011

European Journal of Soil Biology 59 (2013) 8-14

Contents lists available at ScienceDirect

European Journal of Soil Biology

journal homepage: http://www.elsevier.com/locate/ejsobi

Original article

Oribatida (Acari) in grassy arable fallows are more affected by soil properties than habitat age and plant species



Janet Wissuwa^{*}, Jörg-Alfred Salamon¹, Thomas Frank

University of Natural Resources and Life Sciences, Department of Integrative Biology & Biodiversity Research, Institute of Zoology, Gregor Mendel Straße 33, A-1180 Vienna, Austria

ARTICLE INFO

Article history: Received 18 May 2013 Received in revised form 24 July 2013 Accepted 12 August 2013 Available online 28 August 2013 Handling editor: Stefan Schrader

Keywords: Oribatida Arable fallows Habitat age Plant functional group Soil type Soil properties Assemblage analysis

ABSTRACT

Oribatid mites are one of the numerically dominant arthropod groups in soils. They play an important role in soil food webs via regulating the decomposition of organic matter and propagating microorganisms within the soil. To our knowledge, the influence of different plant functional groups on oribatid mites has not been studied in abandoned farmland with undisturbed succession before. The density and assemblage structure of oribatid mites in nine grassy arable fallows relative to three habitat age classes (2–3, 6–8, 12–15 years) and three selected plant species (legume: *Medicago sativa*, forb: *Tar-axacum officinale*, grass: *Bromus sterilis*) were investigated in soil associated with single plants.

Mite density declined marginally not significant with habitat age because of high abundances of the ubiquitous species *Tectocepheus velatus sarekensis* and *Punctoribates punctum* in young and mid-aged fallows and their subsequent decline in old fallows. Oribatid mite density and species assemblage were not affected by plant species. Only *P. punctum* had significantly higher densities in *B. sterilis* samples than in *T. officinale* samples due to a higher amount of fine roots. Distance-based linear models revealed that 65% of the variation in mite assemblage was explained by soil properties, soil type, exposition and geographic position, while habitat age was of minor importance. Canonical correspondence analysis revealed that the mite assemblage was best explained by soil organic and microbial carbon, water content and pH.

© 2013 The Authors. Published by Elsevier Masson SAS. Open access under CC BY-NC-ND license.

1. Introduction

Over the past several decades agricultural intensification led to enormous land-use changes resulting in dramatic losses of biodiversity [1]. To counteract the loss of biodiversity agricultural land is converted to more natural ecosystems [2] like grassy arable fallows or wildflower areas, which are designed to enhance arthropod diversity and abundance of beneficial arthropods [3]. The establishment of such semi-natural habitats targets mainly plants and above-ground invertebrates [4–6] neglecting the response of soil invertebrates [7]. However, soil biodiversity is considerably higher than above-ground diversity at local scales [8]. Yet, there is relatively little information about the development of soil biodiversity after cessation of agricultural practices [9].

Mites are a major constituent of soil biodiversity in terms of taxonomic diversity, range of behaviors and lifestyles [10]. Oribatid mites are the third largest mite group [11] reaching densities up to 200,000 individuals m^{-2} in boreal forests [12]. They are actively involved in decomposition and nutrient cycling as well as the dispersal of microorganisms. Their fecal pellets are an integral component of soil structure in organic horizons [13].

Long-term studies on succession in oribatid mite assemblage structure in agroecosystems following initial disturbance are rare [13] and restricted to Central Europe [9,14–17]. Because most Oribatida groups are generally reduced due to mechanical disturbances [18] they should benefit from the abandonment of arable land. Furthermore, the enhanced habitat diversity due to a welldeveloped vegetation cover with increased successional age [19] provides more microhabitats and food resources facilitating colonization and population growth. Despite being generally sensitive to disturbance oribatid mites show a considerable variation in sensitivity among taxonomic groups [12] from taxa common in



^{*} Corresponding author. Tel.: +43 668 3063150; fax: +43 1 47654 3203.

E-mail addresses: janet.wissuwa@boku.ac.at, janet_wissuwa@yahoo.de (J. Wissuwa), jasalamon@yahoo.de (J.-A. Salamon), thomas.frank@boku.ac.at (T. Frank).

¹ Present address: Kapellenbrink 16, D-30655 Hannover, Germany.

^{1164-5563 © 2013} The Authors. Published by Elsevier Masson SAS. Open access under CC BY-NC-ND license. http://dx.doi.org/10.1016/j.ejsobi.2013.08.002

cultivated soils and heavily disturbed habitats like Tectocepheidae and Oppiidae [13] to very sensitive taxa with long life-cycle and low fecundity like Enarthronota [12]. Such differences in sensitivity likely affect the species composition in different successional stages.

To our knowledge, there are just four investigations about plant species effects on oribatid mites [20–23]. However, plant species vary in palatability to consumers as well as quality and quantity of litter they produce [24], influencing the soil food web [25]. The presence of legumes has been shown to enhance decomposition [26,27], microbial biomass [28] and soil fauna feeding activity [29]. Soil fauna like earthworms [26] and Collembola [30] benefited from the presence of legumes. Similar to Collembola, oribatid mites mainly feed on plant material and microorganisms [13] and are therefore likely affected by resource quality pertaining to plant functional groups or single plant species. Oribatid mites have been shown to vary in abundance and species assemblage between different plant species [20,22]. The effect of plant species on soil organisms has previously been studied in monocultures or artificially established communities with sown mixtures of chosen plant species [20,22,30–33]. In contrast, in the present study the influence of single plant species (Medicago sativa as legume, Taraxacum officinale as forb, Bromus sterilis as grass) on Oribatida in grassy arable fallows belonging to different habitat age classes (2-3, 6-8 and 12-15 years) was studied under natural field conditions where plants could spread out naturally. The mite assemblage of the soil associated with single plants was investigated. This study was designed to test the following hypotheses:

