Exotic earthworm distribution in a mixed-use northern temperate forest region: influence of disturbance type, development age, and soils

Tara E. Sackett, Sandy M. Smith, and Nathan Basiliko

Abstract: The impacts of invasive earthworms in northern North American forests include mixing of soil and litter horizons, changes to nutrient availability, and shifts in understory plant communities. Multi-use forests, with concomitant commercial logging and recreational activities, may have high rates of earthworm dispersal from human activities. Here, we investigated if soil physical and chemical properties, in addition to disturbance type, influence the success of earthworm establishment. We characterized the distribution of earthworms in a multi-use forested area in the Great Lakes St. Lawrence forest region of central Ontario and related earthworm presence and community structure to human influences (i.e., disturbance type, age of development) and edaphic properties. Although soil texture correlated significantly with *Lumbricus* populations, the influence of edaphic properties was small compared with disturbance type and history. Fishing and camp sites were dominated by *Lumbricus*, while gravelled roads had higher populations of epigeic earthworms. The spread of earthworms along gravelled roads may be due to regrading rather than transport in vehicle tires: earthworms were not present more than 200 m off trunk roads on nongravelled trails. Education campaigns to reduce dumping of earthworm bait and changes to road grading practices in multi-use forests could reduce the spread of earthworms.

Résumé : Les impacts des vers de terre dans les forêts de l'Amérique du Nord incluent le mélange des horizons du sol et de la litière, ainsi que des modifications dans la disponibilité des nutriments et les communautés végétales de sous-bois. Les forêts utilisées de façon polyvalente, où des activités récréatives côtoient la récolte commerciale de bois, peuvent avoir des taux plus élevés de dispersion des vers de terre à cause des activités humaines. Ici, nous avons cherché à déterminer si les propriétés chimiques et physiques du sol, en plus du type de perturbation, influencent le succès d'établissement des vers de terre. Nous avons caractérisé la distribution des vers de terre dans une zone de forêt utilisée de façon polyvalente dans la région forestière des Grands Lacs et du Saint-Laurent, dans le centre de l'Ontario, et établi les relations entre la présence et la structure des communautés de vers de terre d'une part et les influences humaines (c.-à-d. le type de perturbation, l'âge de développement) et les propriétés édaphiques d'autre part. Même si la texture du sol était significativement corrélée avec les populations de *Lumbricus*, l'influence des propriétés édaphiques était faible comparativement au type et à l'historique des perturbations. Les zones de pêche et de camping étaient dominées par *Lumbricus* tandis que les populations de vers de terre épigés étaient plus élevées sur les routes gravelées. La dispersion des vers de terre le long des routes gravelées pourrait être due au nivelage plutôt qu'au transport par les pneus des véhicules : les vers de terre n'étaient pas présents à plus de 200 m au-delà des routes à grand trafic sur les chemins non gravelés. Des campagnes d'éducation visant à réduire le rejet de vers de terre utilisés comme appâts et des modifications aux pratiques de nivelage dans les forêts utilisées de façon polyvalente pourraient réduire la dispersion des vers de terre.

[Traduit par la Rédaction]

Introduction

In North America, terrestrial earthworms are generally not native to areas covered by the Wisconsinan glaciation of the late Pleistocene, but due to human transport, they are now found across much of the northern parts of the continent (Gates 1982; Reynolds 1994). Exotic earthworms are recognized as an emerging threat to temperate forest ecosystems, as they can dramatically alter forest floor structure (e.g., Alban and Berry 1994; Hale et al. 2005), soil nutrient and carbon dynamics (e.g., Bohlen et al. 2004; Wironen and Moore 2006), and plant community composition (e.g., Holdsworth et al. 2007*a*). Earthworms may also facilitate the establishment of invasive plants, potentially leading to accelerated changes to plant communities (Nuzzo et al. 2009).

The occurrence of earthworms is strongly related to human disturbance. Forests exposed to human activities have larger

Received 3 May 2011. Accepted 20 December 2011. Published at www.nrcresearchpress.com/cjfr on 6 February 2012.

T.E. Sackett. Department of Geography, University of Toronto Mississauga, 3359 Mississauga Road North, Mississauga, ON L5L 1C6, Canada; Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, ON M5S 3B3, Canada.
S.M. Smith. Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, ON M5S 3B3, Canada.
N. Basiliko. Department of Geography, University of Toronto Mississauga, 3359 Mississauga Road North, Mississauga, ON L5L 1C6, Canada.

