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Original article

Contrasting diversity patterns of soil mites and nematodes in secondary succession

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ABSTRACT

Soil biodiversity has been recognized as a key feature of ecosystem functioning and stability. However, soil biodiversity is strongly impaired by agriculture and relatively little is known on how and at what spatial and temporal scales soil biodiversity is restored after the human disturbances have come to an end. Here, a multi-scale approach was used to compare diversity patterns of soil mites and nematodes at four stages (early, mid, late, reference site) along a secondary succession chronosequence from abandoned arable land to heath land. In each field four soil samples were taken during four successive seasons. We determined soil diversity within samples (α-diversity), between samples (β-diversity) and within field sites (γ-diversity). The patterns of α- and γ-diversity developed similarly along the chronosequence for oribatid mites, but not for nematodes. Nematode α-diversity was highest in mid- and late-successional sites, while γ-diversity was constant along the chronosequence. Oribatid mite β-diversity was initially high, but decreased thereafter, whereas nematode β-diversity increased when succession proceeded; indicating that patterns of within-site heterogeneity diverged for oribatid mites and nematodes. The spatio-temporal diversity patterns after land abandonment suggest that oribatid mite community development depends predominantly on colonization of new taxa, whereas nematode community development depends on shifts in dominance patterns. This would imply that at old fields diversity patterns of oribatid mites are mainly controlled by dispersal, whereas diversity patterns of nematodes are mainly controlled by changing abiotic or biotic soil conditions. Our study shows that the restoration of soil biodiversity along secondary successional gradients can be both scale- and phylum-dependent.

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1. Introduction

A common goal in ecosystem restoration after human disturbance is to recreate the original levels of species diversity found in undisturbed remnant sites. Traditionally, the majority of restoration and succession studies were focused on restoring plant communities (Egler, 1954). More recently, the focus shifted towards a more integrated above-belowground approach (Wardle et al., 2004). At local scales, soil biodiversity is considerably higher than aboveground diversity (De Deyn and Van der Putten, 2005). Perhaps the most compelling explanation for the shear amount of biological diversity found in the soil lies in the extremely heterogeneous habitat in which soil organisms dwell, both spatially and temporally (Ettema and Wardle, 2002). This heterogeneity provides unprecedented potential for niche partitioning and habitat specialization, thereby allowing species coexistence and favoring biodiversity (Bardgett, 2002). The importance of soil biodiversity for ecosystem development after human disturbances becomes increasingly recognized (De Deyn et al., 2003; Kardol et al., 2006, 2009; Mayer, 2008). However, relatively little is known about how soil biodiversity develops along successional sequences, such as restoration trajectories after agricultural disturbance.

Here we examine soil biodiversity patterns of oribatid mites and nematodes in secondary succession following cessation of agricultural practices. In temperate grassland systems, oribatid mites and nematodes are major components of the soil biota; they are

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abundant, typically represent the most species-rich taxa, and are functionally diverse (Petersen and Luxton, 1982; Stanton, 1988). Oribatid mites are involved in decomposition of organic matter, in nutrient cycling and in soil formation (Behan-Pelletier, 1999). Oribatid mites are suggested to be generalistic species (Maraun et al., 2007) and have been shown to feed on a wide variety of substrates (Siepel and De Ruiter-Dijkman, 1993). However, fungi are generally considered to be their preferred food source (e.g. Maraun et al., 1998). Soil nematodes are trophically very diverse and comprise plant-feeding, bacterial-feeding, fungal-feeding, omnivorous, and carnivorous taxa (Yeates et al., 1993). Density and diversity of oribatid mites, having long life cycles of more than one year and little capacity to respond to mechanical perturbations (Maraun et al., 2003), are generally strongly reduced in arable soils (Behan-Pelletier, 1999; Minor and Cianciolo, 2007). In contrast, nematode density can be high in arable soils (Freckman and Ettema, 1993). Most nematode taxa have fast reproduction cycles and, hence, may be less sensitive to agricultural disturbances than oribatid mites. Nevertheless, nematode communities from arable soils are typically dominated by opportunistic bacterial-feeding taxa and show lower richness than communities from undisturbed soils (Yeates and Bongers, 1999; Kardol et al., 2005). Disparate relationships with abiotic and biotic soil properties, as well as differences in life-history traits, make oribatid mites and nematodes ideal taxa to use for a comparative study of diversity patterns in secondary succession.