- 1) The density and species richness of Oribatida increases with fallow age because the impact of the severe disturbances accompanying crop production subsides with increasing habitat age and the abundance and species richness of most Oribatida taxa is generally reduced due to mechanical disturbances [18].
- 2) The Oribatida assemblage differs between the age classes of the fallows because species sensitive to agricultural disturbances are expected to increase with continuing abandonment of farmland.
- 3) The density of Oribatida should be higher in *M. sativa* than in *B. sterilis* and *T. officinale* samples since microphytophagous Oribatida benefit from increased microbial biomass and macrophytophagous Oribatida benefit from the high quality litter in the presence of legumes.
- 4) The Oribatida assemblage differs between the three plant species because plant species differ in their effect on components of soil communities due to differences in quality and amount of organic matter produced [34].

2. Material and methods

2.1. Study region and fallows

This study was carried out in the Marchfeld region, which is part of the Vienna Basin and comprises an area of roughly 1000 km² east and north-east of Vienna, Austria. As a section of the Pannonian Plain it is characterized by a continental climate of high temperature and low precipitation in summer. Mean annual temperature is roughly 9 °C and mean total annual precipitation ranges between 500 and 600 mm [35]. In total, nine grassy arable fallows containing the targeted plant species *M. sativa* as legume, *T. officinale* as herb and *B. sterilis* as grass were selected. The fallows belonged to three different habitat age classes (2–3, 6–8 and 12–15 years) each including three sites. The positions of the fallows ranged from 48.2 to 48.4° northern latitude and from 16.5 to 16.9° eastern longitude. The size of the fallows ranged from 1000 to 29,000 m². The larger fallows were sampled in a smaller area of about 3000 m². The dominant soil types within this region belong to the class chernozem according to the electronic soil map for Austria [36]. The site parameters pH, soil type, geographic position, fallow age and exposition are given in Table 1.

2.2. Sampling and sample treatment

Four plots with at least 20 m distance from each other were randomly selected in the central axis of each fallow in May 2008. Applying a micro-scale approach soil cores (diameter 5.6 cm, height 10 cm) were taken at the base of five plant individuals from aggregations of five to more than ten individuals of each of the chosen three plant species at each plot. Soil fauna was extracted from the pooled material of three randomly chosen cores using a Berlese-Tullgren funnel with stepwise rise of illuminance from approximately 100 lux to maximum intensity with an intermediate step of 1000 lux in the course of three days. The material of two randomly selected cores per plant species and plot was mixed and sieved with a 2 mm mesh for the measurement of abiotic soil parameters and microbial parameters. Fractions for the different measurements were weighted into snap cap vials and stored in the fridge until measurement. Per fallow 12 samples (four plots \times three plant species) were gathered for the investigation of soil fauna and 12 samples for the measurement of soil properties resulting in 108 samples for all nine fallows. Soil fauna was gathered in 10% sodium benzoate solution, transferred into 70% ethanol and determined to species level using the identification key of Weigmann [37].

Soil moisture was gravimetrically measured after drying at 105 °C for 24 h. A fraction of the dried soil was milled and prepared for the analysis of total carbon and nitrogen with an elemental analyzer (Carlo Erba, Milan). The pH was determined in an aqueous suspension of 10 g soil adjusted to 25 ml volume with 0.01 M CaCl₂ solution after shaking for 1 h applying the WTW pH-meter pH95 with SenTix 61 pH-electrode. Organic carbon was calculated as difference of total and inorganic carbon after carbonate measurement with a Scheibler apparatus. Microbial parameters were determined from respiration measurements using an automated respirometer based on electrolytic oxygen microcompensation [38] in fresh soil samples equivalent to 3.5 g dry weight. Basal respiration was calculated by averaging respiration rates at 10 and 20 h after starting the measurements. Microbial carbon was calculated from maximum initial respiratory response after addition of glucose in aqueous solution [7].

Table 1

Parameters of the nine investigated grassy arable fallows within the Marchfeld region (soil types were taken from http://gis.lebensministerium.at/eBOD/frames/ index.php?&gui_id=eBOD, correlations with soil units according to the World Reference Base for Soil Resources were obtained from the Austrian Agency for Health and Food Safety).

Fallows Abandoned in		Geographi position	с	Soil type	Exposition	Mean soil
		Longitude	Latitude			рН
Site 1	2006	16.871	48.225	Gleyic phaeozem	Plain	7.4
Site 2	2006	16.668	48.300	Calcaric phaeozem	Plain	6.6
Site 3	2006	16.490	48.307	Calcaric phaeozem	Plain	7.1
Site 4	2001	16.872	48.225	Gleyic phaeozem	Plain	7.3
Site 5	2000	16.591	48.306	Calcic chernozem	South	7.3
Site 6	2002	16.783	48.280	Calcaric phaeozem	Plain	7.0
Site 7	1994	16.723	48.341	Calcic chernozem	Plain	7.2
Site 8	1996	16.570	48.366	Calcareous tilled soil	South	7.4
Site 9	1993	16.574	48.201	Calcic chernozem	Plain	7.1

2.3. Statistical analyses

Mite density and the densities of the most abundant species, occurring in at least five fallows, were analyzed with the procedure GLM (General Linear Model) of the statistical software SAS 9.1 according to a design with habitat age and plant species as factors, an interaction term (age \times plant) and site as random effect nested within habitat age. Species richness was tested with habitat age as fixed factor and site as random effect nested within habitat age. A post-hoc multi-comparison Tukey test was applied to verify differences between means at the 5% probability level.

