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Soil nematode genera that predict specific types of disturbance

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ABSTRACT

Nematode community indices would be more cost-effective and interpretable if ambiguous genera were removed and indices reduced to only genera with known sensitivity or response to specific types of disturbance. The objective of the present study was to perform a methodical multivariate analysis of existing datasets of high quality and enumerate the genera that respond universally consistent to a specific type of disturbance, treatment, or management worldwide. We collected 20 sources of original data from land used for agricultural purposes, whether cropland, livestock grazing or fruit orchard with manipulated treatments in cultivation, inorganic or organic fertilization or contaminated by heavy metals. Canonical correspondence analysis was performed to determine the effect of disturbance type on the composition of soil nematode communities. Genera that performed consistently in a single direction and across at least two seasons were identified. Briefly, cultivation reduced abundances of *Diphtherophora*, *Prismatolaimus* and *Tylenchorhynchus*. Application of synthetic chemical fertilizers reduced numbers of *Plectus*. Application of organic fertilizers resulted in increased numbers of *Cruznema*, *Mesorhabditus*, *Mesodorylaimus* and *Nygolaimus*. No genera met the criteria for responding positively to either cultivation or inorganic fertilization or negatively to organic fertilization. The source of nutrients apparently affected nematode communities differently. Selected nematode genera were correlated positively with the heavy metals Cd, Cu and Zn, while nematode genera correlated negatively with Cr and Se. These genera need to be verified by independent data to confirm that they respond predictably and consistently to these specific types of disturbance. Once verified, this subset of genera will improve interpretation of index values and can be the initial targets for developing molecular probes that can be made accessible to non-specialists.

1. Introduction

Nematodes have attributes that make them useful as ecological indicators (Ferris et al., 2001; Freckman, 1988; Neher, 2001b). Various kinds of perturbations to soils, such as addition of mineral (de Goede and Dekker, 1993; Wasilewska, 1989) or organic (Ferris and Bongers, 2006; Neher and Olson, 1999) nitrogen fertilizers, cultivation (Hendrix et al., 1986), and accumulation of heavy metals (Ekschmitt and Korthals, 2006; Shao et al., 2008) affect the species richness, trophic structure and successional status of nematode communities. As indicators, soil nematodes reflect changes in soil quality from management practices and changes in policy (H. John Heinz III Center for Science, 2008). It is the relationship of bioindicators to soil function or ecological processes, rather than the taxonomic identity of a specific invertebrate, that is of primary concern. For example, in forest soils across a wide and realistic spatial variability in environmental factors, nematode communities explained 2.3–12.4% of the variation associated with nitrogen availability (Neher et al., 2012).

There are many methods of measuring nematode community structure. Through a series of experiments on sampling and experimental design at various spatial scales, Neher and colleagues concluded that maturity and trophic diversity indices are capable of differentiating among sampling sites better and more efficiently than measures based on populations or ratios of individual trophic groups (Neher et al., 1995; Neher, 2001a,b). Maturity and trophic diversity indices measure different aspects of soil communities and are complementary when used together. "Maturity" is a measure of successional status and trophic diversity measures food web structure (Neher, 2001a).

There are two major impediments to implement nematode communities in large-scale environmental monitoring programs, i.e., ecological interpretation and accessibility to non-specialists capable of identifying a multitude of free-living nematode taxa. Molecular probes are one way to expedite identification and enumeration of nematodes within whole community samples (Chen

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et al., 2010; Holterman et al., 2006; van Megen et al., 2009). Although this approach is available to non-taxonomists, it does not address concerns about interpretation and potential errors in assignments. Alternatively, nematode community indices would be more cost-effective and interpretable if ambiguous genera were removed and indices reduced to only genera with known sensitivity or response to specific types of disturbance (Neher et al., 2004).

Identification of taxa can be achieved by employing a combination of tools. First, meta-analysis of published data can be performed to quantify 'effect' sizes, based on means and standard deviation, in response to particular types of disturbance. Second, ordination analysis can be used to identify patterns in complex data from regional-scale field studies (Fiscus and Neher, 2002; Neher et al., 2005; Zhao et al., 2013). Fortunately, we have access to raw data that allows implementation of multivariate analysis. Multivariate analysis has the advantage over univariate analyses because soil nematodes are interrelated and interactive with each other within the nematode communities (Neher and Darby, 2009). Further, ordination analyses, such as canonical correspondence analysis, manages for non-independence of data and preserves taxon identity rather than collapsing them into a diversity index and analyzing by analysis of variance or categorical analysis.

