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Effects of habitat age and plant species on predatory mites (Acari, Mesostigmata) in grassy arable fallows in Eastern Austria

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ABSTRACT

Density, diversity and assemblage structure of Mesostigmata (cohorts Gamasina and Uropodina) were investigated in nine grassy arable fallows according to a factorial design with age class (2–3, 6–8, 12–15 years) and plant species (legume: *Medicago sativa*, herb: *Taraxacum officinale*, grass: *Bromus sterilis*) as factors. The response of Mesostigmata to habitat age and plant species was explored because this group belongs to the dominant acarine predators playing a crucial role in soil food webs and being important as biological control agents. To our knowledge, this combination of factors has never been studied before for Mesostigmata. A further rarely applied aspect of the present study is the micro-scale approach investigating the Mesostigmata assemblage of the soil associated with single plants. Four plots were randomly chosen at each fallow in May 2008. At each plot plant roots and the adjacent soil of five randomly selected plant individuals per plant species were dug out with steel cylinders for heat extraction of soil fauna and measurement of environmental parameters. In total, 83 mite taxa were identified, with 50 taxa being new to Austria. GLM analysis revealed a significant effect of plant species on mite density, with significantly more mites in *B. sterilis* than in *T. officinale* samples, and *M. sativa* samples being intermediate. This was in contrast to the assumption that the mite density is highest in *M. sativa* samples due to the propagation of plant quality effects to higher trophic levels. These results were probably caused by a higher amount of fine roots in grass samples leading to high densities of Collembola, which are preferred prey of predatory mites. Mite density did not significantly differ between the three age classes. A canonical analysis of principal coordinates (CAP) showed that the mite assemblage exhibited a weak yet significant separation between plant species, and a highly significant separation between age classes. Accordingly, different mite assemblages were found for the three age classes, while only few mite species were clearly associated with a single plant species. Finally, canonical correspondence analysis (CCA) revealed that the mite assemblage was best explained by soil organic carbon, total density of Collembola and water content.

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1. Introduction

Conversion of intensive farmland towards more natural and species rich ecosystems needs to be included into the management of sustainable agriculture. Less or undisturbed habitat islands like fallows can serve as refuges for endangered species and increase species richness in rural landscapes (Gulvik et al., 2008). The transition of arable land to later successional habitats such as grassland includes changes in vegetation composition, soil fauna and microbial communities (Gormsen et al., 2006). Soil biota is an

important component of terrestrial ecosystems because it governs essential ecosystem functions such as decomposition and recycling of organic residues, which influence plant community composition and primary production (Wardle et al., 2004). Furthermore, soil fauna may be of considerable importance for initial colonization as a vector for seed, spores and microbial propagules (Koehler, 2000; Walter and Proctor, 2004). Besides the increased interest in belowground communities over the last few decades, the knowledge of the factors regulating the composition of belowground communities remains limited (Nielsen et al., 2010). Microarthropods constitute a considerable and important part of soil fauna (Siepel and Maaskamp, 1994). Among the microarthropods, mites and Collembola are the most important groups in soil with overwhelming species richness and densities within the range of hundreds of thousands of individuals per m² (Koehler, 1999). As major predators of root pests, especially nematodes, mites are

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generally considered beneficial in soil (Walter and Proctor, 2004). The dominant acarine soil predators are found among the mite taxa Mesostigmata (Gamasida) and Prostigmata (Ruf and Beck, 2005; Walter and Proctor, 2004). The majority of Gamasina, which are a subset of Mesostigmata, are mobile predators feeding on nematodes, Collembola, enchytraeids, insect larvae and mites (Koehler, 1999). As main predators among soil mesofauna, Gamasina have a crucial position in the soil food web contributing significantly to energy and matter turnover (Ruf and Beck, 2005). They have an indirect influence on overall ecosystem performance by affecting population growth of other organisms and are used as bioindicators due to their functional role, high species richness, high abundance and robustness to sampling and extraction (Koehler, 1999). Despite their importance, studies about the succession of Mesostigmata are rare. In most cases there are short-term investigations ranging from less than three (Purvis and Curry, 1980; Streit et al., 1985; Wasyluk, 1995) to five years (Lagerlöf and André, 1988; Koehler, 1991). Furthermore, in most studies the investigated habitats are industrial reclamation sites (Hutson, 1980; Koehler, 1984; Madej and Stodolka, 2008) or reclaimed mining wastelands (Christian, 1993; Dunger, 1968; Madej and Skubala, 1996; Zerling and Prasse, 1986). In general, studies on soil mite communities in traditional, multi-functional farmland and on secondary succession following the abandonment of traditional farmland are lacking in Europe (Gulvik et al., 2008). Only one German study (Koehler, 2000) matches the age profile and habitat type investigated in the present work.

Studies concerning plant effects on soil mites are even scarcer (Badejo et al., 2002; Bezemer et al., 2010; St. John et al., 2006). However, plant species and plant functional group effects on different trophic levels of a soil food web have been studied using nematodes (Viketoft et al., 2005; Wardle et al., 2003) and Collembola (Salamon et al., 2004). Plant species identity influenced the community composition of soil organisms within each of three consumer levels meaning that community compositional effects are propagated through food chains (Wardle et al., 2003). For a long time, most soil organisms have been viewed as generalists, which are relatively insensitive to plant species identity (Bezemer et al., 2010). Yet plant species vary in their chemistry, physiology, rhizodeposition and the quality and quantity of the litter they produce (Maharning et al., 2009). Especially legumes increase soil fertility by nitrogen fixation and returning high quality litter to soil organisms (Mulder et al., 2002; Spehn et al., 2002; Temperton et al., 2007).

In the present study, we investigated the influence of single plant species (*Medicago sativa* as legume, *Taraxacum officinale* as forb, *Bromus sterilis* as grass) on predatory mites in grassy arable fallows belonging to different age classes (2–3, 6–8 and 12–15 years). A micro-scale approach, investigating the mites of the soil associated with single plants, was applied. To our knowledge, the combined effects of habitat age and plant species on soil mites under natural field conditions have not been studied so far. This study is designed to test the following hypotheses:

- 1) The density of mites is higher in *M. sativa* than in *T. officinale* and *B. sterilis* samples due to the propagation of plant quality effects to higher trophic levels. The high nitrogen content of *M. sativa* litter increases the growth of microorganisms attracting microbivorous soil fauna (e.g. Collembola), which is preyed upon by mesostigmatid mites.
- 2) The density and species richness of mites will increase with the successional age of fallows due to the decreased intensity of disturbances and increased habitat diversity because of a well developed vegetation cover.
- 3) The mite assemblages of the different age classes differ from each other due to the occurrence of early, intermediate and late species during succession (Koehler, 1998).

2. Material and methods

2.1. Sites

This study was carried out in the Marchfeld region comprising an area of roughly 1000 km² east and north-east of Vienna, Austria. It is part of the Vienna Basin, a section of the Pannonian Plain, characterized by a continental climate of high temperature and low precipitation in summer, with mean annual temperature over 9 °C and mean total annual precipitation between 500 and 600 mm (Hadatsch et al., 2000). 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 age classes (2–3, 6–8 and 12–15 years) each including three sites representing different stages of secondary succession (Scheu and Schulz, 1996). The dominant soil types were Chernozem, Parachernozem and Wet Chernozem. Most of the fallows were established via spontaneous succession and a few of the fallows were sown with a Lucerne fallow seed mixture. All fallows were mown once a year. The site parameters soil type, geographic position and size are given in Salamon et al. (2011).

2.2. Sampling and sample treatment

In May 2008, four plots with at least 20 m distance from each other were randomly selected in the center of each fallow. Within each plot roots and the associated soil of five individuals of *M. sativa*, *T. officinale* and *B. sterilis* were extracted using square steel cylinders (5.6 cm × 5.6 cm, length 10 cm) from aggregations of the chosen plant species. Altogether 108 samples were obtained (nine sites × four plots × three plant species). The material of two cylinders per plant species was pooled for the measurement of abiotic soil parameters and microbial biomass. The soil of three cylinders (approximately 940 cm³) was combined for the extraction of the soil fauna.

Extraction was carried out in a Berlese–Tullgren funnel with stepwise temperature rise from lowest possible output power to maximum intensity with an intermediate step in the course of three days. The soil fauna was gathered in 10% sodium benzoate solution, transferred into 70% ethanol and stored therein until identification. Mites from the group Mesostigmata were mounted in Marc Andre reagent, dried for about one week and identified to species level using a differential interference contrast microscope and the identification key of Karg (1993).