Prior to analyses of the mite assemblage species abundance data were transformed into a Hellinger distance matrix between all 108 samples, which is one of the best similarity measures for species composition analyses [39]. The assemblage data were analyzed for differences between factor levels using non-metric Multidimensional Scaling (NMDS) and permutational multivariate variance analysis (PERMANOVA) with the software PRIMER v6 with PERMANOVA + add-on. Homogeneity of multivariate dispersion was tested via permutations using the same program. Geographic position, soil type, exposition, measured soil properties, habitat age and plant species were included in a distance-based linear models analysis (DistLM) in PRIMER because the fallows differed in their soil type, exposition and were scattered over a rather large area. Distance-based linear models analysis does a quantitative partitioning of multivariate variability for the included predictor variables. The contribution of predictor variables to the model is tested with appropriate permutation methods as part of a sequential test. Forward selection with Akaike information criterion for small sample sizes was used [40]. Six different sets of predictor variables were defined: (1) geographic position with easting and northing Universal Transverse Mercator coordinates zone 33 north as continuous variables, (2) soil type binary coded, (3) exposition binary coded, (4) plant species binary coded, (5) habitat age as continuous variable and (6) the measured continuous soil properties. Prior to analyses, the measured soil properties were summarized in a correlation matrix and inspected via principal component analysis for possible inter-correlations. Total nitrogen, total, organic, inorganic and microbial carbon as well as C-to-N ratio and pH were correlated. For reasons of parsimony total nitrogen and carbon, inorganic carbon and C-to-N ratio were excluded. The remaining five soil properties water content, pH, basal respiration, microbial and organic carbon were used for the DistLM analysis and the following canonical correspondence analysis (CCA). CCA was applied to investigate the influence of single soil properties on mite assemblage using CANOCO 4.5 with forward selection of variables and Monte Carlo Permutation tests [41]. Only species with at least ten individuals in total were included in the CCA analysis after a log transformation.

To inspect for spatial auto-correlation the Spearman rank correlation coefficient (rho) was calculated between the similarity matrix of species assemblage per sample and the corresponding distance matrix of geographic coordinates. The same procedure was performed for the similarity matrix of the mean species assemblage per fallow and the distance matrix of geographic positions of the fallows. The null hypothesis of no agreement in multivariate pattern between the matrices was tested with 999 permutations in PRIMER [42].

3. Results

3.1. Effect of habitat age and plant species on mite density

Oribatida density decreased marginally not significant from young fallows (8600 ind./m²) over mid-aged fallows (7800 ind./m²)

to old fallows (5000 ind./m², $F_{2,14} = 2.76$, p < 0.1). Species richness was not affected by habitat age and was rather low with a mean of four species per sample. Oribatida density was not affected by plant species. Only one species exhibited a preference. The density of Punctoribates punctum was significantly higher in B. sterilis samples (3240 ind./m²) than in *T. officinale* samples (1640 ind./m²), with *M. sativa* samples (2340 ind./m²) being intermediate ($F_{2,14} = 5.44$, p < 0.01). A few species were associated with a specific age class. P. punctum was significantly more abundant in mid-aged $(4720 \text{ ind.}/\text{m}^2)$ than in old fallows (920 ind. $/\text{m}^2)$, with the young fallows (2790 ind./m²) being intermediate ($F_{2,14} = 5.84$, p < 0.01). The density of Tectocepheus velatus sarekensis was significantly higher in young (2900 ind./m²) than in mid-aged (1090 ind./m²) and old fallows (990 ind./m², $F_{2.14} = 4.73$, p < 0.05). Both species occurred in all fallows and were the most abundant species with relative abundances of 38% and 23%, respectively. They contributed to the assemblage in most of the samples with sample frequencies of 55% and 75%, respectively (Table 2). The density of Epilohmannia *cylindrica* was significantly higher in young (615 ind./m²) and old $(860 \text{ ind.}/\text{m}^2)$ than in mid-aged fallows (25 ind./m², $F_{2,14} = 15.64$, p < 0.001). The density of Ceratozetes laticuspidatus was significantly higher in old (260 ind./m²) than in mid-aged (45 ind./m²) and young fallows (45 ind./m², $F_{2.14} = 12.26$, p < 0.001).

3.2. Assemblage analysis

Nineteen taxa comprising only 45 individuals were omitted. because their accidental occurrence introduced a large number of zeros in the data matrix, without providing relevant information about changes in the assemblage. Non-metric multidimensional scaling did not show any influence of plant species on the mite assemblage because the samples of the three plant species were stochastically distributed without any sign of clustering (Fig. 1). There was a tendency for clustering within the NMDS ordination for habitat age. Mid-aged fallows were slightly separated from young and old fallows although with some overlap (Fig. 2). Yet, this tendency was not significant according to the permutation test (F = 0.91, p < 0.56) probably attributed to significant differences in multivariate dispersion (F = 15.3, p < 0.01). Distance-based linear model analysis revealed that all variable sets (p < 0.01) except plant species (p > 0.9) explained a significant proportion in mite species variation when considered alone within the marginal test. The sequential test with forward selection incorporated all variable sets except plant species into the model. The set of measured soil properties explained the largest proportion of variation in mite assemblage (28%), followed by soil type (12.5%), exposition (12.4%) and geographic position (10.6%). Even though habitat age contributed only 1% to the explained variation, its inclusion significantly improved the model (p < 0.05), which explained 65% of the variation in species assemblage. The correlation coefficient for the similarity matrix of species assemblage per sample and the matrix of sample coordinates was low but significant (rho = 0.103, p < 0.01). There was no correlation between the similarity matrix of the mean species assemblage per fallow and the matrix of fallow coordinates (rho = -0.145, p = 0.76).