Corresponding author: Tara E. Sackett (e-mail: tara.sackett@utoronto.ca).

doi:10.1139/X11-195

earthworm populations than more remote stands (Gundale et al. 2005). Particular earthworm species, such as *Dendrobaena octaedra*, occur near roads (Dymond et al. 1997; Cameron et al. 2007), with a higher probability of occurrence with increasing road age (Cameron and Bayne 2009). Other earthworm species, such as those used for fishing bait (e.g., *Lumbricus terrestris*, *Lumbricus rubellus*, *Aporrectodea* species), are found near boat launches (Cameron et al. 2007). Earthworm occurrence in forests is also positively related to the proximity of agricultural areas (Suarez et al. 2006; Cameron and Bayne 2009). Although the relationship between earthworm communities and site use is fairly consistent in different parts of North America (Gundale et al. 2005; Cameron et al. 2007), there may be site-specific variables that influence earthworm populations as well.

Environmental and habitat characteristics can also influence earthworm populations. Earthworm occurrences have been shown to be higher in mixed-hardwood forest stands as compared with areas with hemlock or beech (Suarez et al. 2006), often reflecting differences in litter quality (Curry 2004). Although different earthworm species have varying preferences for soil pH, highly acidic soils tend not to support high earthworm populations (Curry 2004). Soil texture can also influence earthworms, with fine- to medium-textured soils supporting larger populations (Hendrix et al. 1992; Baker et al. 1998). Earthworm abundance may be limited by low soil moisture during dry periods (McLean et al. 1996; Eggleton et al. 2009).

Mixed-use temperate forests in North America are at particular risk for the establishment of invasive species, including earthworms, due to multiple routes of dispersal via recreational and commercial activities and the higher number of potential introduction events that come with frequent use. However, the distribution of earthworms may also be influenced by soil properties. The goal of this study was to relate earthworm presence and community structure to human influences (i.e., disturbance type, age of development) and soil physical and chemical properties. We addressed three specific questions: (1) How do typical disturbances in a mixed-use temperate forest (fishing/cabin sites, large gravelled roads, small skid trails) and soil properties influence the distribution of earthworm groups? (2) Is the occurrence of earthworms more strongly influenced by the time since disturbance/age of development (e.g., time since construction of a well-used gravelled road) or by soil physical and chemical properties? (3) What is the spatial extent of spread of earthworms along small trails that lead from frequently used sites (e.g., gravelled roads) into the forest interior where human activity is less prevalent?

Methods

We conducted the study at Haliburton Forest and Wildlife Reserve (HF), a 30 000 ha mixed-use forested area in central Ontario. HF abuts the southern extent of Ontario's Algonquin Park (45.29′N, –78.64′W) and is dominated by sugar maple (*Acer saccharum* Marsh.), eastern hemlock (*Tsuga canadensis* L. Carrière), yellow birch (*Betula alleghaniensis* Britt.), and American beech (*Fagus grandifolia* Ehrh.). The Haliburton and Algonquin Highlands are at a regional topographic high position in central-eastern Ontario, and the site receives approximately 1100 mm of precipitation annually and has an average temperature of 4.9 °C. Haliburton Forest was first settled in the 1870s as a base and site for logging operations. The forest timber harvests are managed sustainably with Forest Stewardship Council accreditation first awarded in 1997. HF is Ontario's largest producer of forest products from private land holdings and, in addition to logging, there is consistent recreational use at the forest, including fishing, hunting, cycling, and cottages and semiwilderness camping. Although no earthworm surveys had been done at HF prior to this study, a survey of Haliburton County in 1971 reported 12 exotic species (Reynolds 1972), indicating that earthworms have been present in the region for at least 40 years. Earthworm and soil surveys at HF for this study were conducted from May to September 2010.

To answer question 1, we sampled earthworms and soils at 34 sites exposed to four different types of human disturbance: along gravelled roads ($n = 11$), beside boat launches at lakes ($n = 12$), adjacent to cabins (primarily seasonal hunting camps) ($n = 5$), and at the base of skid trails (logging paths from the forest interior) ($n = 6$). These sites were in areas that had been accessible by road for 20–80 years. The unequal sample size was due to the limited number of cabins and skid trails in the area we were working.