The samples for the determination of soil parameters were sieved with a 2 mm mesh and partitioned for different measurements in the laboratory. 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 ascertained 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 in fresh soil samples equivalent to 3.5 g dry weight. For details on determination of microbial carbon and basal respiration see Salamon et al. (2011).

2.3. Statistical analyses

To detect differences in mite density and species richness as well as for soil parameters the procedure GLM (General Linear Model) of the statistical software SAS 9.1 was used according to the design

with age class and plant species as factors, an interaction term (age \times plant) and site as random effect nested within age class. The Tukey test was applied to verify differences between means at the 5% probability. The same analysis was applied to the abundant species within the dominance classes eudominant ($>10\%$) to subdominant ($>1\%$), which have also a high frequency, i.e. being present on at least five fallows. Dominance classes were used according to Engelmann (1978) resulting in the following six classes eudominant $>10\%$, dominant 3.2–10%, subdominant 1–3.1%, rezedent 0.32–0.99%, subrezedent 0.1–0.31% and sporadic $<0.1\%$. The frequency classes euconstant $>50\%$, constant 30.1–50%, subconstant 15.1–30%, accessory 5–15% and accidents $<5\%$ were taken from Napierala et al. (2009).

To detect a potential effect of age class and plant species on species assemblage, the data were visually explored using non-metric Multi-Dimensional Scaling (MDS) and Principal Coordinates Analysis (PCO) in a first step. Afterward, the data were analyzed applying the nonparametric procedures PERMANOVA (Permutational ANOVA/MANOVA) and CAP (Canonical Analysis of Principal Coordinates) of the software PRIMER v6 with Add-on PERMANOVA. Both routines utilize a permutation method to test for group differences, which avoids the need to conform to normality (Anderson et al., 2006). According to Anderson et al. (2006), PERMANOVA examines if between-group variation explains a significant proportion of the total variation in the system as a whole, whereas CAP, which is a kind of discriminant analysis, is designed to find axes in the multivariate space that are best at separating groups, even if the differences occur in obscure directions that are not apparent when one views the data cloud as a whole. The approach of both analyses is different. First, in PERMANOVA, the relative importance of each PCO axis is in proportion to its eigenvalue (its variance), whereas in CAP, each PCO is given equal weight in the analysis. The latter ensures that directions that otherwise might be of minor importance in the data cloud as a whole, are given equal weight when it comes to searching for groups. Second, the purpose of the CAP routine is to seek out separation of the group centroids. As a consequence, it effectively completely ignores, and even destroys, differences in dispersions among the groups, while PERMANOVA will be sensitive to differences in dispersion among groups (Anderson et al., 2006). Multivariate homogeneity of dispersion was tested with the routine PERMDISP, which is a dissimilarity-based extension of Levene's test (Anderson et al., 2006).

As resemblance measure Bray–Curtis similarity was chosen for the mite assemblage data because it is the most commonly applied similarity measure for biological data (Clarke and Warwick, 2001). Euclidian distance was used for density, species richness, Shannon diversity, Pielou's evenness and environmental parameters, because it is an appropriate similarity measure for environmental data (Clarke and Gorley, 2006). Species counts were subjected to a $\log(1 + y)$ transformation being a practical choice that retains quantitative information and downplays dominant species (Clarke and Warwick, 2001).

The influence of the environmental parameters on mite assemblage was investigated with CCA (Canonical Correspondence Analysis) using CANOCO (Ter Braak, 1988) with forward selection of environmental variables. Only species belonging to the dominance classes subrezedent to eudominant (1%– $>10\%$) were included in the CCA analysis after a log transformation. The factors age and plant species were included as centroids in the CCA bi-plot.

3. Results

3.1. Overall species richness and abundance structure

In total, 83 taxa were found comprising 37 genera and 16 families. 79 taxa were identified to species level. Five taxa could only be determined to subgenus or genus level. One of the non-

identified taxa could be matched quite closely to another occurring species, which was used to assign a provisional species name. Only 34 of the identified species have been reported for Austria before.

Only 19% of all taxa were abundant and observed in nearly all fallows with the three species *Asca bicornis*, *Rhodacarellus silesiacus* and *Hypoaspis aculeifer* being eudominant and comprising 47.3% of the total amount of individuals. They were classified as euconstant with sample frequencies of 63%, 67% and 83%, respectively. The next most abundant species ranked as dominant and constant were *Leiioseius bicolor*, *Hypoaspis kargi*, *Hypoaspis vacua* and *Alliphis siculus*. Further ten species were assigned to the class subdominant (Table A1). 81% of all taxa were comparatively rare comprising the abundance classes rezedent to sporadic with the latter class containing 42% of all taxa however only less than 2% of all individuals. The frequencies of rare species were in general less than 25%.

3.2. Age and plant species effects on density

The density of Gamasina was significantly higher in the *B. sterilis* than in the *T. officinale* samples, with the *M. sativa* samples being intermediate ($F = 3.18$, $p < 0.05$). There was no age effect on Gamasina density (Fig. 1a). The density of the cohort Uropodina decreased significantly from young to old fallows ($F = 5.46$, $p < 0.01$), while the plant species had no significant effect (Fig. 1b). In Fig. 1, total Mesostigmata are not shown because their patterns found with GLM were nearly equivalent to the cohort Gamasina, which comprised 97.7% of all individuals. Species richness, Shannon diversity index and Pielou's evenness remained unaffected by both factors. GLM revealed significant "age \times plant species" interactions for Mesostigmata density and species richness. One-way ANOVA revealed that these interactions occurred only for *M. sativa*. Mesostigmata density was significantly higher in young fallows than in mid-aged and old ones ($F = 10.19$, $p < 0.001$). Species richness was significantly higher in young than in mid-ages fallows, with the old ones being intermediate ($F = 4.76$, $p < 0.05$).

The pattern of the plant species effect was identical for three of the abundant Gamasina species. The densities of *H. aculeifer* ($F = 3.81$, $p < 0.05$), *A. bicornis* ($F = 3.04$, $p = 0.053$) and *Amblyseius alpinus* ($F = 3.42$, $p < 0.05$) were significantly higher in *B. sterilis* than in *T. officinale* samples with *M. sativa* samples being intermediate (Fig. 2a,b,d). In contrast, the number of individuals of *H. vacua* was significantly higher in *T. officinale* than in *M. sativa* and *B. sterilis* samples ($F = 7.09$, $p < 0.01$, Fig. 2c). A significant age effect was observed for eight out of the 17 most abundant species. The density of *H. aculeifer* ($F = 10.16$, $p < 0.001$, Fig. 3a) increased steadily with significantly more individuals in old than in mid-aged and young fallows. The densities of *R. silesiacus* ($F = 7.68$, $p < 0.001$, Fig. 3b), *Arctoseius cetratus* ($F = 5.76$, $p < 0.01$, Fig. 3d) and *Protogamasellus singularis* ($F = 7.85$, $p < 0.001$, Fig. 3h) were significantly higher in young than in mid-aged and old fallows. The density of *Amblyseius bidens* was significantly higher in mid-aged than in young fallows, with the old ones being intermediate ($F = 6.61$, $p < 0.01$, Fig. 3c). The density of *Nenteria breviunguiculata* ($F = 6.54$, $p < 0.01$, Fig. 3e) and *Pergamasus crassipes* ($F = 4.09$, $p < 0.05$, Fig. 3f) decreased continuously, with significantly higher abundances in young than in old fallows, and mid-aged fallows being intermediate. The density of *Pachylaelaps karawaiwii* ($F = 9$, $p < 0.001$, Fig. 3g) was significantly higher in young than mid-aged fallows, with old fallows being intermediate.

