bohlen, P.J. 2002. Exotic earthworm invasions in North America: ecological and policy implications. *BioScience*, **52**: 801–811.
- Hendrix, P.F., Mueller, B.R., Bruce, R.R., Langdale, G.W., and Parmelee, R.W. 1992. Abundance and distribution of earthworms in relation to landscape factors on the Georgia Piedmont. *Soil Biol. Biochem.* **24**: 1357–1361.
- Ingham, E.R., Coleman, D.C., and Moore, J.C. 1989. An analysis of food-web structure and function in a shortgrass prairie, a mountain meadow, and a lodgepole pine forest. *Biol. Fertil. Soils*, **8**: 29–37.
- Kajak, A., Chmielewski, K., Kaczmarek, M., and Rembalkowska, E. 1991. Experimental studies on the effect of epigeic predators on

- organic matter decomposition processes in managed peat grasslands. *Polar Ecol. Stud.* **17**: 289–310.
- Kalisz, P.J., and Dotson, D.B. 1989. Land-use history and the occurrence of exotic earthworms in the mountains of eastern Kentucky. *Am. Midl. Nat.* **122**: 288–297.
- Kalisz, P.J., and Powell, J.E. 2000a. Invertebrate macrofauna in soils under old growth and minimally disturbed second growth forests of the Appalachian Mountains of Kentucky. *Am. Midl. Nat.* **144**: 297–307.
- Kalisz, P.J., and Powell, J.E. 2000b. Effect of prescribed fire on soil invertebrates in upland forests on the Cumberland Plateau of Kentucky, USA. *Areas J.* **20**: 336–341.
- Kampichler, C., Bruckner, A., Kandeler, E., Bauer, R., and Wright, J. 1995. A mesocosm study design using undisturbed intact soil monoliths. *Acta Zool. Fenn.* **196**: 71–72.
- Kolstrom, M., and Lumatjarvi, J. 1999. Decision support system for studying effects of forest management on species richness in the boreal forest. *Ecol. Model.* **119**: 43–55.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.* **74**: 187–228.
- Liiri, M., Setälä, H., Haimi, J., Pennanen, T., and Fritze, H. 2002. Relationship between soil microarthropod species diversity and plant growth does not change when the system is disturbed. *Oikos*, **96**: 137–149.
- Lövel, G.L. 1997. Global change through invasion. *Nature (London)*, **388**: 627–628.
- Mikola, J., and Setälä, H. 1998. Relating species diversity to ecosystem functioning — mechanistic background and an experimental approach with a decomposer food web. *Oikos*, **83**: 180–194.
- Oughton, J. 1948. A zoogeographical study of the land snails of Ontario. *Univ. Toronto Biol. Ser.* **57**.
- Parmelee, R.W., Wentsel, R.S., Phillips, C.T., et al. 1993. Soil microcosm for testing the effects of chemical pollutants on soil fauna communities and trophic structure. *Environ. Toxicol. Chem.* **12**: 1477–1486.
- Petersen, H., and Luxton, M. 1982. A comparative analysis of soil fauna populations and their role in decomposition process. *Oikos*, **39**: 288–308.
- Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. 1999. Environmental and economic costs of nonindigenous species in the United States. *BioScience*, **50**: 53–65.
- Port, C.M., and Port, G.R. 1986. The biology and behaviour of slugs in relation to crop damage and control. *Agric. Zool. Rev.* **1**: 253–299.
- Prezio, J.R., Lankester, M.W., Lautenschlager, R.A., and Bell, F.W. 1999. Effects of alternative conifer release treatments on terrestrial gastropods in regenerating spruce plantations. *Can. J. For. Res.* **29**: 1141–1148.
- Prior, D.J. 1989. Contact-rehydration in slugs: a water regulatory behaviour. *In Slugs and snails in world agriculture*. British Crop Protection Council, Guildford, U.K. *Br. Crop Prot. Counc. Monogr.* **41**. pp. 217–223.
