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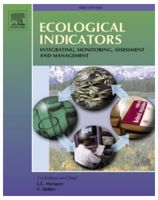

The integration of nematode communities into the soil biological health framework by factor analysis

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ABSTRACT

A critique of the soil health framework is that biological indicators currently lag behind chemical and physical indicators of soil health. Incorporating nematode communities into the soil health framework could help to better reflect key aspects of soil food web structure and function and significantly contribute to ecosystem processes. However, little is understood regarding how nematode communities relate to soil biological health indicators such as permanganate oxidizable carbon (POXC), soil protein, mineralizable C, and enzyme activities in agroecosystems. Here, we use an exploratory factor analysis (EFA) to quantitatively explore which set of soil health indicators best explain a given factor (i.e. soil health trait) using data from two long term experimental trials and 44 farm fields across Ohio. Specifically, this paper aims to 1) integrate our understanding of nematode structure and function with other soil biological health indicators to describe soil health traits; and 2) determine how management practices alter soil health traits. We found that soil biological health indicators represented four underlying soil health traits: fungal organic matter processing pathway, the rate of nutrient cycling, trophic complexity, and cumulative disturbance. Results indicated that soil biological health indicators, such as enzyme activities, POXC, mineralizable C and soil protein were more integrated with nematode feeding groups than with nematode indices. Additionally, tillage intensity had a significant effect on the fungal organic matter processing pathway and the rate of nutrient cycling. This study indicates that nematode feeding groups can be readily incorporated into the soil health framework and future soil health assessments.

1. Introduction

Understanding belowground biodiversity and soil biological processes is essential for sustained soil health (Ferris, 2010a; Dose et al., 2015). Soil health is a growing field and is commonly defined as the ability of the physical, chemical, and biological components of the soil to sustain plant productivity, maintain animal health, and enhance water and air quality (Doran and Zeiss, 2000). Soil biological health is less understood because specific indicators are not as well developed or readily available compared to physical and chemical measures of soil health (Bünemann et al., 2018; O'Neill et al., 2021). As a result, there are growing calls from both the farming and scientific communities for soil biological health indicators to be further developed (Baveye, 2021). Currently, soil biological health indicators that quantify the soil microbiome are hard to interpret and costly (Fierer et al., 2021; Sprunger, 2015). Furthermore, soil metagenomic DNA sequencing does not necessarily inform ecological function, which is an essential linkage for understanding nutrient availability and overall soil health (Brussaard et al., 2007; Graham et al., 2016).

In contrast to quantifying bacterial and fungal communities, nematodes have the potential to serve as strong soil biological health indicators because of their trophic interactions with the microbial community and their ability to respond rapidly to changes within the soil environment (Ferris et al., 2001; Neher, 2001; Sánchez-Moreno et al., 2011; Hua et al., 2021). Nematodes span the trophic food web and function as both colonizing *r*-strategists and persistent *K*-strategists (Ritz and Trudgill, 1999; Yeates and Bongers, 1999; Yeates, 2003). Nematodes can be grouped into functional guilds that reflect several different niches within the soil food web based on feeding groups (Ferris et al., 2001; Ferris, 2010b). For instance, the five main feeding groups consist of bacterial feeders (bacterivores), fungal feeders (fungivores), plant root feeders (plant parasitic), predators that prey on other nematodes

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(predators), and omnivorous feeders (omnivores) (Ferris and Bongers, 2009). Additionally, each nematode family has a specific colonizer-persister (cp) value and feeding group, which can be further aggregated into nematode indices that relate to soil food web function (Yeates and Bongers, 1999; Ferris et al., 2001; Neher, 2001; Ferris, 2010b). These indices can be used to infer soil food web disturbance (basal index (BI)), the microbial decomposition channel (channel index (CI)), nutrient inputs (enrichment index (EI)), trophic complexity (structure index (SI)), plant infestation (plant parasitic index (PPI)), and soil food web succession (maturity index (MI)) (Bongers, 1990; Bongers and Bongers, 1998; Yeates, 2003). Nematode indices can be easily integrated into the soil health framework because of their relationship to ecological function (Ferris et al., 2001; Ferris, 2010b). The quantification of nematode communities is affordable, reliable, and can provide extensive information on soil food web dynamics (Höss and Williams, 2009; Zhao et al., 2016). However, specific tradeoffs do exist, including extensive and laborious training in nematode identification (Neher, 2001).

Nematode communities have yet to be integrated into the soil health framework. Moreover, we know very little regarding how nematode communities relate to soil biological health indicators such as soil mineralizable carbon (C), soil protein, permanganate oxidizable carbon (POXC), and enzyme activity (Tabatabai, 1994; Culman et al., 2012; Hurisso et al., 2018). Specifically, these soil biological health indicators are recommended by the Natural Resource and Conservation Service (NRCS), and are also measured within common soil health testing packages such as the Cornell Comprehensive Assessment of Soil Health (CASH) and Haney Soil Health Test (Strauss et al., 2015; Moebius-Clune et al., 2016).

Evidence suggests that nematode community structure and soil biological health indicators may be strongly integrated with similar soil health processes related to nutrient cycling and decomposition (Gao et al., 2016; Martin and Sprunger, 2021a; Martin and Sprunger, 2021b; Neher, 2001). Verhoef and Brussaard, (1990) found that nematodes heavily impact nitrogen (N) cycling and account for 30% of N mineralization via microbial grazing. Specifically, bacterivores, fungivores, and omnivorous nematodes prey on microbes and excrete excess nutrients as ammonium for plant uptake (Ingham et al., 1985; Bonkowski et al., 2009). Microbivorous nematodes directly regulate organic matter decomposition through preying on microbial communities that are responsible for the breakdown of organic matter (Freckman, 1988). Soil health indicators such as soil protein or enzyme activity can estimate labile N pools and organic matter decomposition, but the lack of integration of nematode community structure with these soil health indicators provides an incomplete representation of nutrient cycling processes (Dupont et al., 2009).

Nematode indices and soil biological health indicators are affected by similar soil functions such as organic matter decomposition and C cycling. For example, the SI represents nematode trophic food web complexity, where an enhanced SI indicates increased predator–prey interactions which can control the rate of organic matter decomposition (Wardle et al., 1995). Additionally, the EI and CI can serve as an indicator of N-enrichment and whether the decomposition channel is fungal or bacterial dominated, respectively (Ferris et al., 2001). Organic matter decomposition can be estimated through soil health indicators such as mineralizable C or enzyme activity, however, the relationships between these soil health indicators and the SI, EI, and CI are severely understudied. The SI has also been linked to soil health indicators that represent the labile C pools (Margenot and Hodson, 2016; Zhong et al., 2017; Liu et al., 2021). In forest systems, Margenot and Hodson, (2016) demonstrate that soil C lability drives nematode trophic complexity, whereby predatory nematodes are more concentrated in areas where soil C pools are less labile. Permanganate oxidizable carbon (POXC) and mineralizable C, two key soil health indicators that reflect different pools of soil C, should be further integrated with the SI to better understand how nematode communities drive soil C dynamics (Bardgett and van der Putten, 2014; Jiang et al., 2018).

Exploratory factor analysis (EFA) may serve as a quantitative solution for integrating the relationship between common soil biological health indicators and nematode community structure and function. Specifically, EFA can quantitatively determine the underlying soil health traits that nematode communities and soil health indicators may share (Fabrigar and Wegener, 2011; Wade et al., under review). Thus far, a large effort has been made to use EFA for the quantification of soil parameters, including soil chemical and physical properties (Dobermann, 1994; Shukla et al., 2006; Mairura et al., 2008; Lambrecht et al., 2016; Barlog et al., 2017; Liu et al., 2018; Zhang et al., 2018; Zhang et al., 2020). However, Wade et al., (2020) is the only study to use sensitive soil biological health indicators including soil protein, POXC, and mineralizable C as the measured variables to determine soil health traits through EFA. Moreover, very few studies have used nematodes as measured variables to determine soil health traits (Bastida et al., 2008; Meng et al., 2013; Igalavithana et al., 2017; Horakova et al., 2020). Understanding how soil fauna fit and relate to soil health indicators is essential to further strengthen our understanding of soil biological health. Moreover, the creation of a conceptual framework to derive the relationships between soil biological health indicators and nematode communities can only be performed through the use of a quantitative analysis.

The use of EFA is a powerful and quantitative tool that can aid in integrating nematodes into the soil health framework. Here, we used EFA on a suite of soil biological health indicators—both recommended soil biological health indicators and nematode measurements—from long-term experimental trials and farmer fields across Ohio. Specifically, this study aims to: 1) integrate our understanding of nematode structure and function with other soil biological health indicators to describe underlying soil health traits; and 2) determine how management practices alter these soil health traits. We hypothesize that 1) nematode indices will be more strongly integrated with soil health indicators than nematode feeding groups; and 2) management practices with decreased management intensity will enhance soil health traits. The ultimate goal of this work is to construct a more ecologically-integrated and biologically-based representation of soil health traits.

2. Methods

2.1. Experimental station sample collection

All soil samples were collected from The Ohio State University Triplett-Van Doren long-term research trials, which includes two identical experiments located in the northwestern and eastern parts of Ohio. The northwestern and eastern experiment were both founded in 1963. The northwestern experiment soil series is a Hoytville clay loam and the eastern experiment soil series is a Wooster silt loam. Both experiment sites are full factorial randomized complete block designs that have three replicated blocks with two factors. The first factor is tillage, which consists of no-till (NT) and chisel till (CT) treatment. The second factor is crop rotation, which consists of a corn (*Zea mays* L.)-soybean (*Glycine* max L.) (CS) rotation , and a corn-forage-forage (CFF) rotation. In the northwest experiment the forage crop was alfalfa (*Medicago sativa)*. Forage crops in the eastern experiment were an oat (*Avena sativa)* and red clover (*Trifolium pratense)* mix. Soil sampling occurred in the corn phase of each rotation. Soil samples were collected using a 1.9 cm diameter push probe to a depth of 10 cm. During planting (May 2020) and harvest (October 2020) ten soil cores were collected within each plot using stratified random sampling to make one composite sample. Soil was then subsampled for routine soil analyses (NCERA-13, 2015), soil moisture, POXC, protein, mineralizable C, nematode identification, and enzyme activity.