Earthworms were collected via two methods: an initial 10 min visual search followed by liquid mustard extraction (Lawrence and Bowers 2002) of earthworms from three 25 cm × 25 cm quadrats selected randomly within the disturbed area of the site. The visual search was conducted across the site (site areas on average were <100 m^2) and involved hand sorting of leaf litter and surface soil and lifting of logs. We did not look for earthworm cocoons. For mustard extraction of earthworms, leaf litter was manually removed from the quadrat and 2 L of mustard solution (10 g of Colman's mustard powder (Unilever PLC, London, UK) per litre water) was applied to the soil over a 10 min period, prompting the emergence of earthworms from the soil. Following application of the mustard solution, the soil within the quadrat was manually searched for any remaining earthworms. All earthworms were immediately placed in a 75% isopropyl alcohol solution, transferred to a 10% formalin solution for fixing for 24–48 h, and then stored in 75% isopropyl alcohol. Soil samples (10 cm × 10 cm) from the top 0–10 cm of the profile were collected from areas within 0.5–1 m of each of the three worm sampling quadrats. The three soil samples were pooled for analysis.

Earthworms were identified to genus and, if possible, species using the key from Reynolds (1977). For analysis, earthworms were divided into three groups based on taxonomic and functional characteristics. (*i*) The small epigeic (surface dwelling) group included the species *Dendrobaena octaedra* and *Dendrodrilus rubidus*, (*ii*) the endogeic (soil-dwelling) group included *Aporrectodea* species — mature *Aporrectodea* individuals found at HF were within the *Aporrectodea caliginosa* complex, a group of species that are difficult to differentiate morphologically (Pérez-Losada et al. 2009), and (*iii*) the third group included *Lumbricus* species — both the anecic (deep soil dwelling) *Lumbricus terrestris* and the epi-endogeic (soil and surface dwelling) *Lumbricus rubellus*. Although these *Lumbricus* species are in different functional groups, the high number of immature *Lumbricus* individuals meant that the species could not be distinguished from each other. Voucher specimens have been deposited in the invertebrate collection at the Royal Ontario Museum, Toronto, Ontario.

Soil particles were separated into size fractions using an adapted pipette method (Kroetsch and Wang 2008) that uses sedimentation rates based on Stokes' law to measure the relative proportion of clay (0–2 μm), silt (2–50 μm), and sand (50 μm – 2 mm). Sand fractions were further separated into two size fractions, 0.5–2 and <0.5 mm, because earthworms may show preferences for smaller sand particles over larger sand particles (Madge 1969). The pH of the soils was measured in a well-mixed slurry using 10 g of fresh soil and 40 mL of distilled, deionized water (Hendershot et al. 2008).

All statistical analyses were done using R version 2.11.1 (R Development Core Team 2010). A likelihood ratio test (function odTest in the R package {pscl} (Jackman 2011)) revealed overdispersion of the site count data due to a high number of zero occurrence events, so we used a negative binomial regression to estimate the most important predictors of the abundance of each of the three groups of earthworms. Initial models for each group included a categorical predictor of type of site disturbance (road, lake, skid trail, cabin) and continuous predictors of soil pH and percent clay, silt, and the sand fractions (percent variables were arcsine transformed). Variance inflation factors had indicated high multicollinearity (>10; Myers 1990) between the sand fractions; thus, we retained only the 0.5–2 mm fraction in the models. The silt and clay fractions were significantly higher at the skid trail sites, and so we did not include silt or clay as a predictor; sand fractions were not different among disturbance types.

We used stepwise regression (both directions) and selection of the model with the lowest Akaike information criterion value to determine the best model predicting earthworm group abundance. Maximum likelihood methods were used to estimate parameters, and for significant categorical predictors (i.e., site type), we used the Tukey test to determine pairwise significant differences between factor levels. We exponentiated the model estimates to express them as odds ratios. The function glm.nb in the R package {MASS} (Venables and Ripley 2002) was used for the negative binomial regression models.

