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Environmental indicators reflective of road design in a forested landscape

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Abstract. Roads cause both chemical and physical disturbance at the time of creation and through the maintenance of the road. However, none have fully considered the extent of above- and below-ground impacts related to roads. Our study seeks to fill this gap with three objectives: (1) quantify differences in the nematode community by road-use intensity, (2) estimate distance of environmental impact of roads using nematode community indices, and (3) relate nematode communities to abiotic soil and above-ground plant communities for a relatively comprehensive environmental assessment of the spatial footprint of roads on the landscape. Soil and plant samples were co-located at six distances from the road edge (shoulder, sideslope, ditch, backslope, 10 m from forest edge, and 50 m from road crown) for each of 10 transects perpendicular to each of three road types (highways, two-lane paved, and gravel). There were differences in all nematode community measures based upon distance as a main effect, correlating with patterns of plant communities. Nematode community index values reflect increased disturbance closer to the road, particularly at the shoulder, with later ecological succession and a shift in the decomposer food web with increased distance from the road and in reference forest sites. In contrast, chemical properties of soil were influenced more by road type and the two-way interaction of road type and topography. Salt concentrations were greatest by two-lane paved roads, while heavy metal concentrations were greatest near highway roads. This study is one of the most comprehensive assessments of environmental impact by roads, providing data for accurate transportation system models. The results suggest that conscious design and management of the forest buffer and intentional inclusion of a ditch as a roadside feature may minimize pollutant movement and protect surrounding landscapes.

Key words: co-correspondence analysis; deicer; impact assessment; nematode community composition; plant community composition; plant–soil interactions; road salt; soil chemistry; transportation models; Vermont.

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INTRODUCTION

In the northeastern United States, native forests are a particular focus of conservation which provides important functions including provision of wildlife habitat, biodiversity conservation, filtration of air and water, and soil conservation. While the benefits of trees and other above-ground vegetation are most often highlighted, soil fauna are increasingly recognized for the role they play in soil quality, defined by the capacity of the soil to sustain biological productivity and health, maintain environmental quality through decomposition, buffering and filtering processes, and effectively mediate water flow through the environment (Karlen et al. 1997). Nematodes are among the key contributors to the soil community, as they are known to influence nitrogen cycling and plant biomass, are a key driver in the relationship between microbial communities and plants in the rhizosphere, and can play a functional role in regulation of native plant populations (Neher 2010). Nematodes have been used in many contexts as biological indicators of ecosystem status because of their unique properties: occupying many levels on the food web, being adaptable to most habitats, having close contact with nutrients and pollutants as they dwell in soil water pores, being responsive to both chemical and physical disturbance and finally being relatively easy to extract and enumerate (Bongers and Ferris 1999, Neher 2001). Therefore, nematodes can be useful in quantifying the degree to which a soil ecosystem is altered through the course of human-created landscape changes.

Roads have been shown to alter the landscape and affect the function and composition of ecological communities near the road edge, a condition termed the "edge effect zone" (Forman and Alexander 1998, Forman and Deblinger 2000, Delgado et al. 2007). While it is estimated that these edge effects may extend into at least 20% of the land area of the United States (Forman 2000), little research has examined below-ground effects on road ecology. Increasing pressure on existing roads coupled with pressure of building new roads in response to population growth and urbanization makes this question more relevant. Ecological implications relevant to soil ecology include alteration of landscape form; fragmentation of habitats; modification of hydrological flow, light, wind, and heat regimes; compaction of soil; shifts in composition of primary producers; and the accumulation of nutrients and pollutants (Forman and Alexander 1998).

Roads cause both chemical and physical disturbance at the time of creation and through the maintenance of the road. Heavy metals may accumulate on the roadside from the sourcing of road material, from leaded gasoline used in the past, from abrasion between tires and the road surface, and from brakes (Lagerwerff and Specht 1970, Davis et al. 2001, Adachi and Tainosho 2004, Pierzynski et al. 2005). Nitrogen and sulfur oxides originating from car exhaust may deposit locally (Vaitiekunas and Banaityte 2007). In regions with freezing rain and snow, such as is seen in the northeast of United States, sands and salts are used commonly to improve driving conditions. Salt can cause water stress in plants and result in reduced plant vigor or death (Goodrich et al. 2009). Both chemical and physical disturbances that alter plant assemblages likely also have a feedback relationship with the soil assemblages, as soil communities may shift in response to changes in litter quality and quantity (Wardle et al. 2004).

In other contexts, nematode community composition is responsive to heavy metals (Korthals et al. 1996, Bongers et al. 2001, Shao et al. 2008) and salts (Le Saux and Queneherve 2002, Nkem et al. 2006). Compaction also affects nematode communities, as they depend upon soil pore films for habitat space (Görres et al. 1999, Neher et al. 1999). A single study examining soils near a highway in China does suggest reduction in higher trophic groups of nematodes, though common nematode indices were not calculated (Han et al. 2009). Urbanization has been shown to impact nematodes (Amosse et al. 2016), with roadside soils in older cities showing more complex trophic structure than newer cities; however, distance from the road was not studied rigorously (Werkenthin et al. 2014), and only grassy areas were sampled (Park et al. 2011). Interestingly, urbanization has been shown to alter the composition, but not the diversity of forest soil nematodes (Pavao-Zuckerman and Coleman 2007). However, forest harvesting has been associated with a disturbance in the soil nematode community (Haskell 2000, Marshall 2000, Yeates 2007, Malmivaara-Lamsa et al. 2008). The very limited set of studies, none of which have fully considered the extent of impacts related to roads, leaves an important gap in the literature.

Our study seeks to fill this gap through three primary objectives: (1) quantify differences in the nematode community by road-use intensity, (2) estimate distance of environmental impact of roads using nematode community indices, and (3) relate nematode communities to abiotic soil factors and above-ground plant communities for a relatively comprehensive environmental assessment of the spatial footprint of roads on the landscape. We hypothesized that greater road-use intensity and closer proximity to the road would result in conditions that alter nematode communities with lower abundance, diversity, trophic structure, and maturity index values. However, our sampling design also recognized that the roadside environment and topography are not homogenous. For example, ditches may both accumulate pollutants and have moister conditions, while forest edges may serve as a filter for both chemical and physical disturbance (Neher et al. 2013).

To our knowledge, this study is the first to link below- and above-ground environmental impacts of a transportation–road interface in the context of a forested landscape matrix, comparing different road types, and generating recommendations for roadside landscaping. Our approach uses nematode communities as biological indicators of soil, and relates their predictions to those of soil chemistry and plant communities as co-located points. Detailed chemistry and plant community composition for this study were published elsewhere (Neher et al. 2013). This paper focuses on linking plant and chemistry indicators to soil biological indicators and implications for road design.

METHODS

Site description and selection

The study was conducted in the Chittenden County, Vermont, within a forested landscape classified as Northern Hardwood and White Pine Northern Hardwood Forest, mixed with mostly rural residential areas and through roads (Eyre 1980, Thompson and Sorenson 2005). Sampling was located within two watersheds, the Muddy Brook (8262 ha centered at 44°24′34″ N, 73°08′00″ W) and Allen Brook (2900 ha centered at 44°25′28″ N, 73°04′01″ W). Within both watersheds, all potential forest sections were identified by Google Earth digital photography and ESRI ArcMap.