According to CCA, organic carbon (7.9%), microbial carbon (5%), pH (5%) and water content (4.4%) contributed most to the explained variance (p < 0.01). Basal respiration (1.9%) was also significant but less influential (p < 0.05). Axis 1 (eigenvalue 0.303) mainly represents organic carbon and pH whereas axis 2 (eigenvalue 0.198) represents water content and basal respiration (Fig. 3). Microbial carbon was correlated with both axes. *Hypochthonius luteus* and *Oppiella obsoleta* correlated with organic carbon. *Protoribates dentatus* and *P. punctum* correlated with organic carbon and pH and were associated with mid-aged fallows. *Liebstadia similis*,

Table 2

Abundance (individuals m⁻²) of Oribatida species in arable grassy fallows of the region Marchfeld, Austria.

Species	Young fallows			Mid-aged fallows			Old fallows			RA	SF
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3		
Achipteria coleoptrata	0	0	0	0	0	0	0	95	0	0.01	0.93
Caenobelba montana ^a	0	0	95	0	0	0	0	0	0	0.01	0.93
Carabodes labyrinthicus	0	0	95	0	0	0	0	0	0	0.01	0.93
Ceratocetes laticuspidatus ^a	190	475	760	1330	0	0	8075	0	95	1.60	21.30
Cosmogneta kargi ^a	0	1235	0	760	0	0	0	0	0	0.29	2.78
Ctenobelba pectinigera	0	0	95	0	0	0	0	0	95	0.03	1.85
Epilohmannia cylindrica	190	16,435	3040	0	665	95	475	11,115	15,295	6.95	48.15
Eupelops occultus	0	0	0	0	0	95	0	0	0	0.01	0.93
Graptoppia paraanalis ^a	0	0	1995	0	0	0	0	0	0	0.29	1.85
Hypochthonius luteus	285	0	0	760	0	0	0	0	0	0.15	6.48
Liebstadia similis	0	0	0	1615	0	0	0	0	0	0.24	2.78
Luccoppia burrowsi ^a	0	0	0	0	0	0	0	0	665	0.10	3.70
Metabelba pulverosa ^a	0	0	0	0	0	0	0	0	190	0.03	0.93
Oppiella nova	0	285	95	380	0	0	475	190	0	0.21	8.33
Oppiella obsoleta	190	0	95	5130	0	190	190	0	0	0.85	15.74
Oppiella sp.	0	0	95	0	0	95	0	0	0	0.03	1.85
Phauloppia rauschenensis ^a	0	0	0	0	95	0	0	0	0	0.01	0.93
Phthiracarus compressus ^a	0	0	95	0	0	0	0	0	0	0.01	0.93
Pilogalumna crassiclava	0	1615	95	0	0	40,185	0	13,015	285	8.10	18.52
Protoribates capucinus	950	1520	380	285	95	0	95	1330	9785	2.12	17.59
Protoribates dentatus ^a	665	0	0	190	0	0	475	0	0	0.20	3.70
Punctoribates punctum	89,205	95	760	105,735	33,250	665	95	28,595	285	37.98	54.63
Ramusella elliptica ^a	95	95	7885	0	0	0	10,355	1235	0	2.89	10.19
Ramusella fasciata	0	0	0	0	0	95	0	0	0	0.01	0.93
Ramusella insculpta ^a	0	0	0	0	0	0	0	0	380	0.06	0.93
Ramusella sp.	0	0	0	0	0	0	95	0	95	0.03	1.85
Rhysotritia ardua	0	6080	1140	0	8360	95	0	1520	7600	3.64	34.26
Scheloribates laevigatus	0	31,635	0	665	0	0	95	0	0	4.76	14.81
Spatiodamaeus boreus ^a	0	0	0	380	0	0	0	0	0	0.06	2.78
Steganacarus spinosus	0	0	95	0	0	0	0	190	0	0.04	2.78
Suctobelbella acutidens	0	0	0	0	95	0	0	475	0	0.08	2.78
Suctobelbella sp.	0	0	95	95	0	0	0	0	0	0.03	1.85
Tectocepheus velatus sarekensis	72,390	4085	17,385	15,295	5890	11,210	760	27,835	2280	23.07	75.00
Tectoribates ornatus	95	0	0	0	0	0	0	0	0	0.01	0.93
Trichoribates novus ^a	285	0	0	0	0	0	0	0	0	0.04	1.85
Zygoribatula glabraª	0	0	19,285	0	0	0	0	21,850	0	6.04	17.59

RA = relative abundance, SF = sample frequency.

^a New record for Austria.

Cosmogneta kargi, C. laticuspidatus and Protoribates capucinus correlated positively with water content. T. velatus sarekensis was associated with microbial carbon. A large group of species such as E. cylindrica, Ramusella elliptica, Rhysotritia ardua and Zygoribatula glabra were associated with young and old fallows and correlated negatively with microbial carbon. Scheloribates laevigatus, E. cylindrica and Z. glabra correlated negatively with pH. Pilogalumna crassiclava was associated with low soil moisture.



Fig. 1. NMDS ordination of oribatid mite assemblages for the 17 most abundant species based on Hellinger distance matrix for the factor plant species (Ms = Medicago sativa, To = Taraxacum officinale, Bs = Bromus sterilis).

4. Discussion

4.1. Effect of habitat age on Oribatida density and assemblage

During natural succession many factors simultaneously affect oribatid mite assemblages masking the influence of few selected factors under field conditions. This seems to be true for the chosen factors habitat age and plant species.



Fig. 2. NMDS ordination of oribatid mite assemblages for the 17 most abundant species based on Hellinger distance matrix for the factor habitat age.