3.3. Assemblage analysis

Ordinations with MDS and PCO did not reveal any patterns in Mesostigmata species composition for plant species, whereas a slight

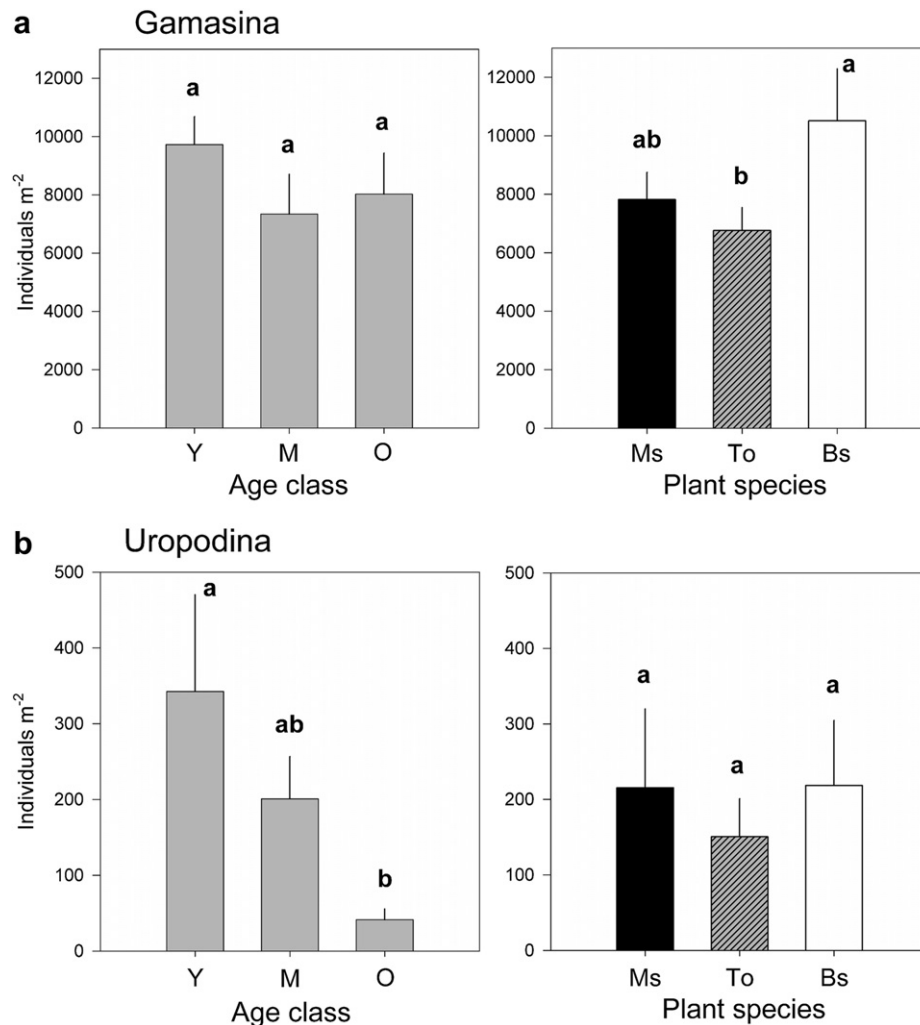


Fig. 1. Density of the Mesostigmata mite cohorts a) Gamasina and b) Uropodina in *Medicago sativa* (Ms), *Taraxacum officinale* (To) and *Bromus sterilis* (Bs) samples and in the three age classes (Y = young, M = mid-aged, O = old) of the fallows ($n = 9$). Means with 1 SE, bars sharing the same letter do not differ significantly from each other ($p > 0.05$; Tukey test).

separation could be detected for the factor age in the PCO plots. Correspondingly, CAP showed a weak discrimination between the plant species (Fig. 4a) and a clear separation of the three age classes (Fig. 4b). CAP calculates two test statistics, which were both significant for plant species and highly significant for age class. In a leave-one-out cross validation as an integral part of CAP 47.7% of the samples were reclassified correctly into their respective plant species group whereas 80.4% of the samples were reclassified correctly into their respective age class. In contrast, PERMANOVA was significant for plant species ($p(\text{perm}) < 0.05$) but not for age class. CAP offers the possibility of a species overlay on the CAP-chart showing which mite species belong to the different groups. Arbitrary species that occurred on less than three fallows were omitted. For plant species only species with correlations above 0.2 to one or both CAP-axes are mentioned. According to CAP, *H. vacua*, *H. vacua* variation' and *Hypoaspis procer* were associated with *T. officinale*, while *L. bicolor*, *Parasitus fimetorum* and *Uropoda orbicularis* correlated with both *T. officinale* and *M. sativa*. *Parasitus beta*, *Ameroseius corbiculus* and *Amblyseius meridionalis* were grouped with *M. sativa*. *A. cetratus*, *Punctodendrolaelaps strenzkei*, *H. aculeifer* and *A. alpinus* were related to both *M. sativa* and *B. sterilis*, where the latter two species tended to be closer to *B. sterilis*. *Hypoaspis*, *Antennoseius bacatus* and *Machrocheles pontina* were associated with *B. sterilis*. For most mite species the assignments to the plant species are supported by significant GLM results and the CCA analysis.

For habitat age correlations between mite species and CAP-axes were higher than for plant species, therefore only species with correlations greater than 0.3 were considered. Altogether, quite characteristic assemblages were observed for the three age classes. *R. silesiacus*, *Parasitus hyalinus*, *P. strenzkei*, *A. cetratus*, *P. beta* and *P. karawaiewi* differentiated the early successional stage from the older stages. To some extent also *H. kargi*, *P. singularis* and *N. breviunguiculata* can be considered characteristic of young fallows, where *N. breviunguiculata* tended to be related to young and mid-aged fallows. *Proprioiseiopsis sororculus*, *Amblyseius filixis*, *Veigaia exigua*, *Rhodacarus furmanae* and *Antennoseius avius* characterized the mid-aged fallows. *H. aculeifer*, *H. vacua*, *Macrocheles glaber*, *P. fimetorum* and *Veigaia planicola* were associated with old fallows. For most of these species the relations found with CAP were supported by significant GLM and CCA results placing them into the same groups.

Mesostigmata assemblage was examined in relation to environmental parameters using CCA which explained 19.03% of the total variance. Organic carbon (4.38%), density of Collembola (3.56%), water content (3.28%), C/N ratio (2.74%), microbial carbon (1.64%) and density of Oribatida (1.64%) contributed significantly to the mite assemblage ($p < 0.01$) and explained together 17.25% of the total variance. Axis 1 mainly represents organic carbon and the densities of Collembola and Oribatida. Axis 2 represents C/N ratio, microbial carbon and basal respiration (Fig. 5). Some species, e.g.

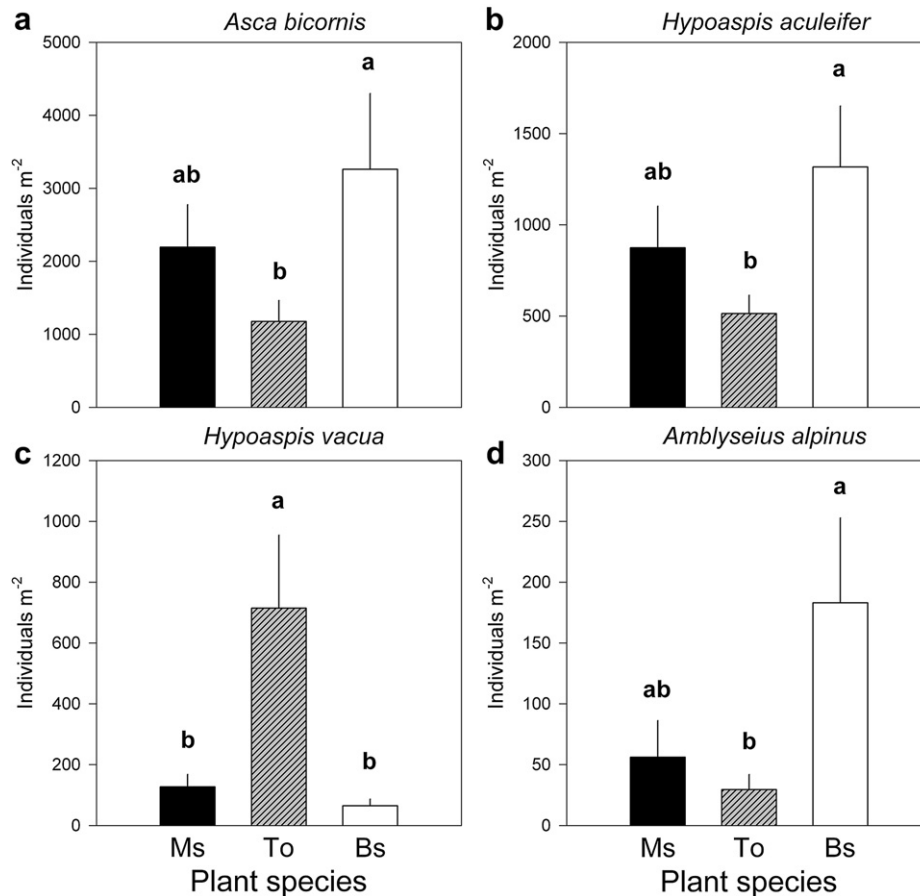


Fig. 2. Density of four common Mesostigmata mite species with significant plant species effect in *Medicago sativa* (Ms), *Taraxacum officinale* (To) and *Bromus sterilis* (Bs) samples ($n = 9$). Means with 1 SE, bars sharing the same letter do not differ significantly from each other ($p > 0.05$; Tukey test).