In total, 180 samples were collected (3 road types × 10 transects × 6 distances). Road types examined in this study are classified broadly as “highways,” “two-lane paved,” and “gravel” which correspond approximately with the Federal Highway Administration’s classification of arterial, collector, and local (US Department of Transportation 2011). For each road type, 10 transects were chosen randomly from all potential transects that met the criterion of a minimum of 100 m of contiguous forest, perpendicular to the road (Delgado et al. 2007). Other studies report that the maximum dust and pollution attenuation occurs within 100 m (Tamm and Troedsson 1955, Yin et al. 2011).

The sampling strategy within the transect was adapted from a study of roadside vegetation in Terra Nova National Park which defined modified roadway zones as the shoulder, sideslope, ditch, backslope, and native vegetation (Karim and Mallik 2008). The shoulder is located next to the driving surface of the road, and the sideslope is the adjacent area built up during road construction to support the main road surface. The ditch is a low point that carries away water from the road surface, and the backslope is the cleared area that maintains ditch functions. In this study, each road type was sampled at the roadside shoulder, middle of the sideslope, middle of the ditch, middle of the backslope, 10 m into the forest from the forest edge, and 50 m from the roadside (Fig. 1). The 50-m location was designed to be our reference of native vegetation and soil. Although these features were common for all road types, the actual distance from the road varied.

Data collection

Sampling for plants, soil chemistry, and nematode communities occurred from 11 May to 3 June 2009. Spring was chosen to capture the greatest effects of salts after final snow melt, but once ground had completely warmed up. Deicing treatments included direct applications of NaCl and pickled sand (5% by mass NaCl to prevent caking) at rates of 14.1, 19.0, and 1.0 $\mathrm{kg \cdot m^{-1} \cdot yr^{-1}}$ for highway, two-lane paved, and gravel roads, respectively. In addition to NaCl, gravel roads received liquid 35% solution calcium (Ca) chloride to suppress dust and bind small particles during the summer months (2.0 $\mathrm{L \cdot m^{-1} \cdot yr^{-1}}$), but no other road types received this treatment.

Percentage cover of herbaceous flora and woody shrub species was quantified in 1- and 10-$\mathrm{m^2}$ circles, respectively, at each sample point. Independent samples were taken for nematodes and other soil properties. Chemistry and bulk density samples were collected with an intact soil core probe (AMS, American Falls, Idaho, USA; 5.08 cm diameter, 7.62 cm length). Nematode samples were a composite of five cores taken using a Dutch auger (5 cm diameter), to a depth of 30 cm, or as deep as possible in the case of compaction. In the forest, leaf duff and large woody debris were gently removed to reveal the organic horizon before sampling. Samples were stored in labeled sealable plastic bags at 15°C in a mechanical convection incubator until soil extraction was completed (Barker 1969).

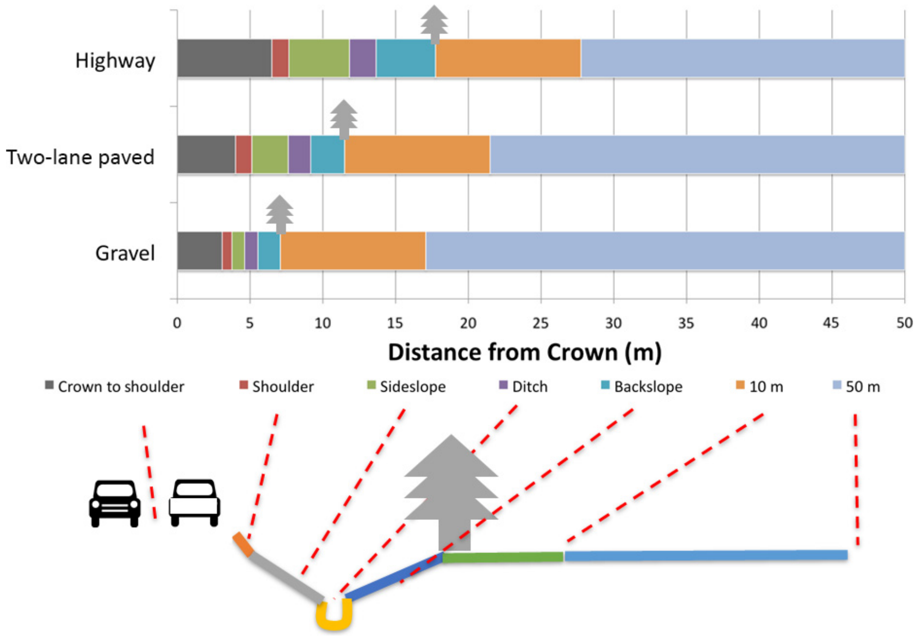


Fig. 1. Measured dimensions of roadside microtopography. Tree icon represents the edge of the forest defined as visually in line, and parallel the road, with the first tree >8 cm diameter at breast height. The road crown (0 m) represents the effective "center" of each road type. Reprinted from Neher et al. (2013, p. 322, fig. 1) with permission from Elsevier (https://doi.org/10.1016/j.scitotenv.2013.01.062).

Chemical and physical analysis

Percent organic matter was determined through loss on ignition for 2 h at 500°C. Nickel (Ni), lead (Pb), sodium (Na), and Ca contents were quantified by inductively coupled plasma mass spectrometry as previously reported (Neher et al. 2013). Quality control and quality assurance were achieved by including an internal standard reference material in each batch of 20 samples, replicating 10% of samples, and correcting output for calibration and reagent blanks (Hoskins 2006).

Nematode community analysis

Nematodes were extracted from 200 cm^3 of soil using a Cobb's sieving and decanting method, modified by triplicate passes through 600, 250, 150, 75 μm and finally 44 μm mesh sieves. Extraction was followed by Oostenbrink cotton-wool filter extraction method for 48 h (Hygia brand rapid milk filter 220 mm; s'Jacob and van Bezooijen 1984). A total of 200 nematodes were identified per sample using a compound light microscope. Nematodes were enumerated and identified by taxonomic genus (Appendix S1) according to Bongers (1987), with the exception of Rhabditidae. Community indices were computed as described previously (Neher and Darby 2006). Specifically, diversity of genera was computed using the Hills N1 index as $\exp - \Gamma[P_i(\ln P_i)]$, where P_i is the proportion of genus group i in the total nematode community and reflects the number of abundant genera (N1 is eH', where e is the base of the natural logarithm and H' is Shannon index). Ecological succession indices were computed in three ways: (1) $F{:}B = \text{fungivores}/(\text{fungivores} + \text{bactervores}) \times 100$, (2) $\text{MI} = \Sigma[\text{CP-value }(i) \times f(i)]/[\text{total numbers of nematodes}]$, where CP-values range from 1 to 5, with 1 representing r-strategists and 5 representing K-strategists, (i) is the individual taxon, and $f(i)$ is the frequency of the free-living taxa in a sample, and (3) ΣMI, where $f(i)$ is the frequency of each plant-parasitic and free-living taxon. Two extensions of the maturity index were also computed: (1) enrichment index (EI) and structural index (SI; Ferris et al. 2001).

