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The Response of Invertebrate Populations in Three Undisturbed Soils in Southwestern Ontario, Canada, to Variations in Local Soil Properties, Seasonal Changes, and Climate

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Three distinctly different undisturbed mature forested sites at the northern limits of the Carolinian forest system in Lambton County, Ontario, were examined to test the hypothesis that the abundance of each order of soil invertebrates captured is dependent on a unique set of soil properties, seasonal changes, and climate variations. Sixteen independent variables were recorded over five consecutive years. With the exception of rainfall, air temperature, and soil temperature, means of the measured variables differed significantly ($P < 0.05$) among soils. Twenty-eight taxa of invertebrates were captured, of which Acari, Collembola, and Nematoda were most abundant. Only the mean of total abundance and the mean abundance of Acari, Nematoda, and Haplotaxida differed significantly ($P < 0.05$) among soils. Haplotaxida was the only taxon in all three soils found to be influenced significantly ($P < 0.05$) by seasonal variation. The usual mid-summer minimum in the abundance of Haplotaxida was latest and most clearly defined in the clay soil and earliest and least clearly defined in the sand soil. Regression analysis showed that each site is sufficiently separated in the factor space observed that the abundance of each invertebrate taxon is dependent on different combinations of local variables. The hypothesis was rejected.

Key Words: micro-invertebrates; abundance; richness; soil properties; self-organization; climate; seasonal effect; Haplotaxida; Carolinian forest; Ontario; Canada

Quantitative data on the character of invertebrate populations in undisturbed mature soils and their dependence on the environmental and seasonal variables can provide a baseline against which changes resulting from forestry or agricultural activity or from proximity to industrial or urban centres can be evaluated. The scarcity of such data has long been recognized, as reported by Marshall et al. (1982) in an extensive review of the need for more research on Canadian soil arthropod populations. In a subsequent review, Marshall (2000) again noted the need for baseline studies to allow the impact of forest harvesting practices to be evaluated.

Recently, several studies have been undertaken to gather data on undisturbed soils. Addison et al. (2003) reported a multi-year study of invertebrates captured from ground litter on undisturbed forest floor on Vancouver Island, British Columbia. Soil and climate data were not reported. Also in British Columbia, Berch et al. (2006) reported data on the response of some soil invertebrates to enhanced levels of nitrogen in evergreen forest plots that had been clear-cut 30 years previously. A detailed study of the correlations of fungi with soil biota in the United Kingdom includes limited data on effects of seasonal variation and soil properties on selected invertebrates (Krivtsov et al. 2004). The relationships between some soil invertebrate populations and soil properties have been investigated by Hishi et al. (2006) in "natural" forests in Japan. Sylvain and Buddle (2010) studied oribatid mites in the soils of undisturbed hardwood forests in southern Quebec.

The Centre for Ecology and Hydrology in the United Kingdom has been conducting periodic intensive surveys of the properties of undisturbed soils and the indigenous invertebrate populations throughout the United Kingdom since 1978. The most recent report from this group (Emmet et al. 2010) matched invertebrate abundance and richness with chemical and physical properties, producing a comprehensive picture of the current status of invertebrate populations in several different environments and long-term trends. Seasonal effects were not examined.

To contribute to the development of a more complete understanding of the dynamics of invertebrate populations in undisturbed soils, I conducted a five-year study (2005–2009) of several variables affecting the abundance and richness of invertebrate populations in three distinctly different undisturbed Carolinian forest sites in rural Lambton County, Ontario. The results of this study apply only to the three sites selected (other sites in Lambton County where these soil types are found would be expected to exhibit generally similar population structures but differ in detail). The hypothesis for this study was that the abundance of each invertebrate taxon captured at these sites was related to a unique combination of local environmental variables.

Methods

Study sites

The study area is in southwestern Ontario in the northeastern corner of Lambton County near the shore

TABLE 1. Independent variables recorded at each sampling in Lambton County, 2005 to 2009, and their definition.

Time	Climate	Soil	Surface biomass
Sampling week number counted from the first week of January (WEEKNO)	Total rainfall at Thedford, Ontario, for the 14–day period prior to each sampling (mm) (RMM)	Soil temperature at the time of sampling (°C) (SOILTMP) Percentage of water content of the soil at the time of sampling by weight (W) Percentage of soil particles >0.05 mm by weight (WC) Percentage of soil particles <0.05 mm and >0.002 mm by weight (WM) Percentage of soil particles <0.002 mm by weight (WF)	Dry weight of ground litter (g/m^2) (DLIT) Percentage of water content of ground litter by weight (LITW)
	Mean air temperature at Thedford, Ontario, for the 14–day period prior to each sampling (°C) (AIRTMP)	Soil bulk density (kg/L) (SOILBLKD) pH (deionized water) (PH) Available phosphorus (Olsen) (µg/g) (SPUGG) Total phosphorus (Olsen) (µg/g) (PUGG) Total nitrogen (Kjeldahl) (µg/g) (NUGG) Total carbon (ignition) (µg/mg) (CUGMG)	

of Lake Huron (Figure 1). The underlying rock formation is reported by the Geological Survey of Canada (1969) to be part of the Middle Devonian Hamilton group, an argillaceous and crinoidal limestone. In this area, three types of soil, representative of 50% of the county, occur within a radius of 3 km: Brookston clay (Dark Grey Gleisolic, poorly drained), Brisbane loam (Grey Brown Podzolic, imperfectly drained), and Plainfield sand (Regosol, excessively drained) (Soil Survey of Lambton County 1979). The environment is rural, with the nearest urban/industrial centre (Sarnia) 50 km to the southwest. The study area is essentially free of urban/industrial stresses, except for long-range atmospheric deposition. The land varies from 5 to 20 m above mean lake level, including a line of dunes along the lake. A few small creeks drain to the north.

Level sites, 50 m^2, were selected for sampling in forests growing in the above soil types. On the UTM grid, the centres of these sites are as follows:

Plainfield sand	4785380 northing	427425 easting
Brookston clay	4783420 northing	426610 easting
Brisbane loam	4781325 northing	424375 easting

The loam site is near plot number of the Ontario Hardwood Forest Survey (4780990 northing, 424965 easting), as reported by McLaughlin et al. (2000).

Tree ring counts showed the soil in each of the sites chosen had not been disturbed for at least 200 years. The loam site differed from the clay and sand sites in that it had a more dense understory of shrubs and vines. All three sites exhibited moder type humus formation, as described by Green et al. (1993).

Total rainfall and mean air temperature data for the 14-day period preceding each sampling were obtained from the Environment Canada weather station about 6 km to the southeast at Thedford (Environment Canada 2005–2009*).

Field methodology and processing of soil biota

Lists of the abbreviations used in the following text, figures and tables and their definiitions are provided in Table 1 and Table 4. A set of soil samples was collected at each site of 50 m^2 once in the spring (weeks 21–23 counting from the first week of January), once in the summer (weeks 32–34), and once in the autumn

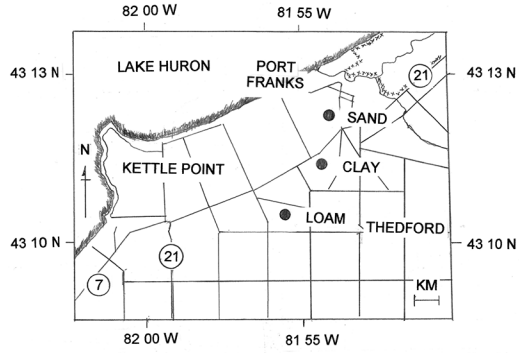

FIGURE 1. Sampling sites in Lambton County, Ontario, 2005 to 2009.