Fig. 3. Ordination of the 17 most abundant oribatid mite species in relation to environmental variables according to Canonical Correspondence Analysis based on forward selection with 499 Monte Carlo permutations. Environmental variables: basal respiration (BR), microbial carbon (Cmic), water content (H₂O), pH value (pH), organic carbon (Corg). Mite species: C karg = *Cosmogneta kargi*, C lati = *Ceratocetes laticuspidatus*, E cyli = *Epilohmannia cylindrica*, G para = *Graptoppia paraanalis*, H lute = *Hypochthonius luteus*, L simi = *Liebstadia similis*, O nova = *Oppiella nova*, O obso = *Oppiella obsoleta*, P capu = *Protoribates capucinus*, P cras = *Pilogalumna crassiclava*, P dent = *Protoribates dentatus*, P punc = *Punctoribates lavigatus*, T vesa = *Tectocepheus velatus sarekensis*, Z glab = *Zygoribatula glabra*. Age classes of the fallows ($\gamma = \gamma$ oung, m = mid-aged, o = old) are included as centroids.

In contrast to the first hypothesis, mite density did not increase with increasing habitat age but declined instead. Such a decline of density in intermediate successional stages was observed in only few other succession studies [14,19,43]. The high densities in the young fallows probably resulted from sampling during the pioneer phase of the parthenogenetically reproducting, opportunistic mite species T. velatus sarekensis and P. punctum [12]. Both species benefited from the release from disturbances and accumulation of organic matter after cessation of agricultural land-use reaching high densities in the two year old fallows. Correspondingly, maximum mite density was observed three years after the setup of experimental succession and reclamation sites [19]. Declining density in intermediate successional stages is assumed to be caused by reduced availability of resources [19], increased competition [44] or predation. The density of predatory beetles, mainly staphylinids and a few carabids, increased significantly from young to mid-aged fallows [45]. Among staphylinid predatory beetles are specialized predators of armored mites like Oribatida and Uropodina [46]. Furthermore, gamasid mites have been shown to reduce oribatid mite density [47]. The density of gamasid mites exceeded oribatid mite density by roughly 3000 individuals m⁻² in the old fallows [48] imposing predation pressure upon weakly sclerotized and juvenile oribatid mites [49].

Species composition did not change between age classes contrary to hypothesis two. The mite assemblages in all nine fallows were characterized by only ten moderately abundant species with relative abundances above one percent (Table 2). Most of them were common species with a worldwide distribution colonizing different habitats from ruderal habitats over meadows to forests [38]. Many species found in young fallows like *E. cylindrica*, *P. capucinus*, *R. elliptica*, *P. punctum* and *T. velatus sarekensis*, also persisted in later successional stages, contributing to old-fallow assemblages. The lack of differences in species composition between the age classes is probably caused by the K-style life history traits of oribatid mites. Many oribatid species have a long life-cycle, slow larval development, low fecundity [13] and low dispersion ability [50]. Therefore, they recolonize formerly disturbed habitats very slowly [12] and need a comparable long time period for the recovery from initial disturbance. Oribatid mites seem to be a fairly conservative element of the decomposer fauna [51]. This is noticeable as the largest shift in species composition and diversity of oribatid mites occurred between a beech forest and a 50 year old woody fallow [15]. In light of the influence of initial conditions on succession and issues with space for time substitution an investigation period of 20 years is considered rather short [19]. The chosen age gradient of up to 15 years for the present study was presumably too short to show considerable changes in species assemblage.

4.2. Effect of plant species on Oribatida density and assemblage

Contrary to hypothesis three, the chosen legume did not support higher oribatid mite densities. This is related to differences in plant traits across species [33] rather than plant functional group. Several plant species belonging to the same functional group differed in their effect on nematode fauna [32]. *M. sativa* develops a long taproot [52], providing less fine root biomass for microorganisms and detritivorous soil fauna than legumes with different root architecture. Therefore, the proposed beneficial effect of nitrogen fixation was less pronounced than for other legumes like some *Trifolium* species [31–33]. Only *P. punctum* was affected by plant species since it preferred the grass species being attracted by the higher amount of fine roots of *B. sterilis* compared to *M. sativa* and *T. officinale* [52] similar to euedaphic Collembola at the same study sites [7].

There were no differences in mite composition between the plant species contradicting the fourth hypothesis. Most oribatid mites likely do not depend on the presence of specific plant functional groups because they feed on a variety of material like plant debris, fungi, mosses, lichens and carrion [13], which contrasts to several more specialized, herbivorous Collembola [30] and nematodes [33]. Similarly, different grass species did not affect soil mite abundance indicating that resource quantity may be of greater importance than resource quality [32]. Likewise, only three out of 79 oribatid mite species were identified as host-habitat specialists [53]. While food preferences have been found under laboratory conditions [54] in the field most soil animals show a rather generalized feeding habit [55] because resources are infinitely intermingled and preferred food likely hard to find and difficult to separate from the surrounding soil [56]. Additionally, several oribatid mite species showed marked seasonal changes in feeding habit reflecting the temporal availability of food [55]. Furthermore, the plant species did not show differences in their microsite conditions indirectly affecting soil mites via altered soil properties. Soil properties like water content, microbial biomass or C-to-N ratio were similar for all three plant species [45]. A further reason for the lacking plant species effect was probably the rather small patch size of plant individuals given under field conditions. Therefore, it cannot be excluded that individual patches were affected by the surrounding plant species masking the effect of the chosen plant species.

