Mini-review

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Non-target effects of herbicides on soil nematode assemblages

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Abstract

BACKGROUND: Herbicides are used extensively to control weeds. However, little is known about the non-target effects of herbicides on soil nematode assemblages. The objective of this study was to determine whether herbicides affect the abundance of nematodes in specific trophic groups. Meta-analysis was performed, and the calculated effect size, *lr*, quantified the impact of herbicides on the abundance of total nematodes and five trophic groups (bacterivores, fungivores, plant parasites, omnivores and predators).

RESULTS: Measurements of *lr* indicated that herbicides decreased abundance of both fungivores and predators; however, abundance of bacterivores, plant parasites and omnivores increased. Overall, total nematode abundance tended to increase in response to herbicide application.

CONCLUSION: The decrease in predator abundance suggests that herbicide application disturbs soil food webs. The increase in bacterivore and decrease in fungivore abundance suggest that bacterivores are more tolerant and both fungivores and predators more sensitive to herbicide applications. Herbicides also have non-target effects on omnivores, which may be due to the increased amount of food resources for omnivores after weed control. Additionally, the use of herbicides may result in a risk of an increase in plant-parasitic nematode abundance.

Keywords: herbicide; nematode; trophic group; meta-analysis

1 INTRODUCTION

In the United States, conservation no-till agriculture technologies have greatly reduced soil loss compared with conventional agriculture technologies.[1] In many agroecosystems worldwide, herbicides are used extensively to control weeds, reduce soil erosion, conserve soil structure and improve labor efficiency. However, herbicides affect more than just weeds; they also impact upon soil biota directly or more frequently indirectly, through the alteration of plant cover and root exudates.[2–5] However, different types of herbicide are associated with negligible, positive or negative effects on various soil organisms (e.g. microorganisms, nematodes, arthropods and earthworms).[4,6–10]

Soil nematodes are the most abundant metazoa and occupy key positions at most trophic levels (bacterivore, fungivore, plant parasite, omnivore and predator) in soil food webs.[11–14] Therefore, the composition of the soil nematode community can indicate ecosystem processes and environmental conditions.[11,12,15] A considerable number of studies have focused on the effects of herbicides on plant-parasitic nematodes, especially root-knot nematodes and cyst nematodes.[16–18] Generally, herbicides are usually less toxic to nematodes than insecticides.[19] In most cases, herbicides are usually applied with other agricultural management practices (e.g. other pesticides, fertilization and tillage).[20] Because little is known about the effects of herbicides alone on soil nematode assemblages, the objective of the present study was to determine whether herbicides affect nematode trophic group composition. Because meta-analysis is a powerful approach for analyzing existing data to obtain general conclusions, this approach was employed to determine herbicide effects on soil nematode communities.

2 MATERIALS AND METHODS

The first step of meta-analysis of the effect of herbicides on total soil nematode numbers and nematode trophic group abundance was to utilize 'herbicide' and 'soil nematode' as topics to search the literature via the ISI WEB OF KNOWLEDGE^{SM} in October 2011. This search resulted in 3050 studies, which were then inspected for further references that isolated control and herbicide treatments. Most of the studies used herbicides as auxiliary management practices in agriculture; some studies focused on certain species of plant-parasitic nematodes; some studies showed relative abundance (percentage data) of nematode

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trophic groups, which was not suitable for the present study, and therefore those studies were omitted. Eventually, 18 literature citations that isolated control and herbicide treatments were identified (Table 1). Nematode taxa were assigned to the main trophic groups (bacterivores, fungivores, herbivores, omnivores, predators) according to Yeates *et al.*[13] when trophic group abundance was not displayed in the tables and/or in the figures of the 18 collected studies. Next, control and herbicide-alone treatment groups were used to calculate effect size, *lr*.[21] Means of total nematode, bacterivore, fungivore, herbivore, predator and omnivore abundance under control and herbicide treatments were extracted from the 18 investigations. When data were shown in figures, the data were extracted with the Digitize module of Origin 7.5 software (OriginLab Corp., USA). Sixty-two observations of total nematode abundance, 26 observations of bacterivores, 20 observations of fungivores, 27 observations of plant parasite abundance, 16 observations of omnivore abundance and 14 observations of predator abundance were used to calculate effect size *lr* as follows:

$$lr = \ln\left(\frac{M_H}{M_C}\right) \tag{1}$$

where M_C is the mean of the control group, and M_H is the mean of the herbicide treatment group. The calculated mean effect sizes across the studies for the fixed-effect model were weighted by reciprocal of the variance. Then, 95% confidence intervals were calculated following the method of Gurevitch and Hedges[21] and utilized to investigate whether the 95% CI overlapped zero (neutral effect). Briefly, there are significant positive effects of herbicides on nematode assemblages when 95% CI exceeds zero; there are significant negative effects of herbicides on nematode assemblages when 95% CI is less than zero. There are no significant effects of herbicides on nematode assemblages when 95% CI overlaps zero. The *lr* of the six variables (i.e. total nematode abundance and five trophic group abundances) were calculated independently. The variances between these six variables were not compared directly. Heterogeneity of each dataset was calculated using the *Q*-statistics method via the procedures of Gurevitch and Hedges.[21] A chi-square distribution table was used to determine *P*-values of heterogeneity.

3 RESULTS

The *P*-values of the within-class heterogeneity test were less than 0.05 in all six datasets (abundance of total nematodes and the five trophic groups), which indicated apparent variation within dataset. By comparing 62 observations with and without herbicide treatments, *lr* of total nematode abundance tended to exceed zero; the mean value equaled 0.008 with 95% CI ranging from −0.005 to 0.021 (Fig. 1). The *lr* values of fungivore and predator nematode abundances were significantly less than zero (Fig. 1). The mean value of *lr* describing the effect of herbicide application on fungivorous nematodes was 0.153 with 95% CI ranging from −0.188 to −0.119; for the effect of herbicide application on predatory nematodes it was 0.719 with 95% CI ranging from −0.872 to −0.566 (Fig. 1). However, the *lr* values of bacterivore, plant-parasitic and omnivore abundances were remarkably greater than zero (Fig. 1). The mean value of *lr* describing the effect of herbicide application on bacterivorous nematodes was 0.115 with 95% CI ranging from 0.095 to 0.134 (Fig. 1); for the effect of herbicide application on plant-parasitic nematodes it was 0.069 with 95% CI ranging from 0.038 to 0.101 (Fig. 1). Additionally, the mean value of *lr* summarizing the effects of herbicide application on omnivorous nematodes was 0.265 with 95% CI ranging from 0.140 to 0.390 (Fig. 1).

4 DISCUSSION

Although some previous studies report that herbicides have negative effects on total soil nematode abundance,[10,22–24] others indicate that herbicides have positive effects on total soil nematode abundance.[25–27] One likely reason is that the different types and concentrations of herbicides used in those studies led to different impacts on total nematode abundance.[4,28–32] In the present meta-analysis, herbicide treatment did not significantly affect total nematode abundance, a result that might be due to heterogeneity within the original dataset for total nematode numbers.

Soil nematodes are the most numerous mesofauna in soil.[33] They are ubiquitous and contribute to many soil ecosystem processes. For example, they are important components of both the soil detrital food chain and the grazer food chain. Therefore, they are involved in soil decomposition and N mineralization.[34,35] The increasing N availability may increase net primary production (NPP); however, an outbreak of plant-parasitic nematodes may significantly reduce NPP.[12,34] The response of different soil nematode trophic groups to herbicide application may indicate a change in soil ecosystem processes (e.g. soil decomposition and nutrient mineralization). In the present study, fungivore abundance decreased and bacterivore abundance increased after herbicide application. Therefore, herbicide application may cause the soil food web to become more bacterially dominated. The meta-analysis results suggest that bacterivores dominated, and most of them were tolerant to herbicide application. Furthermore, although fungi and fungivores are usually considered to be primary decomposers of soil surface residues, bacteria and bacterivores may be more important in the decomposition of underground residues.[36] Therefore, surface fungi and fungivores are more directly exposed to the impact of herbicides than underground bacteria and bacterivores. Herbicide application decreases weed biomass remaining in a field and increases crop biomass that is harvested. Therefore, herbicide application generally decreases total post-harvest above-ground plant biomass, a decrease that may be detrimental to fungi and fungivorous nematodes.