(weeks 42–44) of 2005–2009 inclusive (15 samples per soil type, 45 samples in total). In 2005 and 2008, each site was surveyed to establish the genera of trees present.

Before invertebrate sampling was done, ground litter and growing vegetation were removed down to the mineral soil from a randomly selected sampling plot of 1 m^2 and placed in a sealed tared plastic bag. The air-dried weight of the collected material is considered to be a measure of the above-ground biomass present. Each plot sampled was flagged to prevent resampling at the same point.

The ground litter samples were weighed as taken and then dried to a constant weight at room temperature to estimate the above-ground biomass present and the water content.

A large sample, 26 cm in diameter and 5 cm deep, was taken within each cleared sampling plot of 1 m^2 and placed in a sealed, tared plastic bag. This sample was weighed as taken to estimate the soil bulk density. Subsamples were removed from this sample to estimate water content, particle size distribution, and chemical composition. In 2007, at each sampling, two supplementary small core samples were taken to evaluate the sampling and analytical error of the chemical analyses. Soil temperature was measured at each sampling.

Water content was measured by drying two subsamples of 50–60 g each to a constant weight at 120°C.

Soil particle size distribution was estimated using the hydrometre method described by Day (1965). Chemical analyses for total nitrogen (Kjeldahl), total carbon (ignition), total and available phosphorus (Olsen), and pH (deionized water) were performed by Agriculture and Agri-Food Canada (Harrow, Ont.). The analytical procedures used were those of Carter and Gregorich (2008).

From each cleared plot of 1 m^2, eight soil core samples, 5 cm in diameter and 5 cm deep, were taken at each season over the five-year period. These were held in a cooled container for the invertebrate extraction process, which was started within four to six hours after the samples were collected. Annelid worms were extracted from a closely adjacent plot 50 cm^2 using the hot mustard technique (Clapperton et al. 2008).

Four of the small core samples were extracted separately to estimate the abundance of Nematoda present in each plot using the Baerman funnel technique described by Shurtleff and Averre (2000). The remaining four small cores were used separately to extract other micro-invertebrates using the Merchant-Crossley high-gradient extractor, as modified by Norton (1986). For both sets of four core samples, extractions were run for seven days under temperature control (25–35°C) using 7-watt incandescent bulbs as the heat source in insulated cells. The Baerman extractions were run using chlorine-free aerated water. In the case of the high-gradient extractions, the invertebrates were captured in a water solution (0.05% vol.) of liquid detergent.

All the organisms larger than 0.1 mm were identified to the order level (Collembola, and Haplotaxida were identified to the family level) and counted under water using a stereo microscope at 10× and 40× magnification. Several keys were used (Borror and White 1970; Barnes 1974; Reynolds 1977; Bland and Jaques 1978; Arnett et al. 1980; Chu and Cutkomp 1992).

Invertebrates of each taxon were preserved separately in a 70% isopropanol/water solution containing 0.2% glycerin and stored in screw-topped glass containers. This archive has been deposited in the laboratories of Agriculture and Agri-Food Canada at Harrow, Ontario.

Data processing

A field study of soil invertebrates is usually constrained by the existing values of the many independent variables in the factor space under examination, namely the physical, chemical, and climate characteristics of the locality. The investigator cannot set the values of the independent variables at the levels most useful for identifying the dominant effects on the dependent variables. Under such conditions, analysis of variance (ANOVA) and regression analysis are the most helpful techniques for determining differences and trends, which may then be examined under more controlled conditions. However, for all types of analysis, care must be taken to separate cause and effect from mere correlation.

Statistical analysis was performed using software developed by the Centres for Disease Control and Prevention in Atlanta, Georgia (EPI6, version 6.04d), and Systat 11. Statistical significance was set at the 95% confidence level for analysis of variance. For the regressions, significance was claimed if the 95% confidence limits of the coefficients for the independent variables did not include zero.

For multiple regressions, relative significance of each independent variable was established using the forward selection procedures described by Christensen (2001) and Draper and Smith (1981). Backward selection was then used to develop any significant first order multiple regressions using those independent variables with F values greater than 1.0. Second-order models were tested if the data showed strong curvature.

Draper and Smith (1981) suggest, with reference to work by G. E. P. Box and J. M. Wetz, that the regression F should exceed the value in the F distribution table for 95% confidence at the appropriate degrees of freedom by a factor of at least four if the correlation is to be considered a satisfactory predictor. The regression F values that meet this criterion are identified in the tables. The partial F test noted in the tables is a measure of the relative power of multiple significant variables in accounting for the variation in the dependent variable.

A copy of the complete database for this study is available from the author in several commonly used software systems.

Results

Soil properties

The distribution of tree genera in the three sample sites is shown in Figure 2. *Prunus, Tilia, Populus, Acer,*

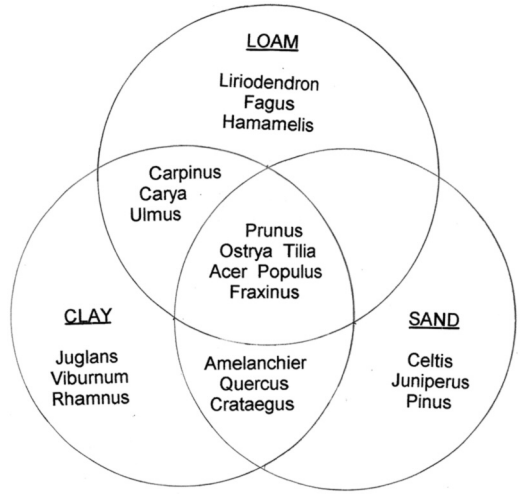

FIGURE 2. Genera of trees on the sampling sites in Lambton County, 2005 to 2009.

Ostrya, and *Fraxinus* were common to all three. *Pinus, Juniperus,* and *Celtis* were found only in the sand site. *Liriodendron, Fagus,* and *Hamamelis* were found only in the loam site, while *Juglans, Rhamnus,* and *Viburnum* occurred only in the clay site. The clay site harboured the greatest number of genera.

The spring-to-autumn variation in climate causes a closely similar weekly variation in soil temperature in all three sites. Figure 3 shows the variation for all three sites combined. The mean soil temperature for the spring samplings was 15°C, for summer was 19°C, and for autumn was 10°C.

The means and the associated standard error of the physical and chemical properties of the soils at each site are recorded in Table 2. For those properties showing significant differences between means ($P < 0.05$), the observed scatter is illustrated in Figures 4a to 4e. Analysis of variance showed that, all soil properties except for total rainfall fourteen days prior to sampling, mean air temperature fourteen days prior to sampling and soil temperature at the time of sampling showed that significant differences ($P < 0.05$) existed between sample plots within each site.

