Temperature and precipitation affect seasonal changes in mite communities (Acari: Mesostigmata) in decomposing litter of broadleaved and coniferous temperate tree species

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Abstract

Key message: We identified the effect of microclimatic conditions on soil mite communities (Mesostigmata) during the decomposition of broadleaved and coniferous litter. The abundance, species richness, and diversity of mite communities decreased from spring to autumn regardless of litter quality and was related to changes in temperature and precipitation.

Context: Litter decomposition is one of the fundamental soil-supporting processes in terrestrial ecosystems. However, there is still a lack of knowledge on some general patterns of the relationships between litter quality (tree species), microclimate, and structure of soil mite assemblages.

Aims: The study aimed to analyze the impact of climatic conditions (temperature and precipitation) on mesostigmatid mite communities in the litter of 11 tree species through the vegetation season.

Methods: The experiment tested litter decomposition of 11 different tree species (693 litterbags), for seven consecutive months (April-October) under homogenous Scots pine (*Pinus sylvestris* L.) canopy monocultures in common garden conditions. Soil mites were extracted in Tullgren funnels.

Results: Mesostigmatid mite abundance was positively correlated with the temperature of the sampling month and negatively with the temperature of the previous month. Species richness depended on the sampling month temperature. Changes in litter mass loss in late autumn (after litterfall) and overwinter were important for colonization of litterbags by soil mesostigmatid mites in the following spring.

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Conclusions: Changes in climatic conditions, i.e., temperature and precipitation between the sampling months (during the following vegetation period), may cause significant changes in mesostigmatid mite abundance and thus may impact ecosystem functions. The winter period is important for mesostigmatid mite abundance in the following vegetation period.

Keywords: Mesostigmatid mite assemblages, Leaf litter, Coniferous forests, Seasonal changes, Tree species effect, Soil invertebrates

1 Introduction

Plant litter decomposition is the most important biological process in the cycling of carbon and nutrients in terrestrial ecosystems, driven by a range of complex and interacting physical and chemical properties of soils, soil organisms, substrate, and climate (Wang et al. 2009; Jurkšienė et al. 2017). Among the climatic factors, moisture and temperature determine the decomposition (Fujii and Takeda 2017), and the functional structure of the soil food web (Whitford 1989). For instance, protozoa can form cysts to survive dry conditions, and soil nematodes can reach anhydrobiosis (a survival strategy that confers protection from environmental stress, which refers to the ability to survive the loss of water and enter into a state when their metabolism comes reversibly to a standstill) when water is limiting, while the microarthropods exhibit diurnal migration between litter and soil due to differences in moisture conditions (van Vliet et al. 2000).

The decomposition of litter is also controlled by soil fauna activity (Schaefer et al. 2009). Soil microarthropods rely on the quantity and quality of plant-derived substrate and soil microbes for food (Wu et al. 2014). Among many groups of soil animals, Mesostigmata represents a species-rich and moderately abundant (4 to 10 thous. m^{-2}) soil fauna group, which is important in decomposition processes, as these mites feed primarily on important decomposer groups such as nematodes, springtails, and other mites which are pivotal in decomposition (Karg 1993; Wissuwa et al. 2012; Bolger et al. 2018). They do not change the soil structure, but they markedly affect the population size of their prey, including decomposer Oribatida (Seniczak et al. 2018). Consequently, they indirectly influence the overall productivity of ecosystems (Madej et al. 2011; Manu et al. 2018). Although there are studies on the relationship between soil fauna including Mesostigmata and the decomposition process (Gergocs and Hufnagel 2016; Urbanowski et al. 2018, 2021; Kamczyc et al. 2019), they do not cover changes in climatic conditions (Kampichler and Bruckner 2009).

Studies on litter decomposition and soil fauna include many factors. For instance, they focused on various forests and habitats (Gergocs and Hufnagel 2016; Horodecki and Jagodziński 2019), tree species (Hansen and Coleman 1998; Hansen 1999; González and Seastedt 2000), single or mixed litter (Kaneko and Salamanca 1999; Reynolds et al. 2003), and litter type (leaf and root) (Reynolds et al. 2003; Fujii and Takeda 2017), with different sampling schedules (González and Seastedt 2000; Reynolds et al. 2003; Gan et al. 2013). However, studies that included climatic conditions (temperature and precipitation) are limited and came from studies on latitudinal gradients (Franca et al. 2018). Climatic conditions in these studies are generally presented as general climatic characteristics of the study sites and are referred to as, for instance, continental, marine, or mountain climates (Frouz 2008) or by analyzing the sampling dates in the seasons. The relationships between soil mesostigmatid mite communities and temperature and precipitation in the decomposed leaf and needle litter during the vegetation period are still poorly known.

The abundance dynamics of a population depend on environmental conditions as well as on intra-population parameters (Kaczmarek et al. 2011). Population density directly depends on population parameters, food base, and also climatic conditions (Błoszyk 1999). Abundance changes in a population during the year might also result from the periodic aggregation of individuals in places of optimum humidity or temperature or to reproduce (Kaczmarek et al. 2011). Published data conducted on Mesostigmata suggest that population density may depend on temperature and moisture, but results do not allow to draw conclusions regarding any general seasonal pattern. For instance, Kaczmarek et al. (2011) reported two peaks of densities (in winter—January and late spring and summer) from central Poland, whereas Salmane (2000) reported the highest abundance in spring, which decreases to June when the temperature is the highest and moisture is rapidly decreasing. After that period temperature and humidity increase which causes an increase in mite population density in August. Finally, the increase of moisture and decrease of temperature in autumn lead to a decrease of the mite population (Salmane 2000). An increase of precipitation enhanced the Mesostigmata abundance by 179%, whereas warming increased it only by 8.2%. However, these data have limited use for forest environments as they were conducted in semiarid grasslands and include only herbaceous species (Wu et al. 2014).

Moreover, some studies on mesostigmatid mites show taxon-specific responses to varying or stable temperatures and moisture (Huhta and Hänninen 2001); however, these data come from microcosm experiments in jars and include only three mesostigmatid mite species, which imposes limitations regarding conclusions on responses at the forest ecosystem level. Although higher temperature and lower humidity may lead to the reduction of Mesostigmata population densities, when they probably move deeper into the soil, there is still a lack of data on their densities in upper litter layers during the vegetation period, especially when variation in litter quality is considered. Our previous data on Mesostigmata communities in the decomposed litter of different tree species revealed that mite community structures differed between April and October; however, we did not analyze changes in communities across the vegetation period (Kamczyc et al. 2019). Moreover, given the increasing temperature trend and predicted increase in precipitation (IPCC 2021), it is reasonable to predict the role of environmental factors such as temperature and precipitation in shaping soil fauna and, consequently, soil Mesostigmata communities. Additionally, covering this knowledge gap may be key for predicting how forest ecosystems will respond to climate change, as was described for the microbial community (Glassman et al. 2018).