Statistical analysis

Effect of road features on soil nematode communities was analyzed by an incomplete three-way ANCOVA. The procedure was performed with relative abundance of nematodes by trophic group and community indices as response variables and topography, road type, distance, and a two-way interaction between topography and road type as independent variables. Two-way interactions of road type or topography with distance and the three-way interaction were omitted from the model because they were not significant and for parsimony. Organic matter, Pb, Ni, Ca, and Na were treated as covariables. Lead and Ni relate to automobiles and are correlated with other metals including aluminum, copper, and zinc (Neher et al. 2013). Organic matter is correlated positively with clay which represents texture and is also positively correlated with bulk density (Neher et al. 2013).

Effect of road features on chemical properties treated as covariables above was analyzed by an incomplete three-way ANOVA with topography, road type, distance, and all two-way variable combinations as independent variables. A three-way interaction was omitted from the model because it was not significant and for parsimony.

Single degree of freedom contrasts were performed for both the ANCOVA and ANOVA above to compare road types and distances of a priori interest. Specifically, gravel vs. paved (highway or two-lane) roads were compared to determine whether the road surface explained treatment effects. Rural roads (gravel, two-lane paved) were compared to highways to determine whether traffic volume and speed explained effects. Distance comparisons were (1) shoulder and grass (backslope, upslope), (2) grass and ditch, and (3) forest (10, 50 m) with non-forest (shoulder, backslope, ditch, upslope). Distance comparisons were designed to decipher whether responses were related to solely to distance, vegetation differences, and/or gravity flow into ditches. All variables were tested for normality using the univariate procedure. As a result, proportions of trophic groups and soil chemistry were transformed as arcsine ($\sqrt{x}$) and $\log(x + 0.01)$, respectively. Analyses were performed using the Mixed procedure in SAS version 9.4 software (SAS Institute, Cary, North Carolina, USA).

Co-correspondence analysis (Co-CA) of soil nematode and plant communities was performed as a single-step, direct approach to identify the ecological gradients of road type and distance from road edge that are common to both communities (ter Braak and Schaffers 2004). The single-step approach makes Co-CA superior to canonical correspondence analysis in this situation because the number of (predictor) species exceeds the number of sites (n = 142 plant species, n = 119 nematode genera, n = 180 co-located sites) by an order of magnitude (ter Braak and Schaffers 2004). The symmetric explanatory version is based on weighted averaging. The method works by maximizing the weighted covariance between weighted averages species of one community and weighted averages species scores of the other community. Symmetric Co-CA provides a value that is most intuitively comparable to that provided by other gradient analysis approaches (Gioria et al. 2011). Biplots illustrate the syntaxonomic unit for each type of site rather than spatial location of sites. Significance is determined with a Monte Carlo randomization of 499 permutations to test the correlation between the two resemblance matrices. Co-correspondence analysis was performed using Canoco version 5 software (ter Braak and Šmilauer 2012). Our approach was modeled after application of Co-CA to investigate associations of plant communities with soil communities of microbes (Mitchell et al. 2010, 2012), insects (Raemakers et al. 2001, Schaffers et al. 2008), carabids, and other arthropods (Harvey et al. 2008).

RESULTS

There were 117 nematode genera identified across the three road types and six distances from the road edge (Appendix S1). Of these genera, one was an algivore, 37 were bacterivorous, 21 fungivorous, 11 omnivorous, 20 predaceous, and 27 plant-parasitic.

Topography and road type

Topography and road type had main effects on contrasting variables after accounting for variance explained by soil chemistry covariables. Specifically, topography explained relative abundance of algivorous and predaceous nematodes,

Table 1. Three-way incomplete factorial ANCOVA of soil nematode trophic group (relative abundance) and community indices.

	Independent variables				Covariables					Single df contrasts				
Response	Topo (df = 1) *F*	Road (df = 2) *F*	Dist (df = 5) *F*	Topo × road type (df = 2) *F*	OM *P*	Pb *P*	Ni *P*	Na *P*	Ca *P*	Gravel vs. pavement[a] *F*	Rural vs. highway[b] *F*	Shoulder vs. grass[c] *F*	Ditch vs. grass[d] *F*	Forest vs. else[e] *F*
Bacterivores	0.20 ns	5.76**	5.65***	0.53 ns	ns	ns	ns	ns	ns	0.00 ns	7.01**	17.87***	2.53 ns	3.92*
Algivores	9.51**	0.15 ns	5.56***	0.48 ns	ns	ns	ns	ns	ns	0.28 ns	0.04 ns	4.54*	6.84**	4.2*
Fungivores	3.44§	2.07 ns	3.91**	0.47 ns	ns	ns	*	***	ns	0.79 ns	0.73 ns	11.9***	0.12 ns	6.82**
Omnivores	0.60 ns	0.27 ns	3.59**	0.09 ns	ns	ns	ns	*	ns	0.04 ns	0.18 ns	8.14**	3.32§	0.67 ns
Predators	9.15**	0.80 ns	1.97§	0.01 ns	ns	ns	ns	ns	ns	1.39 ns	0.16 ns	3.80§	1.00 ns	3.55§
Plant parasites	0.36 ns	7.82***	2.04§	2.04 ns	ns	ns	ns	ns	***	5.92*	15.63***	2.72 ns	1.35 ns	3.36§
F:*B*	1.02 ns	4.49*	5.08***	0.49 ns	ns	ns	*	***	ns	0.62 ns	3.01 ns	17.74***	0.05 ns	6.76*
EI	6.43*	1.91 ns	2.11§	0.53 ns	ns	ns	ns	*	ns	0.06 ns	1.81 ns	3.69§	0.69 ns	0.06 ns
SI	6.02*	0.31 ns	5.78***	2.92§	ns	ns	*	*	ns	0.02 ns	0.46 ns	18.00***	2.36 ns	0.6 ns
MI	3.64§	0.34 ns	4.52***	3.01§	***	ns	**	***	ns	0.58 ns	0.53 ns	9.83**	0.26 ns	1.39 ns
ΣMI	1.42 ns	0.57 ns	4.60***	3.08*	***	ns	§	**	ns	0.78 ns	1.06 ns	7.91**	0.21 ns	3.02 ns
Genus N1	8.28**	0.18 ns	6.52***	0.72 ns	ns	ns	ns	*	ns	0.04 ns	0.09 ns	19.75***	0.46 ns	3.39§

Notes: Trophic groups were arcsine ($\sqrt{x} + 0.01$)- and soil properties as $\ln(x + 0.01)$-transformed before analysis. Soil properties are abbreviated as percent organic matter (OM), lead (Pb), nickel (Ni), sodium (Na), and calcium (Ca). Community indices are abbreviated as fungivores/(fungivores + bacterivores) ratio (*F*:*B*), enrichment index (EI), structural index (SI), maturity index of free-living nematodes (MI), maturity index of free-living and plant-parasitic nematodes (ΣMI), and Hills 1 diversity of genera (genus N1).

Single degree of freedom contrasts of: [a]gravel roads contrasted with all paved roads combined, [b]gravel and two-lane paved roads contrasted with highway roads, [c]shoulder distance contrasted with sideslope and backslope distances combined, [d]ditch distance contrasted with sideslope and backslope distances combined, and [e]both forest distances (10 m from edge and 50 m) combined and contrasted with all other distances.