2.2. On-farm sample collection

Soil samples were collected from 44 farmer fields located across Ohio

(Table S1). Additionally, coordinates of sampling location, sampling date, livestock, tile drainage, tillage intensity, crop type, organic management, and soil texture class data were recorded for each sampling point (Table S1). Each participating farm was mailed a soil sampling kit and asked to collect 10 soil cores to a depth of 10 cm to make one composite sample per field. Once the soil samples were collected, the farmers mailed the soil samples to the Ohio Agriculture Research and Development Center (Wooster, OH) for soil health testing. Once received, soils were subsampled for routine soil analyses (NCERA-13, 2015), soil moisture, POXC, protein, mineralizable C, nematode identification, and enzyme activity.

2.3. *Soil health test analysis*

A suite of soil biological health indicator analyses were conducted for both on-station and on-farm samples. Enzyme activities of acid phosphatase (AP), β-glucosidase (GLU) , N-acetyl-β-glucosaminidase (NAG) (which is often also referred to as chitinase), and arylsulfatase (AS) were analyzed using protocols adapted from (Tabatabai, 1994; Deng and Popova, 2011). Enzyme activity was determined colorimetrically from the quantitative assessment of the recovery of *p*-nitrophenol added to the soil (Tabatabai, 1994). Soil, buffer, and substrate were incubated at 37C for 1 h. The reaction was terminated with 0.5 M $CaCl_2$ and 4 mL of Tris (hydroxymethyl) aminomethane (THAM) (0.1 M, pH 12). Absorbance was measured colorimetrically at 415 nm. Permanganate oxidizable carbon (POXC), which measures a slightly processed pool of organic matter in the soil was measured using methods adapted from Culman et al., (2012). Briefly, potassium permanganate ($KMnO_4$) was reacted with soil (2.5 g) and absorbance was measured in a 96-well plate reader. Autoclave-citrate extractable (ACE) soil protein (soil protein), which infers organic N was analyzed (Hurisso et al., 2018). Specifically, sodium citrate solution was added to the soil, autoclaved, and the supernatant was measured using the colorimetric bicinchoninic-acid (BCA) assay (Thermo Scientific, Pierce, Rockford, IL) in a 96-well spectrophotometric plate reader at 562 nm. Mineralizable C—which indicates the pool of soil C available to microbial communities—was measured via a 24-hour laboratory incubation (Hurisso et al., 2016; Franzluebbers and Haney, 2018). Mineralizable C was measured using a LI-820 infrared gas analyzer (LI-COR, Biosciences, Lincoln, NE) to determine the concentration of carbon dioxide (CO_2). Organic matter (OM) was measured by Spectrum Lab (Washington Court, OH) through loss of ignition and verified using the Walkley-Black method (Roper et al., 2019).

2.4. *Nematode structure and function analyses*

Free-living nematodes were extracted using the elutriation and centrifugal flotation method (Oostenbrink, 1960; Hooper et al., 2005). Briefly, soil samples were passed through an elutriator. The collected solution was processed using centrifugal sugar flotation to bring the nematodes into the supernatant solution. Total nematode abundance was determined by counting individuals under a dissecting microscope at 50x magnification. Each nematode was classified as an adult or juvenile to allow for the determination of population stage. From each sample, 100 nematodes were identified to family and assigned to trophic and colonizer-persister groups using live identification with a compound microscope (Yeates et al., 1993; Bongers and Bongers, 1998). The identification of nematodes to family allowed for the determination of nematode feeding group composition for each soil sample (bacterivore, fungivore, predator/omnivore, and plant parasitic). Nematode indices, which can serve as indictors of soil health were calculated using Nematode INdicator Joint Analysis (NINJA) (Sieriebriennikov et al., 2014).

2.5. *Statistical analysis*

We used exploratory factor analysis (EFA)—a form of latent variable analysis—to examine the underlying soil health traits described by our soil health indicators and nematode measurements (Fabrigar and Wegener, 2011). The underlying constructs that EFA describes will be referred to as soil health traits within this study. The measured variables used in the EFA (i.e., soil biological health indicators) were: AP, GLU, NAG, AS, POXC, soil protein, mineralizable C, organic matter, EI, SI, BI, CI, MI, PPI, bacterivores, fungivores, predator-omnivores, and plant parasitic nematodes.

Four built-in quantitative analyses within the *nfactors* package in R were used to determine the number of underlying constructs (i.e., soil health traits) for this study (Fig S1; R Core Team, 2021; Raiche et al., 2013). Soil health indicators were retained on each underlying construct if the loading of the soil health indicator onto the underlying construct was > 0.45 (Hu and Bentler, 1999). Fig. 1 displays a conceptual figure of an EFA in which the soil health indicators are reduced into four underlying latent variables. The *psych* package in R was used to conduct the EFA (Revelle, 2021). Latent variables were named after careful analysis of the retained soil health indicator loadings.

2.6. *Confirmatory factor analysis*

A confirmatory factor analysis (CFA) using the variables retained for each latent variable was used to test the model fit (Fig. 1). To evaluate model fit, a combinatorial approach as recommended by Hu and Bentler (1999) was used. Specifically, the Root Mean Square Error of Approximation (RMSEA) and Standardized Root Mean Square Residual (SRMR) were used to assess the goodness of fit of the retained soil health indicators on each of the latent variables. The CFA was used to derive individual scores for each of the soil health traits for each soil sample. The confirmatory factor analysis was conducted using the *cfa()* command in *lavaan* in R (Rosseel, 2012).

To determine how management practices alter soil health traits an analysis of variance (ANOVA) was conducted on the scores generated for the validated latent variables using the *lmerTest* package in R (Fig. 1; Kuznetsova et al., 2017). Using soil textural class as a covariate in a linear model, significant effects were determined at $p < 0.05$. Graphing was conducted using *ggplot2* (Wickham, 2016).

3. Results and discussion

3.1. *Bivariate relationships between soil health indicators*

To determine the strength of relationship between soil health indicators and nematode community structure and function (hypothesis 1), a total of 125 observations were collected for 18 soil health indicators: AP, AS, NAG, GLU, MI, PPI, CI, EI, SI, BI, plant parasitic, bacterivores, fungivores, omnivore and predators, POXC, mineralizable C, protein, and organic matter (Table S1). As EFA is dependent on the correlation matrix produced from the measured variables, a correlation analysis was conducted for the 18 soil health indicators. Strong correlations ($r > 0.80$) were found between POXC and mineralizable C ($r = -0.81$), GLU and NAG ($r = 0.91$), and GLU and AS ($r = 0.85$) (Table 1). The strong negative relationship found between POXC and mineralizable C is not surprising given that POXC and mineralizable C represent soil C stabilization and C mineralization, respectively (Hurisso et al., 2016). For example, Sprunger et al., (2020) reported that average residuals from a linear regression model comparing mineralizable C and POXC demonstrated that a continuous corn system was influenced by mineralization processes (mineralizable C) compared to perennial systems that were generally more influenced by C stabilization processes (POXC). Like our study, enzyme activities have been found to be strongly and positively correlated with each other as increased microbial mineralization causes the simultaneous breakdown of nutrients (Zhu et al., 2014). Weak correlations were found between nematode indices and soil biological health indicators. However, it is likely that there is extensive collinearity between these variables (Dormann et al., 2013),

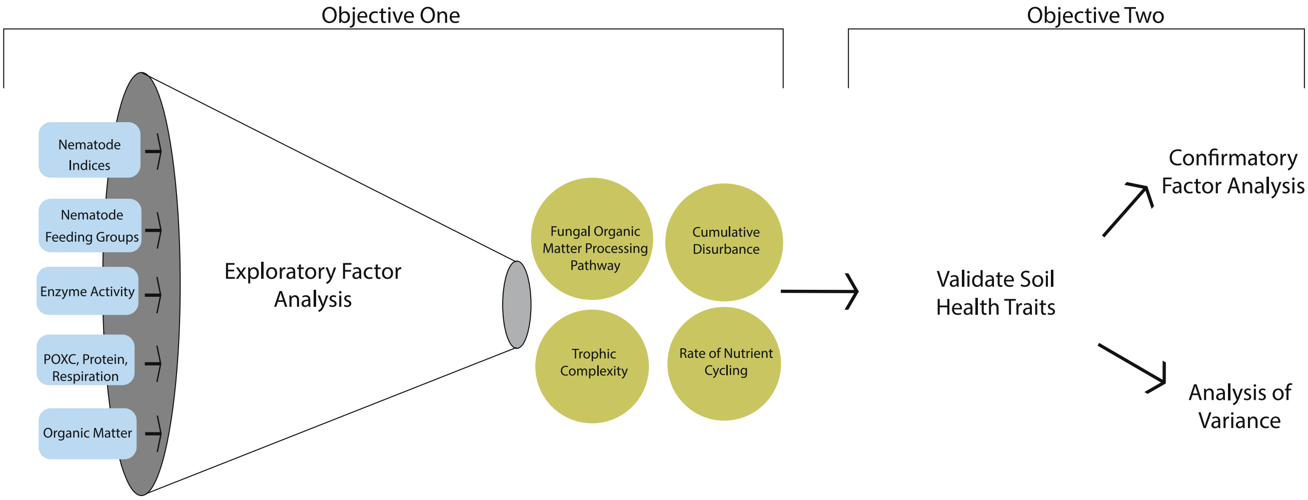

Fig. 1. Conceptual figure of the methodology for describing latent variables from soil biological health indicators using an exploratory factor analysis and determining the effect that management practices have on soil health traits.

suggesting that a more intensive investigation into the quantification of the relationships between nematode community function and soil biological health is warranted.