In general, *k*-selected species (i.e. organisms that successfully compete for limited resources in an environment and tend to occur near the carrying capacity for that environment) are relatively sensitive to disturbance, and *r*-selected species (i.e. those with high potential to reproduce quickly) are relatively tolerant to disturbance,[37] as reflected in the colonizer-persister (*cp*) scale of soil nematodes.[11,12] Therefore, nematodes that are *r*-selected have life-history characteristics including a short generation time, many offspring and tolerance of disturbance; *k*-selected nematodes have life-history characteristics including a longer generation time, fewer offspring and sensitivity to disturbance. The colonizer-persister (*cp*) value ranges from an extreme colonizer (*cp* value = 1) to an extreme persister (*cp* value = 5), with the index values representing life-history characteristics associated with *r*- and *k*-selection respectively. According to this system, predator and omnivorous nematodes are assigned to high *cp* (*cp*4 or *cp*5) guilds because of their long life-history characteristics and sensitivity to disturbance. In the present study, however, predators and omnivores showed significantly different responses to herbicide. The significant decrease in predators indicates that herbicide application disturbs the soil food web and shortens the food chain.

Table 1. Studies investigating herbicide effects on soil nematode assemblages and used in the meta-analysis

Study	Ecosystem	Field/laboratory	Nematode taxa	Herbicide treatment
Das *et al.* (2010)[22]	Crop farm	Field	Total nematode	1. Atrazine 1.0 kg ha^{-1} as pre-emergence 2. Atrazine 1.0 kg ha^{-1} as pre-emergence followed by 0.25 kg ha^{-1} as post-emergence 3. Atrazine 2.0 kg ha^{-1} as pre-emergence 4. Atrazine 2.0 kg ha^{-1} as pre-emergence followed by 0.25 kg ha^{-1} as post-emergence 5. Atrazine 0.25 kg ha^{-1} as post-emergence 6. 2,4-D-amine 0.75 kg ha^{-1} as post-emergence 7. 2,4-D-amine 1.0 kg ha^{-1} as post-emergence 8. Pendimethalin 1.5 kg ha^{-1} as pre-emergence 9. Pendimethalin 2.0 kg ha^{-1} as pre-emergence
Salminen *et al.* (1997)[23]	Forest	Laboratory	Total nematode	1. Terbuthylazine
Sanchez-Moreno and Ferris (2007)[10]	Forest	Laboratory	Total nematode Bacterivore Fungivore Plant parasite Omnivore Predator	1. Simazine 2.68 kg AI ha^{-1} 2. Diuron 1.79 kg AI ha^{-1}
Zhang *et al.* (2010)[24]	Crop farm	Laboratory	Total nematode Bacterivore Fungivore Plant parasite	1. Acetochlor
Griffiths *et al.* (2008)[28]	Crop farm	Laboratory (under three types of maize crop)	Total nematode Bacterivore Fungivore Plant parasite	1. Glufosinate-ammonium 2.5 L ha^{-1}
Hoagland *et al.* (2008)[29]	Orchard	Field	Total nematode	1. A clove oil-based herbicide (Matran) 13.5 L ha^{-1}
Ishibashi *et al.* (1983)[25]	Crop farm	Field	Total nematode Bacterivore Plant parasite Omnivore Predator	1. Paraquat 2. Chlormethoxynil 3. Thiobencarb-Simetryne
Ishibashi *et al.* (1978)[44]	Orchard	Field	Total nematode Predator	1. Paraquat in spring, paraquat and bromacil in summer
Liphadzi *et al.* (2005)[30]	Crop farm	Field	Total nematode Bacterivore Fungivore Plant parasite Omnivore	1. Glyphosate 0.56 kg AI ha^{-1} 2. Glyphosate 1.12 kg AI ha^{-1} 3. Glyphosate 2.24 kg AI ha^{-1} 4. Glyphosate 3.36 kg AI ha^{-1} 5. Glyphosate 3.48 kg AI ha^{-1}
Mohammad (1984)[45]	Crop farm	Field	Total nematode Plant parasite	1. Fluorodifen 1.5 kg AI ha^{-1}
Parfitt *et al.* (2010)[31]	Pasture	Field	Total nematode Bacterivore Fungivore Plant parasite	1. Mecoprop and dicamba