To address the second research question, we grouped road development at HF into three eras: early (1930–1960), middle (1960–1990), and recent (1990–present). We established transects along a random subset of the major roads of Haliburton Forest, including roads from the three eras of development, and every 1.5 km along the roads, we sampled for earthworms and collected soil samples from the area beside (within 1–2 m) the road for a total of 52 road sites. Thirteen sites were along recently developed roads, 27 sites were along roads developed in the middle era, and 16 sites were along early roads. The different number of sites within each developmental era was due to the relative number of roads of different ages that were accessible. Earthworm presence or absence was recorded after a combination of manual searching and liquid mustard extraction. Specifically, we visually searched through litter and soil on both sides of a 10 m stretch of road for earthworms, and after 10 min, we used mustard extraction on three 25 cm × 25 cm quadrats. Because the goal of the search was to accurately determine presence or absence of earthworms at the site, and not relative abundance, quadrats were placed nonrandomly on areas that appeared to be disturbed by earthworms (if visible). This search method was chosen after 10 initial searches showed that an initial earthworm occurrence detected over a 20 min search period had been found within the initial 10 min. As with the first survey, soil samples consisted of three 10 cm × 10 cm subsamples of the top 10 cm of soil. Earthworm identification and soil sample analysis were as described above. We used mixed-effects logistic regression to determine the significant predictors of earthworm occurrence, and maximum likelihood methods were used to estimate parameters. Initial models for each group included road age, soil particle size groupings, and pH. Since sand fractions were again collinear, only the 0.5–2 mm sand fraction was included in the model. Sites along the same roads are likely independent because of the 1.5 km distance between them, but we also included a random grouping factor due to road in the model to account for any nonindependence: roads that shared a common origin from the main county road were classified as belonging to the same group. We determined the best model predicting earthworm abundance using stepwise regression (both directions) and selection of the model with the lowest Akaike information criterion value. The function glmmPQL in the R package {MASS} (Venables and Ripley 2002) was used for the general linear mixed modelling.

To address the third question, 10 nongravelled trails leading off of trunk gravelled roads with earthworm populations were randomly chosen across the forest. These trails were exposed to vehicular traffic: four were most recently used as skid trails and six were primarily recreational (cars, bicycles) trails. Six of the trails were from areas developed from 1930 to 1960 and four from 1960 to 1990. With the junction of the trail and gravelled road as distance zero, we sampled for earthworms every 50 m along the trail. Earthworm presence or absence was recorded after extraction search as described for the second question. If no earthworms were found at two sequential transect points, we judged that we had reached the extent of spread and ceased sampling. We used mixed-effects logistic regression to determine the probability distribution of earthworms by distance along smaller trails; maximum likelihood methods were used to estimate parameters. The type of trail (skid trail versus recreational) and era of development of the road were also included in the model as potential predictors, while the trail itself was included as a random effect in the model. As for question 2, the function glmmPQL in the R package {MASS} (Venables and Ripley 2002) was used for the general linear mixed modelling.

Results

(1) How do disturbances and soil properties influence the distribution of earthworm species?

Earthworm genera and species densities across the 34 sites are presented in Table 1. No *Lumbricus* occurred at skid trail sites, and so these sites were removed from the model because the estimation of regression parameters is invalid when there are all zero events in a treatment. For the remaining sites, *Lumbricus* abundance was best predicted by a negative

Table 1. Mean abundance (and range) per square metre of earthworm genera and species collected from four types of disturbed sites at Haliburton Forest.

	Lake (n = 12)	Road (n = 11)	Skid (n = 6)	Cabin (n = 5)
Lumbricus terrestris	4.3 (0–5)	0.5 (0–5)	0	4.3 (0–11)
Lumbricus rubellus	4.9 (0–32)	1.0 (0–11)	0	0
Lumbricus spp. (immature)	15.6 (0–53)	3.4 (0–37)	0	14.9 (0–48)
Dendrobaena octaedra	6.7 (0–21)	26.7 (0–80)	15.1 (0–27)	8.5 (0–16)
Dendrodrilus rubidus	1.8 (1–16)	3.4 (1–21)	0	1.1 (0–5)
Aporrectodea spp. (mature plus immature)	16.9 (0–171)	3.9 (0–37)	0	20.3 (0–69)

binomial model including site type and proportion of sand. The odds of *Lumbricus* occurring at lake sites was 12.3 times those at road sites (z = 3.4, P = 0.002), and the odds of *Lumbricus* occurrence increased by 1.1% per percent increase in the 0.5–2 mm sand fraction (z = 2.5, P = 0.01). Epigeic earthworm abundance was best predicted by a model that included disturbance site type, but no edaphic predictors, and the odds of epigeic earthworm occurrence was 4.7 times higher at road sites than at lake sites (z = 3.2, P = 0.007). Soil pH, which ranged from 4.1 to 5.9, did not affect *Lumbricus* or epigeic abundance. Endogeic earthworm abundance was not significantly associated with any of the measured predictors.

(2) Is the occurrence of earthworms more strongly influenced by the time since road development or by soil physical and chemical properties?

The presence or absence of earthworms along road sites was only significantly associated with road age (t = 2.61, P = 0.01) (Fig. 1). This pattern was primarily driven by the absence of earthworms at road sites developed on average within the last 10 years. Soil pH, which ranged from 4.1 to 6.1, did not affect earthworm occurrence. Neither did soil texture, with sand showing a range of 58%–98%, silt 0.2%–39%, and clay 0%–4%.