3.2. *Soil health trait one: Fungal organic matter processing pathway*

We interpreted the indicators associated with soil health trait one as representing the fungal organic matter processing pathway. The soil biological health indicators associated with this soil health trait are mechanistically linked with fungal organic matter breakdown (Ferris and Bongers, 2006; Cloutier et al., 2020) and are therefore best interpreted as representing this soil process (Fig. 2). Within this soil health trait, nematode structure was more strongly associated than function, disproving our first hypothesis that nematode indices will be more strongly integrated with soil health indicators than nematode feeding groups. For example, soil biological health indicators of AP, fungivores, and POXC had strong and positive loadings of 0.74, 0.70, and 0.90, respectively on to soil health trait one (Table 2). Additionally, soil biological health indicators of plant parasitic nematodes, soil protein, and mineralizable C had strong and negative loadings of −0.60, −0.66, and −0.81, respectively (Table 2).

Supporting our interpretation, we found that fungal feeding nematodes (fungivores) are highly integrated with soil biological health indicators of POXC and AP. The relationships between fungivores and the more processed, stable C pools were expected as the fungal decomposition pathway has been found to dominate in systems where substrates have high C:N ratios (Hodge et al., 2000; Güsewell and Gessner, 2009; Gebremikael et al., 2016; Trap et al., 2016). Our findings are like those reported by Margenot and Hodson, (2016) which found that more processed pools of SOM supported greater fungal abundance. Given that POXC represents a more processed pool of C (Arachchige et al., 2018; Culman et al., 2012; Sherrod et al., 2019) it is expected that fungivore abundance would be related to POXC. Moreover, the fungal decomposition channel is more commonly associated with slow decomposition where organic matter is incorporated into stable C pools (Okada and Ferris, 2001; Ferris and Matute, 2003; Steel et al., 2010). The positive loadings of AP and total fungivores is also supported by other studies that have reported that the fungal decomposition pathway is linked to soil P availability (Olusanya et al., 2019). Specifically, fungi have been found to dominate the decomposition channel when under P-limiting conditions (Güsewell and Gessner, 2009). Moreover, the loadings of soil health indicators on soil health trait one suggests that fungal feeding nematodes may be essential for supplying essential ecosystem services of C stabilization and P mineralization (Wang et al., 2004; Maina et al., 2021).

Given that fungal decomposition was positively associated with POXC, a pool that reflects more processed pools of C, it is not surprising that soil protein, mineralizable C, and plant parasitic nematodes were inversely related to fungivores as these measured variables are associated with low C:N ratios and increased nutrient mineralization (Bongers et al., 1997; DuPont et al., 2009). Additionally, given that soil protein is largely of fungal origin it is expected that fungal based protein would be inversely related with fungivore abundance (Rosier et al., 2006). Mineralizable C and soil protein represent microbial activity and the organic N pool that is available for mineralization, respectively (Franzluebbers et al., 2000; Franzluebbers and Stuedemann, 2008; Haney et al., 2018; Hurisso et al., 2018). Moreover, increased mineralizable C and greater pools of inorganic N can result in C loss through increased microbial activity, which supports our findings of an inverse relationship between indicators that represent C stabilization and C mineralization (Nunes et al., 2020; Oldfield et al., 2021). Additionally, plant parasitic nematode infestation of plant roots can enhance microbial populations through the breakdown of root tissue which can cause an influx of organic material that is high in N (Tu et al., 2003). Therefore, it is not surprising that plant parasitic nematode abundance loaded opposite to indicators of C stabilization and slow nutrient decomposition.

3.3. *Soil health trait two: rate of nutrient cycling*

We interpreted the second soil health trait as representing the “rate of nutrient cycling” due to the strong positive loadings from enzyme activities and specific nematode feeding groups (Table 2; Fig. 2). Specifically, the loadings of NAG, AS, and predator/omnivore nematode feeding groups were 0.74, 0.87, and 0.49, respectively (Table 2). These results disproved our first hypothesis, given that nematode feeding groups rather than nematode indices loaded with soil biological indicators.

Predator/omnivore nematode feeding groups are essential for the maintenance of ecosystem function (IPBES, 2019; Wardle, 2005; Sánchez-Moreno et al., 2009). Moreover, omnivore and predator nematodes are essential for the top-down control of the microbivorous nematode populations, and are limited by primary productivity (Ingham et al., 1985; Wardle et al., 1995; Yeates and Wardle,1996; Conti et al., 2020). The predator–prey relationship between predator/omnivore nematodes and microbivorous nematodes allows for nutrient processing up the soil food web, which is crucial for nutrient storage and assimilation (Neher, 2001; Yeates, 2003). Our results indicate that greater

Table 1
Correlation matrix between soil health indicators measured on on-farm and experimental trials.

	AP	AS	GLU	NAG	MI	PPI	CI	BI	EI	SI	Plant Parasitic	Bacterivore	Fungivore	Omnivore/ Predator	POXC	MineralizableCarbon	Protein
AP	1.00																
AS	0.59	1.00															
GLU	0.73	0.85	1.00														
NAG	0.78	0.75	0.91	1.00													
MI	0.23	0.12	0.19	0.18	1.00												
PPI	−0.01	−0.12	−0.15	−0.06	0.01	1.00											
CI	0.10	0.06	0.04	0.04	0.16	−0.39	1.00										
BI	−0.06	0.01	−0.06	0.02	−0.19	−0.14	0.36	1.00									
EI	0.02	0.00	0.07	0.05	−0.48	0.05	−0.27	−0.44	1.00								
SI	0.23	0.16	0.21	0.16	0.69	0.04	0.00	−0.56	−0.04	1.00							
Plant Parasitic	−0.58	−0.44	−0.51	−0.47	−0.35	0.09	−0.12	0.12	0.06	−0.33	1.00						
Bacterivore	−0.05	0.09	0.09	−0.03	−0.09	−0.28	0.20	0.04	0.14	0.03	−0.30	1.00					
Fungivore	0.52	0.27	0.33	0.38	0.40	0.15	0.03	−0.17	−0.13	0.30	−0.71	−0.20	1.00				
Omnivore/Predator	0.20	0.29	0.40	0.21	0.27	−0.18	0.07	−0.17	0.04	0.33	−0.31	0.04	−0.05	1.00			
POXC	0.79	0.49	0.60	0.63	0.28	−0.05	0.21	−0.05	−0.03	0.30	−0.58	−0.01	0.57	0.21	1.00		
Mineralizable Carbon	−0.78	−0.51	−0.66	−0.63	−0.31	0.11	−0.12	−0.00	0.11	−0.26	0.64	−0.03	−0.51	−0.29	−0.81	1.00	
Protein	−0.62	−0.42	−0.56	−0.53	−0.21	0.15	−0.12	−0.05	0.02	−0.11	0.50	−0.04	−0.38	−0.24	−0.64	0.72	1.00
Organic Matter	0.25	0.03	0.11	0.14	0.08	0.06	0.21	0.07	−0.08	0.03	−0.10	−0.10	0.24	−0.02	0.27	0.04	−0.03

nutrient cycling by microbial populations may play a role in augmenting the top-down regulation of soil food webs. Predator/omnivore nematode feeding groups have been linked to the regulation of N mineralization through the consumption of bacterivorous nematodes (Beare, 1997; Culman et al., 2010). Additionally, AS is an indicator of greater plant available SO_4 (Bandick and Dick, 1999). Nematode abundance has been reported to increase with greater AS activity (García-Álvarez et al., 2004), yet the relationship between predator/omnivore nematodes and AS has not been mechanistically linked before. These results therefore point to the importance of a structured soil food web for enhanced S and N cycling, which has implications for improved soil health. The AS enzyme cleaves C–O–S bonds and the overall activity is strongly correlated to organic C pools, thus enhanced S cycling through predator/omnivore nematodes may lead to greater organic C pools (Ekenler and Tabatabai, 2003). Additionally, increased NAG activity has been linked to enhanced ecosystem and soil health as greater N cycling through the microbial pool allows for reduced input of inorganic N fertilizer and enhanced organic N pools (Drinkwater and Snapp, 2007; Cenini et al., 2016; Martin and Sprunger, 2021b). Consequently, the integration of predator/omnivore nematode feeding groups with NAG activity indicates that structured soil food webs are essential for maintained nutrient cycling and sustained organic N pools.

3.4. Soil health trait three: trophic complexity

Soil health trait three was interpreted to represent “trophic complexity” given the nematode index loadings from the MI, SI, and EI (Fig. 2). Moreover, these loadings reflect soil food web complexity, structure, and nutrient input which is why soil health trait three was inferred to be linked to trophic complexity. Soil health trait three had positive loadings from the MI and SI of 0.98 and 0.58, respectively (Table 2). Additionally, the EI had a factor loading of −0.59 onto soil health trait three. Nematode indices were the only measurements to load onto soil health trait three. This suggests that nematode indices and other soil biological indicators, such as nematode feeding groups are not regulated by similar underlying soil health traits. These results are contrary to our first hypothesis that indicators of nematode function and soil health indicators would be related to similar soil health traits.

The positive relationship between the MI and SI was not surprising given that both indices are influenced by the abundance of *K*-strategist nematodes (Bongers and Bongers, 1998, Ferris et al., 2001). Moreover, the negative relationship between the EI and SI is supported by soil faunal profiles, which demonstrate the inverse relationship between the EI and SI (Ferris et al., 2001). For example, as the EI increases and SI decreases soil food webs become disturbed, bacterial dominated, and N-enriched (Ferris et al., 2001), whereas systems that have moderate EI and high SI are found to be undisturbed, fungal dominated, and moderately N enriched (Ferris and Matute, 2003). Our results further support the strong linkage between the EI and SI, as these nematode indicators were all governed by the same underlying soil health trait. Moreover, it was notable that common soil biological health indicators and nematode indices did not describe similar underlying soil health traits. Specifically, these results reveal that nematode indices may be poorly suited for integration with soil biological health indicators in agricultural systems of the Midwest.

3.5. Soil health trait four: cumulative disturbance

We interpreted soil health trait four as “cumulative disturbance” due to the positive loadings from the EI and SI and negative loading from the BI, the latter of which is strongly associated with ecosystem disturbance. Soil health trait four had moderate and positive loadings from the EI and SI, with loadings of 0.51 and 0.50, respectively (Table 2). Additionally, the BI loaded strongly and negatively onto soil health trait four, with a loading of −0.90. Similar to soil health trait three, only nematode indices of the EI, SI, and BI loaded onto soil health trait four.