Table 1. Continued

Study	Ecosystem	Field/laboratory	Nematode taxa	Herbicide treatment
Rahman *et al.* (2009)[46]	Vineyard	Field	Bacterivore Plant parasite Omnivore Predator	1. Diquat and paraquat, or carfentrazone-ethyl and glyphosate
Salminen *et al.* (1996)[26]	Forest	Laboratory	Total nematode	1. Terbuthylazine 1.0 g m^{-2} 2. Terbuthylazine 15.0 g m^{-2} 3. Terbuthylazine 50.0 g m^{-2}
Saly (1989)[32]	Vineyard	Laboratory	Total nematode	1. 30% atrazine, 11.5% MCPP, 5.2% 2,4,5-T applied repeatedly 2. 7.5% chlorthiamide applied repeatedly 3. 50% 2-chlorine-4,6 ethylamine-1,3,5-triazine treated repeatedly 4. 25% terbuthylazine, 25% terbumethone applied repeatedly 5. 40% amitrole, 20% methabenzthiazurone, 20% MCPA applied repeatedly 6. 48.5% simazine applied once 7. 25% terbuthylazine, 25% terbumethone applied once 8. 7.5% chlorthiamide applied once
Saly and Ragala (1977)[47]	Vineyard	Laboratory	Total nematode	1. 30% atrazine, 11.5% MCPP, 5.2% 2,4,5-T treated repeatedly 2. 7.5% chlorthiamide applied repeatedly 3. 50% 2-chlorine-4,6 ethylamine-1,3,5-triazine treated repeatedly 4. 25% terbuthylazine, 25% terbumethone treated repeatedly 5. 40% amitrole, 20% methabenzthiazurone, 20% MCPA treated repeatedly
Saly and Ragala (1984)[48]	Vineyard	Laboratory	Total nematode	1. Isopropylamino 12.0 L ha^{-1} 2. Isopropylamino 30.0 L ha^{-1}
Yeates *et al.* (1999)[4]	Crop farm	Field	Total nematode Bacterivore Fungivore Plant parasite Omnivore Predator	1. Atrazine 2. Sulfonylurea 3. Terbumeton/terbuthylazine 4. Bromacil
Zhang *et al.* (2002)[27]	Crop farm	Field	Total nematode Bacterivore Plant parasite	1. Acetochlor

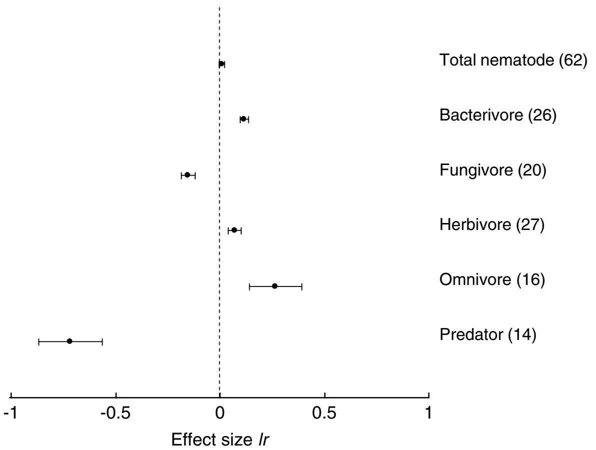

Figure 1. The effect of herbicides on the abundance of total nematodes and five nematode trophic groups (bacterivore, fungivore, plant parasite, omnivore and predator). Data are presented as natural-log-transformed response ratios (*lr*) of treated-to-control group means. The numbers of observations are in parentheses following the nematode taxa. Bars indicate ±95% confidence intervals.