The goal of the study was to conduct a methodical multivariate analysis on existing nematode community assemblage data to discern whether there are particular genera or families of nematodes that correlate consistently to specific types of disturbance, treatment, or management worldwide. We chose four contrasting types of disturbance: (1) physical, (2) inorganic fertilizer, (3) organic fertilizer, and (4) heavy metals. We included heavy metal contamination because they may occur in some sources of organic fertilizer, such as municipal sludge. Our goal was to glean as much information from existing data that are published, rather than invest the time and resources into a gigantic experiment across the globe. The timing of our study is such that we wanted to work with data while authors are still living and available for consultation, and to generate new hypotheses that can stimulate design of future experiments to test the hypothesized genera.

2. Materials and methods

2.1. Data collection

We performed a literature search in Web of Science for the years 1980–2011 using key words combined with 'nematodes' including bioindicators, sentinel taxa, disturbance, cultivation, organic agriculture, fertilizer, heavy metals, and compost. This search yielded 48 citations that met our criteria. Our criteria were data from experiments that include a reference base or control and provide some quantification of the intensity of disturbance, whether induced by management practices or natural phenomena; internally consistent sampling methods across all sites and treatments; availability of raw data including original values for each replicate; and identification of nematode communities to genus. We contacted the corresponding author of each publication to request raw data for nematode communities ($n = 14$ cultivation, $n = 16$ chemical fertilizer, $n = 20$ organic fertilizer, $n = 9$ heavy metals). Of the publications identified, 3 included treatments that controlled for 3 of the 4 types of disturbance, 9 controlled for 2 types of disturbance, and 36 controlled for 1 type of disturbance. We received original data from 21 publications of the original 48 requests that included forest and grasslands in addition to agricultural lands. Of the data received, 20 were of agricultural lands, so we narrowed our focus to land that was used for production of crops, fruit orchards or animal grazing (Table 1). Of the data received, 12 were sampled multiple times and 8 were sampled once. Sample season information was maintained and considered in the analysis to provide a measure of constancy. The experiments were conducted in temperate climates of the northern hemisphere (United States, China, Canada, Great Britain, Netherlands, Japan, Hungary and northern Africa) with the exception of New Zealand. We adjusted stated sampling times of calendar year to 'seasons' to standardize across hemispheres.

2.2. Data analysis

To make all data comparable, nematode community data were transformed to relative abundance (proportion) before analysis. Canonical correspondence analysis (CCA) was used to determine the direct effect of disturbance type on the composition of soil nematode community composition. Treatments were converted to nominal (0, 1) environmental variables (Lepš and Šmilauer, 2003). Original data controlled for cultivation, chemical or organic fertilization were analyzed separately by season (spring, summer and autumn). Original data of heavy metal contamination were not divided into different seasons because of too few data were available. Monte Carlo permutation tests were applied to compute statistical significance. All statistical analyses were performed using CANOCO 4.5 software (Ter Braak and Šmilauer, 2002).

2.3. Prediction ratings

A genus that has a CCA score in the same quadrant (or within the range of 45° of the vector close to an axis) of the biplots as the vector for the type of disturbance (i.e., cultivation, chemical or organic fertilizer, heavy metals) was rated as positive (Fig. 1). Conversely, a genus that scored in the diagonally opposite quadrant was rated as negative (Fig. 1). Genera that fit neither of those criteria were considered independent of the disturbance type and, thus, not correlated (Fig. 1.). The direction of relationship of each genus to each type of disturbance was tallied across studies by disturbance type and season (Table 2). Responses were recorded as positive (increased), negative (decreased) or independent (unchanged). Taxa were considered a 'good indicator' (finalist) if the directional response was consistent in at least 80% of the studies where it occurred. Taxa exhibiting these attributes in 60–80% of the studies where it occurred were considered to have potential as good indicators. Additionally, good indicator needs to be consistency in the response across two or more seasons. If a genus was present in only one study, the genus was eliminated from further consideration because too few data were available to be considered reliable.

3. Results

Genera, that performed consistently in a single direction and across at least two seasons, correlated negatively to cultivation and chemical fertilizers but correlated positively to organic fertilizers. If genera responded positively to either cultivation or inorganic fertilization or negatively to organic fertilization it was limited to a single season.