A. filixis, *P. sororculus*, *R. furmanae*, *Arctoseius insularis* and *V. exigua*, were associated with mid-aged fallows and correlated with basal respiration. Other species like *Veigaia nemorensis*, *H. aculeifer*, *H. kargi* and *A. bicornis* correlated with old fallows. A group of species (e.g. *R. silesiacus*, *A. cetratus*, *P. karawaiewi* and *P. hyalinus*) correlated positively with the density of Collembola and young fallows. Only few species were grouped with single plant species: *H. aculeifer* and *M. pontina* with *B. sterilis*, and *A. corbiculus* and *P. fimetorum* with *M. sativa*. *U. orbicularis*, *H. vacua*, *H. vacua vari-ation*, *L. bicolor*, *P. singularis* and *M. glaber* were associated with *T. officinale*. Some species could not be assigned to a plant species or age class but were clearly correlated with high organic carbon (*Ameroseius plumigerus*, *V. planicola*, *A. alpinus*, *P. crassipes*) or density of Oribatida (*P. crassipes*, *N. breviunguiculata*). Moreover, a group of species was associated with samples that had low organic or microbial carbon, pH or C/N ratio.

4. Discussion

Mesostigmata densities of the chosen arable fallows varied from 3050 to 13,460 with a mean value of 8560 individuals m⁻² averaged over all samples. Similar high densities were found on lucerne ley in the second and fourth year of a Swedish study (Lagerlöf and Andrén, 1988). In contrast, densities reported elsewhere in Central Europe were lower (Buryn and Hartmann, 1992; Koehler, 2000; Madej and Stodolka, 2008; Schulz, 1991). Higher mite densities in the present study might be caused by a higher survival rate perhaps resulting from the former agricultural use as well as

higher immigration rates due to a rather small-scale heterogeneous mosaic of different crop fields and other fallows in the vicinity of the investigated fallows.

4.1. Effect of plant species on Mesostigmata density and species richness

Individual plant species may affect components of the soil biota and associated processes because they differ in quantity and quality of resources, which are returned to the soil decomposer system (Wardle et al., 2004). Sometimes it might be impossible to separate the effects of plant quality and quantity, with soil fauna groups being more sensitive to the amount of nutritive resources (Laossi et al., 2008). Because many soil biota are generalists in terms of feeding habit and habitat preference, they may show a relatively weak response to slight differences in resource quality (Wardle et al., 2006), which could also be true for soil mites. St. John et al. (2006) found several mite suborders to be nonspecific to the identity of grass species with no significant differences in abundance, species richness and diversity of mites between the grass species. They concluded that most soil mites may be sensitive to the original plant source, as long as similar amounts of resources are provided, which means that resource quantity and habitat diversity may be more influential than resource quality. This insensitivity might be explained by indirect interactions, polyphagy and multiple resource channels (root, bacteria, fungi) in soil systems (Hunt et al., 1987; Setälä, 2002). By contrast, the predatory mites in our study were found to be sensitive to plant species identity. In

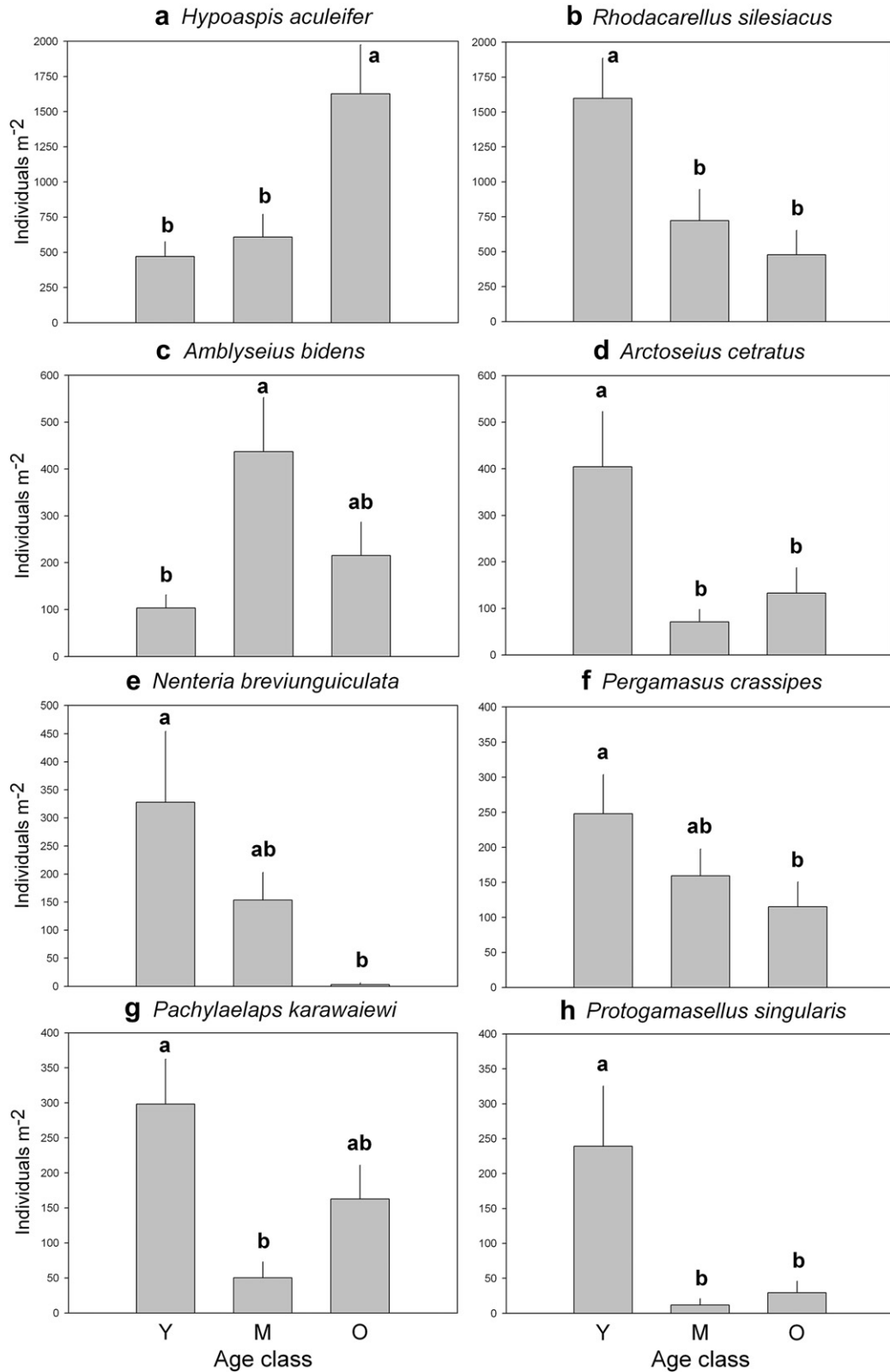


Fig. 3. Density of the eight most abundant Mesostigmata mite species with significant age effect in the three age classes (Y = young, M = mid-aged, O = old) of the fallows (n = 9). Means with 1 SE, bars sharing the same letter do not differ significantly from each other (p > 0.05; Tukey test).

contrast to our hypothesis which states, that the legume effect of higher plant quality may trickle up to higher trophic levels (Bezemer et al., 2010), mite density was significantly higher in the grass species reflecting the pattern of the Collembola studied in the

same fallows (Salamon et al., 2011). This seems to support a greater importance of resource quantity over quality due to the higher amount of fine roots of the grass *B. sterilis* compared to *M. sativa* and *T. officinale* (Kutschera, 1960), which attracts potential prey like