Although herbicides may not be directly toxic to omnivores, the likely reason for this effect is that herbicide application increased the amount of food resources for omnivorous nematodes. Omnivores feed on a wide range of foods (e.g. fungi, bacteria, substrate, protozoa, rotifers, algae and nematodes);[13] herbicide application might increase the abundance of food resources (e.g. bacteria and bacterivorous nematodes) for omnivorous nematodes. Alternatively, because herbicides kill weeds, there is potentially greater light transmission to the soil surface, which subsequently favors growth of soil algae, which are an important food for some omnivores.[13,38,39] Another possible reason is that some genera of omnivorous nematodes are not *k*-selected species (e.g. *Epidorylaimus*).[40,41] Additionally, omnivores may live in deeper soil layers which protect them from being exposed to the direct impact of herbicides. However, further studies of this topic are needed. For any or all of these reasons, the omnivores may never respond negatively to herbicide application. Although previous studies yielded inconsistent conclusions as to how herbicides impact upon plant-parasitic nematodes, the present study shows that numbers of plant-parasitic nematodes tend to increase after herbicide application. One possible reason is that herbicide application suppresses predators (e.g. nematophagous fungi, carnivorous nematodes), and herbicide application did indeed suppress predators in the present study. Even though weed species are hosts of plant-parasitic nematodes,[42,43] herbicides may kill weed hosts, thereby resulting in a shift of some plant parasites to parasitize or feed on crop species. This increase in plant-parasitic nematodes, if large enough, may decrease crop productivity.

The main contribution of this study is that meta-analysis performed across multiple studies indicated that herbicides clearly impact upon all five trophic groups of soil nematode assemblages. To improve the understanding of the effects of herbicides on the soil nematode community, additional large-scale, long-term and comparable (control and treatment) research experiments with different agroecosystems are needed. The change in nematode community structure may alter the soil decomposition pathway. Additionally, the use of herbicides may enhance the risk of increased abundance of plant-parasitic nematodes and a possible loss of crop yield.