It is difficult to distinguish between the role of temperature and moisture in modulating the effect of soil fauna (García-Palacios et al. 2013). However, recent studies with litterbags on cypress, oak, and birch along an arid valley on the eastern Tibetan plateau (Liao et al. 2016) suggest that water rather than temperature impacts soil fauna, but it is important to note that the response may depend on litter quality. In our study, the impact of temperature and precipitation is considered as one among many environmental factors which impact soil fauna communities. However, it may help to understand the seasonal dynamics of soil Mesostigmata communities under ambient precipitation and temperature in decomposed litter of various quality. To minimize the effect of other environmental factors, we conducted a common garden experiment using litter of 11 tree species in nutrient-poor Scots pine (*Pinus sylvestris* L.) forests. We hypothesized that (1) there are seasonal changes in mesostigmatid mite abundance driven by changes in microclimatic conditions (temperature and precipitation) and (2) Mesostigmata communities change during litter decomposition, depending on litter quality, as they prey on the detritivores directly.
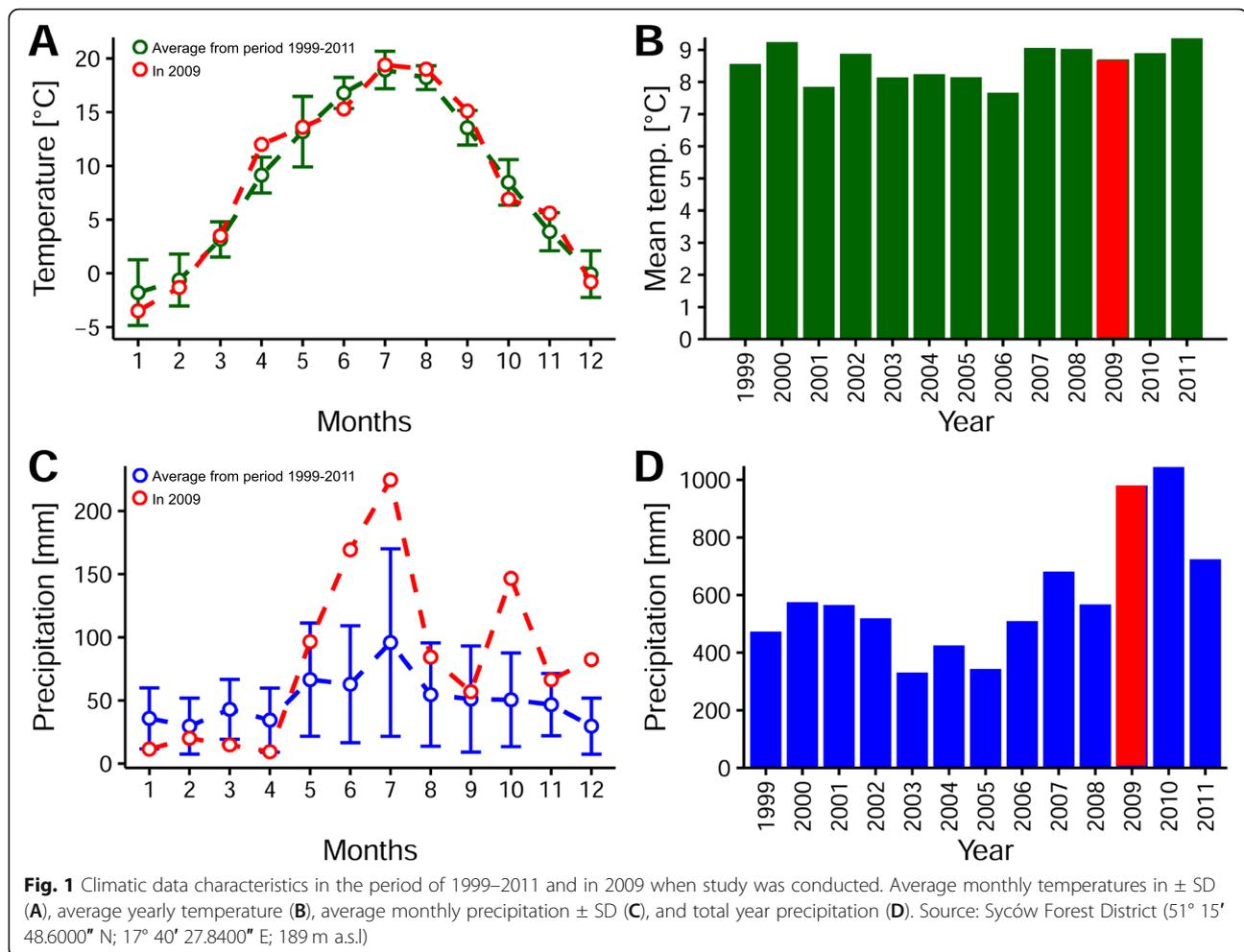
2 Materials and methods
2.1 Study site
The study was conducted in Scots pine forest located in the Siemianice Experimental Forest near Biadaszki

village (51° 14.87′ N, 18° 06.35′ E, elevation 150 m), SW Poland, which belongs to the Poznań University of Life Sciences. The experimental stands were established in 1974, in the podsolic, sandy, and nutrient-poor soil, in vegetation typical of oligotrophic coniferous forests *Leucobryo-Pinetum* (Ceitel 1982). The mature Scots pine stand was clear-cut, stumps, and coarse roots were dug up and removed and deeply plowed to depths of 60–70 cm. In the spring of 1974, 2-year-old Scots pine seedlings were planted at nine different spacings (3 replicates/spacing; area of each plot was 0.11 ha, 27 m × 41 m; 3.07 ha in total with buffer zone), with initial stand densities from 2500 to 20,833 trees per ha. No cleanings and thinnings were done in the study area from the onset of the experiment. Stand densities changed only as a result of natural mortality (Kamczyc et al. 2019).

The climate of the study site is transitional between maritime and continental. Mean annual precipitation was 591 mm, while the mean annual temperature was 8.2 °C (weather data recorded 300 m from the field site from 1968 to 1997) (Reich et al. 2005; Hobbie et al. 2006). During the study which was conducted in 2009, average monthly temperatures ranged from − 6.6 °C in January 2010 to 19.4 °C in July 2009, while monthly precipitation sums ranged from 9.4 mm in April 2009 to 224.6 mm in July 2009 (Kamczyc et al. 2019). Climatic data analyzed in the present study come from the nearest weather station in Syców Forest District (51° 15′ 48.6000″ N, 17° 40′ 27.8400″ E, 189 m a.s.l.). Temperature and precipitation were recorded with an accuracy of ± 0.01. The mean monthly temperatures recorded in 2009 when the litterbag experiment was conducted were in the same range that was recorded for a longer period from 1999 to 2011. Mean monthly temperature for the longer period ranged from − 1.8 ± 3.0 °C in January to 18.9 ± 1.7 °C in July (Fig. 1A). Also, the mean annual temperature in 2009 was similar to the values recorded for the 1999–2011 period (Fig. 1B). Total monthly precipitation in 2009 was slightly higher in June, July, and October than values recorded for 1999–2011 (Fig. 1C). Total annual precipitation was slightly higher in 2009 than in the longer period (Fig. 1D).

We established the decomposition experiment within the three research stands (plots), covering ca. 35-year-old Scots pine stands, with an initial density of 11,111 trees ha^{-1}. We chose only three plots to exclude the influence of initial stand density on ecosystem functioning, especially light availability and nutrient inputs (Jagodziński and Oleksyn 2009a, b, c). The stands were characterized by eight variables, i.e., mean (± SE) diameter at breast height (9.4 ± 0.28 cm), mean tree height (12.9 ± 0.15 m), stand basal area (37.4 ± 0.90 m^2 ha^{-1}), stand density (4908 ± 399 trees ha^{-1}), litter biomass of the organic horizon (30.45 ±

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Fig. 1 Climatic data characteristics in the period of 1999–2011 and in 2009 when study was conducted. Average monthly temperatures in ± SD (**A**), average yearly temperature (**B**), average monthly precipitation ± SD (**C**), and total year precipitation (**D**). Source: Syców Forest District (51° 15′ 48.6000″ N; 17° 40′ 27.8400″ E; 189 m a.s.l)

2.10 Mg ha^{-1}), annual litterfall (2.89 ± 0.16 Mg ha^{-1}) and pH$_{H2O}$ of the Ol horizon (4.71 ± 0.09), and pH$_{H2O}$ of the Of horizon (3.91 ± 0.06) (Kamczyc et al. 2019).