F-statistics and level of significance illustrated for topography (Topo), road types (road), and distance (dist) and two-way interactions of these three variables as $^{***}P \leq 0001$, $^{**}P \leq 0.001$, $^{*}P \leq 0.05$, $^{\S}0.05 > P \leq 0.07$, ns $P > 0.07$. Topo compares overall topography up or down; road compares highway, two-lane paved, and gravel; dist compares shoulder, sideslope, ditch, backslope, 10-m forest, and 50-m forest.

and index values of EI, SI, and N1, whereas road type explained relative abundance of bacterivorous, plant-parasitic nematodes, and *F*:*B* index values. Neither topography nor road type main effects explained relative abundance of fungivorous or omnivorous nematodes or MI values. However, there was a two-way interaction of topography and road type on ΣMI values. Bacterivorous nematodes were relatively more abundant on two-lane paved rural roads than on highways (Table 1). Plant-parasitic nematodes were more abundant on paved than on un-paved gravel roads and on highways compared to two-lane paved roads (Table 1, Fig. 2). Values of *F*:*B* were less for two-lane paved than on gravel or highway road types (Fig. 3).

There were genus-specific relationships to road type (Table 2). For example, *Plectus* and *Mylonchulus* were less abundant with greater road-use intensity, whether highway or two-lane paved. *Cephalobus*, *Eudorylaimus*, *Filenchus*, and *Tylenchus* were more abundant with gravel roads than with two-lane paved roads. *Prismatolaimus* was far more abundant in two-lane paved roads, than either gravel or highway. *Aphelenchus* was most abundant in highway roads, and least in two-lane paved roads.

Chemical properties were influenced more by main effects of road type and a two-way interaction of road type and topography than nematode community assessments (Table 4, Fig. 4). Sodium content was greater downslope than upslope on two-lane paved roads. In contrast, Ca content was greater upslope than downslope for gravel roads. Nickel content was greater for highway than for rural roads (Fig. 4). Concentrations of Ca and Pb were greatest near the road edge. Sodium and Ni tended to accumulate in ditches (Fig. 4).

Distance from road

Distance from the road explained significant or trend differences for all trophic groups and community indices (Table 1). Abundance of bacterivorous nematodes was greater at the shoulder than further distances from the road, including forested distances (Table 1). In contrast, relative abundance of fungivores, omnivores, algivores, *F*:*B*, SI, EI, MI, and ΣMI were less at the shoulder than at grassy areas. Relative abundance of fungivores, omnivores, and *F*:*B* values were greater in forested than in non-forested distances. Relative abundance of algivores was greatest in the ditch compared to the shoulder, grass, or forest (Table 1, Fig. 2).

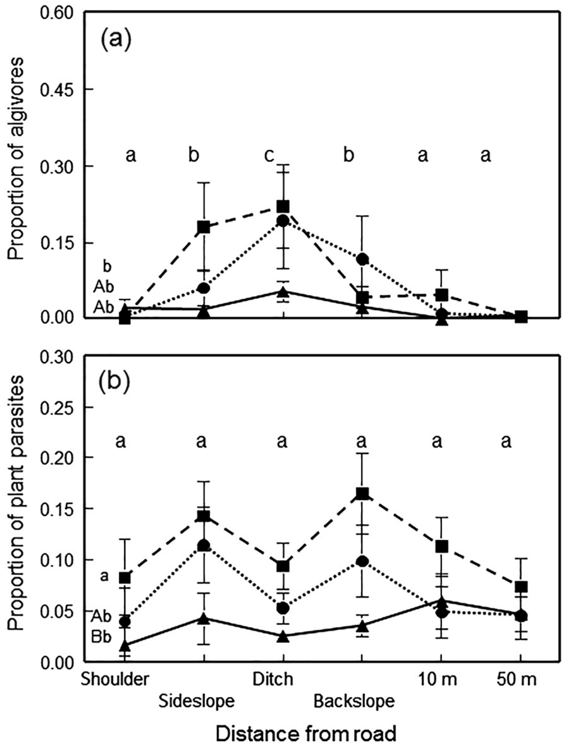


Fig. 2. Proportion of (a) algivorous and (b) plant-parasitic nematodes as a function of distance from the edge of gravel (solid line, triangle), two-lane paved (dotted, circle), and highway (dashed, square) roads in Vermont hardwood forests. Symbols represent means, and bars represent 1 standard error. Contrasting letters represent differences detected with single degree of freedom contrasts among road types (lower left) and distances from the road (middle horizontal row). For road type, uppercase letters compare gravel vs. two-lane paved roads, and lowercase letters compare highway vs. two-lane paved and gravel road types.

While there was a higher prevalence of bacterivores in the roadside, analysis at the genus level showed that different genera of bacterivores were associated with contrasting distances along the transect (Table 3). For example, *Acrobeloides* was abundant at the shoulder, *Eucephalobus* at the shoulder and sideslope, and *Paramphidelus* and *Alaimus* with backslope and forest.

Both plant and nematode communities correlated with distance from road edge more than road surface (Fig. 5). *Acrobeloides*, *Cephalobus*, Rhabditidae, *Eucephalobus*, and *Aphelenchus*

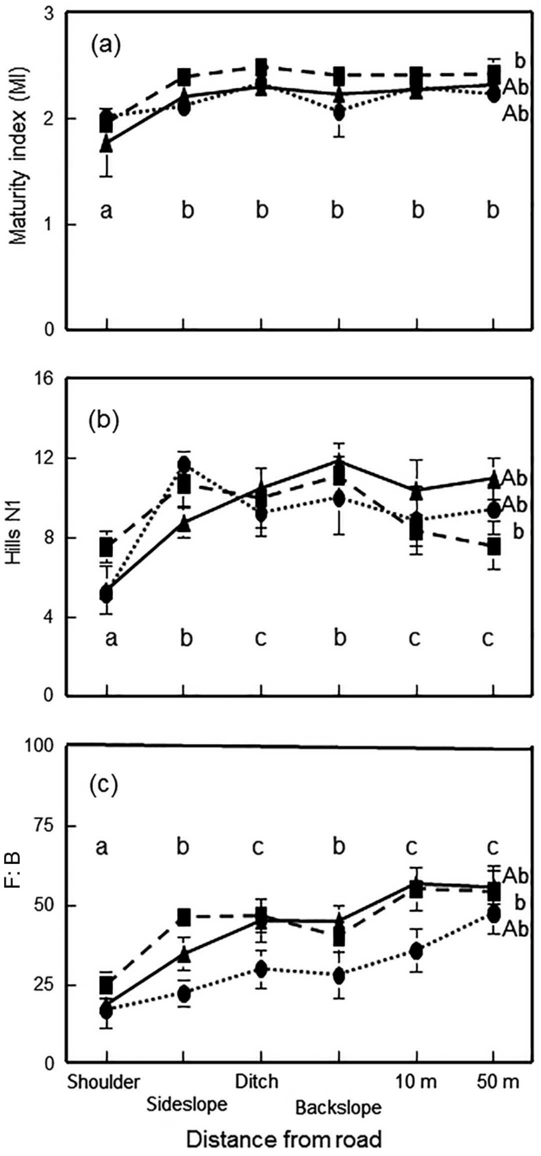


Fig. 3. Nematode community indices as a function of distance from the edge of gravel (solid line, triangle), two-lane paved (dotted, circle), and highway (dashed, square) roads in Vermont hardwood forests. Indicator indices are represented as (a) maturity index, (b) Hills N1 genus diversity, and (c) fungivores/(fungivores + bacterivores) × 100. Symbols represent means, and bars represent 1 standard error. Contrasting letters represent differences detected with single degree of freedom contrasts among road types (upper right) and distances from the road (middle horizontal row). For road type, uppercase letters compare gravel vs. two-lane paved roads and lowercase letters compare highway vs. two-lane paved and gravel road types.