Many of the variables measured to establish the character of the soils at the sampling sites were significantly correlated ($P < 0.05$). By definition, some have correlation coefficients of 1.0, for example the percentage of soil particles >0.05 mm, the percentage of soil particles <0.05 mm and >0.002 mm, and the percentage of soil particles <0.002 mm. Other variables

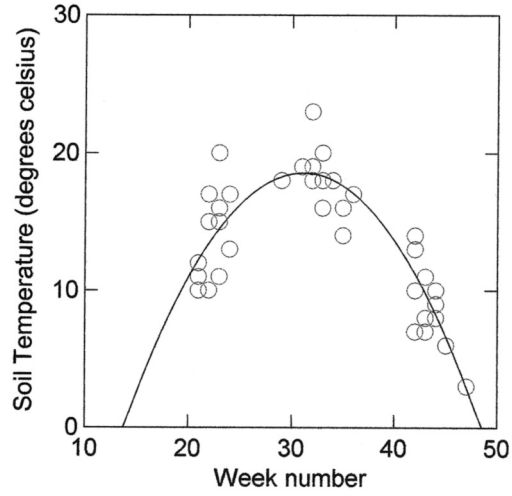

FIGURE 3. Soil temperature at the time of sampling in Lambton County, 2005 to 2009.

TABLE 2. Mean and standard error of climate and soil properties in Lambton County, 2005 to 2009, by soil type.

	Brookston clay			Brisbane loam			Plainfield sand		
	n	x̄	se (+/–)	n	x̄	se (+/–)	n	x̄	se (+/–)
Total rainfall (mm)*	15	36.6	7.7	13	27.9	6.3	14	39.5	7.6
Mean air temperature (C)*	15	13.6	1.6	13	16.4	1.3	14	15.4	1.8
Soil Temperature (C)*	15	14.0	1.4	14	14.3	0.8	14	13.2	1.2
Percentage of water in soil by weight#	15	31.8	2.3	14	23.5	1.9	15	17.1	1.7
Percentage of soil particles >0.05 mm by weight#	15	55.0	1.5	14	78.0	1.2	15	89.2	1.4
Percentage of soil particles <0.05 mm and >0.02 mm by weight#	15	30.5	2.0	14	19.5	1.0	15	10.4	1.3
Percentage of soil particles <0.02 mm by weight#	15	14.4	2.3	14	3.1	0.7	15	0.3	0.1
Soil bulk density (kg/L)	15	1.255	0.05	14	1.192	0.04	15	0.910	0.05
pH	15	6.79	0.10	14	6.30	0.18	15	5.65	0.19
Available phosphorous (Olsen) (µg/g)	15	13.9	1.4	14	6.4	0.92	15	9.7	1.4
Total phosphorous (Olsen) (µg/g)	15	838	69.2	14	341	50.9	15	180	18.4
Total nitrogen (Keldjahl (µg/g)	15	5178	350	14	3140	287	15	2378	295
Total carbon (ignition) (µg/mg)	15	80.6	4.82	14	54	3.79	15	57.8	7.49
Dry weight of ground litter (g/m^2)	15	692	58	14	1049	94	15	875	51
Percentage of water in ground litter by weight	15	43	3	14	30	4	15	38	4
Ratio of carbon to nitrogen (CNRATIO)	15	15.7	0.48	14	17.8	1.09	15	24.0	0.68
Ratio of carbon to total phosphorous (CPRATIO)	15	104	9.0	14	177	13.5	15	325	29.5
Ratio of carbon to available phosphorous (CSPRATIO)	15	6468	691	14	10050	1431	15	6301	534
Ratio of nitrogen to total phosphorous (NPRATIO)	15	6.64	0.56	14	10.0	0.66	15	13.4	1.08
Ratio of nitrogen to available phosphorous (NSPRATIO)	15	415	42.3	14	573	83.1	15	259	18.4
Ratio of total phosphorous to available phosphorous (PSPRATIO)	15	65.9	8.2	14	56.4	5.2	15	21.2	2.5

* ANOVA shows means do not differ significantly
\# Analysis run in duplicant or triplicate

Calculated variables: CNRATIO = (total carbon*1 000)/total nitrogen: CPRATIO = (total carbon*1 000)/total phosphorous; CPRATIO = (total carbon*1 000)/total phosphorous; CSPRATIO = (total carbon*1 000)/available phosphorous; NPRATIO = total nitrogen/total phosphorous; NSPRATIO = total nitrogen/available phosphorous; PSPRATIO = total phosphorous/available phosphorous.

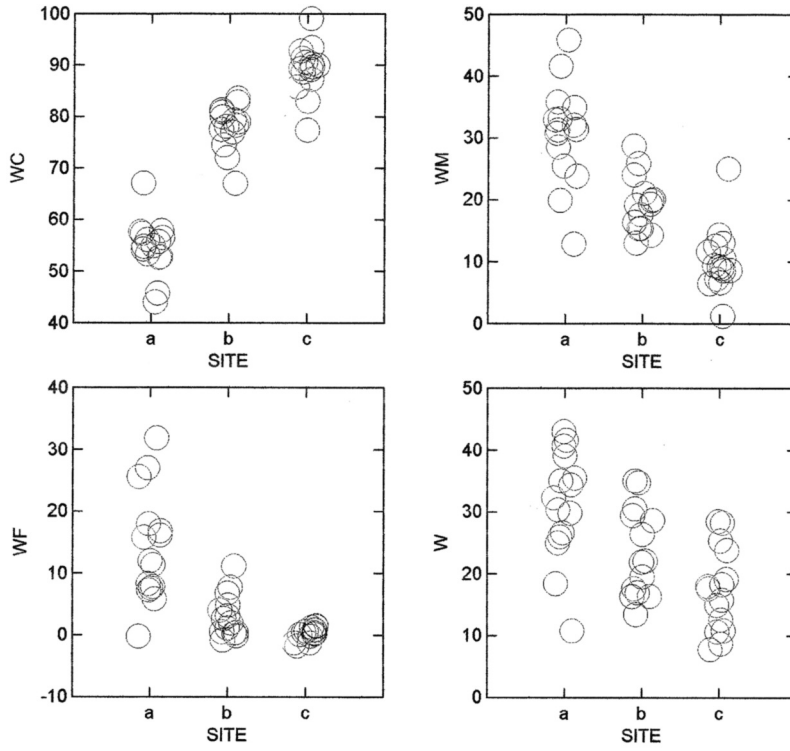

FIGURE 4a. Soil properties at each sampling site. WC = weight % of soil particles > 0.05 mm. WM = weight % of soil particles < 0.05 mm and > 0.002 mm. WF = weight % of soil particles < 0.002 mm. a = clay. b = loam. c = sand.

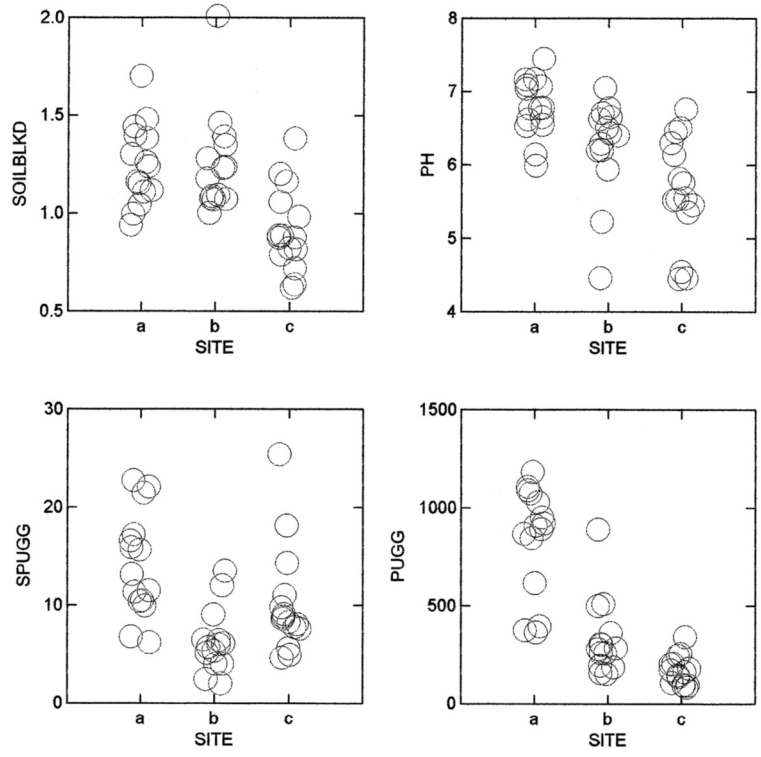

FIGURE 4b. Soil properties at each sampling site. SOILBLKD = soil bulk density (kg/L). PH= pH. SPUGG = available phosphorous (μg/g). PUGG = total phosphorous (μg/g). a = clay. b = loam. c = sand.