2.2 Litterbag experiment design

The litter of 11 tree species for the litterbag experiment was collected from plots of the common garden experiment located ca. 500 m from the Scots pine forest. The litter included seven broadleaved and four coniferous species. Litter traits were characterized in detail by Hobbie et al. (2006). The broadleaved species were as follows: Norway maple (*Acer platanoides* L.), sycamore maple (*A. pseudoplatanus* L.), European hornbeam (*Carpinus betulus* L.), European beech (*Fagus sylvatica* L.), small-leaved lime (*Tilia cordata* Mill.), English oak (*Quercus robur* L.), and invasive Northern red oak (*Q. rubra* L.). The coniferous species were as follows: silver fir (*Abies alba* Mill.), European larch (*Larix decidua* Mill.), Norway spruce (*Picea abies* (L.) H. Karst.), and Scots pine (*Pinus sylvestris* L.). The litter for the experiment was oven-dried (at 65 °C) to constant mass. This

also eliminated all living organisms, which could influence our inference about litter colonization. We placed homogenous litter of each tree species in nylon bags (mesh size of 1 mm) to allow free access of living animals to migrate into the sample with organic matter. The litterbags (size of 18 × 18 cm) were randomly distributed within study plots. The experiment started on 14 October 2008. The litterbags overwintered and were sampled in equal numbers (99 litterbags), seven times at monthly intervals in the vegetation season 2009, on 15.04, 18.05, 18.06, 14.07, 17.08, 16.09, and 19.10. In total, we collected 693 litterbags (11 tree species × 3 plots × 3 replications per plot × 7 sampling periods).

After extraction of mites from litterbags (see Section 2.3), the collected samples were dried to a constant weight at 65 °C, after which any additional material such as other vegetation, insects, sand, etc., was removed from each sample manually using tweezers. Samples were then weighed with an accuracy of 0.001 g to determine leaf mass loss for each litterbag. Litter mass losses (%) used in this paper are the average values of real mass

loss of nine samples obtained for each leaf litter type (species) at each collection date.

We used litter decomposition changes over the experiment as the background for the study of mite assemblages. At the beginning of the litterbag experiment (April), the lowest litter mass loss was found for *A. alba* (11.2%), *F. sylvatica* (14.0%), and *P. sylvestris* (15.2%), whereas the highest for *A. platanoides* (22.4%), *Q. rubra* (21.5%), and *A. pseudoplatanus* (21.3%). At the end of the experiment (October), the lowest litter loss was in *F. sylvatica* (19.3%), then in *A. alba* (19.4%), *P. abies* (20.2%), *T. cordata* (23.3%), *Q. robur* (23.5%), *P. sylvestris* (25.1%), *C. betulus* (25.3%), *L. decidua* (25.8%), *A. pseudoplatanus* (30.6%), *Q. rubra* (32.6%), and the highest in *A. platanoides* (35.8%). This means that the litter decomposition rate of *A. platanoides* is two times higher than of *F. sylvatica* (Fig. 2).

2.3 Mite extraction and identification

Litterbags were carefully placed in a portable cooler and transported to the laboratory. Mites were extracted from samples in Tullgren funnels, according to the recommendations for studies concerning organic substrata such as those in the *Pinus sylvestris* forest floors in this study (Crossley and Blair 1991; Edwards 1991). We set samples within Tullgren funnels (with 40 W bulbs) as quickly as possible (5 h after sampling) and the extraction procedure lasted 7 days until the samples were dry. Then, we selected mesostigmatid mites from the samples, and we identified them to the species level and developmental stages using taxonomical keys of Karg (1993), Ghilarov and Bregetova

(1977), and Micherdziński (1969). Mite species nomenclature follows Błoszyk (2008) and Skorupski (2008).

2.4 Data analyses

All statistical analyses were conducted using R software (R Core Team 2019). To avoid pseudoreplications, we pooled all mite records coming from the same plots, sampling date, and litter types to allow conclusions about diversity within sample plots. This produced three replications (pooled values) of each study date and litter type which gave 231 (3 replications × 3 plots × 7 sampling periods) data points for the analysis. We evaluated species richness as number of taxa recorded within the study plot and litter type, we accounted for species alpha diversity using the Shannon index, and we calculated abundance per sample. Data were presented as mean values followed by the standard error (SE).

To assess the impact of weather conditions (mean temperature and precipitation sums of sampling month and the month before) and litter quality (expressed by its identity, which can be linked with measured litter traits and decomposition constants), we used generalized linear mixed models (GLMM). We assumed Poisson distributions for mite abundance and species richness and a normal distribution for Shannon's index. Abundance was not recalculated per sample mass, as applied Poisson distributions assume integer values. In the models, we accounted for random effects connected with sample dependencies (study plot and collection date), to exclude plot-specific and date-specific factors, which could bias the inference. Models were developed using the lme4
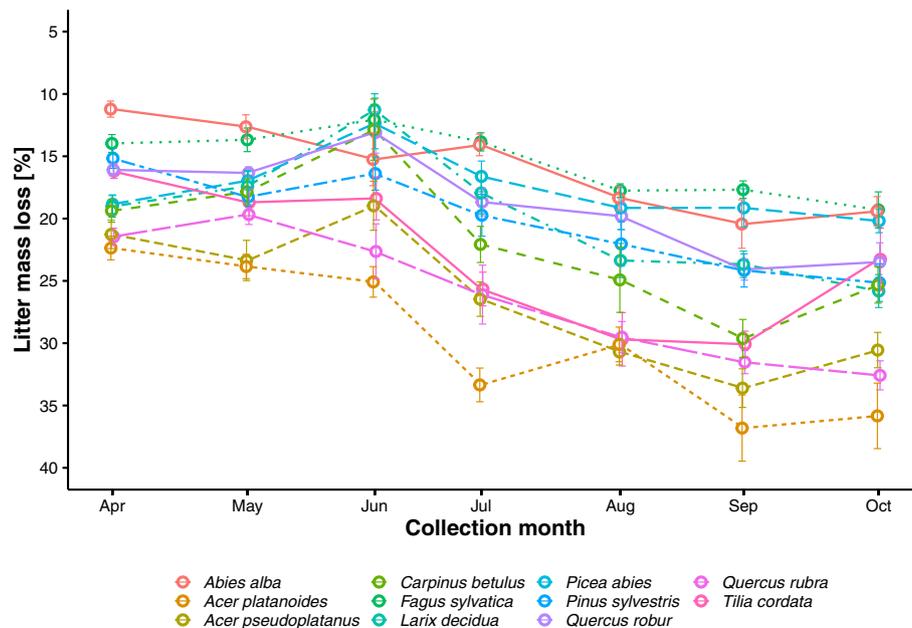

Fig. 2 Litter mass loss of 11 tree species between April and October

package (Bates et al. 2015) while the statistical significance of variables was calculated using z-values implemented in the lmerTest package (Kuznetsova et al. 2017). For all GLMMs, we evaluated the parsimony of models using Akaike's Information Criterion (AIC). We also provided AIC_0 – AIC of models with intercept and random effects only. To evaluate differences between litter origin and collection dates in the models we used Tukey *posteriori* tests. We also calculated marginal (R^2_m) and conditional (R^2_c) coefficients of determination, expressing amount of variance explained by fixed effects only and by both fixed and random effects jointly, respectively (Nakagawa and Schielzeth 2013). These coefficients were calculated using the MuMIn package (Bartoń 2017). Due to high collinearity, we did not include decomposition constant and species identity together in analyses, but we tested variants with each of them separately, to avoid variance inflation, reported by high values of variance inflation factors.