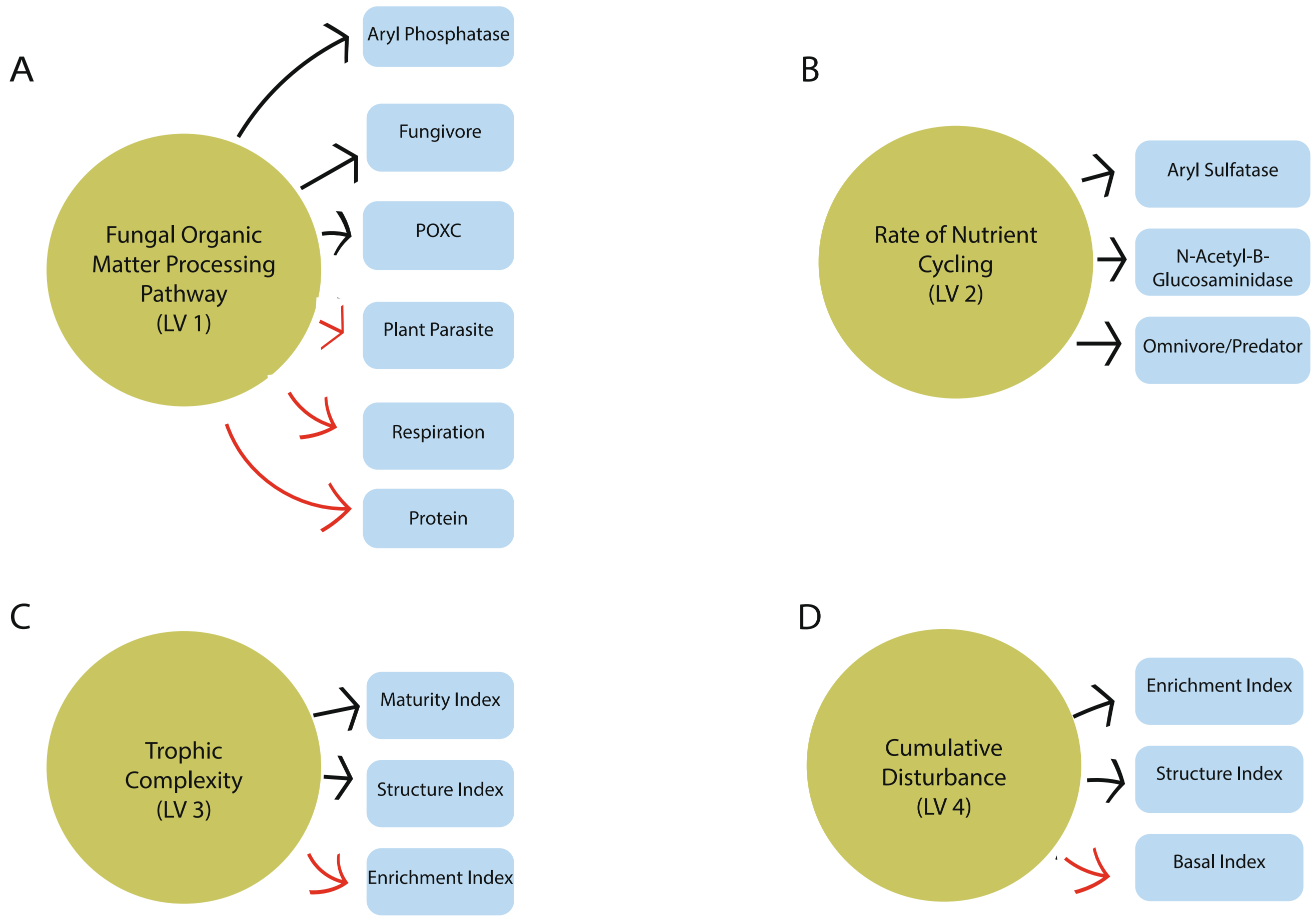

Fig. 2. Named latent variables based on retained soil biological health indicators from the exploratory factor analysis.

Table 2

Factor loadings of measured variables onto the four latent variables. Retained factor loadings at > 0.45 are displayed in bold.

	Fungal Organic Matter Processing Pathway(LV1)	Rate of Nutrient Cycling(LV2)	Trophic Complexity (LV3)	Cumulative Disturbance (LV4)
Acid Phosphatase	**0.74**	0.23	−0.05	0.02
N-acetyl-β-glucosaminidase	0.22	**0.74**	0.02	−0.04
Aryl Sulfatase	−0.03	**0.87**	0.00	−0.05
β-Glucosidase	0.06	**0.96**	0.01	0.02
Fungivore	**0.70**	−0.19	0.12	0.11
Omnivore/Predator	−0.17	**0.49**	0.24	0.15
Plant Parasite	**−0.60**	−0.05	−0.13	−0.09
Bacterivore	−0.13	0.16	−0.02	−0.03
Maturity Index	0.01	0.07	**0.98**	0.02
Structure Index	0.08	0.04	**0.59**	**0.50**
Enrichment Index	−0.06	0.15	**−0.59**	**0.51**
Basal Index	−0.05	0.05	−0.04	**−0.90**
Channel Index	0.18	−0.07	0.18	−0.40
POXC	**0.94**	−0.04	−0.04	0.01
Soil protein	**−0.66**	−0.14	0.02	0.10
Mineralizable Carbon	**−0.81**	−0.12	−0.02	0.05
Organic Matter	0.24	−0.04	0.07	−0.05

Functionally, this suggests that different soil health traits inform nematode feeding group abundance and the derived nematode indices. These results disproved our first hypothesis as feeding group abundances were linked to common soil health indicators, and nematode indices were not linked to any of the soil health indicators.

The BI inverse relationship to the SI and EI is further supported by the nematode community faunal analysis. Specifically, the SI and EI can be positively related to each other under undisturbed and moderately enriched conditions (Ferris et al., 2001). Moreover, when systems are undisturbed and moderately enriched it is not surprising that the BI, which indicates disturbed systems, would be inversely related to the EI and SI (Melakeberhan et al., 2021). Similar to the feeding groups in the "trophic complexity" trait, nematode indices were not functionally linked to other common soil health indicators.

3.6. *Integration of organic matter and soil biological indicators*

One very notable result from our analysis is that organic matter measured via loss-on-ignition and soil biological health indicators did not share underlying soil health traits. Specifically, OM loaded weakly onto all four soil health traits (Table 3). Organic matter is one of the most commonly measured parameters in soil fertility tests and has traditionally been used to infer nutrient retention, soil structure, and fertility (Doran and Parkin, 1994; Tabatabai, 1994; Weil and Magdoff, 2004). However, our results indicate that OM and soil biological health indicators—both nematode and more common soil health measures—may not share similar underlying traits. This suggests that OM may be too coarse of a measurement to reflect changes in organic matter dynamics and the soil nematode community.

3.7. *Using data-model agreement to validate soil health traits*

Our CFA model showed an acceptable level of agreement between the data and the four-trait model implied by our EFA. Our CFA model had RMSEA = 0.13 and SRMR = 0.08, indicating an acceptable fit to the data. In context, the results of the CFA indicated that the soil health traits were accurately represented by the loadings of the various soil biological health indicators. This indicates that while our model sufficiently describes the data, relationships between soil health traits and our measured variables were relatively weak, indicating significant room for improvement. Our results do not give us insight into how to achieve improved model fits in our current dataset. However, the results from the CFA are novel as it is uncommon to have a dependable model fit from a CFA without the further tuning of certain variables (Brown, 2015).

3.8. *Management effects on soil health traits*

Our study determined how management practices would alter the soil health traits. Results demonstrated that reduced tillage intensity can enhance some soil health traits in both on-farm and experimental trials, which partially supported our second hypothesis that decreased management intensity will enhance soil health traits. Tillage intensity had significant effects on the fungal organic matter processing pathway and rate of nutrient cycling ($p < 0.05$; Table 3; Fig. 3). Fungal organic matter processing pathway and the rate of nutrient cycling increased under minimum or no-till conditions (Table 3; Fig. 3). This increase was consistent in both on-farm and experimental trials for the fungal organic matter processing pathway but was not consistent across contexts for the nutrient cycling trait. The decrease in fungal processing with increased tillage intensity is expected given that mechanical disturbance reduces fungal hyphae growth (Carneiro et al., 2019). Additionally, reduced tillage intensity can lead to increased residue input, which has been shown to enhance nutrient cycling (Hendrix et al., 1986; Wardle et al., 1995; Fu et al., 2000). Our finding of increased fungal organic matter decomposition is consistent with previous *meta*-analyses examining the effects of tillage on arbuscular mycorrhizal fungi (Bowles et al., 2017) and the subsequent reflection of that decrease in traditional soil health indicators (Nunes et al., 2020). The mechanical disturbance of tillage degrades the overall structure of the soil food web, often decreasing crop productivity (Brussaard, 1997; Bongers and Bongers, 1998; Mezeli et al., 2019). Additionally, reduced disturbance within minimum and no-till systems improves aggregate formation, enhancing both nematode habitat and the rate of nutrient cycling (Zhang et al., 2012; Zhong et al., 2017).

Table 3
Analysis of Variance of the effect of environmental variables on each latent variable. Texture class was analyzed as a covariate within the model. (*) indicates $p < 0.05$.