3.1. Cultivation effects

Regardless of season, three genera increased with cultivation and four genera decreased with cultivation (Table 2). Genera increasing with cultivation were observed only in autumn, whereas those sensitive (decreasing) to cultivation were observed in spring, summer and autumn. *Diphtherophora*, *Prismatolaimus* and *Tylenchorhynchus* correlated negatively with cultivation more consistently than other genera (Table 2). The response of *Dorylaimoides* to cultivation was inconsistent, which decreased in spring and

Table 1
Metadata associated with data sources used for the analysis of the relationship of nematode genera with different types of disturbances. Sampling occurred in the disturbance type and season indicated by check marks.

Study	Ecosystem	Study location	Time of treatment application	Cultivation			Chemical fertilization			Organic fertilization			Heavy metals ※[b]
				sp[a]	su	au	sp	su	au	sp	su	au	
Okada and Harada (2007)	Farmland	Northern Japan	Once per year in spring	√	√	√	√	√	√	√	√	√	
Sanchez-Moreno et al. (2006)	Farmland	California, USA	Two years earlier	√		√							
Sanchez-Moreno et al. (2009)	Farmland	California, USA	Unclear	√	√		√	√		√	√		
Treonis et al. (2010)	Farmland	Maryland, USA	After harvest in autumn	√		√				√		√	
Zhang et al. (2012)	Farmland	North China	Unclear	√						√			
Liang et al. (2009)	Farmland	Northeast China	Unclear				√	√	√	√	√	√	
Forge and Kempler (2009)	Farmland	BC, Canada	Twice per year, spring and summer				√		√	√		√	
Ferris et al. (2004)	Farmland	California, USA	Once per year in summer							√	√		
Forge et al. (2003)	Apple orchard	BC, Canada	One to three years earlier							√	√	√	
Forge et al. (2008)	Apple orchard	BC, Canada	Once per year in early spring							√	√	√	
Yeates et al. (1999)	Farmland	New Zealand	Cultivation once per year fertilization twice in 7 years	√					√	√			
Scow et al. (1994)	Farmland	California, USA	Fertilization from 1989 to 1992; sample time from 1992 to 1994					√	√		√	√	
Villenave et al. (2010)	Farmland	Burkina Faso	Once per year					√	√		√	√	
Li et al. (2010)	Farmland	Northeast China	Once per year in early summer					√			√		
Hou et al. (2010)	Farmland	Northeast China	One year earlier			√							
Yeates et al. (1997)	Grassland	Wales, UK	Once per year									√	
Nagy (1999)	Farmland	Hungary											√
Nagy et al. (2004)	Farmland	Hungary											√
Korthals et al. (1996)	Grassland	Netherlands											√
Yeates et al. (2003)	Grassland	New Zealand											√

[a] sp, spring; su, summer; au, autumn.
[b] ※indicate soil sampling in different seasons were not separated.