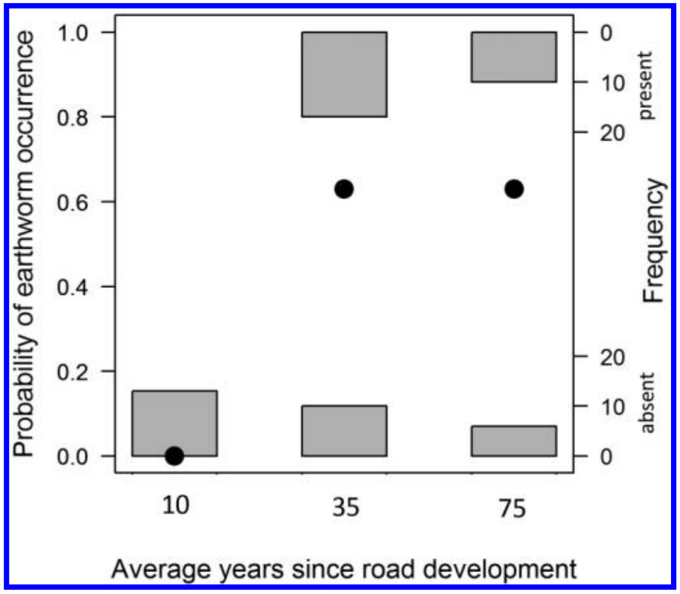
(3) What is the spatial extent of spread of earthworms along small trails into the forest interior where human activity is less prevalent?

Earthworms had not spread more than 200 m along any of the 10 trails sampled, and there was a clear effect of distance on probability of earthworm occurrence (t = –6.2, P < 0.001) (Fig. 2). The type of trail (skid or recreational) or age of development did not influence earthworm spread into the forest interior via these trails.

Discussion

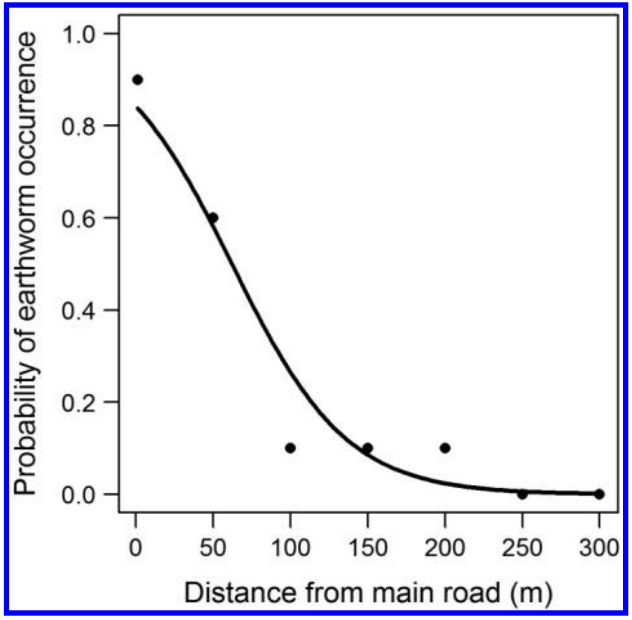
Earthworm distribution in this mixed-use temperate forest region is influenced by multiple factors, particularly disturbance type and time since development, but the soil physical and chemical properties that we measured were not important determinants of distribution. Earthworm species commonly used for fishing were found more at lake sites than at road sites, whereas the smaller, epigeic *Dendrobaena octaedra* more commonly occurred along roads. Soil texture (proportion sand) also influenced earthworm distribution, although to a far lesser degree than disturbance type and age of development.

Fig. 1. Probability of earthworm occurrence along gravelled roads in relation to average years since road development at Haliburton Forest. Circles represent the actual proportion of earthworm occurrences for each road age (y-axis 1) and the histograms illustrate the frequency of earthworm presences and absences within each age class (y-axis 2).



