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Original article

Dynamics of nematode assemblages and soil function in adjacent restored and degraded soils following disturbance

Manqiang Liu [a,*], Xiaoyun Chen [a,b], Bryan S. Griffiths [b], Qianru Huang [c], Huixin Li [a], Feng Hu [a]

[a] Soil Ecology Lab, College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing 210095, People's Republic of China
[b] Teagasc, Environment Research Centre, Johnstown Castle, Wexford, Ireland
[c] Jiangxi Institute of Red Soil, Jinxian 331717, People's Republic of China

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ABSTRACT

Responses of nematode assemblages and soil function (short-term decomposition) in restored and degraded soil following an experimental disturbance (copper, chloroform, heat or drying) were monitored for 65 days. We tested the hypotheses: restoration enhanced the measured soil parameters; stability to disturbance was higher in degraded soil due to induced tolerance; and whether changes of the nematode assemblage were related to soil function. Even after disturbance, greater nematode abundance (>150 vs >10 per 100 g soil), nematode richness ($D' > 1.0$ vs >0.4) and function (>1.0 vs >0.05 mg CO_2 g^{-1} $week^{-1}$) were maintained in restored than in degraded soil, respectively. An increase in nematode enrichment index (from 60 to >75) following all disturbances was attributed to the relatively high abundance of tolerant fungivores. The greater stability of the nematode structure index in degraded soil following heat and drying (120% and 125% respectively of the control), than in restored soil (90% and 30% of control) was due to a higher proportion of tolerant omnivores and carnivores. Thus some higher trophic level nematodes, with high c–p values, were tolerant to disturbance. However, stability of function was greater for restored than degraded soil, with a reduction over time in the degraded soil regardless of disturbance type. The differences in the responses of nematodes and soil function to disturbance suggest that nematodes could provide complementary insights into soil stability.

1. Introduction

Functional stability of soil ecosystems are of concern due to unprecedented rates of biodiversity loss under natural and anthropogenic disturbances [11,20,22,24,30,42–45]. The functional resistance and resilience of soil, considered as two components of stability, match well with the wider concepts of soil quality and health which relate to the soil's continued capacity to deliver human welfare while maintaining biodiversity [25]. The relationship between biodiversity and function in soil is still unclear, though ecological hypotheses suggest that biodiversity may have an important role in the functional stability under a changing environment (i.e. following disturbance) [41], related to functional redundancy [25,46]. Griffiths et al. [22,23] attempted to differentiate the functional stability of soils through dynamically monitoring function during soil incubation following experimental disturbances. However, the extremely high stability of broad-scale function (e.g. decomposition of plant residues) as well as the difficulty of determining multiple functions following disturbance poses a problem in sensitively reflecting soil functional status [25,40,45,46].

The difficulty in characterizing a wide range of broad/specific soil functions led to studies focusing on functional indicators [25,40]. Of those, soil nematodes are good candidates to suitably indicate soil function following disturbances due to their ubiquitous distribution, high diversity, important functional role and their trophic groups being functionally related [1,12,18,35,50]; furthermore, the recently developed community-level diagnosis approach which integrates nematode trophic group and life history, such as maturity index and graphic faunal analysis, reinforce the indicative values of nematodes to interpret the response of the wider soil community following different disturbances [2,15,17,19,32,38,39,50]. A gap in this field is that there are few experiments to monitor the immediate response and recovery trajectory of both nematode assemblage and functional changes following disturbance in a short time scale. Such knowledge is necessary to validate whether nematode analysis are informative for indicating the functional stability of the

* Corresponding author. Tel.: +86 25 84395104.
E-mail addresses: liumq@njau.edu.cn, manqiang-liu@163.com (M. Liu), xychen@njau.edu.cn (X. Chen), Bryan.Griffiths@teagasc.ie (B.S. Griffiths), fenghu@njau.edu.cn (F. Hu).

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soil ecosystem. Current studies focused on the microbial community have provided valuable insights [8,10,20,30,42–46], but nematode analysis may provide a more comprehensive knowledge of the whole soil food web following disturbance.

The objective of our study was to characterize the changes of nematode assemblage and soil function in degraded or restored soils after applying experimental disturbances, in order to test whether nematodes could indicate soil functional stability. Four types of disturbance (i.e. copper, chloroform fumigation, heat and drying) were selected for their environmental relevance to the two soils. Copper, a persistent disturbance, represents heavy metal pollution that receives wide environmental concern. Chloroform fumigation, a transient disturbance, represents a common local practice for controlling soil borne pathogens in vegetable production. Heat or drying shock disturbances are two typical factors for local soils due to the strong seasonal weather cycle. We focused on two soils with distinct management histories, to determine the relationships between nematode assemblage and soil function. Our specific hypotheses were:

(1) Higher absolute values of abundance, diversity, maturity and structure of the nematode assemblage and soil functions will be observed in restored than degraded soil if no experimental disturbances are applied [6,16,29].
(2) The absolute values, in particular the stability of nematode and functional parameters, might be higher in degraded soil for some disturbance types, thanks to their pre-disturbance induced community tolerance to specific disturbance type, as indicated by studies on microbial communities [5,10,43].
(3) Absolute or relative changes of the nematode assemblage will be related to soil functional parameters irrespective of disturbance.