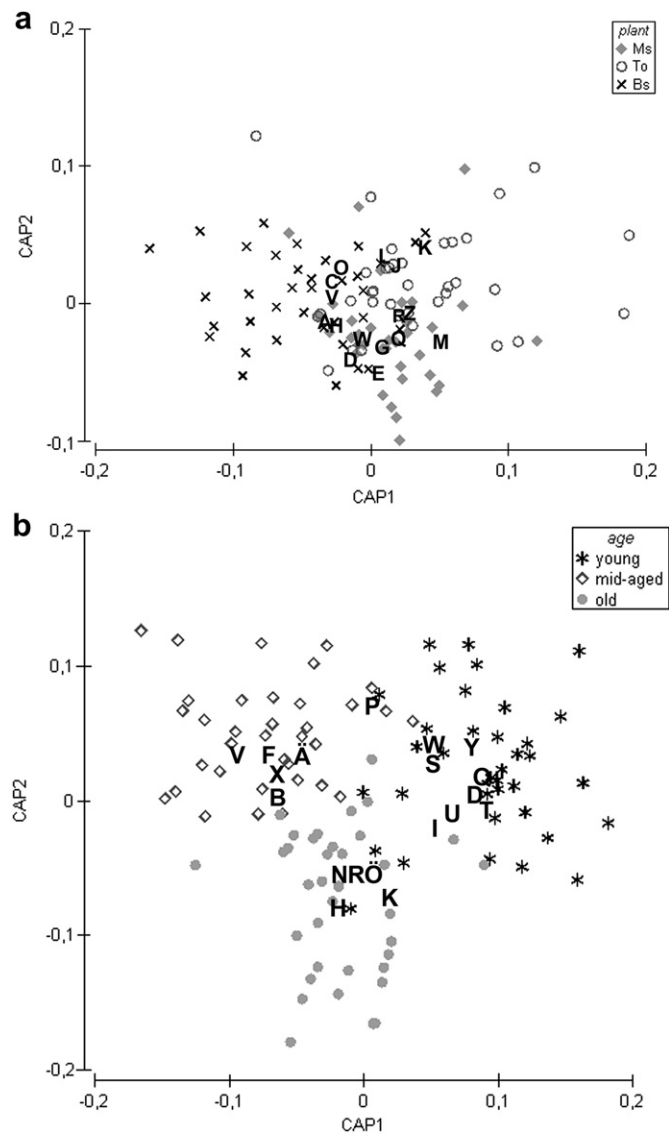


Fig. 4. Canonical Analysis of Principal Coordinates (CAP) for Gamasida assemblage in grassy arable fallows of the Marchfeld region, Austria. The letters represent Gamasida species with correlations to the CAP-axes above 0.2, which occurred on at least three sites. A = *A alp*, B = *A avi*, C = *A bac*, D = *A cet*, E = *A cor*, F = *A fil*, G = *A mer*, H = *H acu*, I = *H kar*, J = *H pro*, K = *H vac*, L = *H vav*, M = *L bic*, N = *M gla*, O = *M pon*, P = *N bre*, Q = *P bet*, R = *P fim*, S = *P hya*, T = *P kar*, U = *P sin*, V = *P sor*, W = *P str*, X = *R fur*, Y = *R sil*, Z = *U orb*, Å = *V exi*, Ö = *V pla* (for abbreviations of mite species see Table A1). a) Plant species effect: Ms = *Medicago sativa*, To = *Taraxacum officinale*, Bs = *Bromus sterilis*; 107 samples; 19 PCO axes; leave-one-out cross validation total correct = 47.7%; test statistic1: $p < 0.05$, test statistic2: $p < 0.01$, 9999 permutations. b) Age effect: 107 samples; 16 PCO axes; leave-one-out cross validation total correct = 80.4%; test statistic1 and test statistic2: $p < 0.001$; 9999 permutations.

Collembola and nematodes promoting higher densities of predators. A further possible explanation might be the high overall abundances of *A. bicornis* and *H. aculeifer*, which had both significantly higher densities in grass plots. In contrast to our results, Lagerlöf and Andrén (1988) observed higher Mesostigmata densities in lucerne ley than in grass and barley fields. Similarly, Oribatida densities were higher in three legume species treatments than in a single grass (Badejo et al., 2002). Some studies detected a plant species or plant functional group effect, while in other studies some of the investigated soil fauna groups remained unaffected (Eisenhauer et al., 2011; Laossi et al., 2008; Van Eekeren et al., 2009;

Viketoft et al., 2005, 2009; Wardle et al., 2003). Furthermore, some studies suggest that the identity of plant species is more important than their functional group (Badejo et al., 2002; Bezemer et al., 2010; Viketoft et al., 2005, 2009; Wardle et al., 2003). In contrast to abundance, species richness was not affected in our study, which agrees with other studies investigating soil mites (Badejo et al., 2002; St. John et al., 2006).

The observed 'age × plant species' interactions do not surprise, since it was shown in a litter quality experiment with Collembola, mites and nematodes that plant effects may change over time (Ilieva-Makulec et al., 2006). Also Badejo et al. (2002) found a seasonal influence of plant species on Oribatida density. Eisenhauer et al. (2011) detected a decrease of the importance of major plant functional groups between 2004 and 2008, with a slight and a significant decrease of the relevance of grasses and legumes, respectively. The latter work corresponds to our results, where mite density and species richness were significantly higher in young fallows in *M. sativa* samples.

4.2. Effect of habitat age on Mesostigmata density and species richness

We found a high initial density of Mesostigmata in young fallows, a decrease in mid-aged ones and a slight recovery in old fallows. Such an age effect has been reported for varying habitats like a graded rubble dump with areas of natural succession and recultivation, investigated in a continuous time series of 20 years (Koehler, 1998, 2000, Koehler and Müller, 2003). Also indirect succession studies with different succession stages on a power plant waste dump (Madej and Stodolka, 2008) or plot age of a reclaimed coal mine (Zerling and Prasse, 1986) and age of rehabilitated nickel- and copper-mine tailings (St. John et al., 2002) as well as abandoned agricultural land (Holtkamp et al., 2008) revealed the same pattern.

The very high densities in the early successional stage result from pioneer optima (Koehler and Müller, 2003), especially of pioneer species or species which are able to survive regular disturbances connected with agricultural practices. These species have suitable attributes, e.g., small and slender shape, high reproduction rate, high agility and phoresy, which allow them to build up large populations in rather short time (Madej and Stodolka, 2008; St. John et al., 2002). *R. silesiacus*, which was dominant in the young fallows, can be considered as survivor tolerating harsh conditions as a small and slender inhabitant of the deeper soil layer (Koehler and Müller, 2003). Further pioneer species are *A. bicornis* (Madej and Stodolka, 2008), which was the most abundant species, *A. cetratus* and *A. siculus* (Heisler, 1995), which were both subdominant and phoretic species (Koehler, 1998; Karg, 1993). Also typical for the early successional stage is *P. singularis* (Madej and Stodolka, 2008), a further subdominant species in the young fallows. Eight of the twelve abundant species in young fallows are rather small with a body size of less than 500 µm including the dominant *H. kargi* as well as *H. vacua*, which both belong to the smaller species within the genus *Hypoaspis*. Most of the abundant species occur repeatedly or regularly in arable fields and grasslands (Karg, 1993). The development of pioneer optima is facilitated by a high availability of nutrients, which stems from the enhanced decomposition of organic matter and minerals due to large fluctuations of climatic factors when vegetation cover is sparse (Vitousek and Walker, 1987). A good supply of nutrients enables the growth of bacteria and fungi supporting the development of large populations of nematodes (Dogan et al., 1996), which in turn provides plenty of food for the mostly nematophagous mite species (Koehler, 1999). Among the abundant taxa in the young fallows predominantly feeding on nematodes were *R. silesiacus* (Sadar and