- Reynolds, J.W. 1977. The earthworms (Lumbricidae and Sparganophilidae) of Ontario. Royal Ontario Museum, Toronto, Ont. Life Sci. Misc. Publ.
- Rowe, J.S. 1972. Forest regions of Canada. Canadian Forestry Service, Department of the Environment, Ottawa, Ont. Inf. Can. Cat. **47**-1300.
- Rushton, S.P., and Hassall, M. 1983. The effects of food quality on the life history parameters of the terrestrial isopod, *Armadillidium vulgare* Latreille. *Oecologia*, **57**: 257–261.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., and Weller, S.G. 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**: 305–332.
- Salmon, S. 2001. Earthworm excreta (mucus and urine) affect the distribution of springtails in forest soils. *Biol. Fertil. Soils*, **34**: 304–310.
- Schaefer, M. 1991a. The animal community: diversity and resources. *Ecosyst. World*, **7**: 51–120.
- Schaefer, M. 1991b. Secondary production and decomposition. *Ecosyst. World*, **7**: 175–218.
- Scheu, S., and Schulz, E. 1996. Secondary succession, soil formation and development of a diverse community of oribatids and saprophagous soil macro-invertebrates. *Biodivers. Conserv.* **5**: 235–250.
- Shirley, M.D.F., Rushton, S.P., Young, A.G., and Port, G.R. 2001. Simulating the long-term dynamics of slug populations: a process-based modelling approach for pest control. *J. Appl. Ecol.* **38**: 401–411.
- South, A. 1992. Terrestrial slugs — biology, ecology and control. Chapman and Hall, New York.
- Strayer, D., Pletscher, D.H., Hamburg, S.P., and Nodvin, S.C. 1986. The effects of forest disturbance on land gastropod communities in northern New England. *Can. J. Zool.* **64**: 2094–2098.
- Symondson, W.O.C., Glen, D.M., Ives, A.R., Langdon, C.J., and Wiltshire, C.W. 2002. Dynamics of the relationship between a generalist predator and slugs over five years. *Ecology*, **83**: 137–147.
- Symstad, A.J., Siemann, E., and Haarstad, J. 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. *Oikos*, **89**: 243–253.
- Thiele, H.U. 1977. Carabid beetles in their environments: a study on habitat selection by adaptations in physiology and behaviour. Springer-Verlag, Berlin.
- van Wensem, J., Verhoef, H.A., and Van Straalen, N.M. 1993. Litter degradation stage as a prime factor for isopod interaction with mineralization processes. *Soil Biol. Biochem.* **25**: 1175–1183.
- Wall, D.H. 1999. Biodiversity and ecosystem function. *BioScience*, **49**: 107–108.
- Wardle, D.A. 1999. How soil food webs make plants grow. *Trends Ecol. Evol.* **14**: 418–420.
- Wilby, A., and Brown, V.K. 2001. Herbivory, litter and soil disturbance as determinants of vegetation dynamics during early old-field succession under set-aside. *Oecologia*, **127**: 259–265.
- Young, A.G., and Port, G.R. 1989. The effect of microclimate on slug activity in the field. *In Slugs and snails in world agriculture*. British Crop Protection Council, Guildford, U.K. *Br. Crop Prot. Counc. Monogr.* **41**. pp. 263–269.
- Young, A.G., Port, G.R., and Green, D.I. 1993. Development of a forecast of slug activity: validation of models to predict slug activity from meteorological conditions. *Crop Prot.* **12**: 232–236.
- Zheng, D.W., Bengtsson, J., and Agren, G.I. 1997. Soil food webs and ecosystem processes: decomposition in donor-control and Lotka-Volterra systems. *Am. Nat.* **149**: 125–148.
- Zimmer, M., and Topp, W. 1997. Surfactants in the gut fluids of *Porcellio scaber* (Isopoda: Oniscidea), and their interactions with phenolics. *J. Insect Phys.* **43**: 1009–1014.
- Zimmer, M., and Topp, W. 2000. Species-specific utilization of food sources by sympatric woodlice (Isopoda: Oniscidea). *J. Anim. Ecol.* **69**: 1071–1082.