



Research paper

A community trait-based approach to ecosystem functioning in soil



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ABSTRACT

Functional traits capture characteristics of organisms that determine their individual response to environmental pressures, providing a mechanistic understanding of habitat responses and the effects on ecological processes. Trait-based approaches have already been reported for separate soil groups like bacteria, nematodes and collembolans but investigating these groups together could bring better insights in assessing both environmental pressures and state of the systems. Still, selecting a suite of single traits that might encompass the large heterogeneity in soil biota remains a challenge for community trait-based analyses.

We sampled arable fields and their adjacent (buffer zone) margins to investigate overall trait-based responses of the soil community to agricultural management. We explored the suitability of three groups of functional traits (i.e. eco-physiological traits, behavioural traits and faunal morphological traits) to analyse how different components of the soil biota (fungi, bacteria, micro- and mesofauna) respond to agricultural management and to what extent the selected traits detect effects on soil functioning. For microbes, we opted for eco-physiological trait proxies due to the difficulties to study these organisms at individual level. Our results showed that eco-physiological traits reflected differences in nutrient cycling dynamics and carbon storage driven by the soil microbial community. The structural organization of micro- and the mesofauna trophic grouping and body mass distribution reflected effects of agricultural management on soil assemblages and revealed differences in the responses of these groups to the environment. We recognize some methodological limitations of our comprehensive community trait-based approach. Yet our analysis reveals characteristics of the soil community structure and belowground ecological processes, as i.e. the partial shift from the bacterial- to the fungal-driven energy channels, that could not be detected by traditional methods, showing the potential of this approach in determining environmental pressures and in evaluating ecosystem services.

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1. Introduction

Trait-based approaches, focusing on the functional characteristics of individuals, provide a mechanistic understanding of habitat responses and ecosystem functioning (Lavorel et al., 2013; Verberk et al., 2013). Functional traits capture characteristics of organisms (i.e. morphological, physiological, phenological or behavioural) that are linked to life-history and ecological functioning, and determine individual response to pressures and subsequent effects on ecological processes (Violle et al., 2007; Díaz

et al., 2013). Hence, traits can be used as indicators of specific ecological processes (e.g. Lavorel et al., 1997; Harrington et al., 2010; Lavorel and Grigulis, 2012) and changes in means and distributions of trait values within a community can be seen as early warning signals of disturbance (Mulder et al., 2012; Mouillot et al., 2013). Over the last three decades, especially in plant ecology (Violle et al., 2007), and more recently in soil ecology (e.g. Mulder et al., 2005a; Pelosi et al., 2014; Pey et al., 2014), the trait-based approach has been widely used in many studies ranging from organism up to ecosystem levels. Trait-based approaches have already been reported for separate soil groups like bacteria, nematodes and collembolans (e.g. Lennon et al., 2012; Vonk et al., 2013; Widenfalk et al., 2015 respectively), but investigating these groups together could bring better insights in assessing both the environmental pressures and the state of the systems. Still, such a

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community trait-based approach is challenging in representing the enormous diversity of soil life across microbial and faunal groups (Pey et al., 2014). Moreover, little is known regarding the distribution of microbial functional traits in nature (Green et al., 2008) and it is still difficult to study microbial communities at individual or species level.

Therefore, for microbes, we selected 'eco-physiological trait proxies' correlated with microbial metabolism that determine most of the primary consumption in soil systems (Mulder et al., 2006). For the rest of the soil groups, we analysed two key behavioural and morphological traits (feeding guild and body mass) that determine most of the decomposition process in soil, as well as nutrient cycling (Peters, 1983; Calder, 1984; Hendriks and Mulder, 2008).

Hence, here we wish to explore the suitability of the three groups of functional traits, i.e. eco-physiological, behavioural, and morphological traits, in detecting the effects of environmental pressures across different groups of soil biota. We used a suite of these traits to analyse how different components of the soil biota (fungi, bacteria, micro- and mesofauna) respond to agricultural management. In particular, we hypothesized that:

- i) The values of the selected eco-physiological traits will reflect differences in the nutrient cycling and carbon storage driven by the soil microbial community;
- ii) Trophic grouping will reflect the environmental filtering acting on soil organisms and hence will reveal potential shifts between the bacterial and the fungal-driven energy channels;
- iii) Trophic grouping, together with the body-mass distribution, will reveal differences in the responses of the micro- and the mesofauna to the environment;
- iv) The structural organization of basal resources and consumer guilds will reflect the effects of agricultural management on soil community assemblages.