Table 2. Relative occurrence and abundance of nematode genera (per 200 cm^3 soil) affected by road type. For simplicity, only genera with significant differences are illustrated.

Trophic group/Genus	Road type		
	Gravel	Two-Lane Paved	Highway
Algivores			
Achromadora	ns	ns	ns
Bacterivores			
Acrobeloides	ns	ns	ns
Alaimus	*58.33*	*31.03*	*38.33*
Cephalobus	141.19 ± 6.45	97.93 ± 25.53	110.97 ± 25.74
Cervidellus	*38.33*	*31.03*	*16.67*
Eucephalobus	ns	ns	ns
Eumonhystera	ns	ns	ns
Paramphidellus	*41.67*	*20.69*	*51.67*
Plectus	105.27 ± 15.05	97.57 ± 17.19	44.26 ± 10.49
Prismatolaimus	31.00 ± 10.60	73.74 ± 36.90	19.88 ± 8.36
Rhabdolaimus	*15.00*	*20.69*	*38.33*
Teratocephalus	ns	ns	ns
Fungivores			
Aphelenchus	40.06 ± 11.49†	32.27 ± 9.67	66.33 ± 18.19
Boleodorus	*56.67*	*31.03*	*50.00*
Ditylenchus	ns	ns	ns
Filenchus	252.23 ± 35.49	108.14 ± 18.00	175.77 ± 29.77
Tylencholaimus	ns	ns	ns
Tylenchus	83.48 ± 3.17	31.87 ± 5.11	50.92 ± 10.67
Omnivores			
Eudorylaimus	41.59 ± 20.21	14.82 ± 4.35	24.27 ± 14.49
Prodorylaimus	*45.00*	*24.14*	*46.67*
Thonus	ns	ns	ns
Predators			
Clarkus	ns	ns	ns
Mylonchulus	19.31 ± 6.05	9.53 ± 1.65	6.26 ± 1.72
Plant-parasites			
Helicotylenchus	*43.33*	*41.38*	*70.00*
Pratylenchus	*15*	*29.31*	*3.005*

Notes: Each genus was analyzed two-ways: (1) contingency table to evaluate proportion of samples containing a genus (i.e., incidence), and (2) analysis of variance (ANOVA) of genus when present within sample. Percentage values are illustrated in italics if incidence was significant but not abundance. Otherwise, means ± 1 standard error ($n = 30$) are illustrated.

† Both incidence and abundance were significant ($P \leq 0.05$).

nematodes were associated with plant species including *Sonchus oleraceus*, *Dactylis glomerata*, and *Rubus allegheniensis*. The sideslope and backslope positions were populated by grasses such as *Festuca* species, *Athyrium filia*, and *Phalaris arundinacea*. Associated with the grasses were nematodes *Ditylenchus*, *Teratocephalus*, *Boloderus*, and *Prodorylaimus*. Forests were relatively depauperate in herbaceous species, but their soils contained nematodes *Prismatolaimus*, *Alaimus*, and *Helicotylenchus*. *Filenchus* was most abundant in the forest, and *Eudorylaimus* specifically at the 50 m (Table 3).

DISCUSSION

Biological indicators are valuable because they integrate effects of pollutants and habitat alterations of the roadside, clearly demonstrating the greatest disturbance at the road shoulder. Compared with impacts to physical and chemical soil properties and above-ground plant communities, soil nematodes are at least as sensitive to environmental disturbance caused by roads in northern temperate forests. As previously noted, soil nematodes are correlated with soil chemistry, but are not redundant (Neher and Campbell 1994).

Table 3. Relative occurrence and abundance of nematode genera (per 200 cm^3 soil) affected by categorical distance from road edge. For simplicity, only genera with significant differences are illustrated.

Trophic group/Genus	Categorical distance					
	Shoulder	Sideslope	Ditch	Backslope	10 m Forest	50 m Forest
Algivores						
Achromadora	40.62 ± 32.33†	163.49 ± 61.41	80.24 ± 2.33	44.76 ± 18.76	30.47 ± 11.43	14.4 ± 3.56
Bacterivores						
Acrobeloides	212.57 ± 55.33	102.32 ± 54.82	37.53 ± 11.78	49.63 ± 16.17	85.02 ± 29.60	126.16 ± 60.26
Alaimus	*6.67*	*23.33*	*41.38*	*63.33*	*60.00*	*62.07*
Cephalobus	ns	ns	ns	ns	ns	ns
Cervidellus	*16.67*	*16.67*	*13.79*	*26.67*	*43.33*	*55.17*
Eucephalobus	268.73 ± 50.68	272.69 ± 47.76	177.49 ± 3.84	178.13 ± 41.96	105.01 ± 24.98	71.49 ± 20.09
Eumonhystera	145.13 ± 36.29	138.09 ± 27.84	68.5 ± 0.45	72.47 ± 15.69	21.2 ± 4.50	24.09 ± 6.39
Paramphidellus	*3.33*	*23.33*	*7.59*	*56.67*	*56.67*	*62.07*
Plectus	*50.00*	*96.67*	*100.00*	*96.67*	*90.00*	*89.66*
Prismatolaimus	ns	ns	ns	ns	ns	ns
Rhabdolaimus	*3.33*	*13.33*	*37.93*	*23.33*	*20.00*	*51.72*
Teratocephalus	23.24 ± 4.96	36.21 ± 9.10	20.28 ± 9.10	9.51 ± 2.46	19.90 ± 6.97	31.08 ± 10.41
Fungivores						
Aphelenchus	90.25 ± 31.92†	49.98 ± 11.78	36.04 ± 5.94	32.32 ± 10.17	14.21 ± 5.18	4.47 ± 0.87
Boleodorus	67.27 ± 59.02†	69.56 ± 17.73	72.62 ± 29.09	125.86 ± 49.60	37.41 ± 10.90	25.26 ± 12.73
Ditylenchus	154.07 ± 71.94	51.67 ± 21.21	33.51 ± 10.01	27.54 ± 8.74	43.95 ± 9.23	36.53 ± 8.86
Filenchus	82.4 ± 22.12	136.42 ± 21.60	110.31 ± 26.80	168.7 ± 44.32	306.54 ± 61.22	249.37 ± 39.82
Tylencholaimus	*0.00*	*50.00*	*48.28*	*53.33*	*76.67*	*65.52*
Tylenchus	*46.67*	*76.67*	*82.76*	*80.00*	*90.00*	*82.76*
Omnivores						
Eudorylaimus	21.13 ± 12.01	16.24 ± 4.84	38.76 ± 32.15	6.01 ± 1.09	25.72 ± 7.52	65.27 ± 41.57
Prodorylaimus	*3.33*	*43.33*	*58.62*	*56.67*	*26.67*	*44.83*
Thonus	*23.33*	*16.67*	*37.93*	*46.67*	*56.67*	*58.62*
Predators						
Clarkus	*0.00*	*13.33*	*13.79*	*20.00*	*46.67*	*37.93*
Mylonchulus	ns	ns	ns	ns	ns	ns
Plant-parasites						
Helicotylenchus	106.82 ± 80.79†	64.90 ± 20.17	32.01 ± 8.87	51.41 ± 11.67	48.55 ± 11.45	38.72 ± 16.36
Pratylenchus	*23.33*	*60.00*	*41.38*	*30.00*	*3.33*	*0.00*

Notes: Each genus was analyzed two-ways: (1) contingency table to evaluate proportion of samples containing a genus (i.e., incidence), and (2) analysis of variance (ANOVA) of genus when present within sample. Percentage values are illustrated in italics if incidence was significant but not abundance. Otherwise, means ± 1 standard error (n = 30) are illustrated.