Within-ecosystem estimates of diversity comprise numerous organismal and ecological entities across a wide range of spatial and temporal scales (Wolters, 2001; Caruso et al., 2005). Basically, three main types of diversity can be distinguished: α-diversity as the property of a defined spatial unit, β-diversity as a measure of dissimilarity between two or more spatial (or temporal) units, and γ-diversity as the overall number of taxa across units within a larger area (Whittaker, 1960). In secondary succession following cessation of agricultural practices, release from physical and chemical disturbance may enable α- and γ-diversity of oribatid mite and nematode communities to increase (Maraun and Scheu, 2000). Changes in soil acidity (Van Straalen et al., 1988) and build-up in the amount, complexity and diversity of organic matter as driven by changes in the vegetation (Bardgett and Shine, 1999) may further enhance α- and γ-diversity. After cessation of agricultural practices, plant community development, plant species heterogeneity and organic matter input to the soil may enhance spatial variation in soil micro-habitats and food resources, and thereby, increase soil β-diversity (Hansen and Coleman, 1998).

Using a multi-scale approach, we studied diversity patterns of oribatid mite and nematode communities during four subsequent seasons at three stages along a 22-year old chronosequence of abandoned agricultural fields, which we called ‘early’, ‘mid’, ‘late’. As a possible end-point reference, we included a semi-natural heath land, which was the predominant ecosystem type before the land became cultivated. Specifically, we compared successional patterns of α-, β-, and γ-diversity for oribatid mites and nematodes and tested the basic hypothesis that across-scale diversity of both phylogenetic groups of soil organisms increases during the transition from arable land towards a semi-natural ecosystem.

2. Methods

2.1. Study area and sampling

Soil samples were collected in 2004 from three former agricultural sites, which were abandoned in 2002 (early), 1995 (mid) and 1982 (late) (Holtkamp et al., 2008). The sites were selected out of 26 former agricultural sites based on their similarity in agricultural history and physical soil characteristics, and their distinct positions along plant and soil successional axes (Kardol et al., 2005; Van der Wal et al., 2006; Appendix 1); therefore, the sites could be regarded as representative for early, mid and late stages of secondary succession. A semi-natural heath land from medieval origin was selected as a reference system. Sites were located within the same geographical region in the central part of the Netherlands on well-drained, sandy soils originating from former glacial deposits. The sites were managed by low-intensive grazing of native and introduced vertebrate herbivores. Within each site a 50×50 m^2 plot was chosen in an area at a minimum distance of 20 m from the edge. In April, June, September and November 2004, at each site, four soil monoliths of $25 \times 25 \times 10$ cm^3 each were collected from four random positions at minimally 5 m distance from each other. The inter-sample distance was large enough to consider the samples collected within each site as independent from each other. However, samples taken within each field are strictly speaking pseudoreplicates for successional stage. Therefore, this resulted in 4 (sites) $\times$ 4 (seasons) $\times$ 4 (spatially-separated pseudoreplicates per site) $=$ 64 samples in total. Within each monolith a sub-sample of 10 cm diameter and 10 cm depth was taken for oribatid mites. The remaining part of the sample was sieved through a 4 mm mesh and homogenized, before collecting sub-samples for isolating soil nematodes. Additionally, in February 2006, we collected four random soil samples for oribatid mites (10 cm diameter and 10 cm depth) in the surrounding forest of each of the sites.

2.2. Mite and nematode extraction

The samples included the organic layer and the top layer of the mineral horizon. Oribatid mites were extracted using Tullgren funnels (Van Straalen and Rijninks, 1982) for a period of three weeks to ensure optimal extraction. Emerging mites and other soil animals were collected in Gisin-medium (750 ml 95% alcohol, 250 ml ethyl ether, 30 ml glacial acetic acid, 3 ml 40% formaldehyde). Prior to counting, oribatid mites were manually separated from other soil animals and soil particles. Adult oribatid mites were identified to species or genus level. Juvenile oribatid mites could not be identified and were not included in the diversity measurements. Nematodes were extracted from the soil by Oostenbrink elutriators (Oostenbrink, 1960). Nematodes present in 10% of the extracted soil were heat-killed and fixed (35% formaldehyde diluted to 4%). From each sample, about 150 nematodes were identified to family or genus level. The group *Dorylaimoidea* was used to specify a heterogeneous group of omnivorous dorylaimids comprising Dorylaimidae, Qudsianematidae, Thornenematidae and Aporcelaimidae.

2.3. Data analyses

Differences between sites in the total abundance and taxon richness of oribatid mites and nematodes were tested using one-way Analysis of Covariance (ANCOVA) with site as fixed factor and season as covariable. Contrasts were specified for individual comparisons. Oribatid mite and nematode α-diversity were calculated as the Shannon Index, $H' = -\sum p_i \ln p_i$, where $p_i = n_i/N_i$, $n_i =$ the density of the i-th taxon, and $N =$ the total density. Both for oribatid mites and for nematodes, α-diversity was not affected by season (ANOVA or non-parametric Kruskal–Wallis test: $P > 0.10$). Therefore, we considered the 16 samples collected from each site (4 seasons $\times$ 4 samples) as independent pseudoreplicates. Between-site comparisons of nematode α-diversity were tested using one-way ANOVA with each individual sample as replicate ($n = 16$) and