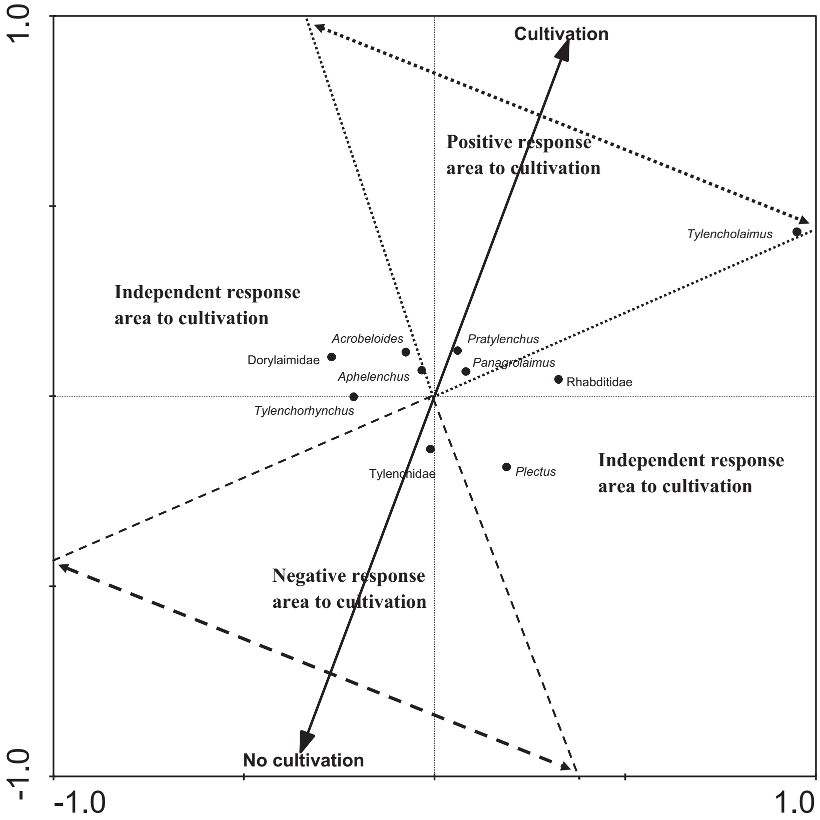

Fig. 1. Example of a canonical correspondence analysis (CCA) bi-plot to illustrate the method of assigning response scores to intensive agricultural practices. The positive response area between the 90°-angled dotted lines in the direction of cultivation represents nematode taxa that correlated positively with cultivation; the negative response area between the right angled dash lines against the direction of cultivation represents nematode taxa that correlated negatively with cultivation; the other two areas include nematode taxa considered independent of cultivation. The angles between the direction of cultivation and the two dotted lines and between the direction of cultivation and the two dashed lines are 45° and 135°, respectively, of the effect of cultivation on soil nematode communities Sanchez-Moreno et al. (2006).

increased in autumn (Table 2). Positive responses of *Ditylenchus* and *Psilenchus* to cultivation were only found in autumn (Table 2).

3.2. Chemical fertilization effects

Many genera correlated negatively with chemical fertilization. *Plectus* correlated negatively with chemical fertilization in both spring and summer (Table 2). Of the other genera, eight correlated negatively with chemical fertilization in summer but only five correlated negatively with chemical fertilization in spring or autumn (Table 2).

3.3. Organic fertilization effects

A majority of the genera correlated positively with additions of organic fertilizer in one or more seasons (Table 2). However, positive effects were seen consistently across multiple seasons for only four genera, i.e., *Cruznema* (spring and autumn), *Mesorhabditus* (spring and autumn), *Mesodorylaimus* (summer and autumn) and *Nygolaimus* (spring and autumn) (Table 2).

3.4. Heavy metals

When correlations of abundance of a genus occurred, there were typically positive with increasing concentration of Cd and Zn and negatively with Cr and Se (Table 3). Genera tended to demonstrate specificity toward metals rather than have a general response.

4. Discussion

In the present study, we found many soil nematode genera that demonstrated potential for their predictable and consistent response to intensive agriculture practices (cultivation, chemical or organic fertilization) and heavy metal contamination. They are organized relative to type of disturbance below.

4.1. Cultivation effects

In the present study, there were few genera that consistently responded to cultivation. In general, cultivation is considered as a severe physical disturbance to soil and soil biota (Neher and Campbell, 1994; Moore and de Ruiter, 1991; Hendrix et al., 1986; Fu et al., 2000; Wardle, 1995). Consistent with our finding, the abundance of *Diphtherophora*, *Prismatolaimus* and *Tylenchorhynchus* were fewer under standard cultivation than conservation tillage of long-term research at agriculture systems in Davis, California (Sanchez-Moreno et al., 2006, 2009). Both *Diphtherophora* and *Prismatolaimus* are reported to be more abundant in restored prairie and Conservation Reserve Program (CRP) plots than in annually cultivated corn (T.O. Powers, personal communication). Sensitivity of *Prismatolaimus* to cultivation was also observed in the Piedmont region of North Carolina (Fiscus and Neher, 2002). In addition to cultivation, *Prismatolaimus* is also slow to recover after fire and grazing disturbance in grasslands (Todd et al., 2006). In contrast to our finding, *Tylenchorhynchus* has been reported to be common in soils that are cultivated (Zhang et al., 2012) with wheat and corn (T.O. Powers, personal communication), and in moist, low areas of grassland (Todd et al., 2006). Perhaps, studies vary by species or

Table 2
Response of nematode genera to applications of intensive agriculture practices. Seasons of sampling are represented. The trio of numbers[†] in parentheses represents a tally of studies reporting a positive (increased), negative (decreased) or independent (unchanged) response.