† Both incidence and abundance were significant ($P \leq 0.05$).

Soil chemistry is affected more by topography and road type as a main effect or interactions, whereas nematode communities are affected more by distance from roads. The "edge effect" is at least partially a measure of the size of the road verge. Categorical distance is confounded by vegetation and microtopography.

Topography

One would expect that downsloping transects would carry runoff further distances, and therefore have pollutant accumulation farther from the roadside in downsloping transects. Indeed, many chemical properties had greater values in downsloping samples, and showed potential for farther surface movement, such as Na. However, there were some unexpected cases where the upsloping transects, particularly at the ditch, actually contained a greater concentration of pollutants. It is possible that the upsloping ditch is more effective than the downsloping ditches at retaining those pollutants. Depending on surrounding topography, downsloping ditches were not always present. In those cases, samples were simply taken equidistant from the sideslope and backslope.

Table 4. Three-way analysis of variance of chemical properties used as covariates in ANCOVA.

	Independent variables						Single df contrasts				
Response	Topo (df = 1) *F*	Road (df = 2) *F*	Dist (df = 5) *F*	Topo × road (df = 2) *F*	Topo × dist (df = 5) *F*	Road × dist (df = 10) *F*	Gravel vs. pavement[a] *F*	Rural vs. highway[b] *F*	Shoulder vs. grass[c] *F*	Ditch vs. grass[d] *F*	Forest vs. else[e] *F*
OM	13.32***	7.68***	29.72***	3.09*	0.43 ns	3.44***	15.34***	3.41§	24.26***	0.08 ns	94.00***
Pb	7.58**	58.68***	3.60**	9.42***	2.21§	6.04***	96.96***	77.47***	9.39**	0.0 ns	0.87 ns
Ni	1.10 ns	20.11***	3.35**	7.93***	4.06**	1.69 ns	18.43***	38.41***	8.03**	12.81***	0.29 ns
Na	6.38*	20.41***	10.00***	11.90***	3.17**	2.08*	31.20***	0.02 ns	8.84**	0.60 ns	33.85***
Ca	16.62 ***	43.50***	18.77***	6.68**	0.24 ns	4.51***	82.54***	41.09***	12.45***	0.78 ns	74.81***

Notes: Response variables were ln (x + 0.01)-transformed before analysis and are abbreviated as percent organic matter (OM), lead (Pb), nickel (Ni), sodium (Na), and calcium (Ca). All variables are expressed as mg/kg except for Ca which is g/kg.

Single degree of freedom contrasts of: [a]gravel roads contrasted with all paved roads combined, [b]gravel and two-lane paved roads contrasted with highway roads, [c]shoulder distance contrasted with sideslope and backslope distances combined, [d]ditch distance contrasted with sideslope and backslope distances combined, and [e]both forest distances (10 m from edge and 50 m) combined and contrasted with all other distances.

F-statistics and level of significance are illustrated for topography (Topo), road type (road), and distance (dist) and two-way interactions of these three variables as $^{***}P \leq 0001$, $^{**}P \leq 0.001$, $^{*}P \leq 0.05$, $^{§}0.05 > P \leq 0.07$, ns $P > 0.07$. Topo compares overall topography up or down; road compares highway, two-lane paved, and gravel; dist compares shoulder, sideslope, ditch, backslope, 10-m forest, and 50-m forest.

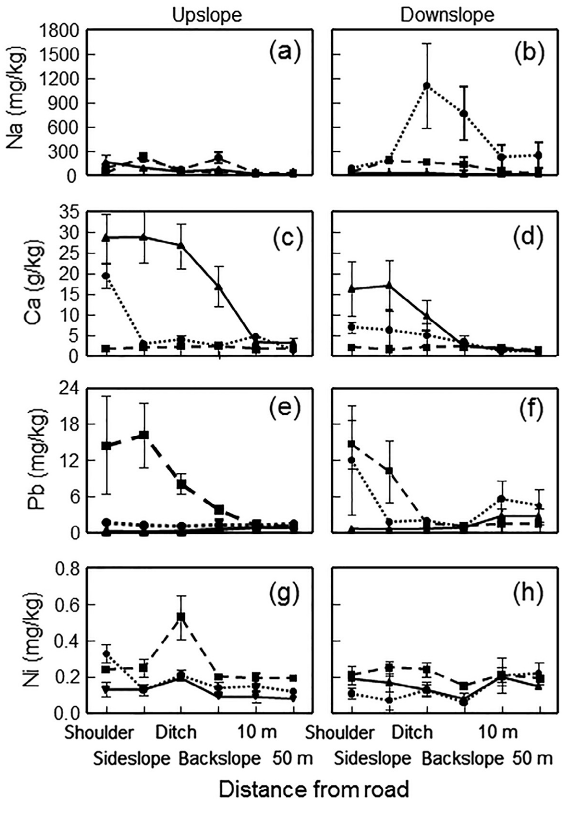


Fig. 4. Concentrations of (a, b) sodium, (c, d) calcium, (e, f) lead, and (g, h) nickel as a function of upslope (left column) or downslope (right column) and distance from the edge of gravel (solid line, triangle), two-lane paved (dotted, circle), and highway (dashed, square) roads in Vermont hardwood forests.

Road type

At least in this study, traffic volume and speed varied depending on terrain type. Gravel roads were most often found in rural, hilly areas, while two-lane roads were near stream valley areas, and highways were in elevated valley paths. Annual average daily trips were greatest for highway, intermediate for two-lane paved roads, and fewest for gravel roads (Neher et al. 2013). Increased traffic volume requires more winter road maintenance, thus greater applications of salts to avoid slick conditions associated with temperatures below freezing. Nematode response to salinity varies by family both in terms of tolerance and in terms of sensitivity to specific salt forms (Le Saux and Queneherve 2002, Nkem et al. 2006). If not directly causing death, salinity may affect other processes in nematodes such as their ability to reproduce or to infect their food host (Finnegan et al. 1999, Moens and Vincx 2000). Pollutant levels may shift through the season; most notably, the source of Na is probably more seasonally concentrated, being carried in the snow melt in a spring flush. Because samples were taken in the spring, Na levels at this time may be greater than at other times of the year.