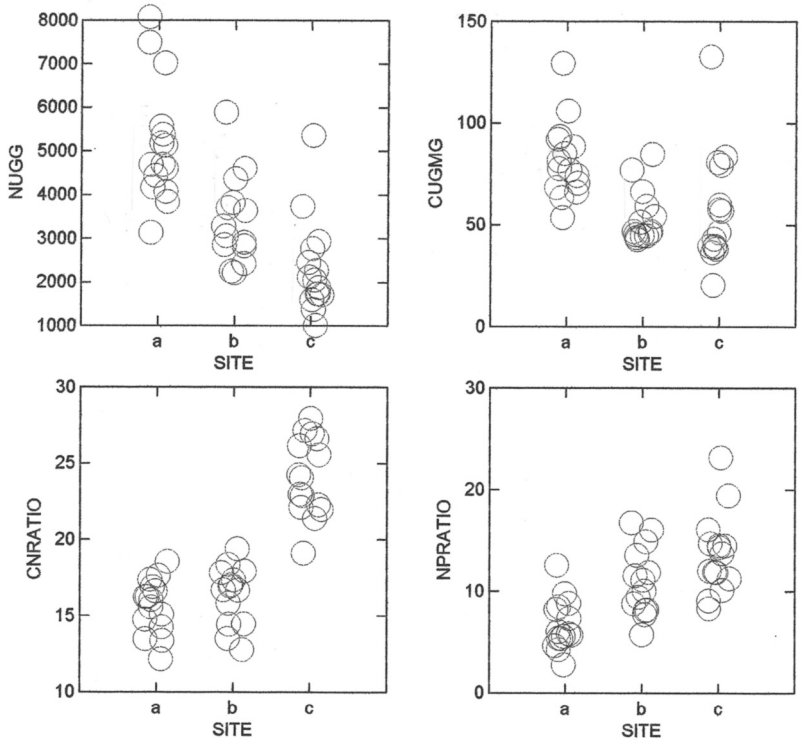

FIGURE 4c. Soil properties at each sampling site. NUGG = total nitrogen (µg/g). CUGMG = total carbon (µg/mg). CNRATIO = (CUGMG*1 000)/NUGG. NPRATIO = NUGG/PUGG. a = clay. b = loam. c = sand.

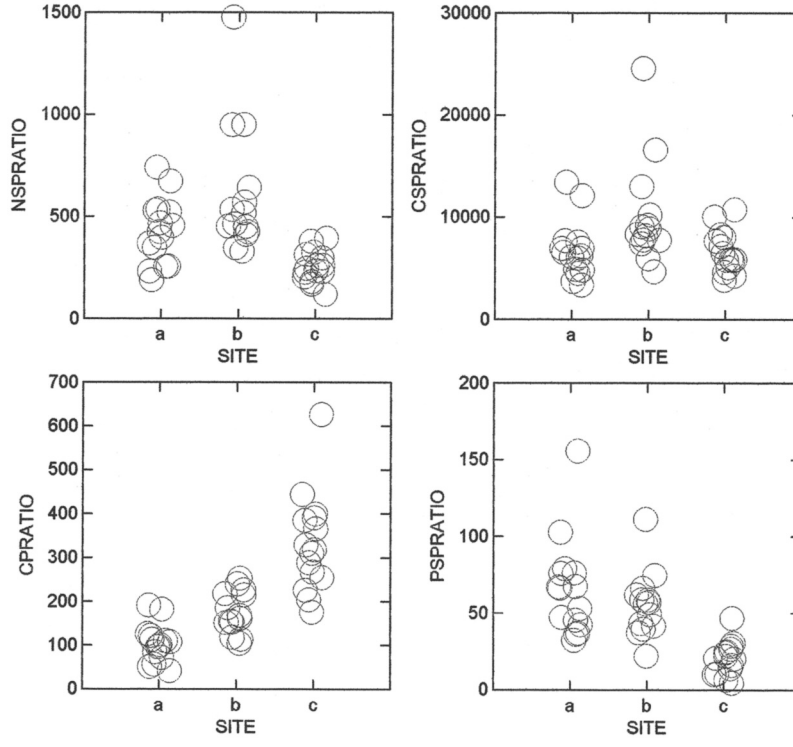

FIGURE 4d. Soil properties at each sampling site. NSPRATIO = NUGG/SPUGG. CSPRATIO = (CUGMG*1 000)/SPUGG. CPRATIO = (CUGMG*1 000)/PUGG. PSPRATIO = PUGG/SPUGG. a = clay. b = loam. c = sand.

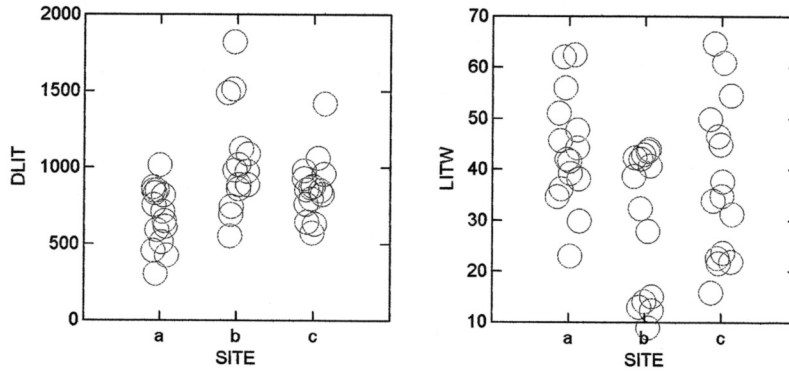

FIGURE 4e. Soil properties at each sampling site. DLIT = dry weight of ground litter (g/m^2). LITW = water content of ground litter (weight %). a = clay. b = loam. c = sand.