To assess the importance of temperature and precipitation in shaping mite species communities, we used Canonical Correspondence Analysis (CCA), implemented in the vegan package (Oksanen et al. 2018). CCA is the method of constrained ordination of the multivariate data (mite species abundances). In contrast to unconstrained ordination, CCA also allows to evaluate the importance of environmental variables in ordered sample coordinates within reduced analytical space. We tested the importance of temperature and precipitation using permutation analysis of variance (PERMANOVA), also implemented in the vegan package (Oksanen et al. 2018). Before analyses, we transformed species abundances using Hellinger's square root transformation (Legendre and Gallagher 2001), and we downweighted rare species (i.e., those with total abundance < 5). The selection of variables used to constrain the ordination (environmental variables) was based on forward selection and variable elimination to decrease AIC.

We described relationships between litter origin and mite species using bipartite network metrics (*bipartite* package in R), assuming litter species as the lower-level group and mite species as the higher-level group in the data processing. We also calculated network metrics—connectiveness and coefficient of network specialization H2'. Connectiveness is a proportion of links between species related to all possible links in the network. Network specialization H2' is an index describing the level of so-called complementarity specialization of the whole network. The H2' index describes how much observed interactions deviate from those that would be expected given the species marginal totals. Therefore, higher values of H2' indicate higher selectiveness and specialization of species (Blüthgen et al. 2006; Dormann

et al. 2009). At the species level, we determined the number and proportion of litter (among 11 litter types) where a particular mite species was recorded. We also calculated species diversity in the litter, i.e., diversity of litter species where a particular species was recorded, using the Shannon index, where species abundance on a particular litter type was used as a weight (Dormann 2011). To assess the level of specialization, we determined specialization index d', derived from Kulback-Leibler distance, which indicates the strength of a species deviation from a random sampling of all available taxa from the lower-level group (in our case—from litter origin species). Specialization index d' ranges from 0 to 1, and higher values indicate a higher level of specialization (Blüthgen et al. 2006; Dormann 2011). All network analyses were conducted using a bipartite package (Dormann et al. 2008): for abundances, species richness and Shannon diversity, litter decomposition and climatic data for the analyses—check complete dataset (Kamczyc et al. 2022).

3 Results

In total, 22,972 mites were collected and classified in 34 taxa. Species richness per sample ranged from 0.0 to 13.0 species, with an average of 8.0 ± 0.1 species, Shannon index from 0.00 to 2.25 (1.47 ± 0.02), and abundance from 0.0 to 100.0 ind. per sample (33.7 ± 1.2 ind. per sample) (Table 1). Species richness was quite constant during the whole study period, slightly decreasing at the beginning and end of the growing season, similar to the Shannon index (Fig. 3). For mite abundance, we found decreasing numbers of mites recorded in samples from later study dates. The best fit model explaining mite abundance comprised species identity, the temperature of the current month, and temperature of the previous month (Table 2; AIC = 2464.6, AIC_0 = 2589.9, df = 15, R^2_m = 0.641, R^2_c = 0.857). The highest mean abundance was found in *P. sylvestris* (41.5 ± 4.3 ind. per sample) and *A. alba* litter (39.3 ± 4.3 ind. per sample), while the lowest was in *F. sylvatica* (27.3 ± 2.8 ind. per sample). Abundances were positively correlated with the temperature of the sampling month and negatively correlated with the temperature of the month before sampling. Mean species richness of mites depended on the temperature of the sampling month (Table 2; AIC = 1020.8, AIC_0 = 1026.1, df = 4, R^2_m = 0.046, R^2_c = 0.147). Species diversity of mites was best explained by the model with intercept only (Table 2; AIC = AIC_0 = 74.9, df = 4, R^2_m = 0.000, R^2_c = 0.422).

CCA of soil mite communities in litterbags (Fig. 3A, B) revealed that 90.0% of explained variability was related to unconstrained factors (i.e., species composition) while constrained factors (i.e., environmental constraints) explained 10.0%. The first two unconstrained

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Table 1 Characteristics of the mite communities from various litter types. Data are presented as ranges (min. and max.) and mean values (per sample for abundance and species richness) followed by standard error (SE)

Tree species	Abundance			Species richness			Shannon		
	Min	Mean ± SE	Max	Min	Mean ± SE	Max	Min	Mean ± SE	Max
Abies alba	6.0	39.3 ± 4.3	79.0	5.0	8.4 ± 0.4	11.0	0.856	1.476 ± 0.068	2.019
Acer platanoides	0.0	29.4 ± 4.1	72.0	0.0	6.9 ± 0.6	12.0	0.000	1.282 ± 0.110	2.075
Acer pseudoplatanus	5.0	38.0 ± 4.5	88.0	5.0	8.3 ± 0.4	12.0	0.497	1.494 ± 0.085	2.065
Carpinus betulus	9.0	28.5 ± 3.9	82.0	5.0	7.4 ± 0.4	11.0	0.665	1.384 ± 0.070	1.882
Fagus sylvatica	6.0	27.3 ± 2.8	54.0	4.0	7.4 ± 0.3	10.0	0.844	1.398 ± 0.070	1.999
Larix decidua	9.0	32.3 ± 4.0	85.0	6.0	8.4 ± 0.4	12.0	0.832	1.546 ± 0.059	2.034
Picea abies	6.0	31.7 ± 3.3	61.0	5.0	8.0 ± 0.5	13.0	1.068	1.535 ± 0.059	2.034
Pinus sylvestris	14.0	41.5 ± 4.3	90.0	6.0	8.9 ± 0.4	13.0	0.792	1.530 ± 0.071	2.038
Quercus robur	3.0	38.0 ± 4.6	92.0	3.0	7.7 ± 0.5	12.0	0.708	1.486 ± 0.076	2.083
Quercus rubra	7.0	30.8 ± 3.2	53.0	5.0	8.4 ± 0.4	12.0	0.680	1.522 ± 0.077	2.252
Tilia cordata	12.0	33.0 ± 4.5	100.0	5.0	8.3 ± 0.5	12.0	0.507	1.509 ± 0.084	2.082

axes explained 17.1% and 15.5% of species composition variability, respectively. In the final model, we found important impacts of temperature and precipitation (from both sampling month and previous month; $p < 0.001$) on species composition of mites (Table 3). However, litter origin was not included in the most parsimonious model. Points representing particular litter origin were not separated in the ordination space (Fig. 4A). We also found that mite communities representing the same litter origin grouped along the CCA1 axis in the order of sampling—samples from April grouped at the left of ordination space while those from October—at the right side (Fig. 4B). Most of the species scores were grouped in the middle of the ordination space, revealing a lack of response to ordination gradients.