2. Materials and methods

2.1. Sampling and experimental design

2.1.1. Locations and sampling

The sampling took place in 2012, September 22nd–29th in Hoeksche Waard (The Netherlands) and was spread over an area of about 55 km² (from 51°43'54" N to 51°48'21" N and from 4°25'45" E to 4°36'21" E). This area has been investigated in many projects which facilitated the access to the farms (Heijting et al., 2011; Rutgers et al., 2012) and holds the promise to contribute to transdisciplinary approaches for improving agro-environmental management schemes (Alebeek et al., 2006). Four farms were selected to be comparable in terms of type of crop, rotation scheme and presence of adjacent field margins as buffer zones (Mulder et al., 2017). All the arable fields were under conventional management (Crittenden et al., 2015) whereas their field margins, always between the investigated arable field and a ditch, were not seeded, ploughed, or manured at least since four years. At each farm, we sampled eight spots: four spots in the arable field (1 × 1 m²) and four spots (1 × 1 m²) in the field margin. The distance between each sampling spot was close to 20 m. We considered this distance sufficient to ensure independence between each spot within the same management (field margins and arable fields), and between the two habitats in terms of, for instance, movements of the soil fauna. For each sampling spot, 50 soil cores (Ø 2.3 cm, depth 10 cm) were collected and mixed to measure soil abiotics and microbial parameters, and to extract nematodes. Three larger intact soil cores (Ø 5.8 cm, depth 10 cm) were used for analysis of mesofauna (collembolans and mites).

2.1.2. Soil parameters

Soil characterisation and chemical analysis of soil samples were performed according to the standard methods used in the Netherlands Soil Monitoring Network (Rutgers et al., 2009): the soil pH was measured in 1 M KCl solution at a soil to solution ratio of 1:1 (weight:volume). Total soil C (C-tot: mg kg⁻¹) was determined by thermogravimetric analysis while total soil N (N-tot: mg kg⁻¹) was determined by a titrimetric method after distillation using Kjeldahl destruction. Total soil P (P-tot) was determined by Automated Ion Analyzer after sample digestion. Pore water-extractable phosphorus (P_w) was determined as mg PL⁻¹, after extraction at a soil to water ratio 1:60 (volume: volume). Soil organic matter (OM%) was measured by loss on ignition and hot water extractable carbon (HWC) was analysed according to Sparling et al. (1998). Clay percentage (Clay%) was estimated after sieving by granulometric analysis. Bulk density was measured in the 5–10 cm layer below the soil surface in ring samples containing 100 cm³ of soil.

2.1.3. Microbial parameters

Bacterial biomass was estimated from numerical abundance and biovolume using a carbon content of $3.1 \times 10^{-13} \text{ g C} \times \mu\text{m}^{-3}$ (Bloem et al., 1995). Fungi were counted under an epifluorescence microscope at 400× magnification and the biomass was calculated assuming a mean hyphal diameter of 2.5 μm and a specific carbon content $1.3 \times 10^{-13} \text{ g C} \times \mu\text{m}^{-3}$ (Van Veen and Paul, 1979; Bakken and Olsen, 1983). The potential C mineralization (based on O₂ consumption) was measured between week 1 and week 6 by soil incubation at 20 °C and 50% water holding capacity (Bloem et al., 1994). Potentially mineralizable N was determined by anaerobic incubation of soil samples in slurry for 1 week at 40 °C (Keeney and Nelson, 1982). The metabolic quotient (qCO₂) was calculated by dividing the basal respiration rate by the amount of microbial carbon (Anderson and Domsch, 1993). The growth response of the bacterial community on a range of carbon and energy substrates was analysed in Biolog EcoPlates™ through the measurement of colour formation in the plates. The multiwell plates were incubated in the dark at 20 °C and 85% relative humidity (Rutgers et al., 2006). Colour development was measured daily during 7 days using a semi-automatic sampler and a spectrophotometer (Spectra MAX250; Molecular Devices, Oxford, UK). The amount of inoculum that caused 50% of the maximum theoretical response for one specific substrate conversion (individual well colour development) was compared with the amount of inoculum that caused 50% of the maximum average response of all 31 substrates, resulting in a value for the relative abundance of catabolic units (heterotrophic bacteria) for that specific substrate.

2.1.4. Soil fauna

Nematodes were extracted from 100 g of fresh soil using funnel elutriation complemented by sieving and cottonwood extraction (Oostenbrink, 1960). For each nematode sample, the individuals were counted. A subsample of 150 randomly chosen individuals was identified to genus; body length and width were measured using a microscope. Lengths and widths were used to estimate body mass using a regression according to Andrassy (1956). Per sample, the average body mass of identified taxa was derived from estimated weights. The total abundance of each taxon was derived as a proportion of the number of taxon identified within the 150 individuals. Enchytraeids were extracted from soil cores by wet-funnel extraction (O'Connor, 1955) and counted. Adults were identified at genus level. Based on visual observation, each enchytraeid was allocated to one body size class with known body length and width. We used length-weight regressions to convert the body size parameters to body-mass averages as described by Abrahamsen (1973). Soil microarthropods (i.e.

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