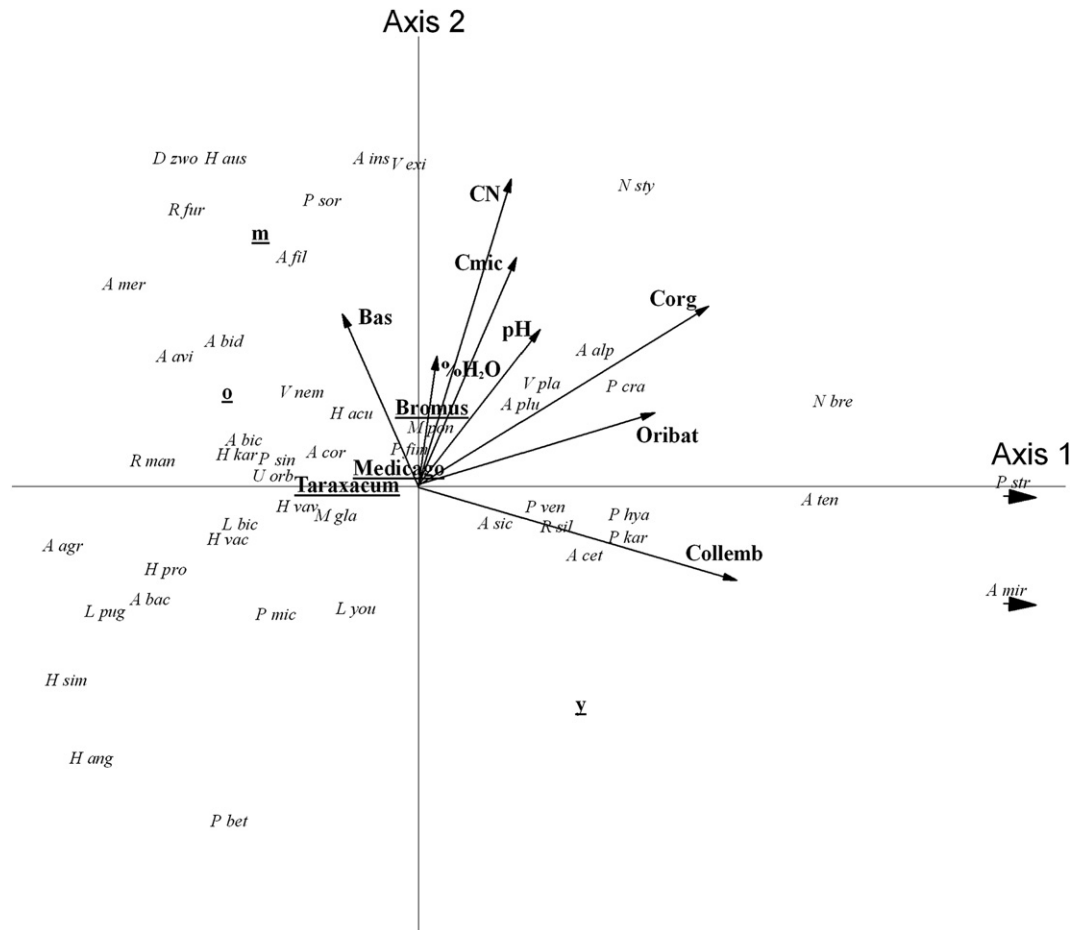


Fig. 5. Ordination bi-plot of the Canonical Correspondence Analysis (CCA) for Gamasida taxa considering eudominant (>10%) to subrezedent (>0.1%) species. For abbreviations of mite species see Table A1. Species with short arrow are located out of scale. Environmental variables: basal respiration (Bas), C/N ratio (CN), microbial carbon (Cmic), water content (%H₂O), pH value (pH), organic carbon (Corg), density of Oribatida (Oribat) and Collembola (Collemb). Age classes of the fallows (y = young, m = mid-aged, o = old) and presence of *Medicago sativa*, *Taraxacum officinale* and *Bromus sterilis* are included as centroids.

Murphy, 1987), *A. cetratus* (Binns, 1974), *H. aculeifer*, *Pachylaelaps* (Karg, 1993), *Protogamasellus* (Krantz and Walter, 2009) and Uropodina (Koehler, 1999). *A. siculus* even feeds exclusively on nematodes (Koehler, 1999). In our study high availability of nutrients might be a remnant of the former use of our study sites as conventional crop fields, and the influence of adjacent fields still in agricultural use. The population decline after the observed pioneer maxima might be due to the timely limitation of easily available nutrients (Koehler, 2000), which are readily taken up by the developing vegetation, increasing immobilization of nutrients (Koehler and Müller, 2003) and intensified competition among soil biota (Ettema and Bongers, 1993). The increase in mite density in later successional stages presumably results from the overall increased diversity of habitats, which is caused by the developing vegetation balancing microclimate during the consolidation phase (Koehler and Müller, 2003) as well as burrowing animals like earthworms creating nutrient-rich microhabitats by repeated small-scale disturbances (Scheu and Sprengel, 1989). Vegetation structure is one of the most important factors influencing soil conditions. The increase in plant cover, plant species richness, humus content and the appearance of shrubs and trees improve soil conditions supporting the establishment of another mite species sequence (Madej and Stodolka, 2008). Zaitsev et al. (2006) observed a shift in the major factors on the oribatid community from soil conditions to vegetation conditions and further

a combination of both. Szymkowiak (1999) found a significant effect of undergrowth cover on four mesostigmatid mite species including *V. nemorensis* in terms of a positive correlation between mite abundance and vegetation cover. The Gamasina assemblage was influenced by small pioneer species, herbs, tall forbs and grasses according to Koehler and Müller (2003).

In contrast to earlier studies showing an increase in species richness with habitat age (Koehler and Müller, 2003; Madej and Stodolka, 2008; Schulz, 1991; St. John et al., 2002) we did not find increasing species numbers. In our study species richness varied only slightly with 11 ± 1 species between age classes due to the high variation between samples as well as sites.

4.3. Effects of habitat age and plant species on Mesostigmata assemblage

Plant species identity had a significant effect on mite assemblage according to PERMANOVA, which explained a significant proportion of the overall variation of the system. Also CAP, which serves as a discriminant analysis, revealed significant differences between the plant species. Similar to the present work, Bezemer et al. (2010) found a significant plant species effect on communities of nematodes, mites, enchytraeids, macrofauna and microorganisms as well as food web structure as a whole for plant individuals of *Plantago lanceolata* and *Lotus corniculatus*. A plant

species effect on nematode community even with different composition between plant species of the same functional group was found by Viketoft et al. (2005). However, there was no significant plant effect for predatory (Viketoft et al., 2009; Wardle et al., 2003) and omnivorous nematodes (Viketoft et al., 2009). It seems that the effect of plant species composition on soil communities is context-dependent with a range of effects being met. This context dependency is likely to be determined primarily by spatial and temporal scale and by abiotic factors (Wardle et al., 2004).

Such context-dependency might be a possible reason for the non-significant PERMANOVA result for habitat age. Yet, CAP showed that the mite assemblage differed significantly between the three age classes. This may be due to the different approach of both routines (see methods). Furthermore, the greater importance of spatial and soil related or other environmental factors may mask the age effect rendering the influence of habitat age on overall variation not significant. The effect of a single factor may not be detected in field studies because plant-soil food web interactions are complex and comprise many species and variables. Additionally, the response of the soil faunal community and diversity might not be in-step with plant succession. Species of soil biota found in early successional stages persist in later stages, although with changes in dominance and species frequency. Species replacement is either less pronounced or it occurs at a different (longer) time scale (Maharning et al., 2009). This might explain why our results differ partly from other studies. Secondary succession of plants and soil biota start from different boundary conditions. Our study sites were abandoned agricultural fields while in other studies reclaimed dumps were investigated (Koehler, 1998; Koehler and Müller, 2003; Madej and Stodolka, 2008). Despite this, Madej and Stodolka (2008) observed a pattern similar to the present study in terms of abundance in different successional stages for *A. bicornis*, *A. cetratus*, *A. meridionalis*, *P. singularis* and *V. planicola*. Supporting our results, Koehler (1998) also found a similar distribution over time for *R. silesiacus*, *L. bicolor* and *V. planicola*, while Schulz (1991) found a similar abundance pattern over time for *P. crassipes*, *V. exigua* and *V. planicola*. *A. cetratus*, which can establish high populations in disturbed habitats like crop fields as a phoretic early colonizer, was only found within the first four years of succession (Koehler, 1998). However, in the present study this species occurred in all fallows of all age classes with a significantly higher density in young fallows, which corresponds to the pattern observed by Madej and Stodolka (2008). It seems that this species is able to persist in later successional stages or quickly reinvade habitats due to phoretic transport. Similar to Madej and Stodolka (2008), *A. bicornis* remained a dominant species throughout all age classes also in the present study although being considered as pioneer species (Madej and Stodolka, 2008). In concordance to Koehler and Müller (2003), who observed rather clear succession phases with different Gamasina assemblages replacing each other on the successional site, in our study characteristic species assemblages were also observed for the three age classes. A shift in the preferred stratum could be observed too. The proportion of Ascoidea and Rhodacaridae, which both colonize preferably soil porosities and capillaries (Karg, 1994) and Rhodacaridae even frequently encountered in deeper soil layers up to underlying groundwater habitats (Krantz and Walter, 2009), decreased from roughly 60% in young fallows to 40% in old fallows. On the other hand, Phytoseiidae, which are mostly found above-ground on herbs and woody plants (Karg, 1993), increased from 2.6% in young fallows to 12% in mid-aged fallows indicating the increasing importance of the vegetation. Similarly, Zaitsev et al. (2006) found a steady increase of surface-dwelling oribatid species.