Fungal Organic Matter Processing Pathway (LV 1)	Factor	F-Value	P-values
	Tillage	5.43	<0.006*
	Experiment Trial	160.5	<0.0001*
	Tile Drainage	1.67	0.20
	Crop Type	1.3	0.22
	Livestock	0.86	0.35
	Organic System	1.2	0.27
Rate of Nutrient Cycling (LV 2)	Factor	F-Value	P-values
	Tillage	9.2	<0.0001*
	Experiment Trial	194.15	<0.0001*
	Tile Drainage	0.63	0.43
	Crop Type	1.5	0.14
	Livestock	0.39	0.53
	Organic System	0.43	0.51
Trophic Complexity(LV 3)	Factor	F-Value	P-values
	Tillage	9.2	0.50
	Experiment Trial	4.9	0.10
	Tile Drainage	1.2	0.28
	Crop Type	1.5	0.33
	Livestock	1.1	0.29
	Organic System	3.72	0.057*
Cumulative Disturbance(LV 4)	Factor	F-Value	P-values
	Tillage	0.37	0.69
	Experiment Trial	40.54	0.51
	Tile Drainage	0.46	0.52
	Crop Type	1.5	0.34
	Livestock	0.50	0.47
	Organic System	0.08	0.77

Unexpectedly, our results show that rate of nutrient cycling in on-farm trials was greater in minimum tillage systems than no-till systems, which partially disproved our second hypothesis (Fig. 3). There are several potential explanations for this unexpected result. First, this could reflect a bias arising from unbalanced sample sizes between minimum and no-till fields in the on-farm trials. Secondly, differing definitions of no-till between researchers and farmers could confound the data gathered in the on-farm trials (Uri, 2000). While the first two of these explanations suggest a false negative, it is also possible that the factor analytic approach is able to detect more subtle effects than other single-measurement methods. For example, our findings of greater nutrient cycling in minimum tillage than no-till systems could also be attributed to the length of time since no-till was initiated, as it often takes 5 or even 10 years before the benefits are consistently realized (Pittelkow et al., 2015). Thus, our results could reflect transient increases in overall nutrient cycling in on-farm minimum till systems, although our results don't permit further validation of this explanation. Nevertheless, these contrasting results between on-farm and experimental trials demonstrate the potential for factor analytic methods to be utilized as a tool for site-specific soil health assessment.

3.9. *Nematode indices are decoupled from other soil health indicators*

Our results indicate that nematode indices are not linked with other soil health indicators. Specifically, correlations indicate a weak relationship between all nematode indices and soil biological indicators (Table 1). Additionally, soil biological health indicators and nematode indices did not represent similar soil health traits (Fig. 2). Moreover, the soil health traits that nematode indices loaded on were found to be unresponsive to changes in management intensity (Fig. 3). Collectively, this suggests that nematode indices may not be responsive to changes in management or actively cycling fractions of organic matter. Thus, while nematode indices were intended to serve as bioindicators of disturbance and the condition of the soil food web (Ferris et al., 2001), nematode community structure and soil biological health indicators may be more informative in terms of explaining ecosystem processes. Our findings corroborate Wall et al., (2002) where univariate nematodes indices failed to represent structural changes in the nematode community when comparing between sandy dune and beach systems. Thus, future research that aims to investigate ecosystem functioning should utilize nematode community structure rather than nematode indices (Martin

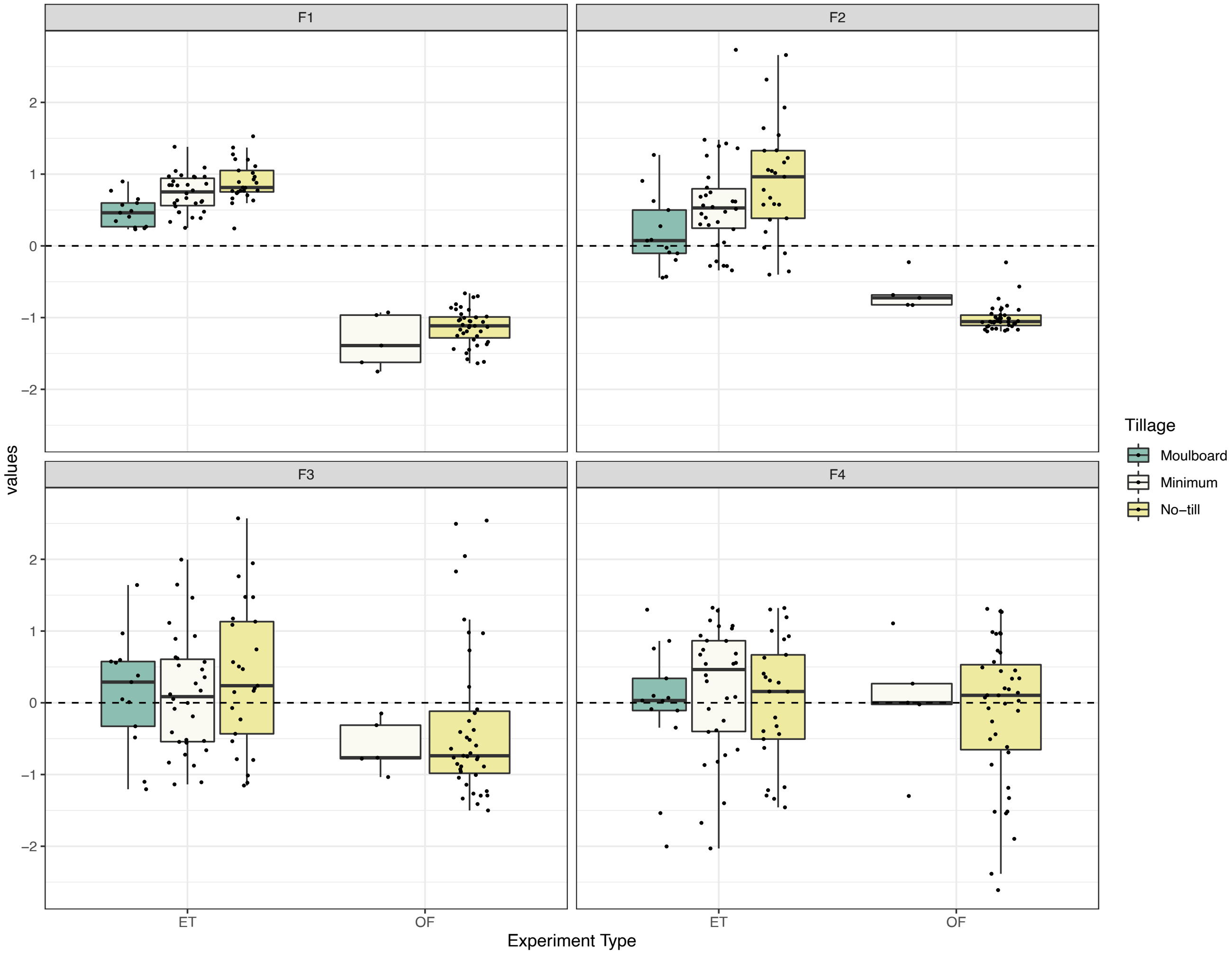

Fig. 3. The effect of tillage (color) and experiment type on each named latent variable. Data points represent individual observations from the confirmatory factor analysis. Error bars represent one standard error from the mean.

and Sprunger, under review).

3.10. Novelty of EFA and future research

Thus far, soil health literature has relied on individual indicators to explore differences in soil health (Harris et al., 1997; Lehmann et al., 2020). Moreover, as individual indicators can represent various aspects of the soil health framework there is an imperative need to determine and quantify the underlying traits that soil health indicators share (Janzen et al., 2021). Exploratory factor analysis can serve as an empirical and rigorous approach for the quantification of underlying soil health traits (Wade et al., under review; Zhang et al., 2018). Quantitative analysis built on EFA can be subsequently linked to soil health outcomes and ecosystems processes (Wade et al., 2020). Moreover, in this study the use of EFA synthesized data to build a strong conceptual foundation to identify and quantify the underlying soil health traits that inform both common soil biological health indicators and nematode communities. Our results demonstrate that this rigorous quantitative model can be used to integrate theory and empirics of soil biological health. Soil health traits that were shared by nematode feeding groups and other common soil biological indicators may be indicative of the ecosystem functions that are essential for C accrual and sustained crop productivity (DuPont et al., 2009; Lindahl and Tunlid, 2015). However, future research should seek to validate the soil health traits we have elucidated here and link those traits to specific ecosystem services.

4. Conclusion

This study utilized factor analytic approaches to incorporate nematode community structure and function into existing interpretations of soil biological health indicators. First, we showed that nematode feeding groups share underlying soil health traits and can be integrated with commonly used soil biological health indicators of enzyme activities, soil protein, mineralizable C, and POXC. Next, we showed that nematode indices did not share underlying soil health traits with other soil biological health indicators. Lastly, we validated our interpretations of specific EFA-derived soil health traits by demonstrating that they are sensitive to management practices, producing consistent effects across both experimental and on-farm studies. Furthermore, our results indicate that organic matter measured via loss on ignition—a measurement included in many commercial soil fertility tests—did not provide meaningful information about our four soil health traits. Taken together, our findings demonstrate the potential to integrate nematode community structure (i.e., nematode feeding groups) and indices within common soil health assessment frameworks. This integration of higher trophic levels of soil food webs with soil health indicators has the potential to better reflect and predict important ecosystem processes and lead to the development of improved soil health. Moreover, nematode communities may serve as valuable soil biological indicators that could help foster more sustainable management practices leading to improved soil health traits including, enhanced nutrient cycling, reduced disturbance, and greater trophic complexity.

CRediT authorship contribution statement

Tvisha Martin: Writing – review & editing, Visualization, Investigation, Data curation, Writing – original draft, Methodology, Software, Conceptualization. **Jordon Wade:** Writing – review & editing, Software, Validation, Methodology, Software, Conceptualization. **Prabhjot Singh:** . **Christine D. Sprunger:** Writing – review & editing, Visualization, Investigation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108676.

References

Arachchige, P.S.P., Hettiarachchi, G.M., Rice, C.W., et al., 2018. Sub-micron level investigation reveals the inaccessibility of stabilized carbon in soil microaggregates. Sci. Rep. 8, 16810. https://doi.org/10.1038/s41598-018-34981-9.

Bandick, A.K., Dick, R.P., 1999. Field management effects on soil enzyme activities. Soil Biol. Biochem. 31, 1471–1479. https://doi.org/10.1016/S0038-0717(99)00051-6.

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511. https://doi.org/10.1038/nature13855.