Roadside soils are often altered at the time of construction, with removal of the topsoil fraction and combined with re-fill, particularly in the cases of highway roads. It is not surprising that these greatly altered soils do not support as complex a nematode community. Ecological succession

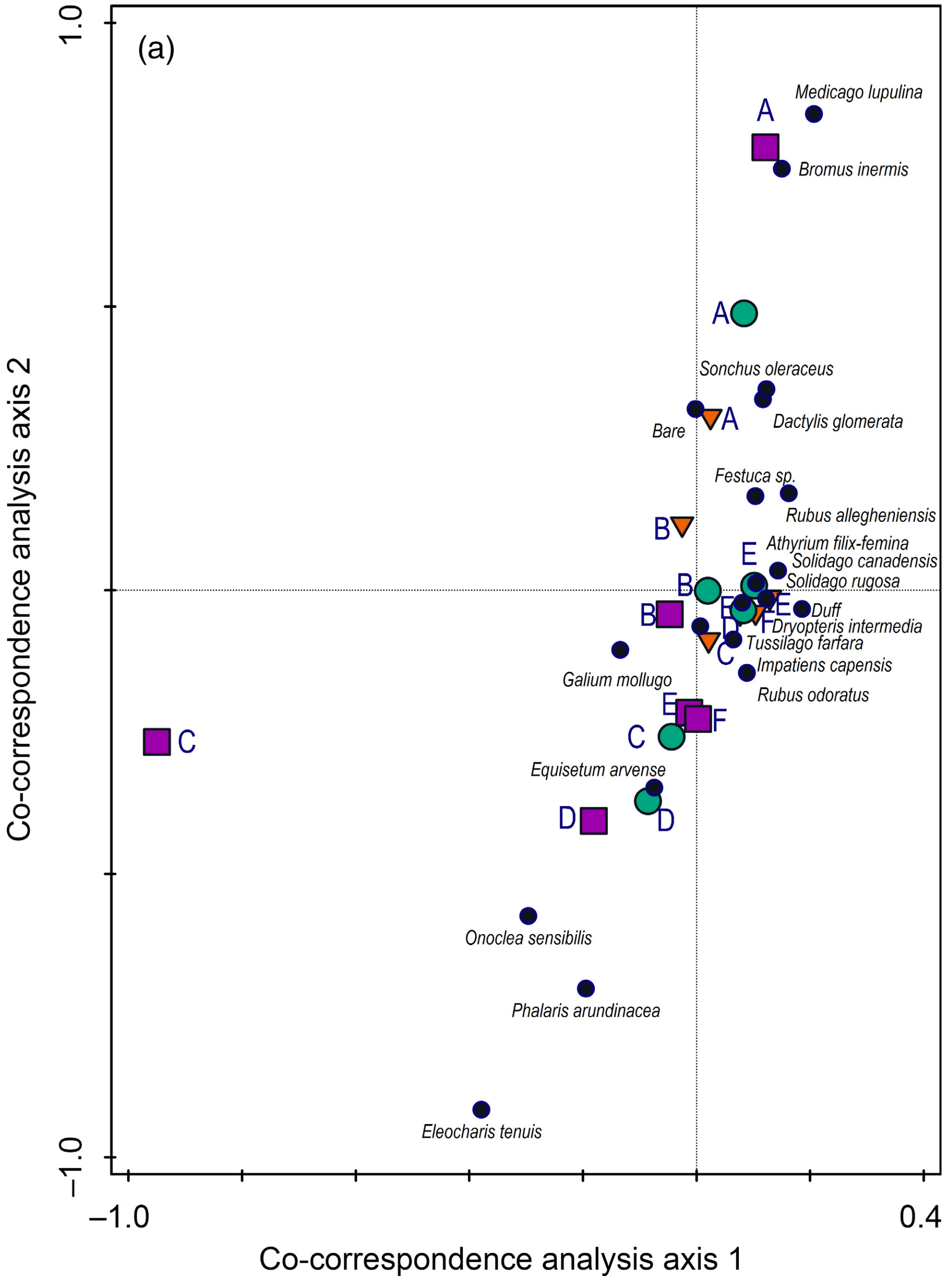
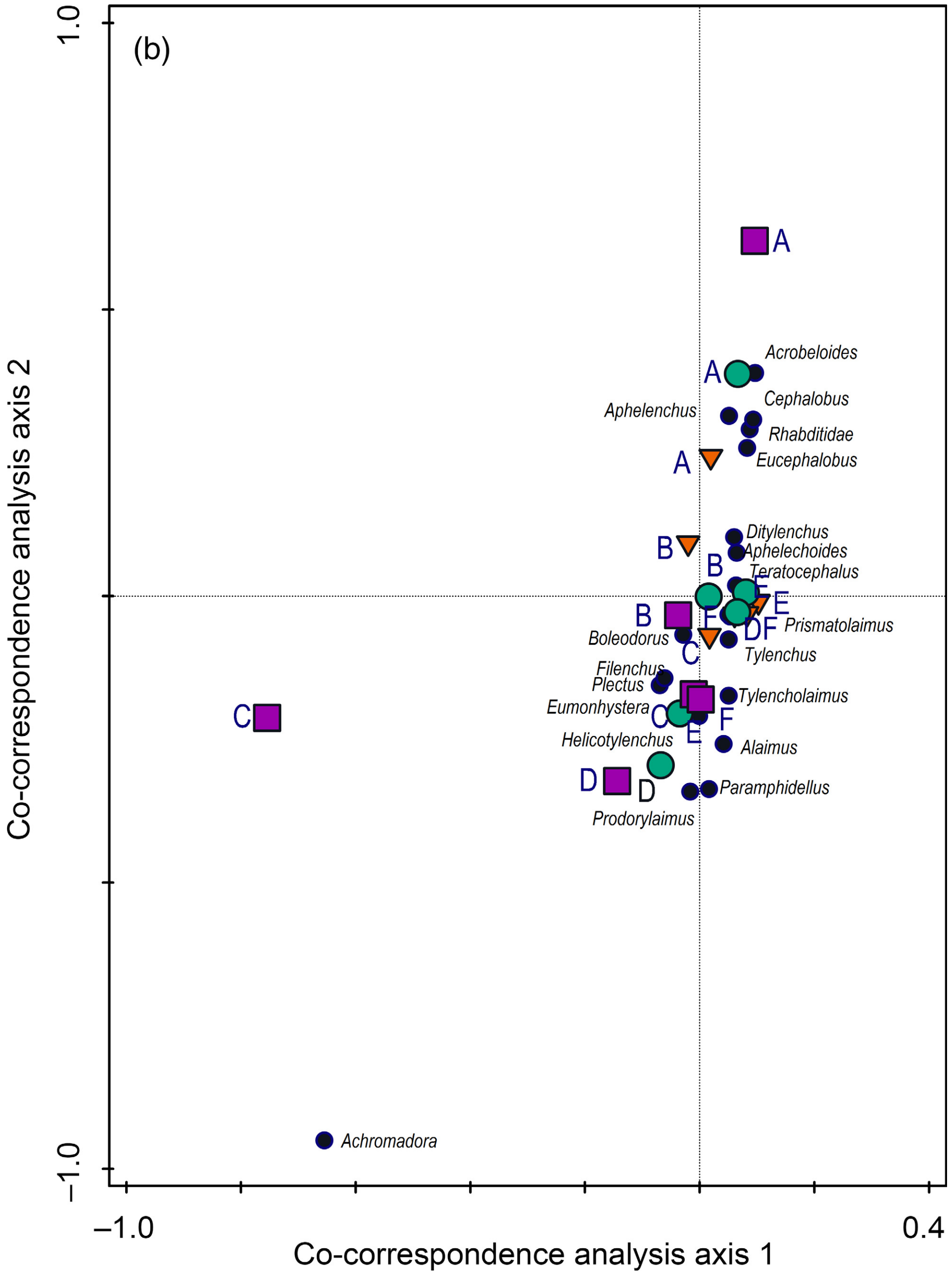


Fig. 5. Biplot based on symmetric co-correspondence analysis, illustrating the top 20 plant species (a) and nematode genera (b) common to different road types and distances from each road edge into Northern Hardwood forests; 20.67% of the total variance of each data set. Correlation coefficients between nematode-derived and plant-derived site scores of the first three axes of symmetric correspondence canonical analysis (axis 1: 0.8793, $\lambda 1 = 0.0840$, $P = 0.0060$; axis 2: 0.7916). Road types are depicted by symbol (highway: purple squares; two-lane paved: turquoise circles; gravel: orange inverted triangles), and distance from road is depicted by contrasting letter (A: shoulder; B: downslope; C: ditch; D: upslope; E: 10 m from forest edge; F: 50 m from forest edge).