4.4. Environmental parameters influencing Mesostigmata assemblage

CCA suggested that six of the eight determined environmental parameters contributed significantly to the structure of the mite assemblage. The greatest influence was linked to organic carbon, Collembola density and water content, which corresponds to other studies. Similarly, the Collembola community was mainly influenced by soil organic matter and water content (Salamon et al., 2011). Soil carbon and water content were found to be highly correlated with mite assemblage among several parameters measured (Koehler, 1998). Furthermore, soil organic matter, soil moisture and pH were considered as main factors structuring mite community (Bedano and Ruf, 2007). A proportional interrelationship of soil organic matter with Gamasina was reported in agricultural cropping systems (Andrén and Lagerlöf, 1983). High amounts of organic matter promote bacterial and fungal growth, which attracts potential prey like Collembola, nematodes and Oribatida thus also influencing higher trophic levels like predatory mites. Soil organic matter is also a direct food resource of Collembola (Scheu and Falca, 2000) and Oribatida, which are particulate feeders of decaying higher-plant material and microorganisms (Norton, 1990). Mesostigmata feed on Collembola and juvenile Oribatida, with some species being specialized on specific groups, e.g., *V. nemorensis*, *P. crassipes* and *Lasioseius* preferring Collembola (Karg, 1993) and *H. aculeifer* preferring Acaridia and Oribatida (Karg and Mack, 1986). *A. bicornis*, *A. cetratus* and other species from the family Ascidae feed on Collembola, juvenile Oribatida, nematodes and soft membranous mites (Karg, 1993). Such feeding habits may explain the observed relationships between Mesostigmata and their prey Collembola and Oribatida.

5. Conclusion

To conclude, we did not find a propagation of a legume effect up to predatory mites as stated in our first hypothesis. Our results rather suggest that resource quantity may be more important than resource quality. We found a bottom-up effect of the grass *B. sterilis*, which was propagated through the soil food web. Probably the higher amount of palatable fine roots of *B. sterilis* compared to the legume *M. sativa*, despite its higher nitrogen content, increased the density of Collembola (Salamon et al., 2011), which in turn may have led to a high density of predatory mites. Likewise, our second hypothesis that mite density and species richness will increase with habitat age was disproven. The pioneer optimum induced by mite species which are well adapted for agricultural habitats often exceeds the recovery of populations in the older successional stage. It seems that the traits of predatory mites, i.e. being r-strategists with fast reproduction or tolerating harsh conditions by moving deeper into the soil, and initial soil conditions are more effective in boosting population growth at the beginning of secondary succession. Increased habitat diversity due to a well developed vegetation cover and less disturbances in later successional stages seem to be less effective in recovering mite populations. In contrast, we found clear mite species assemblages differentiating the three age classes as proposed in our third hypothesis.

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Appendix 1

Table 1

Dominance, frequency and number of sites of Mesostigmata species in arable grassy fallows of the region Marchfeld, Austria. (Abbr = abbreviation, RA = already reported for Austria, TD = total species dominance, DC = adjusted dominance class, SF = sample frequency, FC = frequency class; dominance classes: eudominant (ED) >10%, dominant (D) 3.2–10%, subdominant (SD) 1–3.1%, rezedent (R) 0.32–0.99%, subrezedent (SR) 0.1–0.31%, sporadic (S) <0.1%; frequency classes: euconstant (F5) >50%, constant (F4) 30.1–50%, subconstant (F3) 15.1–30%, accessory (F2) 5–15%, accidents (F1) <5%)