Barlog, P., Lukowiak, R., Grzebisz, W., 2017. Predicting the content of soil mineral nitrogen based on the content of calcium chloride-extractable nutrients. J. Plant Nutr. Soil Sci. 180, 624–635. https://doi.org/10.1002/jpln.201700136.

Bastida, F., Kandeler, E., Moreno, J.L., Ros, M., Garcıa, C., 2008. Application of fresh and composted organic wastes modifies structure, size and activity of soil microbial community under semiarid climate. Appl. Soil Ecol. 12.

Baveye, P.C., 2021. Bypass and hyperbole in soil research: A personal view on plausible causes and possible remedies. Eur. J. Soil Sci. 72, 21–28. https://doi.org/10.1111/ejss.12940.

Beare, M. H, 1997. Fungal and bacterial pathways of organic matterdecomposition and nitrogen mineralization in arable soil. in. Brussaard and R. Ferrera-Cerrato, (Eds.), Soil ecology in sustainable agricultural systems. pp. 37–70.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19. https://doi.org/10.1007/BF00324627.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10, 239–251. https://doi.org/10.1016/S0929-1393(98)00123-1.

Bongers, T., van der Meulen, H., Korthals, G., 1997. Inverse relationship between the nematode maturity index and plant parasite index under enriched nutrient conditions. Appl. Soil Ecol. 6, 195–199. https://doi.org/10.1016/S0929-1393(96)00136-9.

Bonkowski, M., Villenave, C., Griffiths, B., 2009. Rhizosphere fauna: the functional and structural diversity of intimate interactions of soil fauna with plant roots. Plant Soil 321, 213–233. https://doi.org/10.1007/s11104-009-0013-2.

Bowles, T.M., Jackson, L.E., Loeher, M., Cavagnaro, T.R., 2017. Ecological intensification and arbuscular mycorrhizas: a meta-analysis of tillage and cover crop effects. J. Appl. Ecol. 54, 1785–1793. https://doi.org/10.1111/1365-2664.12815.

Brown, T.A., 2015. Confirmatory Factor Analysis for Applied Research, Second Edition. Guilford Publications.

Brussaard, L., 1997. Biodiversity and Ecosystem Functioning in Soil. Ambio 26, 563–570.

Brussaard, L., Pulleman, M.M., Ouédraogo, É., Mando, A., Six, J., 2007. Soil fauna and soil function in the fabric of the food web. Pedobiologia 50, 447–462. https://doi.org/10.1016/j.pedobi.2006.10.007.

Bünemann, E.K., Bongiorno, G., Bai, Z., Creamer, R.E., De Deyn, G., de Goede, R., Fleskens, L., Geissen, V., Kuyper, T.W., Mäder, P., Pulleman, M., Sukkel, W., van Groenigen, J.W., Brussaard, L., 2018. Soil quality – A critical review. Soil Biol. Biochem. 120, 105–125. https://doi.org/10.1016/j.soilbio.2018.01.030.

Carneiro, M.A.C., de Assis, P.C.R., Paulino, H.B., da Rocha, M.R., Teixeira, R.A., Pinto, F. A., dos Santos, J.V., Siqueira, J.O., de Souza, E.D., 2019. Diversity of arbuscular mycorrhizal fungi and nematodes in a 14 years no-tillage chronosequence. Rhizosphere 10, 100149. https://doi.org/10.1016/j.rhisph.2019.100149.

Cenini, V.L., Fornara, D.A., McMullan, G., Ternan, N., Carolan, R., Crawley, M.J., Clément, J.-C., Lavorel, S., 2016. Linkages between extracellular enzyme activities and the carbon and nitrogen content of grassland soils. Soil Biol. Biochem. 96, 198–206. https://doi.org/10.1016/j.soilbio.2016.02.015.

Cloutier, M.L., Murrell, E., Barbercheck, M., Kaye, J., Finney, D., García-González, I., Bruns, M.A., 2020. Fungal community shifts in soils with varied cover crop treatments and edaphic properties. Sci. Rep. 10, 6198. https://doi.org/10.1038/s41598-020-63173-7.

Conti, E., Di Mauro, L.S., Pluchino, A., Mulder, C., 2020. Testing for top-down cascading effects in a biomass-driven ecological network of soil invertebrates. Ecol. Evolut. 10, 7062–7072. https://doi.org/10.1002/ece3.6408.

Culman, S.W., DuPont, S.T., Glover, J.D., Buckley, D.H., Fick, G.W., Ferris, H., Crews, T. E., 2010. Long-term impacts of high-input annual cropping and unfertilized perennial grass production on soil properties and belowground food webs in Kansas, USA. Agric. Ecosyst. Environ. 137, 13–24. https://doi.org/10.1016/j.agee.2009.11.008.

Culman, S.W., Snapp, S.S., Freeman, M.A., Schipanski, M.E., Beniston, J., Lal, R., Drinkwater, L.E., Franzluebbers, A.J., Glover, J.D., Grandy, A.S., Lee, J., Six, J., Maul, J.E., Mirsky, S.B., Spargo, J.T., Wander, M.M., 2012. Permanganate Oxidizable Carbon Reflects a Processed Soil Fraction that is Sensitive to Management. Soil Sci. Soc. Am. J. 76, 494–504. https://doi.org/10.2136/sssaj2011.0286.

Deng, S., Popova, I., 2011. Carbohydrate Hydrolases, in: Methods of Soil Enzymology. John Wiley & Sons, Ltd, pp. 185–209. doi:10.2136/sssabookser9.c9.

Dose, H.L., Fortuna, A.-M., Cihacek, L.J., Norland, J., DeSutter, T.M., Clay, D.E., Bell, J., 2015. Biological indicators provide short term soil health assessment during sodic soil reclamation. Ecol. Ind. 58, 244–253. https://doi.org/10.1016/j.ecolind.2015.05.059.

Dobermann, A., 1994. Factors causing field variation of direct-seeded flooded rice. Geoderma 62, 125–150. https://doi.org/10.1016/0016-7061(94)90032-9.

Doran, J.W., Parkin, T.B., 1994. Defining and Assessing Soil Quality, in: Defining Soil Quality for a Sustainable Environment. John Wiley & Sons, Ltd, pp. 1–21. doi: 10.2136/sssaspecpub35.c1.

Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Appl. Soil Ecol. 15, 3–11. https://doi.org/10.1016/S0929-1393(00)00067-6.

Dormann, C.F., Elith, J., Bacher, S., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Drinkwater, L.E., Snapp, S.S., 2007. Nutrients in Agroecosystems: Rethinking the Management Paradigm, in: Sparks, D.L. (Ed.), Advances in Agronomy. Academic Press, pp. 163–186. doi:10.1016/S0065-2113(04)92003-2.

DuPont, S.T., Ferris, H., Van Horn, M., 2009. Effects of cover crop quality and quantity on nematode-based soil food webs and nutrient cycling. Appl. Soil Ecol. 41, 157–167. https://doi.org/10.1016/j.apsoil.2008.10.004.

Ekenler, M., Tabatabai, M.A., 2003. Responses of phosphatases and arylsulfatase in soils to liming and tillage systems. J. Plant Nutr. Soil Sci. 166, 281–290. https://doi.org/10.1002/jpln.200390045.

Fabrigar, L.R., Wegener, D.T., 2011. Exploratory Factor Analysis, Understanding Statistics. Oxford University Press. doi:10.1093/acprof:osobl/9780199734177.001.0001.

Ferris, H., 2010a. Contribution of Nematodes to the Structure and Function of the Soil Food Web. J. Nematol. 42, 63–67.

Ferris, H., 2010b. Form and function: Metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 8.

Ferris, H., Bongers, A.M.T., 2009. Indices Developed Specifically for analysis of Nematode Assemblages. Nematod. Environ. Indicat. 124–145.

Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. J. Nematol.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29. https://doi.org/10.1016/S0929-1393(01)00152-4.

Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. Appl. Soil Ecol. 23, 93–110. https://doi.org/10.1016/S0929-1393(03)00044-1.

Fierer, N., Wood, S.A., Bueno de Mesquita, C.P., 2021. How microbes can, and cannot, be used to assess soil health. Soil Biol. Biochem. 153, 108111 https://doi.org/10.1016/j.soilbio.2020.108111.

Franzluebbers, A.J., Haney, R.L., 2018. Evaluation of Soil Processing Conditions on Mineralizable C and N across a Textural Gradient. Soil Sci. Soc. Am. J. 82, 354–361. https://doi.org/10.2136/sssaj2017.08.0275.

Franzluebbers, A.J., Stuedemann, J.A., 2008. Soil physical responses to cattle grazing cover crops under conventional and no tillage in the Southern Piedmont USA. Soil Tillage Res. 100, 141–153. https://doi.org/10.1016/j.still.2008.05.011.

Franzluebbers, A.J., Wright, S.F., Stuedemann, J.A., 2000. Soil Aggregation and Glomalin under Pastures in the Southern Piedmont USA. Soil Sci. Soc. Am. J. 64, 1018–1026. https://doi.org/10.2136/sssaj2000.6431018x.

Freckman, 1988. Bacterivorous nematodes and organic matter decomposition. Agriculture Ecosystems and Environment 24, 195–217. https://doi.org/10.1016/0167-8809(88)90066-7.

Fu, S., Coleman, D.C., Hendrix, P.F., Crossley, D.A., 2000. Responses of trophic groups of soil nematodes to residue application under conventional tillage and no-till regimes. Soil Biol. Biochem. 32, 1731–1741. https://doi.org/10.1016/S0038-0717(00)00091-2.

Gao, Y., Dang, X., Yu, Y., et al., 2016. Effects of Tillage Methods on Soil Carbon and Wind Erosion. Land Degrad. Dev. 27, 583–591. https://doi.org/10.1002/ldr.2404.

García-Álvarez, A., Arias, M., Díez-Rojo, M.A., Bello, A., 2004. Effect of agricultural management on soil nematode trophic structure in a Mediterranean cereal system. Appl. Soil Ecol. 27, 197–210. https://doi.org/10.1016/j.apsoil.2004.06.002.