Analysis of the co-occurrence network (Fig. 5) revealed that most mite species preferred more than one type of litter origin. The most abundant species were not specialized and occurred in numerous types of litter. The network of connections covered 63.9% of all possible links. The coefficient of specialization H2` was 0.023, indicating low overall specialization of the network. Analysis of co-occurrence patterns revealed that among 34 recorded taxa, 15 were present in all types of litter (Table 4), while only four were present only in one litter species (*Hypoaspis praesternalis* Willmann, 1949, *Laelapsis astronomica* (C.L. Koch, 1839), *Lasioseius muricatus* (C.L. Koch, 1839), and *Olodiscus minima* (Kramer, 1882)). These four species occurred with only 1–2 specimens in that one litter type. We found the highest diversity of partners for the species present in all litter types and these species were characterized by the lowest d' values (from 0.01 to 0.04). The highest d' values were recorded for *Zercon zelawaiensis* Sellnick, 1944 (0.21), *Rhodacarellus silesiacus* Willmann, 1936 (0.20),

Alliphis halleri (G. & R. Canestrini, 1881) (0.19), and *Hypoaspis vacua* (Michael, 1891) (0.17) (Table 5).

4 Discussion

Our results provide interesting insights on two specific aspects which include (1) the state of the mesostigmatid mite community (abundance and richness) at the beginning of the experiment in April, after overwintering and further changes in the community during the vegetation period, and (2) the impact of analyzed climatic conditions, i.e., precipitation and temperature, on the mite community. Although the distribution patterns of mite communities are well documented, the mechanisms that affect seasonality of mite communities are poorly known (Hufnagel et al. 2011). Seasonal changes may result from several factors such as changes in microclimatic conditions (temperature and precipitation), which may favor the activity of soil mesofauna (Wang and Ruan 2011; Thakur et al. 2018) or from other driving forces like niche dimensionality, resource quality, dispersal ability, local interactions, and environmental filtering processes (Wehner et al. 2018).

Firstly, we expected an increase of mesostigmatid mite abundance during the growing season, with a slowdown or stabilization in summer, during dry and hot months, and a later increase during the wet and colder autumn, reported in previous studies (e.g., Fujii and Takeda, 2017; Seastedt et al. 1983). However, the highest mite abundance was observed in the following spring (in April) after the litterbags were laid out, and then the abundance slightly decreased along with the vegetation period. In our opinion, these patterns may be explained by the interaction of mite population dynamics, feeding strategies of Mesostigmata and microclimatic conditions. For instance, Kaczmarek et al. (2011) reported that humidity is the main factor that enables an increasing mite
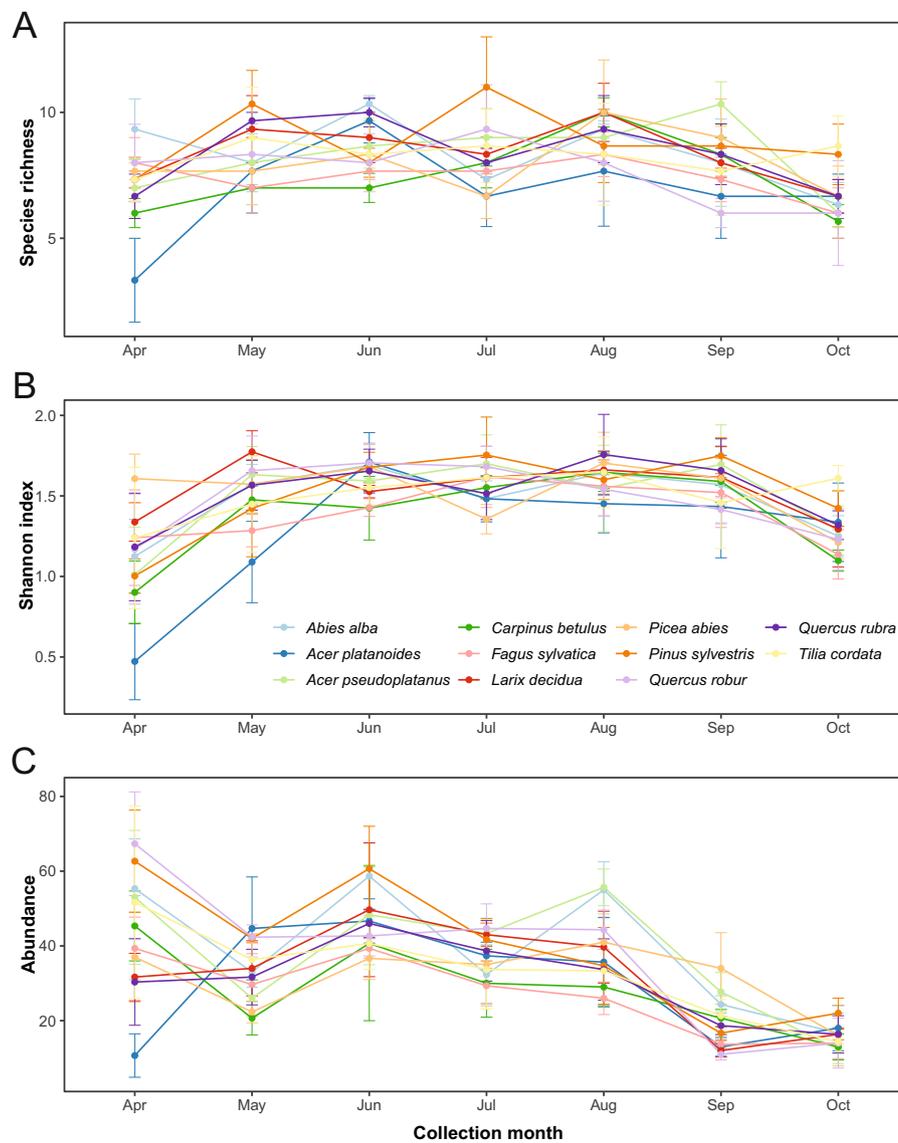
Fig. 3 Mean (+SE) mite species richness (**A**), diversity (**B**), and abundance per sample (**C**) in litterbags in particular collection months

population, which results from the appearance of juvenile instars in spring. Later in summer and autumn, the mite population structure changes and mature instars appear in the environment. Additionally, Mesostigmata (in which almost all species are predators) show dynamics similar to their prey such as nematodes or springtails (Fujii and Takeda 2017). We suppose that mite communities in spring (in April) met both comfortable microclimatic conditions (increasing temperature and humidity) and available food source (e.g., other invertebrates that graze on litter) which both allowed a large increase of the abundance. However, we noticed that the abundance stabilized or even decreased by October, which was surprising as only about 15–35% of the litter was utilized (Fig. 2). This pattern may be explained by a stronger

impact of microclimatic conditions in litterbags on mite communities. It has been documented that litterbags placed on the ground, like those in this study, are strongly affected by abiotic conditions (Fujii and Takeda 2017) which probably exceeded benefits that the mite community could obtain from its food source.