Species	Abbr	RA	Young fallows			Mid-aged fallows			Old fallows			TD	DC	SF	FC	Sites
			Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3					
<i>Alliphis sculus</i>	A sic	X	8.13	2.03	3.43	2.95	0.51	10.40	0.52	0.33	10.48	4.40	D	54.6	F5	9
<i>Amblygamasus mirabilis</i>	A mir	X	2.88	–	–	–	–	–	–	–	–	0.33	R	4.6	F1	1
<i>Amblyseius agrestis</i>	A agr	–	–	–	0.07	–	–	0.60	2.60	–	–	0.21	SR	5.6	F2	3
<i>Amblyseius alpinus</i>	A alp	–	2.16	1.58	–	4.42	1.95	–	0.52	1.27	0.13	1.07	SD	25.0	F3	7
<i>Amblyseius bicaudus</i>	A bic	–	–	–	–	–	–	–	0.26	–	–	0.01	S	0.9	F1	1
<i>Amblyseius bidens</i>	A bid	–	0.10	0.23	2.15	–	6.69	7.14	–	4.82	0.13	3.01	SD	41.7	F4	7
<i>Amblyseius decolor</i>	A dec	–	–	–	–	–	0.10	0.09	–	–	–	0.02	S	1.9	F1	2
<i>Amblyseius filixis</i>	A fil	–	–	–	–	–	2.16	0.26	0.52	0.07	–	0.32	R	11.1	F2	4
<i>Amblyseius graminis</i>	A gra	–	–	0.45	–	–	–	–	0.52	–	0.25	0.09	S	6.5	F2	3
<i>Amblyseius lutezhicus</i>	A lut	–	0.10	–	–	–	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Amblyseius meridionalis</i>	A mer	X	–	–	0.13	–	1.13	0.34	0.26	0.33	–	0.27	SR	10.2	F2	5
<i>Amblyseius obtusus</i>	A obt	X	–	–	–	–	–	0.17	–	0.33	–	0.08	S	3.7	F1	2
<i>Amblyseius tenuis</i>	A ten	–	0.72	–	–	–	–	–	0.52	–	–	0.11	SR	2.8	F1	2
<i>Amblyseius zwoelferi</i>	A zwo	–	–	–	–	–	–	–	0.52	–	–	0.02	S	1.9	F1	1
<i>Ameroseius corbiculus</i>	A cor	X	2.98	0.34	0.47	1.77	0.31	5.59	3.64	0.87	1.14	1.75	SD	43.5	F4	9
<i>Ameroseius plumigerus</i>	A plu	X	3.81	0.23	1.07	4.72	1.03	1.03	3.12	0.74	0.63	1.42	SD	55.6	F5	9
<i>Antennoseius avius</i>	A avi	–	–	–	–	–	0.10	0.95	–	0.40	–	0.21	SR	12.0	F2	3
<i>Antennoseius bacatus</i>	A bac	–	–	–	–	–	–	4.82	0.78	0.13	–	0.72	R	11.1	F2	3
<i>Antennoseius masoviae</i>	A mas	–	–	–	–	–	–	0.52	–	–	–	0.07	S	3.7	F1	1
<i>Arctoseius cetratus</i>	A cet	–	5.86	5.98	1.81	1.47	0.72	1.03	0.26	0.74	4.17	2.43	SD	37.0	F4	9
<i>Arctoseius insularis</i>	A ins	–	–	–	–	–	2.06	–	–	–	–	0.24	SR	3.7	F1	1
<i>Arctoseius venustus</i>	A ven	X	–	–	–	–	–	0.17	–	–	–	0.02	S	1.9	F1	1
<i>Asca bicornis</i>	A bic	X	1.85	31.72	48.02	–	50.31	12.90	2.08	37.58	2.90	26.43	ED	63.0	F5	8
<i>Cheiroseius borealis</i>	C bor	X	–	0.56	–	–	–	–	–	–	–	0.06	S	2.8	F1	1
<i>Cosmolaelaps spec.</i>	Cosm	–	–	–	0.13	–	–	–	–	–	–	0.02	S	0.9	F1	1
<i>Dendrolaelaps spec.</i>	Dendro	–	0.62	–	–	–	–	–	–	0.07	–	0.08	S	3.7	F1	2
<i>Dendrolaelaps zwoelferi</i>	D zwo	–	–	–	0.20	–	0.21	–	–	1.47	0.13	0.33	R	7.4	F2	4
<i>Discourella modesta</i>	D mod	X	0.10	–	–	2.06	–	–	–	–	–	0.09	S	4.6	F1	2
<i>Saprocans baloghi</i>	S bal	–	–	–	–	0.59	–	0.17	0.26	–	–	0.06	S	4.6	F1	3
<i>Holoparasitus calcaratus</i>	H cal	X	–	–	–	–	–	0.09	–	–	–	0.01	S	0.9	F1	1
<i>Hypoaspis aculeifer</i>	H acu	X	3.50	7.79	3.76	4.72	11.73	6.53	7.01	21.57	25.51	10.79	ED	83.3	F5	9
<i>Hypoaspis angusta</i>	H ang	–	–	4.18	–	–	0.62	–	–	–	–	0.51	R	6.5	F2	2
<i>Hypoaspis astronomica</i>	H ast	–	–	–	–	–	–	–	–	0.33	0.38	0.09	S	3.7	F1	2
<i>Hypoaspis austriaca</i>	H aus	X	–	–	–	–	–	0.26	–	3.01	–	0.57	R	5.6	F2	2
<i>Hypoaspis humerata</i>	H hum	X	–	–	0.07	–	–	–	–	–	0.13	0.02	S	1.9	F1	2
<i>Hypoaspis kargi</i>	H kar	–	0.62	3.27	10.07	0.29	–	3.70	0.52	12.59	0.51	4.98	D	40.7	F4	8
<i>Hypoaspis nollii</i>	H nol	X	0.41	–	–	–	–	–	–	–	–	0.05	S	1.9	F1	1
<i>Hypoaspis ornata</i>	H orn	–	–	–	0.40	–	–	–	–	–	–	0.07	S	0.9	F1	1
<i>Hypoaspis procera</i>	H pro	–	–	–	3.29	–	–	0.52	0.52	0.54	–	0.77	R	13.9	F2	4
<i>Hypoaspis similisetae</i>	H sim	–	–	0.79	0.74	–	–	–	–	–	–	0.21	SR	3.7	F1	2
<i>Hypoaspis vacua</i>	H vac	X	–	2.26	7.05	–	0.51	2.32	24.42	0.47	6.19	3.61	D	35.2	F4	7
<i>Hypoaspis 'vacua variation'</i>	H vav	–	–	–	0.27	–	–	–	–	–	0.88	0.13	SR	3.7	F1	2
<i>Iphidozercon gibbus</i>	I gib	–	–	–	0.07	–	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Lasioseius berlesei</i>	L ber	X	–	–	0.07	–	0.31	–	–	–	0.51	0.09	S	5.6	F2	3
<i>Lasioseius youcefi</i>	L you	–	–	0.23	–	–	–	–	0.26	–	1.01	0.13	SR	4.6	F1	3
<i>Leioseius bicolor</i>	L bic	X	0.93	4.74	3.09	0.29	0.31	18.40	17.40	1.74	10.86	5.82	D	50.0	F4	9
<i>Leitneria pugio</i>	L pug	–	–	–	–	–	–	5.50	3.90	–	–	0.93	R	7.4	F2	2
<i>Leptogamasus cuneoliger</i>	L cun	–	–	–	0.07	–	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Lysigamasus digitulus</i>	L dig	–	–	0.11	–	–	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Macrocheles glaber</i>	M gla	X	0.10	–	0.07	–	–	0.60	3.64	–	3.66	0.61	R	9.3	F2	5
<i>Macrocheles mammifer</i>	M mam	–	–	–	–	0.29	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Macrocheles pontina</i>	M pon	–	–	–	–	–	0.21	0.09	–	–	1.01	0.13	SR	7.4	F2	3
<i>Macrocheles rotundiscutis</i>	M rot	–	0.10	–	–	–	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Nenteria breviunguiculata</i>	N bre	X	11.42	–	–	14.45	–	0.09	0.26	–	–	1.93	SD	21.3	F3	4
<i>Nenteria stylifera</i>	N sty	X	0.21	–	–	0.88	–	–	–	0.33	–	0.12	SR	7.4	F2	3
<i>Pachylaelaps karawaiewi</i>	P kar	–	5.76	0.79	2.55	4.72	0.10	–	2.08	–	5.93	2.04	SD	42.6	F4	7
<i>Pachylaelaps multidentatus</i>	P mul	–	–	0.11	–	–	0.10	–	–	–	–	0.02	S	1.9	F1	2
<i>Pachylaelaps pectinifer</i>	P pec	X	–	–	–	0.88	–	–	–	–	–	0.04	S	1.9	F1	1
<i>Parasitus beta</i>	P bet	X	0.10	4.06	0.81	–	–	–	–	–	–	0.58	R	11.1	F2	3
<i>Parasitus coleoptratorum</i>	P col	X	–	–	–	–	–	–	–	–	0.13	0.01	S	0.9	F1	1
<i>Parasitus fimetorum</i>	P fim	X	0.93	–	–	–	0.21	0.43	4.68	0.13	5.93	0.98	R	21.3	F3	6
<i>Parasitus hyalinus</i>	P hya	–	2.37	–	0.74	0.29	–	0.43	–	0.27	0.13	0.53	R	16.7	F3	6
<i>Parazercon radiatus</i>	P rad	X	–	–	–	–	0.10	–	–	–	–	0.01	S	0.9	F1	1
<i>Pergamasus crassipes</i>	P cra	X	6.89	1.24	0.40	2.95	4.42	0.09	–	1.34	2.40	2.08	SD	49.1	F4	8

(continued on next page)

Table 1 (continued)

Species	Abbr	RA	Young fallows			Mid-aged fallows			Old fallows			TD	DC	SF	FC	Sites
			Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3					
<i>Pergamasus quisquiliarum</i>	P qui	X	0.82	–	–	–	–	–	–	–	0.09	S	3.7	F1	1	
<i>Proctolaelaps ventrianalis</i>	P ven	–	–	0.23	0.07	–	–	–	0.07	2.02	0.24	SR	6.5	F2	4	
<i>Proprioseiopsis</i>	Prop	–	–	–	–	–	–	–	0.07	–	0.01	S	0.9	F1	1	
<i>Proprioseiopsis sororculus</i>	P sor	–	–	–	0.59	4.94	0.77	–	1.00	0.13	0.88	R	24.1	F3	5	
<i>Protogamasellus mica</i>	P mic	–	0.51	2.48	0.67	–	0.72	6.10	10.91	0.20	2.27	2.10	SD	32.4	F4	8
<i>Protogamasellus singularis</i>	P sin	–	0.10	1.24	4.63	–	0.41	–	–	0.67	–	1.12	SD	18.5	F2	5
<i>Prozercon traegardhi</i>	P tra	X	–	–	–	0.29	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Punctodendrolaelaps strenzkei</i>	P str	–	5.86	–	–	0.59	–	–	–	–	0.88	0.78	R	13.0	F2	3
<i>Rhodacarellus silesiacus</i>	R sil	X	29.22	23.25	3.43	50.44	0.31	6.10	1.56	6.30	7.83	11.16	ED	66.7	F5	9
<i>Rhodacarus coronatus</i>	R cor	X	–	–	0.13	–	–	–	–	–	–	0.02	S	0.9	F1	1
<i>Rhodacarus furmanae</i>	R fur	–	–	–	–	–	4.84	0.60	–	0.07	–	0.65	R	9.3	F2	3
<i>Rhodacarus mandibularis</i>	R man	–	–	–	–	–	–	0.77	–	–	–	0.11	SR	1.9	F1	1
<i>Trachyuropoda ponticuli</i>	T pon	–	–	–	–	–	–	–	–	–	0.13	0.01	S	0.9	F1	1
<i>Trichouropoda querceti</i>	T que	–	–	–	–	0.29	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Uropoda kargi</i>	U kar	X	–	–	0.07	–	–	–	–	–	–	0.01	S	0.9	F1	1
<i>Uropoda orbicularis</i>	U orb	X	0.10	–	–	–	–	0.43	0.52	0.07	0.51	0.15	SR	8.3	F2	5
<i>Veigaia exigua</i>	V exi	–	0.10	–	–	–	2.37	–	–	0.07	–	0.29	SR	8.3	F2	3
<i>Veigaia nemorensis</i>	V nem	X	–	–	–	–	0.21	–	2.08	–	–	0.12	SR	4.6	F1	2
<i>Veigaia planicola</i>	V pla	–	0.62	0.11	–	–	0.31	–	3.90	–	1.14	0.40	R	12.0	F2	5
Total number of individuals			972	886	1489	339	972	1163	385	1493	792					
Species richness			33	26	33	22	32	36	31	34	33					

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