Gebremikael, M.T., Steel, H., Buchan, D., Bert, W., De Neve, S., 2016. Nematodes enhance plant growth and nutrient uptake under C and N-rich conditions. Sci. Rep. 6, 32862. https://doi.org/10.1038/srep32862.

Graham, D.W., Knapp, C.W., Christensen, B.T., McCluskey, S., Dolfing, J., 2016. Appearance of β-lactam Resistance Genes in Agricultural Soils and Clinical Isolates over the 20th Century. Sci. Rep. 6, 21550. https://doi.org/10.1038/srep21550.

Güsewell, S., Gessner, M.O., 2009. N : P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. Funct. Ecol. 23, 211–219. https://doi.org/10.1111/j.1365-2435.2008.01478.x.

Haney, R.L., Haney, E.B., Smith, D.R., Harmel, R.D., White, M.J., 2018. The soil health tool—Theory and initial broad-scale application. Appl. Soil Ecol. 125, 162–168. https://doi.org/10.1016/j.apsoil.2017.07.035.

Harris, R.F., Karlen, D.L., Mulla, D.J., 1997. A Conceptual Framework for Assessment and Management of Soil Quality and Health, in: Methods for Assessing Soil Quality. John Wiley & Sons, Ltd, pp. 61–82. doi:10.2136/sssaspecpub49.c4.

Hendrix, P.F., Parmelee, R.W., Crossley Jr., D.A., Coleman, D.C., Odum, E.P., Groffman, P.M., 1986. Detritus Food Webs in Conventional and No-tillage Agroecosystems. Bioscience 36, 374–380. https://doi.org/10.2307/1310259.

Hodge, A., Robinson, D., Fitter, A., 2000. Are microorganisms more effective than plants at competing for nitrogen? Trends Plant Sci. 5, 304–308. https://doi.org/10.1016/S1360-1385(00)01656-3.

Hooper, D.J., Hallmann, J., Subbotin, S.A., 2005. Methods for extraction, processing and detection of plant and soil nematodes. In: Luc, M., Sikora, R.A., Bridge, J. (Eds.), Plant Parasitic Nematodes in Subtropical and Tropical Agriculture, 2nd edn. CAB International, Wallingford (GB), pp. 53–86.

Horakova, E., Pospisilova, L., Vlcek, V., Mensik, L., 2020. Changes in the soil's biological and chemical properties due to the land use. Soil and Water Research 15, 228–236. https://doi.org/10.17221/44/2019-SWR.

Höss, S., Williams, P.L., 2009. Ecotoxicity testing with nematodes. In: Wilson, M.J., Kakouli-Duarte, T. (Eds.), Nematodes as Environmental Indicators. CABI, Wallingford, pp. 208–224. doi:10.1079/9781845933852.0208.

Hu, L., Bentler, P.M., 1999. Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. Struct. Eq. Model.: A Multidiscipl. J. 6, 1–55. https://doi.org/10.1080/10705519909540118.

Hua, E., Zhu, Y., Huang, D., Liu, X., 2021. Are free-living nematodes effective environmental quality indicators? Insights from Bohai Bay, China. Ecol. Indicat. 127, 107756 https://doi.org/10.1016/j.ecolind.2021.107756.

Hurisso, T.T., Culman, S.W., Horwath, W.R., Wade, J., Cass, D., Beniston, J.W., Bowles, T.M., Grandy, A.S., Franzluebbers, A.J., Schipanski, M.E., Lucas, S.T., Ugarte, C.M., 2016. Comparison of Permanganate-Oxidizable Carbon and Mineralizable Carbon for Assessment of Organic Matter Stabilization and Mineralization. Soil Sci. Soc. Am. J. 80, 1352–1364. https://doi.org/10.2136/sssaj2016.04.0106.

Hurisso, T.T., Moebius-Clune, D.J., Culman, S.W., Moebius-Clune, B.N., Thies, J.E., van Es, H.M., 2018. Soil Protein as a Rapid Soil Health Indicator of Potentially Available Organic Nitrogen. Agric. Environ. Lett. 3, 180006er. https://doi.org/10.2134/ael2018.02.0006er.

Igalavithana, A.D., Farooq, M., Kim, K.-H., Lee, Y.-H., Qayyum, M.F., Al-Wabel, M.I., Lee, S.S., Ok, Y.S., 2017. Determining soil quality in urban agricultural regions by soil enzyme-based index. Environ. Geochem. Health 39, 1531–1544. https://doi.org/10.1007/s10653-017-9998-2.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of Bacteria, Fungi, and their Nematode Grazers: Effects on Nutrient Cycling and Plant Growth. Ecol. Monogr. 55, 119–140. https://doi.org/10.2307/1942528.

IPBES (2019): Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. pp. 56.

Janzen, H.H., Janzen, D.W., Gregorich, E.G., 2021. The 'soil health' metaphor: Illuminating or illusory? Soil Biol. Biochem. 159, 108167 https://doi.org/10.1016/j.soilbio.2021.108167.

Jiang, Y., Qian, H., Wang, X., et al., 2018. Nematodes and microbial community affect the sizes and turnover rates of organic carbon pools in soil aggregates. Soil Biol. Biochem. 119, 22–31. https://doi.org/10.1016/j.soilbio.2018.01.001.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J. Stat. Softw. 82 (13), 1–26. https://doi.org/10.18637/jss.v082.i13.

Lambrecht, I., Vanlauwe, B., Maertens, M., 2016. Integrated soil fertility management: from concept to practice in Eastern DR Congo. Int. J. Agricult. Sustainab. 14, 100–118. https://doi.org/10.1080/14735903.2015.1026047.

Lehmann, J., Bossio, D.A., Kögel-Knabner, I., Rillig, M.C., 2020. The concept and future prospects of soil health. Nat. Rev. Earth Environ. 1, 544–553. https://doi.org/10.1038/s43017-020-0080-8.

Lindahl, B.D., Tunlid, A., 2015. Ectomycorrhizal fungi – potential organic matter decomposers, yet not saprotrophs. New Phytol. 205, 1443–1447. https://doi.org/10.1111/nph.13201.

Liu, L., Li, S., Wilson, G.W.T., Cobb, A.B., Zhou, C., Li, Jinsheng, Li, Jiahuan, Guo, L., Huang, D., 2021. Nematode communities indicate anthropogenic alterations to soil dynamics across diverse grasslands. Ecol. Ind. 132, 108338 https://doi.org/10.1016/j.ecolind.2021.108338.

Liu, J., Wu, L., Chen, D., Yu, Z., Wei, C., 2018. Development of a soil quality index for Camellia oleifera forestland yield under three different parent materials in Southern China. Soil Tillage Res. 176, 45–50. https://doi.org/10.1016/j.still.2017.09.013.

Maina, S., Karuri, H., Ng'endo, R.N., 2021. Free-living nematode assemblages associated with maize residues and their ecological significance. J. Nematol. 53, e2021–38. https://doi.org/10.21307/jofnem-2021-038.

Mairura, F.S., Mugendi, D.N., Mwanje, J.I., Ramisch, J.J., Mbugua, P.K., Chianu, J.N., 2008. Scientific evaluation of smallholder land use knowledge in Central Kenya. Land Degrad. Dev. 19, 77–90. https://doi.org/10.1002/ldr.815.

Margenot, A.J., Hodson, A.K., 2016. Relationships between labile soil organic matter and nematode communities in a California oak woodland. Nematology 18, 1231–1245. https://doi.org/10.1163/15685411-00003027.

Martin, T., Sprunger, C.D., Under Review. Soil food web structure and function in annual row-crop systems: How can nematode communities infer soil health? Appl. Soil Ecol.

Martin, T., Sprunger, C.D., 2021a. A meta-analysis of nematode community composition across soil aggregates: Implications for soil carbon dynamics. Appl. Soil Ecol. 168, 104143 https://doi.org/10.1016/j.apsoil.2021.104143.

Martin, T., Sprunger, C.D., 2021b. Belowground dynamics influence nitrogen cycling and crop productivity in diversified corn systems. Front. Sustain. Food Syst. 5, 435. https://doi.org/10.3389/fsufs.2021.705577.

Melakeberhan, H., Bonito, G., Kravchenko, A.N., 2021. Application of Nematode Community Analyses-Based Models towards Identifying Sustainable Soil Health Management Outcomes: A Review of the Concepts. Soil Syst. 5, 32. https://doi.org/10.3390/soilsystems5020032.

Meng, Q., Yang, J., Yao, R., Liu, G., 2013. Soil quality in east coastal region of China as related to different land use types. J. Soils Sediments 13, 664–676. https://doi.org/10.1007/s11368-012-0648-0.

Mezeli, M.M., Haygarth, P., George, T.S., Neilson, R., Blackwell, M.S.A., 2019. Soil "organic" phosphorus: an untapped resource for crop production? Better Crops Plant Food 103, 22–25.

Moebius-Clune, B.N., D.J. Moebius-Clune, B.K. Gugino, O.J. Idowu, R.R. Schindelbeck, A. J. Ristow, H.M. van Es, J.E. Thies, H.A. Shayler, M.B. McBride, K.S.M Kurtz, D.W. Wolfe, and G.S. Abawi, 2016. Comprehensive Assessment of Soil Health – The Cornell Framework, Edition 3.2, Cornell University, Geneva, NY.

Neher, D.A., 2001. Role of Nematodes in Soil Health and Their Use as Indicators. J. Nematol. 33, 161–168.

Nunes, M.R., Karlen, D.L., Veum, K.S., Moorman, T.B., Cambardella, C.A., 2020. Biological soil health indicators respond to tillage intensity: A US meta-analysis. Geoderma 369, 114335. https://doi.org/10.1016/j.geoderma.2020.114335.

Okada, H., Ferris, H., 2001. Effect of temperature on growth and nitrogen mineralization of fungi and fungal-feeding nematodes. Plant Soil 234, 253–262. https://doi.org/10.1023/A:1017957929476.

Oldfield, E.E., Bradford, M.A., Augarten, A.J., et al., 2021. Positive associations of soil organic matter and crop yields across a regional network of working farms. Soil Sci. Soc. Am. J. https://doi.org/10.1002/saj2.20349.