Secondly, we expected a strong influence of litter quality on mite community. We have observed the highest differences in abundance among studied litter types in April (based on the same litter quality pool), which started to stabilize during the vegetation period and had the lowest values in October. Similar tendencies were observed for species richness and the Shannon diversity index (Fig. 3A–C) where differences were the highest in April. Additionally, species richness and diversity were

Table 2 Generalized linear mixed-effects models explaining mite abundance, species richness, and diversity

Response	Term	Estimate	SE	z	Pr (>|z|)
Abundance	(Intercept)	3.3754	0.2991	11.2860	< 0.0001
	Litter origin—*Acer platanoides*	− 0.2901	0.0532	− 5.4560	< 0.0001
	Litter origin—*Acer pseudoplatanus*	− 0.0332	0.0496	− 0.6700	0.5029
	Litter origin—*Carpinus betulus*	− 0.3230	0.0537	− 6.0170	< 0.0001
	Litter origin—*Fagus sylvatica*	− 0.3640	0.0543	− 6.7000	< 0.0001
	Litter origin—*Larix decidua*	− 0.1960	0.0518	− 3.7840	0.0002
	Litter origin—*Picea abies*	− 0.2153	0.0521	− 4.1350	< 0.0001
	Litter origin—*Pinus sylvestris*	0.0424	0.0476	0.8920	0.3726
	Litter origin—*Quercus robur*	− 0.0332	0.0496	− 0.6700	0.5029
	Litter origin—*Quercus rubra*	− 0.2458	0.0525	− 4.6810	< 0.0001
	Litter origin—*Tilia cordata*	− 0.1741	0.0515	− 3.3830	0.0007
	mean temperature of previous month	− 0.0623	0.0154	− 4.0390	0.0001
	mean temperature of sampling month	0.0758	0.0195	3.8940	0.0001
	Random effect—sampling date	Variance	0.03352	SD	0.1831
	Random effect—plot	Variance	0.01097	SD	0.1047
Richness	(Intercept)	1.7711	0.1153	15.3560	< 0.0001
	mean temperature of sampling month	0.0208	0.0060	3.4640	< 0.0001
	Random effect—sampling date	Variance	0.0000	SD	0.0000
	Random effect—plot	Variance	0.0147	SD	0.1213
Shannon	(Intercept)	8.0191	0.7835	10.23	0.00319
	Random effect—sampling date	Variance	0.6049	SD	0.7778
	Random effect—plot	Variance	1.5447	SD	1.2429

quite similar in litterbags through the vegetation period, regardless of litter quality (Fig. 3A–C). These results show the strong impact of litter type on the mite community in spring which started to fade along with the vegetation period. This outcome was partially surprising, assuming that litter is considered as a rather stable microhabitat (Wehner et al. 2018). It was proved that the variation in litter quality was of minor importance for soil mites (Bluhm et al. 2019); however, Mesostigmata abundance was correlated with litter mass loss after 1 year of decomposition (Wang et al. 2009). Therefore, lower differences among litter types of varied quality in October may be explained by habitat loss for decomposers. We suppose that as generalist predators, Mesostigmata follow their

prey population densities represented by nematodes, springtails, and other mites (Karg 1993; Koehler 1997), which are associated with fungal and bacterial decomposition of organic matter such as tree litter in our experiment. For instance, we recorded high abundances of several species (Fig. 5), and among them *Zercon peltatus* C.L. Koch, 1836 occurred at the highest abundance (Fig. 5, Table 4). This taxon, which is considered nematophagous (Koehler 1997), reached high abundance in the spring sampling periods. This outcome may suggest a pattern in which litter decomposition was started by microorganisms (fungi and bacteria), which were probably followed by fungi- and *bacteriophagous* nematodes, which are food sources for nematophagous mites. We also recorded

Table 3 PERMANOVA test of the influence of environmental variables on mite species communities in CCA reduced space. AIC_0 refers to the null model (unconstrained analysis)

Term	Abbreviation	df	Variance	F	Pr(>F)
Mean temperature of previous month	temp_prev	1	0.04458	10.6372	0.001
Mean temperature of sampling month	temp_cur	1	0.02908	6.9382	0.001
Mean precipitation of previous month	prec_prev	1	0.01395	3.3291	0.001
Mean precipitation of sampling month	prec_cur	1	0.01834	4.3748	0.001
Residual		227	0.95139	–	–
AIC	759.22	AIC_0	775.72	Adj. R^2	0.08

Fig. 4 CCA analysis of mite community species composition. **A** Scores for samples (each point represents the community from litterbags per plot per date) and species which occurred at least 10 times (names shown for each species are first four letters of the genus and first four letters of the species). **B** Shifts of mite species composition averaged per each litter species and study date, represented by points connected by the lines from April (left) to October (right). Constraining environmental variables are marked by black arrows and labels. Abbreviations of the environmental variables are explained in Table 2

Fig. 5 Co-occurrence network for bipartite relationships between litter origin species (blue boxes) and mite species (red boxes). Boxes are proportional to species abundance; ribbon width is proportional to the proportion of co-occurrences

higher abundances of other mite species such as *Veigaia nemorensis* (C.L.Koch, 1836) or individuals from the *Paragamasus* genus; however, their abundances patterns were not so obvious. For instance, *V. nemorensis* reached high abundances in June, September, and October, whereas *Paragamasus vagabundus* (Karg, 1968), in April and June. Moreover, *Veigaia nemoresis* is an edaphic-detriticolous species with the widest range from ultra-lowland up to the alpine zone. It occurs in various soil microhabitats (including roots, rock cracks, etc.), having a wide ecological plasticity (Manu et al. 2017). Secondly, current study may also suggest that the key time for decomposition of leaves or needles, when litter is the most accessible for soil fauna and thus is crucial for soil mites in temperate pine forests, is the autumn. This result has at least two important ecological aspects for ecosystem functioning, (1) autumn-spring decomposition guarantees the required key litter mass loss, which makes the litter accessible for soil mites and (2) how could the changes in autumn-spring (during winter) temperature impact soil fauna communities? According to litter mass loss, it has been proved that microarthropods do not affect decomposition rates in temperate forests until at least 20% of the mass is lost (Osler et al. 2004). We recorded that the litter mass loss varied between litter types of varying quality (tree