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REFERENCES

1 Pimentel D, Harvey C, Resosudarmo P, Sinclair K, Kurz D, McNair M *et al.*, Environmental and economic costs of soil erosion and conservation benefits. *Science* **267**:1117–1123 (1995).
2 Hendrix PF and Parmelee RW, Decomposition, nutrient loss and microarthropod densities in herbicide-treated grass litter in a Georgia piedmont agroecosystem. *Soil Biol Biochem* **17**:421–428 (1985).
3 Mahn E-G and Kästner A, Effects of herbicide stress on weed communities and soil nematodes in agroecosystems. *Oikos* **44**:185–190 (1985).
4 Yeates GW, Wardle DA and Watson RN, Responses of soil nematode populations, community structure, diversity and temporal variability to agricultural intensification over a seven-year period. *Soil Biol Biochem* **31**:1721–1733 (1999).
5 Andrén O, Paustian K and Rosswall T, Soil biotic interactions in the functioning of agroecosystems. *Agric Ecosyst Environ* **24**:57–67 (1988).
6 Lupwayi NZ, Brandt SA, Harker KN, O'Donovan JT, Clayton GW and Turkington TK, Contrasting soil microbial responses to fertilizers and herbicides in a canola–barley rotation. *Soil Biol Biochem* **42**:1997–2004 (2010).
7 Greenslade PJM, Reid IA and Packer IJ, Herbicides have negligible effects on ants and springtails in an Australian wheat field. *Soil Biol Biochem* **42**:1172–1175 (2010).
8 Freemark K and Boutin C, Impacts of agricultural herbicide use on terrestrial wildlife in temperate landscapes: a review with special reference to North America. *Agric Ecosyst Environ* **52**:67–91 (1995).
9 Chakravarty P and Chatarpaul L, Non-target effect of herbicides: I. Effect of glyphosate and hexazinone on soil microbial activity. Microbial population, and in-vitro growth of ectomycorrhizal fungi. *Pestic Sci* **28**:233–241 (1990).
10 Sanchez-Moreno S and Ferris H, Suppressive service of the soil food web: effects of environmental management. *Agric Ecosyst Environ* **119**:75–87 (2007).
11 Ferris H, Bongers T and de Goede RGM, A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Appl Soil Ecol* **18**:13–29 (2001).
12 Bongers T and Ferris H, Nematode community structure as a bioindicator in environmental monitoring. *Trends Ecol Evol* **14**:224–228 (1999).
13 Yeates GW, Bongers T, Degoede RGM, Freckman DW and Georgieva SS, Feeding habits in soil nematode families and genera – an outline for soil ecologists. *J Nematol* **25**:315–331 (1993).
14 Freckman D, Bacterivorous nematodes and organic-matter decomposition. *Agric Ecosyst Environ* **24**:195–217 (1988).
15 Zhao J and Neher D, Soil nematode genera that predict specific types of disturbance. *Appl Soil Ecol* **64**:135–141 (2013).
16 Gilreath JP, Santos BM, Gilreath PR, Jones JP and Noling JW, Efficacy of 1,3-dichloropropene plus chloropicrin application methods in combination with pebulate and napropamide in tomato. *Crop Prot* **23**:1187–1191 (2004).
17 Dewar AM, Haylock LA, May MJ, Beane J and Perry RN, Glyphosate applied to genetically modified herbicide-tolerant sugar beet and 'volunteer' potatoes reduces populations of potato cyst nematodes and the number and size of daughter tubers. *Ann Appl Biol* **136**:179–187 (2000).
18 Browde JA, Tylka GL, Pedigo LP and Owen MDK, Responses of *Heterodera glycines* populations to a postemergence herbicide mixture and simulated insect defoliation. *J Nematol* **26**:498–504 (1994).
19 Neher D, Soil community composition and ecosystem processes: comparing agricultural ecosystems with natural ecosystems. *Agrofor Syst* **45**:159–185 (1999).
20 Neher DA and Olson RK, Nematode communities in soils of four farm cropping management systems. *Pedobiologia* **43**:430–438 (1999).