Olusanya, A.O., Gong, S., Tariq, A., Pan, K., Sun, X., Chen, W., Zhang, L., Dakhil, M.A., Huang, D., Tan, X., 2019. The effect of phosphorus addition, soil moisture, and plant type on soil nematode abundance and community composition. J. Soil. Sedim. 19, 1139–1150. https://doi.org/10.1007/s11368-018-2146-5.

O'Neill, B., Sprunger, C.D., Robertson, G.P., 2021. Do soil health tests match farmer experience? Assessing biological, physical, and chemical indicators in the Upper Midwest United States. Soil Sci. Soc. Am. J. 85, 903–918. https://doi.org/10.1002/saj2.20233.

Oostenbrink, M., 1960. Estimating nematode populations by some selected methods. In: Sasser, J.N., Jenkins, W.R. (Eds.), Nematology. The University of North Carolina Press, Chapel Hill, pp. 85–102.

Pittelkow, C.M., Linquist, B.A., Lundy, M.E., Liang, X., van Groenigen, K.J., Lee, J., van Gestel, N., Six, J., Venterea, R.T., van Kessel, C., 2015. When does no-till yield more? A global meta-analysis. Field Crops Research 183, 156–168. https://doi.org/10.1016/j.fcr.2015.07.020.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.URL https://www.R-project.org/.

Raiche, G., Walls, T.A., Magis, D., Riopel, M., Blais, J.-G., 2013. Non-graphical solutions for Cattell's scree test. Methodology 9 (1), 23–29.

Revelle, William. (2021) Psych: Procedures for Psychological, Psychometric, and Personality Research. Evanston, Illinois. https://CRAN.R-project.org/package=psych.

Ritz, K., Trudgill, D.L., 1999. Utility of nematode community analysis as an integrated measure of the functional state of soils: perspectives and challenges. Plant Soil 212, 1–11. https://doi.org/10.1023/A:1004673027625.

Roper, W.R., Robarge, W.P., Osmond, D.L., Heitman, J.L., 2019. Comparing Four Methods of Measuring Soil Organic Matter in North Carolina Soils. Soil Sci. Soc. Am. J. 83, 466–474. https://doi.org/10.2136/sssaj2018.03.0105.

Rosier, C.L., Hoye, A.T., Rillig, M.C., 2006. Glomalin-related soil protein: Assessment of current detection and quantification tools. Soil Biol. Biochem. 38, 2205–2211. https://doi.org/10.1016/j.soilbio.2006.01.021.

Rosseel, Yves, 2012. lavann: an R package for Sturcutural Equation Modeling. J. Stat. Softw. 48 (2), 1–36.

Sánchez-Moreno, S., Ferris, H., Young-Mathews, A., Culman, S.W., Jackson, L.E., 2011. Abundance, diversity and connectance of soil food web channels along environmental gradients in an agricultural landscape. Soil Biol. Biochem. 43, 2374–2383. https://doi.org/10.1016/j.soilbio.2011.07.016.

Sánchez-Moreno, S., Nicola, N., Ferris, H., Zalom, F., 2009. Effects of agricultural management on nematode–mite assemblages: Soil food web indices as predictors of mite community composition. doi:10.1016/J.APSOIL.2008.09.004.

Shukla, M.K., Lal, R., Ebinger, M., 2006. Determining soil quality indicators by factor analysis. Soil Tillage Res. 87, 194–204. https://doi.org/10.1016/j.still.2005.03.011.

Sherrod, L.A., Vigil, M.F., Stewart, C.E., 2019. Do Fulvic, Humic, and Humin Carbon Fractions Represent Meaningful Biological, Physical, and Chemical Carbon Pools? J. Environ. Qual. 48, 1587–1593. https://doi.org/10.2134/jeq2019.03.0104.

Sieriebriennikov, B., Ferris, H., de Goede, R.G.M., 2014. NINJA: An automated calculation system for nematode-based biological monitoring. Eur. J. Soil Biol. 61, 90–93. https://doi.org/10.1016/j.ejsobi.2014.02.004.

Sprunger, C.D., 2015. Root production and soil carbon accumulation in annual, perennial, and diverse cropping systems (Ph.D.). Michigan State University, United States –, Michigan.

Sprunger, C.D., Martin, T., Mann, M., 2020. Systems with greater perenniality and crop diversity enhance soil biological health. Agric. Environ. Lett. 5, e20030 https://doi.org/10.1002/ael2.20030.

Steel, H., de la Peña, E., Fonderie, P., Willekens, K., Borgonie, G., Bert, W., 2010. Nematode succession during composting and the potential of the nematode community as an indicator of compost maturity. Pedobiologia 53, 181–190. https://doi.org/10.1016/j.pedobi.2009.09.003.

Strauss, J., Smith, H., Pretorius, W., 2015. New approach: Mimicking nature‘s ratios and values-measuring the health and fertility status of your soil: Soils. SABI Magazine-Tydskrif 7 (6), 26–29.

Tabatabai, M.A., 1994. Soil Enzymes, in: Methods of Soil Analysis. John Wiley & Sons, Ltd, pp. 775–833. doi:10.2136/sssabookser5.2.c37.

Trap, J., Bonkowski, M., Plassard, C., Villenave, C., Blanchart, E., 2016. Ecological importance of soil bacterivores for ecosystem functions. Plant Soil 398, 1–24. https://doi.org/10.1007/s11104-015-2671-6.

Tu, C., Koenning, S.R., Hu, S., 2003. Root-Parasitic Nematodes Enhance Soil Microbial Activities and Nitrogen Mineralization. Microb. Ecol. 46, 134–144.

Uri, N.D., 2000. Perceptions on the use of no-till farming in production agriculture in the United States: an analysis of survey results. Agricult., Ecosyst. Environ. 77, 263–266. https://doi.org/10.1016/S0167-8809(99)00085-7.

Verhoef, H.A., Brussaard, L., 1990. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. Biogeochemistry 11, 175. https://doi.org/10.1007/BF00004496.

Wade J, Culman SW, Gasch CK, Lazcanoe C, Maltais-Landryf G, Margenot AJ, Martin TK, Potter TS, Wayne RR, Ruark MD, Sprunger CD, Wallenstein MD (Under Review) Rigorous, empirical, and quantitative: a proposed pipeline for soil health assessments. Soil Biology and Biochemistry.

Wade, J., Culman, S.W., Logan, J.A.R., Poffenbarger, H., Demyan, M.S., Grove, J.H., Mallarino, A.P., McGrath, J.M., Ruark, M., West, J.R., 2020. Improved soil biological health increases corn grain yield in N fertilized systems across the Corn Belt. Sci. Rep. 10, 3917. https://doi.org/10.1038/s41598-020-60987-3.

Wall, J., Skene, K., Neilson, R., 2002. Nematode community and trophic structure along a sand dune succession. Biol. Fertil. Soils 35, 293–301. https://doi.org/10.1007/s00374-002-0478-0.

Wang, K.H., McSorley, R., Gallaher, R.N., 2004. Relationship Of Soil Management History And Nutrient Status To Nematode Community Structure. Nematropica 83–96.

Wardle, D.A., 2005. How plant communities influence decomposer communities. Biolo. Divers. Funct. Soils 119–138.

Wardle, D.A., Yeates, G.W., Watson, R.N., Nicholson, K.S., 1995. The detritus food-web and the diversity of soil fauna as indicators of disturbance regimes in agro-ecosystems. Plant Soil 170, 35–43. https://doi.org/10.1007/BF02183053.

Weil, R., Magdoff, F., 2004. Significance of Soil Organic Matter to Soil Quality and Health. In: Magdoff, F., Weil, R. (Eds.), Soil Organic Matter in Sustainable Agriculture, Advances in Agroecology. CRC Press. https://doi.org/10.1201/9780203496374.ch1.

Wickham, H., 2016. Ggplot2: Elegant graphics for data analysis. Springer International Publishing, Cham, Switzerland, p. 260.

Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37, 199–210. https://doi.org/10.1007/s00374-003-0586-5.

Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystems. Agricult., Ecosyst. Environ. 74, 113–135.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding Habits in Soil Nematode Families and Genera—An Outline for Soil Ecologists. J. Nematol. 25, 315–331.

Zhang, X., Li, Q., Zhu, A., Liang, W., Zhang, J., Steinberger, Y., 2012. Effects of tillage and residue management on soil nematode communities in North China. Ecol. Ind. 13, 75–81. https://doi.org/10.1016/j.ecolind.2011.05.009.

Yeates, G.W., Wardle, D.A., 1996. Nematodes as predators and prey: Relationships to biological control and soil processes. Pedobiologia 40, 43–50.

Zhao, J., Li, D., Fu, S., He, X., Fu, Z., Zhang, W., Wang, K., 2016. Using the biomasses of soil nematode taxa as weighting factors for assessing soil food web conditions. Ecol. Ind. 60, 310–316. https://doi.org/10.1016/j.ecolind.2015.06.003.

Zhang, X., Yang, W., Xin, X., Zhu, A., Ding, S., 2020. Poor physical structural components restrict soil fertility and crop productivity for wheat–maize cropping. Nutr. Cycl. Agroecosyst. 117, 169–184. https://doi.org/10.1007/s10705-020-10063-z.

Zhang, X., Zhu, A., Xin, X., Yang, W., Zhang, J., Ding, S., 2018. Tillage and residue management for long-term wheat-maize cropping in the North China Plain: I. Crop yield and integrated soil fertility index. Field Crops Res. 221, 157–165. https://doi.org/10.1016/j.fcr.2018.02.025.

Zhong, S., Zeng, H., Jin, Z., 2017. Influences of different tillage and residue management systems on soil nematode community composition and diversity in the tropics. Soil Biol. Biochem. 107, 234–243. https://doi.org/10.1016/j.soilbio.2017.01.007.

Zhu, B., Gutknecht, J.L.M., Herman, D.J., Keck, D.C., Firestone, M.K., Cheng, W., 2014. Rhizosphere priming effects on soil carbon and nitrogen mineralization. Soil Biol. Biochem. 76, 183–192. https://doi.org/10.1016/j.soilbio.2014.04.033.