Genus	Guild[b]	Intensive agriculture practices								
		Cultivation			Chemical fertilization			Organic fertilization		
		Spring	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
Achromadora	Pr3					−−[a] (0, 2, 0)[†]				
Acrobeloides	Ba2				+ (3, 0, 1)					
Aglenchus	Fu2							−− (0, 2, 0)		
Aporcelaimellus	Om5							− (1, 5, 2)		
Cephalobus	Ba2									+ (4, 0, 2)
Cervidellus	Ba2					− (0, 3, 1)				
Chronogaster	Ba2						++ (2, 0, 0)			
Coslenchus	Fu2							++ (2, 0, 0)		
Cruznema	Ba2							++ (3, 0, 0)		++ (2, 0, 0)
Cylindrolaimus	Ba3							−− (0, 3, 0)		
Diphtherophora	Fu3	− (1, 3, 0)	−− (0, 2, 0)							
Ditylenchus	Fu2			++ (2, 0, 0)						
Dorylaimoides	Om5	−− (0, 2, 0)		++ (2, 0, 0)						
Eumonhystera	Ba2									− (1, 3, 1)
Geomonhystera	Ba2									++ (2, 0, 0)
Helicotylenchus	Pl3						−− (0, 2, 0)			
Mesodorylaimus	Om5						−− (0, 2, 0)		+ (4, 1, 1)	+ (3, 0, 1)
Mesorhabditis	Ba1					−− (0, 3, 0)		++ (1, 5, 0)		++ (3, 0, 0)
Microdorylaimus	Om4					−− (0, 2, 0)				
Mononchus	Pr4							− (1, 3, 0)		
Nothotylenchus	Fu2				−− (0, 2, 0)				++ (2, 0, 0)	
Nygolaimus	Pr5							+ (3, 0, 1)		+ (2, 0, 1)
Panagrolaimus	Ba1					− (1, 3, 1)		++ (4, 0, 1)		
Plectus	Ba2				− (0, 3, 1)	−− (1, 4, 0)		+ (6, 1, 2)		
Prismatolaimus	Ba3	− (1, 3, 0)		−− (0, 3, 0)		−− (5, 0, 1)				
Psilenchus	Fu2			++ (2, 0, 0)						
Rhabditis	Ba1								++ (4, 0, 0)	
Sectonema	Om5								++ (2, 0, 0)	
Seinura	Pr3								− (1, 3, 1)	
Tylencholaimus	Fu4					− (0, 3, 1)				
Tylenchorhynchus	Fu2	− (0, 3, 1)		−− (0, 2, 0)	−− (0, 2, 0)					
Tylenchus	Fu2								− (1, 3, 1)	
Xiphinema	Pl5				++ (2, 0, 0)					

[a] −, potentially good indicator (exhibiting negative attributes in 60–80% of the studies where it occurred) that correlated negatively with intensive agriculture practices; +, potentially good indicator (exhibiting positive attributes in 60–80% of the studies where it occurred) that correlated positively with intensive agriculture practices; −−, good indicator (exhibiting negative attributes in at least 80% of the studies where it occurred) that correlated negatively with intensive agriculture practices; ++, good indicator (exhibiting positive attributes in at least 80% of the studies where it occurred) that correlated positively with intensive agriculture practices.

[b] Guild designation is the composite of trophic group and cp value: Ba, bacterivore; Fu, fungivore; Pr, predator; Om, omnivore; Pl, herbivore. Nematode genera were assigned to these trophic groups according to Yeates et al. (1993).

Table 3
Response of nematode genera to applications of heavy metals (Cu, Ni, Cr, Se, Zn, or Cd). The trio of numbers[†] in parentheses represents a tally of studies reporting a positive (increased), negative (decreased) or independent (unchanged) response.

Genus	Guild[b]	Heavy metal contamination					
		Cd	Cr	Cu	Ni	Se	Zn
Acrobeles	Ba2					−−[a] (0, 2, 0)[†]	
Acrobeloides	Ba2					++ (2, 0, 0)	
Aphelenchoides	Fu2			++ (2, 0, 0)			
Aporcelaimellus	Pr5		−− (0, 2, 0)				++ (2, 0, 0)
Cephalobus	Ba2				−− (0, 2, 0)		
Diploscapter	Ba1	++ (2, 0, 0)[4]					
Discolaimium	Pr5					−− (0, 2, 0)	
Discolaimus	Pr5					−− (0, 2, 0)	
Ecumenicus	Om4					−− (0, 2, 0)	
Eucephalobus	Ba2	++ (2, 0, 0)					
Eudorylaimus	Om4					−− (0, 2, 0)	
Filenchus	Fu2						++ (2, 0, 0)
Heterocephalobus	Ba2	−− (0, 2, 0)					
Malenchus	Pl2						++ (2, 0, 0)
Meloidogyne	Pl3	++ (2, 0, 0)					
Paratylenchus	Pl3	++ (2, 0, 0)					
Pratylenchus	Pl3						++ (2, 0, 0)
Prismatolaimus	Ba3	++ (2, 0, 0)					
Seinura	Pr3			++ (2, 0, 0)			
Tylenchorhynchus	Pl3						++ (2, 0, 0)
Wilsonema	Ba2				++ (2, 0, 0)		

[a] −−, good indicator (taxa exhibiting negative attributes in at least 80% of the studies where it occurred) that correlated negatively with heavy metal contamination; ++, good indicator (taxa exhibiting negative attributes in at least 80% of the studies where it occurred) that correlated positively with heavy metal contamination.