2. Materials and methods

2.1. Site and soil description

Soils used for laboratory experiment were collected from a typical red soil region (N28°15′, E116°55′, Yujiang county, Jiangxi province in Southeast China). This area is representative of a typical subtropical moist climate with a mean annual temperature of about 17.7 °C, a maximum daily temperature of around 40 °C in summer and a rainfall of 1750 mm, about 50% of which falls from March to early July. The uneven distribution of hydrothermal resource causes strong seasonal heat and drought in summer and autumn from July to October, respectively [34]. Low hills are the dominant landform in this area and the dominant soil type is typical red soil (Acrisols, WRB) derived from Quaternary red earth. This hilly region is also famous for the susceptibility to degradation from severe erosion.

A typical degraded area of about 10 ha, once called “red desert” in subtropical China, was selected. Within this area, local farmers have grown vegetables for about 20 years, restoring the soil with organic amendments. Two extreme soils (restored and degraded) with distinct physicochemical and biological properties were collected for pretreatment and later experiment, i.e. subjecting to experimental disturbance and incubation (see below). The restored soil has grown vegetables (Chinese cabbage, lettuce, pepper, tomato, bean, radish, intercropped or rotated yearly) and been fertilized with mainly pig manure for at least 20 years; while the degraded soil has not been used for farming and has a sparsely distribution of grass (mainly *Setaria viridis*, *Arunfinella anomala*) and pine (*Pinus massoniana*), with vegetation covering no more than 20% of soil surface.

Briefly, soil properties were markedly improved compared with those in the degraded soil after decades’ restored managements (Table 1). The pH increased 1.6 units mainly due to lime amendments (1500 kg $CaCO_3$ per ha) once five years. The total organic C, organic and mineral N, microbial biomass C and N, soil structural stability increased by more than twice, and bacterial abundance and fungal biomass increased about more than 4 times, in restored soil than degraded soil (Table 1).

2.2. Soil sampling and processing

Soils were collected at a depth of 0–20 cm in autumn of 2007. A total of 40 cores (5 cm diameter) were randomly sampled from within each of two similar ‘plots’ (each about 300 m^2) of restored and degraded soil after consulting with local farmers. Soils were collected in plastic bags and transferred to a refrigerator at 4 °C as soon as possible. Just before nematode extraction, soil samples were gently broken by hand along natural planes of weakness and sieved at <5 mm in order to maintain the original soil aggregate structure and prevent nematodes being damaged. During this process, debris and plant remains were removed in order to avoid any influence on the parameters analyzed in the laboratory. A small portion of soil was air-dried and sieved to determine soil physicochemical parameters. Then the remaining soils were amended to 60% water holding capacity and incubated in the dark at 22 °C for 14 d before conducting disturbance-incubation experiments.

2.3. Soil physicochemical and biological parameters

Basic soil properties were measured before incubation experiment to describe the general status of the two composite soils (Table 1). Total organic carbon and organic nitrogen contents were determined by the methods of Walkley and Black dichromate oxidation and micro-Kjeldahl digestion, respectively. The mineral nitrogen (NH_4^+–N and NO_3^-–N) concentration was determined by Continuous Flow Analytical System AutoAnalyzer 3-Continuous-Flow Analyser (Bran Luebbe, Norderstedt, Germany). Water-stable aggregate distribution was determined by wet-sieving and the mean weight diameter used to express soil structural stability [14]. Bacterial abundance were represented by total cells stained with DAPI (4′,6-Diamidino-2-phenylindole-dihydrochloride) and counted with an epifluorescence microscope [4]. Ergosterol, as an indicator of fungal biomass, was extracted from 1.5 g fresh soil and quantified by high-performance liquid chromatography [36]. Microbial biomass C and N was determined by the chloroform-fumigation extraction

Table 1
Initial properties of restored and degraded soil before the incubation experiment.

Soil	pH	Organic carbon	Organic nitrogen	NH_4^+–N	NO_3^-–N	Structural stability	Bacterial abundance	Fungal biomass	Microbial biomass C	Microbial biomass N
		g C kg^{-1}	g N kg^{-1}	mg N kg^{-1}		mm	10^6 cells g^{-1}	mg kg^{-1}	mg C kg^{-1}	mg N kg^{-1}
Restored	5.8	17.0	1.57	9.8	44.5	0.82	5.36	0.62	401.9	51.1
Degraded	4.2	5.5	0.68	3.8	21.5	0.38	1.05	0.16	190.8	15.6

Note: Structural stability was expressed by mean weight diameter (MWD) of water-stable aggregates. Fungal biomass was presented as ergosterol content.