The type of site disturbance is the strongest predictor of abundance for *Lumbricus* and epigeic earthworms. *Lumbricus* species, which are commonly used as fishing bait, have higher abundance at boat launches than at road sites. Similarly, Cameron et al. (2007) found large populations of fishing worms at boat launches in Alberta. At Haliburton Forest, the significantly higher abundance of epigeic worms (primarily *Dendrobaena octaedra*) at road sites, as compared with boat launches, is also similar to patterns in Alberta (Dymond et al. 1997; Cameron et al. 2007; Cameron and Bayne 2009). *Aporrectodea* were not significantly associated with a particular disturbance type but were marginally more abundant at camp and lake sites than at road sites. *Aporrectodea* distribution has been associated with boat launches (Cameron et al. 2007) and cabins (Holdsworth et al. 2007*b*) due to their use as bait. A stronger association of *Lumbricus* than *Aporrectodea* with lake sites in our study could be due to species differences in ease of establishment after the worms are discarded or due to differences in bait preferences by fishers. Distributional differences highlight the importance of anthropogenic dispersal mechanisms for earthworms. Because *Lumbricus* and *Aporrectodea* were rarely found along roads, their

Fig. 2. Predicted probability of earthworm occurrence along small, nongravelled trails at Haliburton Forest (solid line). Circles represent the actual proportion of earthworm occurrences at each distance.



passive dispersal will be more easily preventable if public educational programs discouraging the dumping of bait are implemented successfully (Callaham et al. 2006). The transport of other species passively along roads is more difficult to control, especially as the transport mechanisms have not been confirmed.

For earthworms living along gravelled roads, we found that the probability of occurrence was related to road age, a pattern also seen for forest roads in Alberta (Cameron and Bayne 2009). At Haliburton Forest, we found no earthworms on roads built since 1990, which suggests that earthworms were not introduced with the gravel fill and that spread and establishment along roads to a degree detectable by our sampling method takes several decades. For roads with earthworms, we found that earthworms were very common in low gravel banks along the side of the forest roads (T.E. Sackett, personal observation); these banks also contained a large quantity of leaf litter and were formed from the periodic regrading of the roads. Thus, one of the major mechanisms of spread at Haliburton Forest may be through regrading, as gravel containing earthworms is pushed along the roads. The mechanisms of earthworm spread along forest roads may share some aspects with exotic plant distribution. Exotic plant frequency on forest roads is positively associated with disturbances such as grading and high traffic, but wind- and animal- dispersed seeds also occur more frequently than heavier seeds (Parendes and Jones 2000). The dispersal of earthworms is likely limited to vehicular or soil transport.

In agricultural systems, earthworms and their cocoons can be transported in soil caught in tractor wheels (Marinissen and van den Bosch 1992), and dispersal along forest roads might also occur in vehicle tires via this mechanism. However, earthworms were found only up to 200 m along nongravelled trails in the forest, even though these trails are used by recreational (cars, bicycles) and operational vehicles, including log skidders. Skidders carry a considerable amount of soil in their wheel treads (T.E. Sackett, personal observation) and thus could potentially be effective vectors of earthworms. However, at this point, there is little evidence of earthworm transport by vehicles along nongravelled trails, although future studies with increased sample sizes could explore this further.

In general, edaphic factors did not influence earthworm abundance or distribution. Although the pH of some sites was as low as 4.1, pH was not correlated with earthworm distribution and abundance. The species found at our sites are widely reported from Canadian coniferous forests (Addison 2009), so these species appear well adapted for acidic soils. Soil texture did not generally affect earthworm abundances, with the exception of *Lumbricus*, for which sand was positively correlated with abundances at sites across Haliburton Forest. The proportion of sand may reflect the drainage capacity of the soil. Earthworms can increase the bulk density of forest soils (Hale et al. 2005), so it is possible that the higher sand fraction in soils compacted by earthworm populations and in heavily used areas maintains water drainage. However, this result is somewhat surprising when considered in the context of previous studies: epi-endogeic earthworm populations are usually positively associated with medium to finer textured soils (Madge 1969; Hendrix et al. 1992). This also may be a location-specific result: although HF is a large and representative multi-use forest site, sampling was confined to a 34 sites within this 30 000 ha area.

The potentially negative ecosystem consequences of exotic earthworms in forests highlight the importance of understanding the factors influencing earthworm spread and distribution. Earthworms are most rapidly spread by human activities; thus, multi-use forests may be particularly at risk. In this study, we investigated whether soil edaphic factors, in addition to human activities, were important in determining earthworm distribution. We found little evidence that soil pH and texture affect earthworm distribution, but our results support previous findings on the role of particular human activities as vectors of earthworm spread, with earthworm species used as fishing bait having established populations near lakes and epigeic species spreading along road routes. We hypothesize that the spread of earthworms along roads at Haliburton Forest was not due to transport on vehicles but rather the movement of earthworms in gravel and litter during the regrading of roads. Changing road maintenance procedures could reduce the invasion of earthworms across mixed-use forested landscapes. For example, roads could be graded in the direction from newer roads to older such that till and litter containing earthworms are not transported over large distances from invaded to uninvaded sites. With respect to lake and cabin sites, the establishment of *Lumbricus* species and other bait earthworm populations is through the active disposal of worms, and there is no indication that these species spread along roads; education campaigns may reduce the disposal of live bait onsite and decrease the rate of establishment of new populations. Mixed-use temperate forests are exposed to increased risk of earthworm spread from recreational and operational activities, and human activities, rather than edaphic factors, are the primary determinant of earthworm occurrence.