4.3. Influence of environmental and site-specific factors on Oribatida assemblage

DistLM attributed the greatest influence on oribatid mite assemblage to the set of measured soil properties and CCA revealed that each of the five properties within this set contributed significantly to the structure of the mite assemblage. The greatest influence was linked to organic and microbial carbon, pH and water content, being similar to Collembola [7], macrofauna [45] and predatory mites [48]. The correlation of mite assemblage with organic and microbial carbon has been observed numerous times [15,57–59]. This can be explained by the fact that oribatid mites mainly feed on microorganisms and dead organic matter [13]. Likewise, soil water content is one of the most decisive factors affecting oribatid communities [15,56,58]. Experimentally induced drought significantly decreased abundance and species richness while irrigation significantly enhanced both [60,61]. The relevance of soil moisture is reflected in the overall low density and species richness in the studied fallows, which are situated in the rather dry Marchfeld region with continental climate [62]. An indication for general dry conditions was the presence of species reported from dry habitats like Z. glabra and H. luteus and the relatively high abundance of E. cylindrica, which is considered to be xerothermophilous [37]. Soil pH is assumed to be one of the main factors influencing oribatid abundance and community [50]. Despite varying slightly between 6.6 and 7.4 soil pH influenced species distribution. P. punctum was strongly associated with the fallows with higher pH, while S. laevigatus and E. cylindrica had higher abundances in fallows with lower pH. On average lower pH values were found in fallows with calcaric phaeozem. As different soil types represent distinct microhabitats [63] they play a modulating role in oribatid assemblage composition [64]. Differences in pore size distribution and volume between soil types will likely affect microarthropod abundance and assemblage through space limitation [65]. Accordingly, the larger species P. crassiclava and S. laevigatus, with body lengths above 500 µm [37], were associated with calcaric phaeozem, which has a texture of loamy sand [36]. Small species like P. punctum, R. elliptica, C. laticuspidatus and *P. capucinus*, all with mean body lengths below 300–400 um [37]. were associated with glevic phaeozem and calcic chernozem, both with a texture of loamy silt [36]. This is an indication for differences in habitable pore space between the soil types causing a slight shift in mite assemblage. Beside soil type, exposition explained a considerable proportion of mite assemblage variation. The exposition may have an indirect effect on soil mites via influencing the local microclimate. Geographic position explained roughly 11% in species variation. This was mainly a result of a higher species assemblage similarity between samples within a fallow than between fallows. Thus, there was no auto-correlation between the fallows.

Acknowledgments

This study was funded by the Austrian Science Fund (FWF, project no. 19988). We would like to thank Bernhard Klarner for the identification of Oribatida, Norbert Schuller for help with soil sampling, Olaf Butenschön and Theodora Volovei for help with determination of microbial biomass. Furthermore, we thank two anonymous reviewers for helpful comments in improving the manuscript.

References

- T. Tscharntke, A.M. Klein, A. Kruess, I. Steffan-Dewenter, C. Thies, Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management, Ecol. Lett. 8 (2005) 857–874.
- [2] G.W. Korthals, P. Smilauer, C. Van Dijk, W.H. Van der Putten, Linking aboveand below-ground biodiversity: abundance and trophic complexity in soil as a response to experimental plant communities on abandoned arable land, Funct. Ecol. 15 (2001) 506–514.
- [3] T. Frank, S. Aeschbacher, M. Barone, I. Künzle, Ch. Lethmayer, C. Mosimann, Beneficial arthropods respond differentially to wildflower areas of different age, Ann. Zool. Fennici 46 (2009) 465–480.
- [4] S.A. Corbet, Insects, plants and succession: advantages of long-term set-aside, Agric. Ecosyst. Environ. 53 (1995) 201–217.
- [5] P. Duelli, M.K. Obrist, D.R. Schmatz, Biodiversity evaluation in agricultural landscapes: above-ground insects, Agric. Ecosyst. Environ. 74 (1999) 33–64.
- [6] E. Siemann, J. Haarstad, D. Tilman, Dynamics of plants and arthropod diversity during old field succession, Ecography 22 (1999) 406–414.