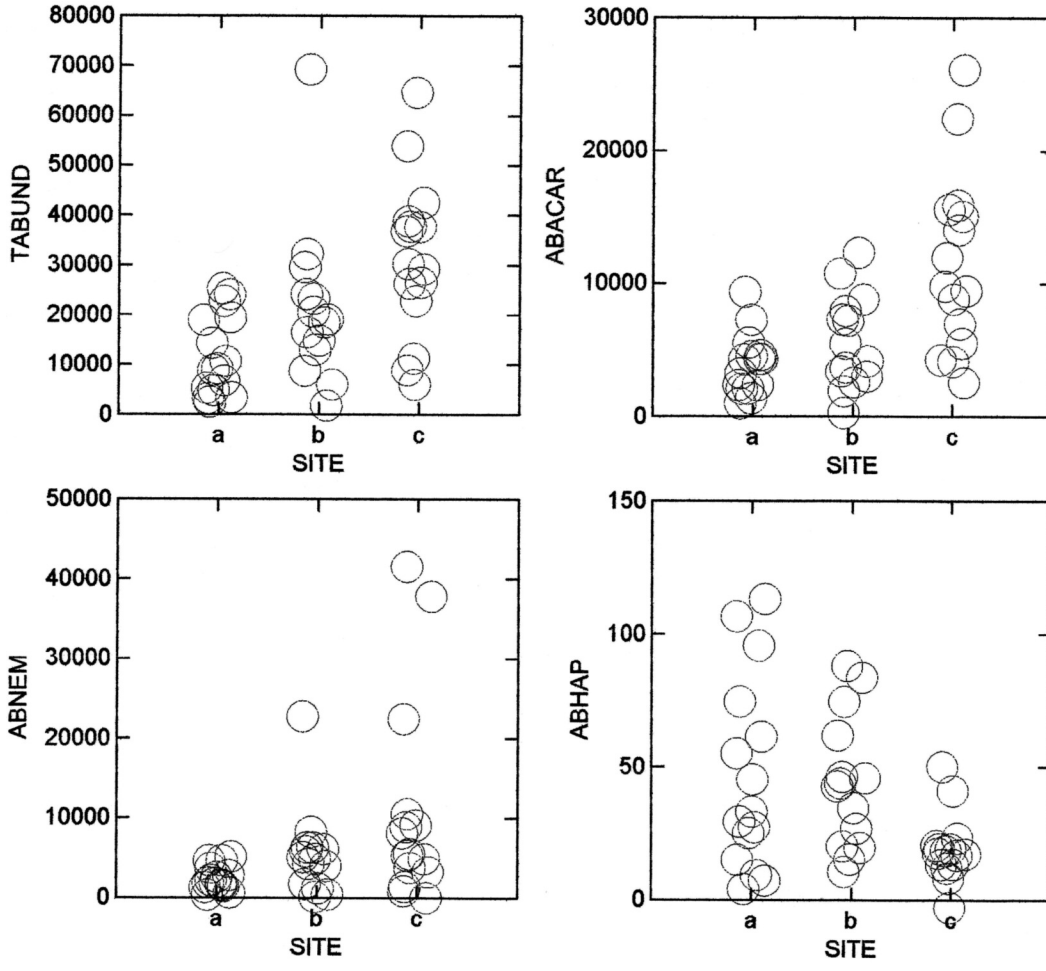

FIGURE 5. Invertebrate abundance at each sampling site. TABUND = total organisms/m^2. ABACAR = Acari/m^2. ABNEM = Nematoda/m^2. ABHAP = Haplotaxida/m^2. a = clay. b = loam. c = sand.

TABLE 3. Statistical details of significant ($P < 0.05$) regressions for soil properties in Lambton County, 2005 to 2009, all sites combined. Partial F in parentheses. Coefficients are rounded to two significant digits.

	Dependent variables						
	Soil temperature	Percentage of water content of the soil at the time of sampling by weight	Percentage of soil particles >0.05 mm by weight	Soil bulk density (kg/L)	pH	Total carbon (ignition) (µg/mg)	Dry weight of ground litter (g/m^2)
Week number	+3.8 (100)	–	–	–	–	–	–
Week number^2	−0.06 (110)	–	–	–	–	–	–
Total rainfall	+0.10 (12)	–	–	–	–	–	–
Mean air temperature	–	−0.35 (6)	–	–	–	–	–
Percentage of soil particles >0.05 mm by weight	–	–	–	–	–	+0.56 (16)	–
Percentage of soil particles <0.002 mm by weight	–	+0.36 (6)	–	+0.020 (27)	–	–	–
Soil bulk density (kg/L)	–	+12 (8)	–	–	–	–	–
Available phosphorus (Olsen) (µg/g)	–	–	–	–	–	+1.4 (17)	−49 (19)
Total phosphorus (Olsen) (µg/g)	–	–	−0.03 (65)	–	–	–	–
Total nitrogen (Kjeldahl) (µg/g)	–	–	–	–	–	+0.013 (72)	–
Total carbon (ignition) (µg/mg)		+0.17 (16)	–	–0.0042 (10)	–	–	+8.4 (10)
Percentage of water content of ground litter by weight	–	–	–	–	–	–	−6.0 (6)
Ratio of carbon to nitrogen (CNRATIO)	–	–	+1.0 (13)	–	–	–	–
Ratio of carbon to total phosphorus (CPRATIO)	–	–	–	–	−0.0042	–	–
Ratio of total phosphorus to available phosphorus (PSPRATIO)	–	–	–	–	–	–	−3.1 (5)
Constant	−41	−1.2	+68	+1.3	+7.1	−38	+1200
r^2	0.78	0.76	0.82	0.40	0.44	0.86	0.45
F	72[1]	22[1]	91[1]	14	33[1]	82[1]	8
n	43	43	43	43	43	43	43

[1]Meets Box–Wetz criterion for prediction

exhibited significant correlations, with low correlation coefficients caused by unmeasured variables or analytic error.

When the data for all three sites were combined, the significant correlations ($P < 0.05$) between soil properties (Table 3) were found. Some of these correlations can be readily rationalized. Observed relationships among the percentage of soil particles >0.05 mm, pH, and the dry weight of ground litter as dependent variables are probably mere correlations, while those for water content and soil bulk density are probably cause and effect. The correlation between total carbon as the dependent variable and total nitrogen, available phosphorus, and the percentage of soil particles <0.05 mm is noteworthy and is discussed further below.

The surveys reported by the Centre for Hydrology and Ecology in the United Kingdom (Emmett et al. 2010) cover a factor space much larger than that of this study in terms of the range of soil types examined. The soils in my study are most closely similar to the woodland and grassland soils in the United Kingdom. However, the available phosphorus levels in the soils in Lambton County are 20% to 50% lower.

Invertebrate populations

The invertebrates found are listed in Table 4 together with an indication of their presence in the three soils in approximate order of decreasing abundance. Of the 28 taxa found, 21 occurred in all three soils. Two orders of Acari and seven families of Collembola were

TABLE 4. Frequency of occurrence of organisms found in Lambton County, 2005 to 2009, in approximate order of decreasing abundance. "+" = present.

Taxon	Brookston clay	Brisbane loam	Plainfield sand
Abundance of taxa >1000/m^2			
Acari	+	+	+
Trombidiformes	+	+	+
Sarcoptiformes	+	+	+
Collembola	+	+	+
Onchyuridae	+	+	+
Isotomidae	+	+	+
Hypogastruridae	+	+	+
Poduridae	+	+	+
Entomobryidae	+	+	+
Sminthuridae	+	+	+
Neelidae	+	+	+
Nematoda	+	+	+
Abundance of taxa <1000/m^2 and >300/m^2			
Diptera	+	+	+
Coleoptera	+	+	+
Protrura	+	+	+
Abundance of taxa <300/m^2			
Pauropoda	+	+	+
Haplotaxida	+	+	+
Tardigrada	+	+	+
Diplura	+	+	+
Hymenoptera	+	+	+
Aranea	+	+	+
Plecoptera	+	+	+
Symphyla	+	+	+
Ephemeroptera	+	+	+
Hemiptera	+	+	+
Pseudoscorpiones	+	+	+
Juliforma	+	+	+
Blattodea	+	+	+
Isopoda	+	+	+
Geophilomorpha	+	+	+
Copepoda		+	
Homoptera	+	+	
Stylommatophora		+	
Orthoptera		+	
Thysanura			+
Lepidoptera			+
Neuroptera			+

identified. All Haplotaxida were found to be Lumbricidae.