Acknowledgements

We thank Haliburton Forest and Wildlife Reserve and Dr. Peter Schleifenbaum for site access, in-kind support in the form of subsidized field lodging, and information about the site histories. E. Marks and two anonymous reviewers provided valuable feedback on earlier versions of this manuscript. Funding for this project came from Haliburton Forest and Wildlife Reserve and MITACS in the form of an industrial-partnered postdoctoral fellowship for T.E. Sackett. Natural Sciences and Engineering Research Council of Canada Discovery Grants to N. Basiliko and S.M. Smith supported other research expenses.

References

Addison, J. 2009. Distribution and impacts of invasive earthworms in Canadian forest ecosystems. Biol. Invasions, **11**(1): 59–79. doi:10.1007/s10530-008-9320-4.

Alban, D.H., and Berry, E.C. 1994. Effects of earthworm invasion on morphology, carbon, and nitrogen of a forest soil. Appl. Soil Ecol. **1**(3): 243–249. doi:10.1016/0929-1393(94)90015-9.

Baker, G.H., Carter, P.J., Curry, J.P., Cultreri, O., and Beck, A. 1998. Clay content of soil and its influence on the abundance of *Aporrectodea trapezoides* Duges (Lumbricidae). Appl. Soil Ecol. **9**(1–3): 333–337. doi:10.1016/S0929-1393(98)00085-7.

Bohlen, P.J., Groffman, P.M., Fahey, T.J., Fisk, M.C., Suárez, E., Pelletier, D.M., and Fahey, R.T. 2004. Ecosystem consequences of exotic earthworm invasion of north temperate forests. Ecosystems (N.Y.), **7**(1): 1–12. doi:10.1007/s10021-003-0126-z.

Callaham, M.A., Jr, Gonzalez, G., Hale, C.M., Heneghan, L., Lachnicht, S.L., and Zou, X.M. 2006. Policy and management responses to earthworm invasions in North America. Biol. Invasions, **8**(6): 1317–1329. doi:10.1007/s10530-006-9016-6.

Cameron, E.K., and Bayne, E.M. 2009. Road age and its importance in earthworm invasion of northern boreal forests. J. Appl. Ecol. **46** (1): 28–36. doi:10.1111/j.1365-2664.2008.01535.x.

Cameron, E.K., Bayne, E.M., and Clapperton, M.J. 2007. Human-facilitated invasion of exotic earthworms into northern boreal forests. Ecoscience, **14**(4): 482–490. doi:10.2980/1195-6860(2007)14[482:HIOEEI]2.0.CO;2.

Curry, J. 2004. Factors affecting the abundance of earthworms in soils. *In* Earthworm ecology. 2nd ed. *Edited by* C.A. Edwards. CRC Press, Boca Raton, Fla.

Dymond, P., Scheu, S., and Parkinson, D. 1997. Density and distribution of *Dendrobaena octaedra* (Lumbricidae) in aspen and pine forests in the Canadian Rocky Mountains (Alberta). Soil Biol. Biochem. **29**(3–4): 265–273. doi:10.1016/S0038-0717(96)00052-1.

Eggleton, P., Inward, K., Smith, J., Jones, D.T., and Sherlock, E. 2009. A six year study of earthworm (Lumbricidae) populations in pasture woodland in southern England shows their responses to soil temperature and soil moisture. Soil Biol. Biochem. **41**(9): 1857–1865. doi:10.1016/j.soilbio.2009.06.007.

Gates, G.E. 1982. Farewell to North American megadriles. Megadrilogica, **4**: 12–77.

Gundale, M.J., Jolly, W.M., and Deluca, T.H. 2005. Susceptibility of a northern hardwood forest to exotic earthworm invasion. Conserv. Biol. **19**(4): 1075–1083. doi:10.1111/j.1523-1739.2005.00103.x.

Hale, C.M., Frelich, L.E., Reich, P.B., and Pastor, J. 2005. Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA. Ecosystems (N.Y.), **8**(8): 911–927. doi:10.1007/s10021-005-0066-x.