- [7] J.-A. Salamon, J. Wissuwa, K. Moder, T. Frank, Effects of *Medicago sativa*, *Tar-axacum officinale and Bromus sterilis* on the density and diversity of Collembola in grassy arable fallows of different ages, Pedobiologia 54 (2011) 63–70.
- [8] G.B. De Deyn, W.H. Van der Putten, Linking aboveground and belowground diversity, Trends Ecol. Evol. 20 (2005) 625–633.
- [9] P. Kardol, J.S. Newton, T.M. Bezemer, M. Maraun, W.H. van der Putten, Contrasting diversity patterns of soil mites and nematodes in secondary succession, Acta Oecol. 35 (2009) 603–609.
- [10] D.E. Walter, H.C. Proctor, Mites Ecology, Evolution and Behaviour, CABI Publishing, Wallingford, 1999.
- [11] M. Maraun, H. Schatz, S. Scheu, Awesome or ordinary? Global diversity patterns of oribatid mites, Ecography 30 (2007) 209–216.
- [12] M. Maraun, S. Scheu, The structure of oribatid mite communities (Acari, Oribatida): patterns, mechanisms and implications for future research, Ecography 23 (2000) 374–383.
- [13] V.M. Behan-Pelettier, Oribatid mites biodiversity in agroecosystems: role for bioindication, Agric. Ecosyst. Environ. 74 (1999) 411–423.
- [14] E. Schulz, Die Milbenfauna (Acari: Mesostigmata und Cryptostigmata) in Lebensräumen auf Kalkgestein: Populationsökologie, Sukzession und Beziehungen zum Lebensraum. Dissertation, in: Göttingen, Berichte des Forschungszentrums Waldökosysteme Göttingen (A), vol. 79, 1991, pp. 1–245.
- [15] S. Scheu, E. Schulz, Secondary succession, soil formation and development of a diverse community of oribatids and saprophagous soil macro-invertebrates, Biodivers. Conserv. 5 (1996) 235–250.
- [16] J. Stary, Changes of oribatid mite communities (Acari: Oribatida) during secondary succession on abandoned fields in South Bohemia, in: K. Tajovsky, V. Pizl (Eds.), Soil Zoology in Central Europe, ISB AS CR, Ceske Budejovice, 1999, pp. 315–323.
- [17] A.S. Zaitsev, V. Wolters, R. Waldhardt, J. Dauber, Long-term succession of oribatid mites after conversion of cropland to grassland, Appl. Soil Ecol. 34 (2006) 230–239.
- [18] M. Maraun, J.-A. Salamon, K. Schneider, M. Schaefer, S. Scheu, Oribatid mite and collembolan diversity, density and community structure in a moder beech forest (*Fagus sylvatica*): effects of mechanical perturbations, Soil Biol. Biochem. 35 (2003) 1387–1394.
- [19] H. Koehler, J. Müller, Entwicklung der Biodiversität während einer 20 jährigen Sukzession als Grundlage für Managementmaßnahmen. Abschlussbericht des BMBF-Forschungsvorhabens FKZ 01 LC 0005 bioDIVEMAN, Universität Bremen Zentrum für Umweltforschung und Umwelttechnologie, 2003.
- [20] M.A. Badejo, G. Tian, Abundance of soil mites under four agroforestry tree species with contrasting litter quality, Biol. Fert. Soils 30 (1999) 107–112.
- [21] S. Migge, M. Maraun, S. Scheu, M. Schaefer, The oribatid mite community (Acarina) of pure and mixed stands of beech (Fagus sylvatica) and spruce (Picea abies) of different age, Appl. Soil Ecol. 9 (1998) 115–121.
- [22] M.A. Badejo, J.A.A. Espindola, J.G.M. Guerra, A.M. de Aquino, M.E.F. Correa, Soil oribatid mite communities under three species of legumes in an ultisol in Brazil, Exp. Appl. Acarol. 27 (2002) 283–296.
- [23] M.G. St. John, D.H. Wall, H.W. Hunt, Are soil mite assemblages structured by the identity of native and invasive alien grasses? Ecology 87 (2006) 1314–1324.
- [24] A.R. Maharning, A.A.S. Mills, S.M. Adl, Soil community changes during secondary succession to naturalized grasslands, Appl. Soil Ecol. 41 (2009) 137–147.
- [25] D.A. Wardle, Communities and Ecosystems Linking Aboveground and Belowground Components, Princeton University Press, Princeton, 2002.
- [26] A. Milcu, S. Partsch, C. Scherber, W.W. Weisser, S. Scheu, Earthworms and legumes control litter decomposition in a plant diversity gradient, Ecology 89 (2008) 1872–1882.
- [27] J.R. McLaren, R. Turkington, Plant functional group identity differentially affects leaf and root decomposition, Glob. Change Biol. 16 (2010) 3075–3084.
- [28] E.M. Spehn, J. Joshi, R. Schmid, J. Alphei, J. Körner, Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems, Plant and Soil 224 (2000) 217–230.
- [29] K. Birkhofer, T. Diekötter, S. Boch, M. Fischer, J. Müller, S. Socher, V. Wolters, Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness, Soil Biol. Biochem. 43 (2011) 2200–2207.
- [30] J.-A. Salamon, M. Schaefer, J. Alphei, B. Schmidt, S. Scheu, Effects of plant diversity on Collembola in an experimental grassland ecosystem, Oikos 106 (2004) 51–60.
- [31] M. Viketoft, C. Palmborg, B. Sohlenius, K. Huss-Danell, J. Bengtsson, Plant species effects on soil nematode communities in experimental grasslands, Appl. Soil Ecol. 30 (2005) 90–103.
- [32] M. Viketoft, J. Bengtsson, B. Sohlenius, M.P. Berg, O. Petchey, C. Palmborg, K. Huss-Danell, Long-term effects of plant diversity and composition on soil nematode communities in model grasslands, Ecology 90 (2009) 90–99.
- [33] D.A. Wardle, G.W. Yeates, W. Williamson, K.I. Bonner, The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups, Oikos 102 (2003) 45–56.
- [34] D.A. Wardle, R.D. Bardgett, J.N. Klironomos, H. Setälä, W.H. van der Putten, D.H. Wall, Ecological linkages between aboveground and belowground biota, Science 304 (2004) 1629–1633.
- [35] S. Hadatsch, R. Kratochvil, A. Vabitsch, B. Freyer, B. Götz, Biologische Landwirtschaft im Marchfeld – Potenziale zur Entlastung des Natur- und Landschaftshaushaltes, in: Monographien, Band 127, Umweltbundesamt GmbH (Federal Environmental Agency - Austria), Wien, 2000.
- [36] http://gis.lebensministerium.at/eBOD/frames/index.php?&146=true&gui_id=eBOD.