[b] Guild designation is the composite of trophic group and cp value: Ba, bacterivore; Fu, fungivore; Pr, predator; Om, omnivore; Pl, herbivore. Nematode genera were assigned to these trophic groups according to Yeates et al. (1993).

season(s). The species in the CRP study is *Tylenchorhynchus maximus*, although some people consider it in the genus *Sauertylenchus* (T.O. Powers, personal communication).

In the present study, we found *Ditylenchus*, *Dorylaimoides*, *Psilenchus* to correlate positively with cultivation in autumn but not in other seasons. However, several other studies report that cultivation had negative or non-significant effects on *Ditylenchus* (Fiscus and Neher, 2002; Griffiths et al., 2011; Sanchez-Moreno et al., 2009).

4.2. Chemical fertilization effects

Plectus was the only genus that responded consistently to chemical fertilization across two or more seasons. Our results align with a number of other studies reporting a reduction in *Plectus* when chemical fertilizers rich in nitrogen are applied to soil (Li et al., 2010; Liang et al., 2009; Sarathchandra et al., 2001; Villenave et al., 2010). Similarly, *Plectus* is common in unfertilized prairie soils (Todd et al., 2006).

4.3. Organic fertilization effects

Abundance of most genera increases, rather than decreases, in response to organic fertilization. Most literature describes relationships at coarse taxonomic levels such as trophic group or colonizer–persister values. Of the studies that identified nematodes to genus, we found general agreement with our results for *Cruznema* and *Mesorhabditus* (Briar et al., 2011; Liang et al., 2009; Sanchez-Moreno et al., 2009; Zhang et al., 2012) and *Mesodorylaimus* and *Nygolaimus* (Wang et al., 2006; Yeates et al., 1997).

4.4. Heavy metal contamination effects

In general, heavy metals usually are considered as xenobiotic substances and have harmful effects on soil nematode communities. However, some metals are micronutrients and show positive affects in small doses (e.g., copper, zinc). Genera that correlated significantly with copper and zinc were always positive in our study. For example, *Aphelenchoides* and *Seinura* are correlated positively with Cu in our study and other reports (Ekschmitt and Korthals, 2006). Additionally, Li et al. (2005) reported that low doses of copper show positive effects on soil nematode community. Korthals et al. (1996) reported that long-term Cu contaminated farmland soils suppressed many soil nematode genera; however, they did not find *Aphelenchoides*, *Heterocephalobus*, and *Seinura* in their soils were which found in this study to be correlated positively with Cu. There are reports of other nematode genera that decrease in abundance when exposed to copper, e.g., *Heterocephalobus* (Ekschmitt and Korthals, 2006). Our finding that *Cephalobus* is correlated negatively with nickel concentration supports previous reports (Ekschmitt and Korthals, 2006; Yeates et al., 2003).

Certainly, we recognize that our approach has its limitations. For example, we were limited to 'direct' analysis and not able to do an 'indirect' analysis because we did not have a uniform cohort of environmental covariables (Fiscus and Neher, 2002). Indirect analysis would lend itself to other types of procedures such as structural equation modeling or partial canonical correspondence analysis (Fiscus and Neher, 2002).

5. Conclusion

This study showed that cultivation reduced abundances of *Diphtherophora*, *Prismatolaimus* and *Tylenchorhynchus*. The application of synthetic chemical fertilizers reduced the numbers of *Plectus*, while organic fertilization increased numbers of *Cruznema*, *Mesorhabditus*, *Mesodorylaimus* and *Nygolaimus*. Selected nematode genera were correlated positively with the heavy metals Cd, Cu and Zn, while nematode genera were correlated negatively with Cr and Se. These genera need to be verified by independent data to confirm that they generally reflect intensive cultivation, fertilization by synthetic or organic types or heavy metal contamination. Once verified, this subset of genera will improve interpretation of index values and can be the initial targets for developing molecular probes that can be made accessible to non-specialists which will make the application of the soil bioindicators more efficient, convenient and comprehensive.

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