Table 5 records mean abundance and the associated standard error for the most frequently captured invertebrates by soil type. Total abundance and richness (total number of taxa) are also included. Of those listed, only the mean abundance for the Acari, Nematoda, and Haplotaxida and mean total abundance exhibited significant differences ($P < 0.05$) among soils. For those means exhibiting significant differences ($P < 0.05$), the variation in abundance observed among sites and within sites is illustrated in Figure 5. The sand site showed the highest abundance for all but Haplotaxida.

Significant correlations ($P < 0.05$) were found between the mean abundance of several invertebrate taxa and soil properties, seasonal changes, and climate variables. Details of these correlations for those taxa found to have a significantly different ($P < 0.05$) mean abundance in the three soils are recorded in Table 6. Four can be considered robust relationships, having correlation coefficients (r^2) greater than 0.60. Two of the Haplotaxida correlations meet the Box–Wetz criterion for prediction. There is, however, little consistency in the pattern of independent variables with the exception of Haplotaxida. For those correlations, week number was the dominant independent variable.

Figure 6 illustrates the variation of Haplotaxida abundance with week number (WEEKNO) for the three sites separately, as derived by second-order least squares modelling. The equations for these relationships are as follows:

Clay: Haplotaxida =
$(-29.7 * \text{WEEKNO}) + (0.409 * \text{WEEKNO}^2) + 551$
Loam: Haplotaxida =
$(-9.10 * \text{WEEKNO}) + (0.137 * \text{WEEKNO}^2) + 185$
Sand: Haplotaxida =
$(-6.20 * \text{WEEKNO}) + (0.100 * \text{WEEKNO}^2) + 107$

The regressions for the clay and sand sites are significant ($P = 0.05$), but the regression for the loam site is not. The minima of abundance for the series clay/loam/sand occur at week numbers 36/33/31, respectively, and become more extended. The minima of abundance at those week numbers are 12/34/11, respectively.

Discussion

The data set developed in this study should be considered generally representative of similar soils in Lambton County. With the exception of the ongoing survey conducted by the Centre for Ecology and Hydrology in the United Kingdom, the available literature on undisturbed soils is focused on small regions in the total factor space affecting the dynamics of indigenous invertebrate populations. My study is intermediate in this regard.

TABLE 5. Abundance (mean number of organisms/m^2 ± standard error) and richness (total number of taxa ± standard error) of the most frequently captured invertebrate taxa in Lambton County, 2005 to 2009.

	Brookston Clay (n = 15)		Brisbane Loam (n = 14)		Plainfield Sand (n = 15)	
Taxon	$\bar{x}$	se (+/-)	$\bar{x}$	se (+/-)	$\bar{x}$	se (+/-)
Acari						
Trombidiformes	877	214	3 964	914	7 013	1 261
Sarcoptiformes	2 823	524	1 832	362	4 523	907
Subtotal*	3 699	656	5 795	1 056	11 537	1 727
Collembola						
Onchiyuridae	1 105	474	1 559	500	1 192	548
Isotomidae	1 911	734	1 061	575	1 113	373
Hypogasruridae	1 403	475	1 841	629	2 402	767
Poduridae	123	35	216	115	430	219
Entomobryidae	246	94	113	57	333	176
Neelidae	298	252	19	19	456	367
Sminthuridae	342	133	38	38	184	82
Subtotal	4 813	982	4 866	779	5 742	860
Nematoda*	2 043	411	5 532	1 566	10 713	3 306
Diptera	701	221	648	240	833	160
Coleoptera	88	38	188	71	324	159
Protrura	105	68	658	292	430	192
Pauropoda	35	20	160	84	254	147
Haplotaxida*	48	3	44	7	18	3
Total abundance*	12 496	2 001	21 094	4 454	32 157	4 459
Richness (total number of taxa captured)	8.4	0.6	9.5	0.4	9.5	0.7

* ANOVA shows these means differ significantly ($P < 0.05$)

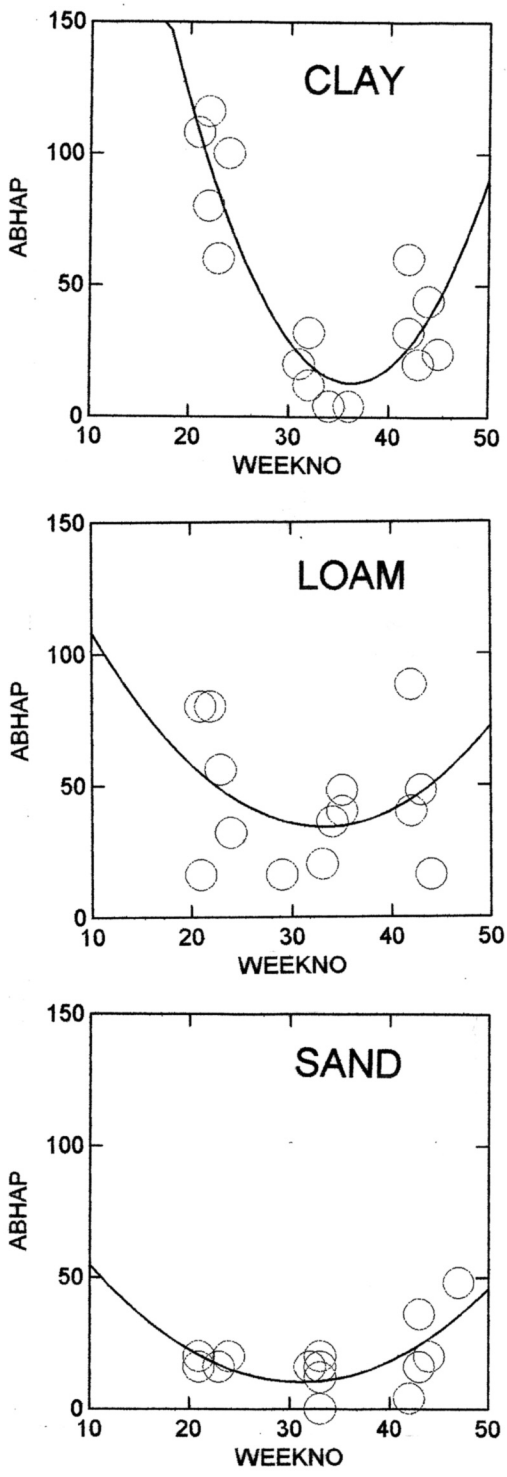

FIGURE 6. Seasonal variation in Haplotaxida abundance in the three soils in Lambton County, 2005 to 2009. ABHAP = Haplotaxida/m^2. WEEKNO = Sampling week number counting from the first week of January.

Soil properties

As noted above, the mean climate data reflect average conditions at the Environment Canada weather station at Thedford for spring, summer, and autumn and therefore do not differ significantly ($P < 0.05$). However, matching the weather data for the two-week period prior to each sampling with the sampling data provides a measure of the effect of local weather on soil and invertebrate populations. Furthermore, since the sampling sites are so close together, it is not surprising that the soil temperature profiles from spring to autumn are virtually identical. Nevertheless, the means of most soil properties at these sites (Table 2) differed significantly ($P < 0.05$).

Analysis of variance for those soil samples analyzed in duplicate or triplicate showed that statistically significant ($P < 0.05$) differences existed between sampling of plots 1 m^2 within each sampling site of 50 m^2, as illustrated in Figures 4a to 4d. Therefore, when conducting studies in undisturbed soils to determine the relationship between soil properties and invertebrate populations, it is necessary to measure soil properties in close proximity to the samples for invertebrate data.