(*Fig. 5. Continued*).

is proportional to the time since disturbance. In this study, gravel roads were oldest, at a mean of 152 yr, followed by two-lane paved roads and highways, at 135 and 47 yr old, respectively (Vermont Department of Motor Vehicles 2011). Age may explain at least partly why the most complex nematode communities were associated with gravel roads (Morse et al. 2016).

Distance from road edge

By design, road features are vegetated with different types of species. Shoulders are highly compacted, allowing few plant species to successfully establish. Shoulders are also the most disturbed, which was reflected in nematodes communities, soil chemistry, and plant communities. Typically, grasses are planted outside the road shoulder to limit woody plant invasion and to allow mowing for better visibility. The grassy areas are wider for highways than for rural roads for improved visibility at longer distances to accommodate greater speeds.

The ditch is a unique environment being wetter and supporting obligate wetland plant species (Ramakrishna and Viraraghavan 2005, Neher et al. 2013). Therefore, it is not surprising that algivorous nematodes were most abundant in ditches. The combination of saturated or semi-saturated soils and the accumulation of road salts probably collectively stimulate algivore growth in ditch soils. *Achromadora* is generally an aquatic nematode, often found in marine environments, though 30–50% of species having been recorded from freshwater environments (Abebe et al. 2006). Ditches may actually have a unique role to play in the greater health of ecosystems, by providing a unique habitat type and by accumulating nutrients and pollutants that might otherwise travel to nearby aquatic or terrestrial ecosystems.

The original sampling design with two distances within forest assumed that more disturbance would be detected 10 m from the forest edge than deeper (50 m) in the forest. However, no differences were detectable. These results mirrored those of soil chemistry, and suggest that the effects of the road were being filtered by the forest edge, and that those effects reflect upon the nematode community, as the forest community was different from that of the road verge. Transition zones, particularly the edge of the backslope and the edge of the forest, are important determinants of plant composition and other road effects. The greater density of shrubs resulting from light penetration in this zone can help to physically separate the roadside environment from forest environment. Our finding supports the hypothesis that forest edges may serve as a filter for biological, chemical, and physical disturbance (Neher et al. 2013).

Interactions above and below ground

Alterations of the roadside environment that lead to changes in plant species composition, diversity, and habitat structure have potential implications for soil biota that are linked to specific plant species or habitat types. For example, some nematodes feed primarily on specific host plants, including some roadside grasses and weeds (Vanstone and Russ 2001, Belair et al. 2007). This type of vegetation was more common at the sides of highway than at rural roads. Our study may be the first to use Co-CA with nematodes and plant communities. Closer investigation of individual plant species and nematode associations could reduce labor-intensive assessment that currently requires identifying entire soil nematode communities.

This study is one of the first to report measuring the spatial extent of habitat structure changes due to roads using biological soil indicators in conjunction with other soil and plant data based on landscape features. Due to the feedbacks between above- and below-ground systems (Wardle et al. 2004), it is likely that successful establishment of the roadside environment by plants would be linked with soil biota. Alterations in local plant community may also have an indirect effect on the soil community through changes in the soil habitat. Altered plant composition may affect the composition of plant exudates including nitrogen compounds, phytotoxins, and associated soil biota (Wardle et al. 2004, Bains et al. 2009).

Indices of ecological succession are useful indicators of disturbance. These indices supported the hypothesis about decreasing disturbance with distance from roads, but did not consistently distinguish road type. Site characteristics suggest that Tylenchidae are more likely fungivores than plant parasites in this study. For example, some distances from roads are not vegetated and mycorrhizae are prolific in these forests, spreading far beyond tree roots as reported for forest soils of similar latitude (Sohlenius et al. 1977). Relatively abundant fungivores occurred in forest soils protected from disturbance. Our results support another study that demonstrated that urbanization results in decreases in fungivorous nematodes (Pouyat et al. 1994, Pavao-Zuckerman and Coleman 2007). This research suggests that road building in rural areas could have an impact aside from development, but the magnitude of the impact is limited to the near roadside.

Implications for road design

While previous studies have investigated different aspects of the roadside environment, there is a paucity of environmental impact data available for rural forest ecosystems necessary for accurate transportation system models. The complicated interactions between road type, traffic volume, and maintenance activities suggest the need for further research, particularly considering variations in different geographic locations. Different road types are specifically designed and managed to host different traffic volumes and speeds. To inform modeling at a national scale, future research should consider a priori how road traffic varies within a particular road type. Additional research that has a greater breadth of road traffic volumes than that of this study is needed. While this research suggests the forest edge is important, there may be a difference in how effectively the forest edge functions as a buffer with higher traffic volumes, and therefore, pollution loading.

Management in the size and scope of the roadside grassy area is one design consideration stemming from these results. Transportation planners and managers should consider adding a structurally diverse vegetated buffer in cases where there is not a priori forested vegetation along roadsides, and consciously design and manage the roadside vegetation even in cases of forested landscapes. Advantages of forested buffers should be weighed with potential side effects on site-specific basis, based upon traffic visibility and potential to attract animals. The latter point is a potential hazard for both humans and animals, in the case of increased road-kill and predation. Areas near major waterways, wetlands, and sensitive or rare forest ecosystems would be priority locations for designed buffers. For those areas, plant communities could be selected for their ability to tolerate and even remediate pollutants of concern.

Roadside ditches could also be expanded to play a greater role in capturing and treating pollutants. In many urban areas, vegetative swales and raingardens have been installed to capture and treat roadway runoff before it enters a storm drain or receiving body. Similarly, the use of rural ditches could be expanded and improved to focus on greater infiltration and treatment of pollutants. Even in a downslope situation, the addition of a roadside ditch could reduce the travel of contaminated stormwater. Further improving these micro-habitats with a wide diversity of tolerant species would increase the environmental benefits.

In northern latitudes, roadways should be designed with special consideration for the impact of salts that are applied in de-icers. The position of the road relative to sensitive ecological features is a serious consideration for the roadside pollutant accumulation, which will have negative impacts on ecosystem function. This concern is particularly relevant for two-lane paved roads, which are often in closer proximity to major water bodies than are highway roads. Alternative paving materials, or reduced speed limits in coordination with reducing salt load application, are potential design features that have to be balanced with traffic concerns. Because studies have shown that salt pulses into waterways after final snow melt, efforts might focus on strategies to mediate the pulse effect so that salt is not loading the system all at once. Snowmelt catchments with salt-tolerant plants could be an appropriate solution in some cases. Strategies to reduce salt application and utilize alternatives to salt application should continue to be developed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1734/full