21 Gurevitch J and Hedges LV, Meta-analysis: combining the results of independent experiments, in *Design and Analysis of Ecological Experiments*, ed. by Scheiner SM and Gurevitch J. Chapman and Hall, New York, NY, pp. 378–398 (1993).
22 Das TK, Sakhuja PK and Zelleke H, Herbicide efficacy and non-target toxicity in highland rainfed maize of Eastern Ethiopia. *Int J Pest Manag* **56**:315–325 (2010).
23 Salminen J, Setala H and Haimi J, Regulation of decomposer community structure and decomposition processes in herbicide stressed humus soil. *Appl Soil Ecol* **6**:265–274 (1997).
24 Zhang J, Li Q and Liang W, Effect of acetochlor and carbofuran on soil nematode communities in a Chinese soybean field. *Afr J Agr Res* **5**:2787–2794 (2010).
25 Ishibashi N, Kondo E and Ito S, Effects of application of certain herbicides on soil nematodes and aquatic invertebrates in rice paddy fields in Japan. *Crop Prot* **2**:289–304 (1983).
26 Salminen J, Eriksson I and Haimi J, Effects of terbuthylazine on soil fauna and decomposition processes. *Ecotoxicol Environ Saf* **34**:184–189 (1996).
27 Zhang W, Duan Y, Chen L and Liang C, Effect of agrochemicals and bio-control productions on soil nematode community dynamics. *Yingyong Shengtai Xuebao* **13**:638–640 (2002).
28 Griffiths BS, Caul S, Thompson J, Hackett CA, Cortet J, Pernin C *et al*., Soil microbial and faunal responses to herbicide tolerant maize and herbicide in two soils. *Plant Soil* **308**:93–103 (2008).
29 Hoagland L, Carpenter-Boggs L, Granatstein D, Mazzola M, Smith J, Peryea F *et al*., Orchard floor management effects on nitrogen fertility and soil biological activity in a newly established organic apple orchard. *Biol Fert Soils* **45**:11–18 (2008).
30 Liphadzi KB, Al-Khatib K, Bensch CN, Stahlman PW, Dille JA, Todd T *et al*., Soil microbial and nematode communities as affected by glyphosate and tillage practices in a glyphosate-resistant cropping system. *Weed Sci* **53**:536–545 (2005).
31 Parfitt RL, Yeates GW, Ross DJ, Schon NL, Mackay AD and Wardle DA, Effect of fertilizer, herbicide and grazing management of pastures on plant and soil communities. *Appl Soil Ecol* **45**:175–186 (2010).
32 Saly A, Evaluation of herbicide influence on the edaphon in vineyards by means of free-living nematodes. *Pol Ecol Stud* **15**:47–54 (1989).
33 Neher DA and Powers TO, Nematodes, in *Encyclopedia of Soils in the Environment*, ed. by Hillel D, Rosenzweig C, Powlson D, Scow K, Singer M and Sparks D. Academic Press, New York, NY, pp. 1–5 (2004).
34 Neher DA, Weicht TR and Barbercheck ME, Linking invertebrate communities to decomposition rate and nitrogen availability in pine forest soils. *Appl Soil Ecol* **54**:14–23 (2012).
35 Zhao J, Wan S, Li Za, Shao Y, Xu G, Liu Z *et al*., *Dicranopteris*-dominated understory as major driver of intensive forest ecosystem in humid subtropical and tropical region. *Soil Biol Biochem* **49**:78–87 (2012).
36 Hendrix PF, Parmelee RW, Crossley DA, Jr, Coleman DC, Odum EP and Groffman PM, Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* **36**:374–380 (1986).
37 Pianka ER, On *r*- and *k*-selection. *Am Nat* **104**:592–597 (1970).
38 Backlund HO, Studies on the soil microfauna II: The soil inhabiting nematodes. *Oikos* **1**:287–289 (1949).
39 Sohlenius B, Influence of clear-cutting and forest age on the nematode fauna in a Swedish pine forest soil. *Appl Soil Ecol* **19**:261–277 (2002).
40 Zhao J, Shao Y, Wang X, Neher DA, Xu G, Li Za *et al*., Sentinel soil invertebrate taxa as bioindicators for forest management practices. *Ecol Indicators* **24**:236–239 (2013).
41 Fiscus DA and Neher DA, Distinguishing sensitivity of free-living soil nematode genera to physical and chemical disturbances. *Ecol Applic* **12**:565–575 (2002).
42 Thomas SH, Schroeder J and Murray LW, The role of weeds in nematode management. *Weed Sci* **53**:923–928 (2005).
43 Duncan LW and Noling JW, Agricultural sustainability and nematode integrated pest management, in *Plant and Nematode Interactions*, ed. by Barker KR, Pederson GA and Windham GL. American Society of Agronomy, Madison, WI, pp. 251–287 (1998).
44 Ishibashi N, Muraoka M, Kondo E, Yamasaki H, Kai H, Iwakiri T *et al*., Effects of annual application of herbicides on nematodes, soil mites, and springtails in satsuma mandarin orchards. *Agric Bull Saga Univ* **44**:43–55 (1978).
45 Mohammad G, Fluorodifen influence on soil microflora and nematode fauna of soybean crop var. bragg at three stages of growth and post-harvest. *Geobios* **11**:69–74 (1984).
46 Rahman L, Whitelaw-Weckert MA, Hutton RJ and Orchard B, Impact of floor vegetation on the abundance of nematode trophic groups in vineyards. *Appl Soil Ecol* **42**:96–106 (2009).
47 Saly A and Ragala P, The effects of herbicides applied in a vineyard on the composition of soil inhabiting nematode populations. *Sb UVTI (Ustav Vedeckotechnickych Informaci) Ochrana Rostlin* **13**:39–46 (1977).
48 Saly A and Ragala P, Free living nematodes bioindicators of the effects of chemical on the soil fauna. *Sb UVTIZ (Ustav Vedeckotechnickych Informaci pro Zemedelstvi) Ochrana Rostlin* **20**:15–21 (1984).