The robust correlation found between the carbon content of the soil as the dependent variable and nitrogen, available phosphorus, and particle size distribution (Table 3) is of interest, since it suggests that mature undisturbed soils can develop a complicated, predictable balance of chemical properties over time. Higher levels of nitrogen (NUGG) and available phosphorus (SPUGG) in coarse soils were associated with higher total carbon content (CUGMG). Such a situation is difficult to rationalize. Exploring this relationship further revealed that, when the sites were examined separately, the relationships for the clay and loam sites were very similar, with only nitrogen (NUGG) as the significant ($P < 0.05$) variable. When the data for these sites were combined, the relationship was as follows:

CUGMG = (0.01 · NUGG) + 16.4;
correlation coefficient: 0.92;
$F = 142$ (meets the Box–Wetz criterion for prediction);
total degrees of freedom: 28.

For the sand soil, the relationship was:

CUGMG = (0.02 · NUGG) − 1.4;
correlation coefficient: 0.96;
$F = 314$ (meets the Box–Wetz criterion for prediction);
total degrees of freedom: 14.

Nitrogen is twice as potent in increasing the carbon content in the sand soil than it is in either the loam or the clay soil. This effect results in the development of a dense mat of the roots of small shrubs, weeds, and grass in the top 5 cm of sand. This mat is absent in clay and loam. The acidic nature of all three soils precludes the presence of carbonates, so the carbon content is present as decomposing ground litter or actively growing ground cover. The sand soil responds to higher levels of nitrogen by developing actively growing low ground cover more readily than either loam or clay

TABLE 6. Statistical details of significant (P < 0.05) correlations between invertebrate abundance and soil properties, climate, and seasonal variables, presented by taxon and total abundance. Coefficients are rounded to two significant digits. Only those taxa showing significant (P < 0.05) differences in means are shown.

Acari			
Clay:	(-140*W) + (200*WC) - 2 800		
	r^2 = 0.56	F = 8	n = 14
Loam:	(300*WEEKNO) - 3 700		
	r^2 = 0.42	F = 9	n = 13
Sand:	no significant correlation		
All sites combined:	-(7 300*SOILBLKD) + (-6.1*PUGG) - 18 000		
	r^2 = 0.31	F = 9	n = 43
Nematoda			
Clay:	no significant correlation		
Loam:	(1 100*AIRTMP) + (3 600*SPUGG) + (-75*PUGG) - 9 300		
	r^2 = 0.68	F = 6	n = 12
Sand:	(-11 000*PH) + 71 000		
	r^2 = 0.35	F = 7	n = 14
All sites combined	(-6 100*PH) + 44 000		
	r^2 = 0.27	F = 16	n = 43
Haplotaxida			
Clay:	(-31*WEEKNO) + (0.42*WEEKNO^2) + (0.34*RMM) + (24*PH) + (43*SOILBLKD) + (-0.25PSPRATIO) + 360		
	r^2 = 0.97	F = 37#	n = 14
Loam:	no significant correlation		
Sand:	(-8.0*WEEKNO) + (0.12*WEEKNO^2) + (0.26*RMM) + 130		
	r^2 = 0.81	F = 14#	n =13
All sites combined:	(-18*WEEKNO) + (0.26*WEEKNO^2) + (18*PH) + 210		
	r^2 = 0.43	F = 10	n = 43
Total abundance			
Clay:	(2 900*CNRATIO) + (-430*W) - 20 000		
	r^2 = 0.63	F = 10	n = 14
Loam:	no significant correlation		
Sand:	no significant correlation		
All sites combined:	(-3.3*NUGG) + (-7 000*PH) + 77 000		
	r^2 = 0.32	F = 10	n = 43

Meets the Box-Wetz criterion for prediction

soil. Gunderson et al. (1998) reported a similar effect in sandy soils in northern Europe.

Invertebrate populations

Total abundance and the abundance of Acari and Nematoda increased across the series clay/loam/sand (Table 5 and Figure 5). For Haplotaxida, that trend was reversed. This result generally supports the findings of Hishi et al. (2008) and Sylvain et al. (2010)—that high density of fine root structure and conifer forests generally favour higher abundance of micro-Arthropoda.

The data set for organisms showing significant ($P < 0.05$) differences between mean abundance of taxa and mean total abundance in the three soils was used to develop correlations (Table 6). Those for Acari show this taxon exhibited no consistent pattern of dependence on any particular set of variables, although a coarse, dry soil seemed to be favoured. This finding is supported by the control data reported by Berch et al. (2006), who showed a higher abundance of Acari in coarse, acidic soil with a lower nitrogen to available phosphorus ratio.

The correlations for Nematoda abundance showed a preference for more acidic soils, but again there was no clear pattern.

Abundance of Haplotaxida showed a consistent seasonal dependence and a positive relationship with pH and rainfall. The correlations for the clay and sand soils are both significant ($P < 0.05$) and robust. The significant ($P < 0.05$) positive effect of total rainfall for the 14-day period preceding sampling (as opposed to soil moisture at the time of sampling) supports the finding of Baker (1998), who reported that annual rainfall was a critical positive variable for Haplotaxida abundance in agricultural soils.

In the three soils studied here, the consistent trend to earlier and more extended minima in the abundance of Haplotaxida across the series of clay/loam/sand (Figure 6) suggests a relationship between the timing of the diapause behaviour of various Lumbricidae or some other seasonal variation not investigated in this study. Millican et al. (2007) reported that different soil compositions exhibit minima in Haplotaxida abundance at

different times in predominantly clay soils with different histories of disturbance. Both Millican et al. and Pothoff et al. (2008) reported a positive effect of pH.

If the seasonal soil temperature profiles of the three soils had been different, it is probable that soil temperature would appear as a significant ($P < 0.05$) variable (Edwards et al. 1972). It is noteworthy that the carbon to nitrogen ratio for all three soils is higher than the optimal range for Haplotaxida reported by Lee (1985).

Data reported Berch et al. (2006) and Emmet et al. (2010) for invertebrate abundance in conifer-forested sandy soil in British Columbia and Great Britain respectively exemplify the range of abundance commonly found. The abundance of Acari and Collembola combined in the British Colunbia soil is about 95 000/m^2. In the Great Britain soil the comparable abundance is about 3 000/m^2 . For Lambton County, this abundance is intermediate at about 18 000 /m^2. Even allowing for the inevitable differences in sampling and processing, such a variation indicates that the organisms have been exposed to entirely different locations in the multivariate factor spaces of soil and climate.

The lower correlation coefficients for the relationships derived for the combined data (Table 6) result in part from variation introduced when the effects of different soil environments are introduced into the calculations.

The complexity of the relationships between soil properties and the dynamics of invertebrate population is illustrated by the response surfaces for richness and abundance in Figure 7 and Figure 8. In these figures, data for all three soils have been combined to produce a least squares approximation at maximum tension. The independent variables in Figure 7 are physical properties of the soil (percentage of coarse particles and soil temperature) selected from the list of properties as being orthogonal and therefore distributed most evenly in the factor space. In Figure 8, the independent variables are chemical properties of the soil (pH and available phosphorus) selected using the same criterion. The irregular character of these surfaces shows why calculation of simple first- or second-order approximations, even with several independent variables, achieves statistical significance ($P < 0.05$) with difficulty.