species). The lowest values were recorded for *Abies alba*, whereas the highest for *Acer platanoides* (Fig. 2). These differences recorded at the beginning of the vegetation period, for all litter types in April, continued for the next 6 months to October. The changes in litter mass loss recorded here were expected because differences in litter mass loss among many tree species were previously reported (Horodecki et al. 2019); however, the differences recorded in April for various litter types came from the initial stages of decomposition between October 2008 and April 2009 (during the first winter season). This tendency has been observed and presented in our previous study (Kamczyc et al. 2019): the litter mass loss from October to April (during the first winter season) ranged from 10 to c.a. 20% for various tree species. Consequently, extreme changes in precipitation, temperature and snow cover during that period could affect soil micro-arthropod (including Mesostigmata mites) communities (Bokhorst et al. 2012). However, the differences were minimized within the next few months as we found decreasing numbers of mites recorded in samples from further study dates in the next vegetation season. The differences in April may be also connected with changes in microbial decomposers, which are the base food source for soil nematodes and
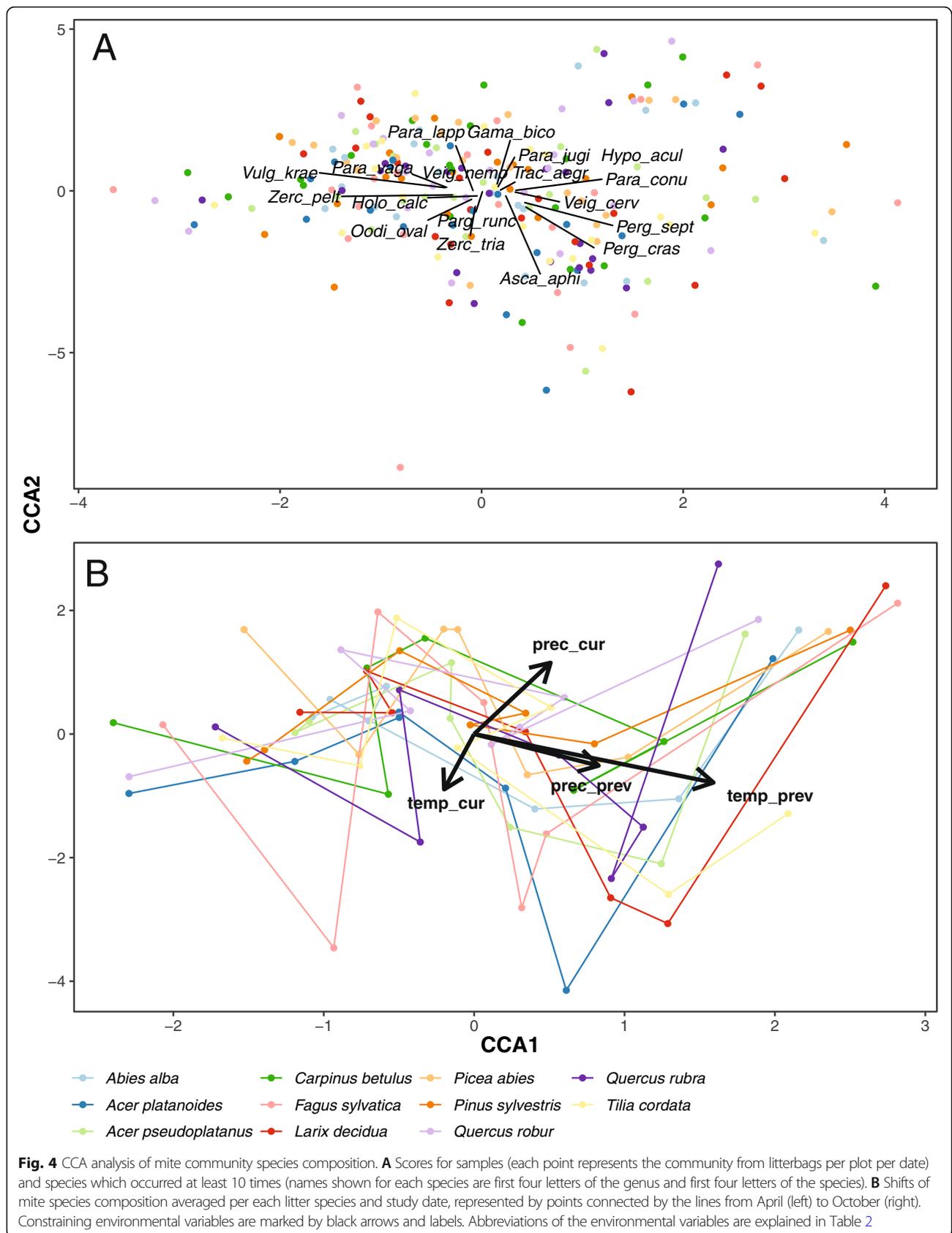
Table 4 Checklist of mite species recorded from litterbags with leaf litter of 11 tree species. Number of individuals in litterbags was summed from seven dates of mite collection

No.	Mite species	Abies alba	Acer platanoides	Acer pseudoplatanus	Carpinus betulus	Fagus sylvatica	Larix decidua	Picea abies	Pinus sylvestris	Quercus robur	Quercus rubra	Tilia cordata	Total
1	Alliphis halleri (G. & R. Canestrini, 1881)	0	0	0	0	0	0	1	0	0	6	1	8
2	Amblyseius sp.	0	0	0	0	0	0	1	0	1	1	0	3
3	Arctoseius cetratus (Sellnick, 1940)	0	0	1	0	0	1	0	1	0	1	3	7
4	Arctoseius semiscissus (Berlese, 1892)	0	0	1	0	0	0	0	2	0	1	0	4
5	Asca aphidioides (Linnaeus, 1758)	12	2	7	3	8	1	5	4	4	7	5	58
6	Dinychus perforatus Kramer, 1882	0	0	0	0	0	1	1	0	0	0	0	2
7	Gamasellodes bicolor Berlese, 1918	1	3	0	0	4	1	0	5	7	4	4	29
8	Holoparasitus calcaratus (C.L. Koch, 1839)	18	9	12	9	12	23	20	35	17	18	26	199
9	Hypoaspis aculeifer (Canestrini, 1883)	3	2	4	1	8	4	0	3	0	1	2	28
10	Hypoaspis praesternalis Willmann, 1949	1	0	0	0	0	0	0	0	0	0	0	1
11	Hypoaspis procera Karg 1965	1	0	0	0	0	0	1	4	0	0	0	6
12	Hypoaspis vacua (Michael, 1891)	2	0	1	1	1	13	0	0	0	3	0	21
13	Laelapsis astronomica (Koch, 1839)	2	0	0	0	0	0	0	0	0	0	0	2
14	Lasioseius muricatus (C.L. Koch, 1839)	0	1	0	0	0	0	0	0	0	0	0	1
15	Olodiscus minima (Kramer, 1882)	0	0	0	0	0	1	0	0	0	0	0	1
16	Oodinychus ovalis C.L. Koch 1839	2	7	2	0	0	2	0	2	2	1	1	19
17	Paragamasus conus Karg, 1971	112	87	161	101	71	175	158	153	157	192	110	1477
18	Paragamasus jugincola (Athas-Henriot, 1967)	183	167	236	173	237	216	380	210	310	232	214	2558
19	Paragamasus lapponicus Trägårdh, 1910	21	20	50	42	14	2	43	18	34	18	14	276
20	Paragamasus vagabundus (Karg, 1968)	47	8	18	14	51	25	55	26	50	13	36	343
21	Paragamasus runcatellus (Berlese, 1903)	292	261	243	126	263	279	357	274	376	282	205	2958
22	Pergamasus crassipes Linnaeus, 1758	10	6	12	18	8	24	9	3	13	9	16	128
23	Pergamasus mediocris Berlese, 1904	2	0	0	0	1	1	0	7	1	1	1	14
24	Pergamasus septentrionalis Oudemans, 1902	20	37	37	28	35	23	37	25	15	45	23	325
25	Rhodacarellus silesiacus Willmann, 1936	0	0	0	0	0	0	1	7	0	0	0	8
26	Rhodacarus coronatus Berlese, 1921	0	3	0	1	0	0	0	0	2	2	2	10
27	Trachytes aegrota (C. L. Koch, 1841)	165	107	130	39	24	80	58	146	119	32	61	961
28	Trichouropoda obscura (C.L. Koch, 1836)	0	0	1	0	0	0	0	0	0	0	1	2
29	Veigaia cervus (Kramer, 1876)	27	8	15	9	20	13	13	29	9	7	14	164
30	Veigaia nemorensis (C. L. Koch, 1839)	500	218	302	307	213	352	357	495	290	287	304	3625
31	Vulgarogamasus kraepelini (Berlese, 1904)	318	130	215	187	131	174	135	314	223	167	107	2101
32	Zercon peltatus C.L. Koch, 1836	696	751	888	713	580	593	336	712	729	574	893	7465
33	Zercon triangularis C.L. Koch, 1836	24	7	30	1	20	8	10	9	9	12	21	151
34	Zercon zelawaiensis Sellnick 1944	0	0	0	0	0	1	0	14	1	1	0	17
	Total	2459	1834	2366	1773	1701	2013	1978	2498	2369	1917	2064	22972

Table 5 Network statistics for mite species recorded in the study, describing their affiliation to litter types (Fig. 4) and specialization