- [37] G. Weigmann, Hornmilben (Oribatida), in: F. Dahl (Ed.), Die Tierwelt Deutschlands und der angrenzenden Meeresteile, Bd. 76, Goecke & Evers, Keltern, 2006.
- [38] S. Scheu, Automated measurement of the respiratory response of soil microcompartements: active microbial biomass in earthworm faeces, Soil Biol. Biochem. 24 (1992) 1113–1118.
- [39] P. Legende, L. Legende, Numerical Ecology, third ed., Elsevier, Amsterdam, 2012.
- [40] M.J. Anderson, R.N. Gorley, K.R. Clarke, PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods, PRIMER-E, Plymouth, UK, 2006.
- [41] C.F.J. Ter Braak, CANOCO a FORTRAN Program for Canonical Community Ordination by Partial Detrended Canonical Correspondence Analysis, Principle Component Analysis and Redundancy Analysis. Technical report, TNO Institute, Wageningen, The Netherlands, 1988.
- [42] K.R. Clarke, R.N. Gorley, PRIMER V6: User Manual/Tutorial, PRIMER-E, Plymouth, UK, 2006.
- [43] W. Dunger, Zur Primärsukzession humiphager Tiergruppen auf Bergbauflächen, Zool. Jahrb. Allg. Zool. 118 (1991) 423–447.
- [44] C.H. Ettema, T. Bongers, Characterisation of nematode colonization and succession in disturbed soil using the maturity index, Biol. Fertil. Soils 16 (1993) 79–85.
- [45] J.-A. Salamon, J. Wissuwa, S. Jagos, M. Koblmüller, O. Ozinger, C. Winkler, T. Frank, Plant species effects on soil macrofauna density in grassy arable fallows of different age, Eur. J. Soil Biol. 47 (2011) 129–137.
- [46] P. Jaloszynski, Adults of European ant-like stone beetles (Coleoptera: Staphylinidae: Scydmaeninae) Scydmaenus tarsatus Muller & Kunze and Scydmaenus hellwigii (Herbst) prey on soft-bodied arthropods, Entomol. Sci. 15 (2012) 35–41.
- [47] K. Schneider, M. Maraun, Top-down control of soil microarthropods evidence from a laboratory experiment, Soil Biol. Biochem. 41 (2009) 170–175.
- [48] J. Wissuwa, J.A. Salamon, T. Frank, Effects of habitat age and plant species on predatory mites (Acari, Mesostigmata) in grassy arable fallows in Eastern Austria, Soil Biol. Biochem. 50 (2012) 96–107.
- [49] W. Karg, Acari (Acarina), Milben, Parasitiformes (Anactinochaeta), Cohors Gamasina Leach, Raubmilben, in: F. Dahl (Ed.), Die Tierwelt Deutschlands 59. Teil, Gustav Fischer Verlag, Jena, Stuttgart, New York, 1993.
- [50] P. Lebrun, N.M. van Straalen, Oribatid mites: prospects for their use in ecotoxicology, Exp. Appl. Acarol. 19 (1995) 361–379.
- [51] A.S. Zaitsev, M. Chauvat, A. Pflug, V. Wolters, Oribatid mite diversity and community dynamics in a spruce chronosequence, Soil Biol. Biochem. 34 (2002) 1919–1927.

- [52] L. Kutschera, Wurzelatlas mitteleuropäischer Ackerunkräuter und Kulturpflanzen, DLG Verlag, Frankfurt am Main, 1960.
- [53] G.H.R. Osler, A.J. Beattie, Contribution of oribatid ans mesostigmatid soil mites in ecologically based estimates of global species richness, Austral Ecol. 26 (2001) 70–79.
- [54] M. Maraun, S. Migge, M. Schaefer, S. Scheu, Selection of microfungal food by six oribatid mite species (Oribatida, Acari) from two different beech forests, Pedobiologia 42 (1998) 232–240.
- [55] J.M. Anderson, Succession, diversity and trohpic relationships of some soil animals in decomposing leaf litter, J. Anim. Ecol. 44 (1975) 475–495.
- [56] M. Maraun, H. Martens, S. Migge, A. Theenhaus, S. Scheu, Adding to 'the enigma of soil animal diversity': fungal feeders and saprophagous soil invertebrates prefer similar food substrates, Eur. J. Soil Biol. 39 (2003) 85–95.
- [57] S. Saitoh, S. Fujii, H. Takeda, Evaluation of the bottom-up force of accumulated organic matter on microarthropods in a temperate forest floor, Eur. J. Soil Biol. 47 (2011) 409–413.
- [58] N.-I. Noti, H.M. André, X. Ducarme, P. Lebrun, Diversity of soil oribatid mites (Acari: Oribatida) from high Katanga (Democratic Republic of Congo): a multiscale and multifactor approach, Biodivers. Conserv. 12 (2003) 767-785.
- [59] J.C. Bedano, M.P. Cantu, M.E. Doucet, Abundance of soil mites (Arachnida: Acari) in a natural soil of central Argentina, Zool. Stud. 44 (2005) 505–512.
- [60] N. Lindberg, J.B. Engtsson, T. Persson, Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand, J. Appl. Ecol. 29 (2002) 924–936.
- [61] M.A. Tsiafouli, A.S. Kallimanis, E. Katana, G.P. Stamou, S.P. Sgardelis, Responses of soil microarthropods to experimental short-term manipulations of soil moisture, Appl. Soil Ecol. 29 (2005) 17–26.
- [62] W. Müller, Agroklimatische Kennzeichnung des zentralen Marchfeldes, 3, in: Beihelfte zu den Jahrbüchern der ZAMG Klimatologie, Zentralanstalt für Meteorologie und Geodynamik (ZAMG), Wien, 1993. Publ. Nr. 348.
- [63] U.N. Nielsen, G.H.R. Osler, C.D. Campbell, D.F.R.P. Burslem, R. van der Wal, The influence of vegetation type, soil properties and precipitation on the composition of soil mite and microbial communities at the landscape scale, J. Biogeogr. (2010) 1317–1328.
- [64] A.S. Zaitsev, V. Wolters, Geographic determinants of oribatid mite communities structure and diversity across Europe: a longitudinal perspective, Eur. J. Soil Biol. 42 (2006) 358–361.
- [65] U.N. Nielsen, G.H.R. Osler, R. van der Wal, C.D. Campbell, D.F.R.P. Burslem, Soil pore volume and the abundance of soil mites in two contrasting habitats, Soil Biol. Biochem. (2008) 1538–1541.