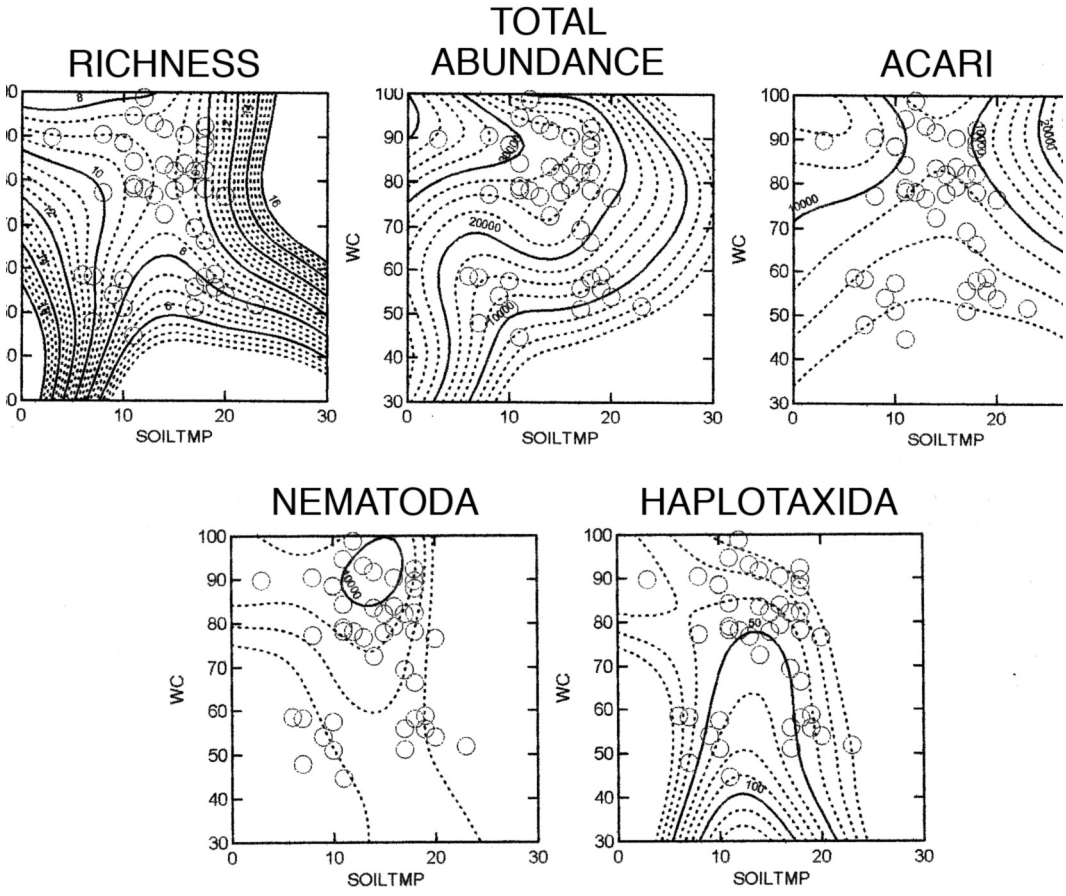

FIGURE 7. Response surfaces for richness and abundance in relation to two physical properties of the soils. WC = percentage of soil particles >0.05 mm by weight. SOILTMP = soil temperaure at the time of sampling (Celsius).

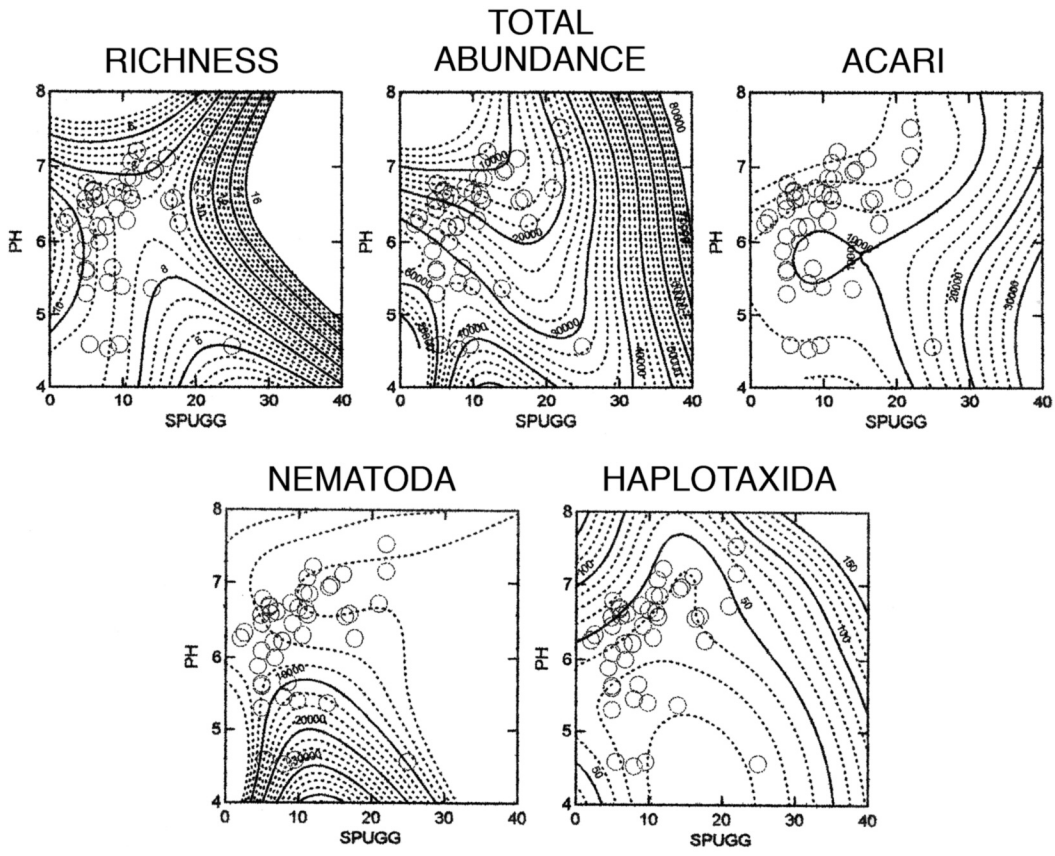

FIGURE 8. Response surfaces for richness and abundance in relation to two chemical properties of the soils. PH = pH. SPUGG = available phosphorous (Olsen) (μg/g).

It is apparent that the three soils examined here are sufficiently separated in the multivariate factor space that differences in the balance of independent variables are critical in changing the response of richness and abundance of individual invertebrate taxa. Krivtsov et al. (2004) observed a similar effect in forested soils in the United Kingdom. The absence of an independent variable in the correlations recorded in Table 6 does not mean that it is unimportant. For a soil occupying another location in the factor space, it might have a significant effect. Furthermore, the high level of adaptability of soil invertebrates is evident from the fact that, in all three distinctly different soils, most of the taxa found were present in all three (Table 4).

Finally, the finding of statistically significant ($P < 0.05$) correlations (Table 6) is evidence, in the three soils studied here, of the self-organization tendency found in wild populations (May 1991). Such systems can oscillate in abundance over time between a chaotic state and an ordered state. Many populations found in this study were in an ordered state for a period of five years over an area of 50 m^2 in at least one soil.

The hypothesis that abundance of each taxon of invertebrates captured is dependent on a unique set of soil properties, seasonal variables, and climate was not supported by this study.

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