Hendershot, W., Lalande, H., and Duquette, M. 2008. Soil reaction and exchangeable acidity. *In* Soil sampling and methods of analysis. 2nd ed. *Edited by* M.R. Carter and E.G. Gregorich. CRC Press, Boca Raton, Fla.

Hendrix, P., Mueller, B., Bruce, R., Langdale, G., and Parmelee, R. 1992. Abundance and distribution of earthworms in relation to landscape factors on the Georgia Piedmont, USA. Soil Biol. Biochem. **24**(12): 1357–1361. doi:10.1016/0038-0717(92)90118-H.

Holdsworth, A.R., Frelich, L.E., and Reich, P.B. 2007*a*. Effects of earthworm invasion on plant species richness in northern hardwood forests. Conserv. Biol. **21**(4): 997–1008. doi:10.1111/j.1523-1739.2007.00740.x. PMID:17650250.

Holdsworth, A.R., Frelich, L.E., and Reich, P.B. 2007*b*. Regional extent of an ecosystem engineer: earthworm invasion in northern hardwood forests. Ecol. Appl. **17**(6): 1666–1677. doi:10.1890/05-2003.1. PMID:17913131.

Jackman, S. 2011. pscl: Classes and methods for R developed in the Political Science computational library, Stanford University. Stanford University, Stanford, Calif. R package version 1.04.1. Available at http://pscl.stanford.edu.

Kroetsch, D., and Wang, C. 2008. Particle size distribution. *In* Soil sampling and methods of analysis. 2nd ed. *Edited by* M.R. Carter and E.G. Gregorich. CRC Press, Boca Raton, Fla.

Lawrence, A.P., and Bowers, M.A. 2002. A test of the “hot”mustard extraction method of sampling earthworms. Soil Biol. Biochem. **34**(4): 549–552. doi:10.1016/S0038-0717(01)00211-5.

Madge, D.S. 1969. Field and laboratory studies on the activities of two species of tropical earthworms. Pedobiologia (Jena), **9**: 188–214.

Marinissen, J.C.Y., and van den Bosch, F. 1992. Colonization of new habitats by earthworms. Oecologia (Berl.), **91**(3): 371–376. doi:10.1007/BF00317626.

McLean, M.A., Kolodka, D.U., and Parkinson, D. 1996. Survival and growth of *Dendrobaena octaedra* (Savigny) in pine forest floor materials. Pedobiologia (Jena), **40**: 281–288.

Myers, R.H. 1990. Classical and modern regression with applications. 2nd ed. PWS Kent, Boston, Mass.

Nuzzo, V.A., Maerz, J.C., and Blossey, B. 2009. Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. Conserv. Biol. **23**(4): 966–974. doi:10.1111/j.1523-1739.2009.01168.x. PMID: 19236448.

Parendes, L.A., and Jones, J.A. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conserv. Biol. **14**(1): 64–75. doi:10.1046/j.1523-1739.2000.99089.x.

Pérez-Losada, M., Ricoy, M., Marshall, J.C., and Domínguez, J. 2009. Phylogenetic assessment of the earthworm *Aporrectodea caliginosa* species complex (Oligochaeta: Lumbricidae) based on mitochondrial and nuclear DNA sequences. Mol. Phylogenet. Evol. **52**(2): 293–302. doi:10.1016/j.ympev.2009.04.003. PMID: 19364539.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org.

Reynolds, J.W. 1972. Earthworms (Lumbricidae) of the Haliburton Highlands, Ontario, Canada. Megadrilogica, **1**: 1–11.

Reynolds, J.W. 1977. The earthworms (Lumbricidae and Sparganophilidae) of Ontario. Royal Ontario Museum, Toronto, Ont.

Reynolds, J.W. 1994. The distribution of the earthworms (Oligochaeta) of Indiana: a case for the post quaternary introduction theory for megadrile migration in North America. Megadrilogica, **5**: 13–32.

Suárez, E.R., Tierney, G.L., Fahey, T.J., and Fahey, R. 2006. Exploring patterns of exotic earthworm distribution in a temperate hardwood forest in south-central New York, USA. Landsc. Ecol. **21L**(2): 297–306. doi:10.1007/s10980-005-1785-2.

Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. Springer, New York.

Wironen, M., and Moore, T.R. 2006. Exotic earthworm invasion increases soil carbon and nitrogen in an old-growth forest in southern Quebec. Can. J. For. Res. **36**(4): 845–854. doi:10.1139/x06-016.