Species	Abbreviation	Number of litter types	Proportion of litter types	Litter types diversity	Specialization index d′
Alliphis halleri (G. & R. Canestrini, 1881)	Alli_hall	3	0.27	0.736	0.192
Amblyseius sp.	Ambl_sp.	3	0.27	1.099	0.026
Arctoseius cetratus (Sellnick, 1940)	Arct_cetr	5	0.45	1.475	0.067
Arctoseius semiscissus (Berlese, 1892)	Arct_semi	3	0.27	1.040	0.047
Asca aphidioides (Linnaeus, 1758)	Asca_aphi	11	1.00	2.240	0.025
Dinychus perforatus Kramer, 1882	Diny_perf	2	0.18	0.693	0.036
Gamasellodes bicolor Berlese, 1918	Gama_bico	8	0.73	1.933	0.066
Holoparasitus calcaratus (C.L. Koch, 1839)	Holo_calc	11	1.00	2.315	0.011
Hypoaspis aculeifer (Canestrini, 1883)	Hypo_acul	9	0.82	2.008	0.061
Hypoaspis praesternalis Willmann, 1949	Hypo_prae	1	0.09	0.000	0.018
Hypoaspis procera Karg 1965	Hypo_proc	3	0.27	0.868	0.105
Hypoaspis vacua (Michael, 1891)	Hypo_vacu	6	0.55	1.234	0.171
Laelapsis astronomica (Koch, 1839)	Lael_astr	1	0.09	0.000	0.097
Lasioseius muricatus (C.L. Koch, 1839)	Lasi_muri	1	0.09	0.000	0.055
Olodiscus minima (Kramer, 1882)	Olod_mini	1	0.09	0.000	0.043
Oodinychus ovalis C.L. Koch, 1839	Oodi_oval	8	0.73	1.873	0.069
Paragamasus conus Karg, 1971	Para_conu	11	1.00	2.357	0.013
Paragamasus jugincola (Athas-Henriot, 1967)	Para_jugi	11	1.00	2.368	0.015
Paragamasus lapponicus Trägårdh, 1910	Para_lapp	11	1.00	2.234	0.035
Paragamasus vagabundus (Karg, 1968)	Para_vaga	11	1.00	2.255	0.032
Pargamasus runcatellus (Berlese, 1903)	Parg_runc	11	1.00	2.365	0.012
Pergamasus crassipes Linnaeus, 1758	Perg_cras	11	1.00	2.281	0.028
Pergamasus mediocris Berlese, 1904	Perg_medi	7	0.64	1.567	0.089
Pergamasus septentrionalis Oudemans, 1902	Perg_sept	11	1.00	2.353	0.018
Rhodacarellus silesiacus Willmann, 1936	Rhod_sile	2	0.18	0.377	0.196
Rhodacarus coronatus Berlese, 1921	Rhod_coro	5	0.45	1.557	0.107
Trachytes aegrota (C.L. Koch, 1841)	Trac_aegr	11	1.00	2.249	0.029
Trichouropoda obscura (C.L. Koch, 1836)	Tric_obsc	2	0.18	0.693	0.023
Veigaia cervus (Kramer, 1876)	Veig_cerv	11	1.00	2.291	0.015
Veigaia nemorensis (C. L. Koch, 1839)	Veig_nemo	11	1.00	2.353	0.010
Vulgarogamasus kraepelini (Berlese, 1904)	Vulg_krae	11	1.00	2.334	0.012
Zercon peltatus C.L. Koch, 1836	Zerc_pelt	11	1.00	2.371	0.022
Zercon triangularis C.L. Koch, 1836	Zerc_tria	11	1.00	2.211	0.034
Zercon zelawaiensis Sellnick, 1944	Zerc_zela	4	0.36	0.634	0.210

mites (Elkins and Whitford 1982), as their functioning depends on an interaction between the community and its climate (Glassman et al. 2018).

Generally, this study indicated that mite abundances were positively correlated with the air temperature of the sampling month, while negatively correlated with the air temperature of the month before sampling. These results are in line with Mueller et al. (2016) who noted that light availability and soil temperature between April and November were the best predictors of soil invertebrate diversity. Moreover, Heneghan et al. (1998) concluded that climate (which differed between analyzed study sites), substrate quality, and fauna affected the decomposition process; however, they only presented the precipitation data for 12 months without detailed analysis. Decreased precipitation is known to reduce soil fauna abundance, especially in forest ecosystems (Blankinship et al. 2011), but this effect is apparently independent of the taxon. Abundance decrease may occur in litterbags which were placed on the ground,

as they were more exposed to changes in climatic conditions than deeper layers in the soil environment. This is supported by Fujii and Takeda (2017), who indicated that changes in species composition of Mesostigmata were primarily determined by abiotic factors like water content. Changes in the mite abundance in our study can also depend on specific requirements of mite species. Each species has its optimal conditions for growth and reproduction at certain ranges of temperature and moisture, which can change during the vegetation period (Huhta and Hänninen 2001). These optimal environmental conditions may vary among developmental stages, and it is also important whether the conditions fluctuate or remain stable (Huhta and Hänninen 2001). Our studies revealed the importance of temperature and precipitation for shaping mite species composition. These results are in line with Huhta and Hänninen (2001), who documented that temperature and moisture had significant effects on mesostigmatid mites in their microcosm experiments; however, certain species may respond differently to these factors. For instance, the common forest species *Veigaia nemorensis*, which feeds mainly on springtails, prefers constant moisture (Huhta and Hänninen 2001). On the other hand, studies of Wu et al. (2014) reported no impact of the soil temperature on mite and Collembola abundances. However, the shifts in soil fauna communities can alter their relationships with soil microbes and ecosystem functions. Wang and Ruan (2011) suggested that the microclimate (moisture and temperature) affects N dynamics via its effects on the composition and diversity of soil mesofauna and is therefore important.

5 Conclusions

In conclusion, the findings from this study have a wide relevance because of high variability in litter quality (11 species), changes of key climatic factors (temperature and precipitation) which affect soil Mesostigmata communities in widely distributed Scots pine forests. The results may support sustainable forestry practices taking into consideration the decomposition processes and considering how tree admixtures affect soil fauna. This study proved that the changes in litter mass loss in autumn (after litterfall) and winter conditions were important for colonization of litterbags by soil mites the following spring, although the local species pool was limited. Moreover, our study proved that changes in climatic conditions, i.e., temperature and precipitation, between the sampling months (during the following vegetation period), may cause significant changes in mite abundance in the following spring and thus may impact ecosystem function.

Authors' contributions
Conceptualization, A.M.J. and J.K; methodology, A.M.J. and J.K; software, A.M.J., J.K., M.K.D., and P.H.; validation, J.K., A.M.J., M.K.D., and P.H.; formal analysis, J.K., M.K.D., A.M.J., and P.H.; investigation, J.K., A.M.J., P.H., and M.K.D.; resources, J.K., A.M.J., P.H., and M.K.D.; data curation, J.K., A.M.J., P.H., and M.K.D.; writing—original draft preparation, J.K., A.M.J., M.K.D., and P.H.; writing—review and editing, J.K., A.M.J., M.K.D., and P.H.; visualization, J.K., P.H., M.K.D., and A.M.J.; supervision, J.K. and A.M.J.; project administration: A.M.J. and J.K.; funding acquisition: A.M.J. and J.K. The authors read and approved the final manuscript.

Declarations

Ethics approval and consent to participate
The authors declare that they follow the rules of good scientific practice.

Consent for publication
All authors gave their informed consent to this publication and its content.

Competing interests
The authors declare that they have no competing interests.

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