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Temporal fluctuations in oribatid mites indicate that density-independent factors favour parthenogenetic reproduction

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Abstract We investigated the oribatid mite density, community structure and the percentage of parthenogenetic individuals in four different forest types across three regions in Germany in 2008 and once again in 2011. We compared temporal (inter-annual) fluctuations in population densities between sexually and parthenogenetically reproducing species of oribatid mites. We hypothesized that population densities in parthenogenetic oribatid mite species fluctuate more than in sexual ones. Further, we expected species composition and dominance of parthenogenetic species to differ between forest types and regions. Oribatid mite community structure did not differ between years but varied with forest type and region, indicating low species turnover in time. As hypothesized, temporal fluctuations were more pronounced in parthenogenetic as compared to sexual species. The percentage of parthenogenetic individuals was significantly higher in coniferous than in beech forests and significantly higher in Schorfheide-Chorin than in Hainich-Dün and Schwäbische Alb. The results indicate that parthenogenetic species flourish if populations are controlled by density-independent factors and dominate at sites were resources are plentiful and easily available, such as coniferous forests, and in regions with more acidic soils and thick organic layers, such as Schorfheide-Chorin. However, historical factors also may have contributed to the increased dominance of parthenogenetic species in the Schorfheide-Chorin, as this region was more heavily glaciated and this may have favoured parthenogenetic species. Overall, our study supports the hypothesis that parthenogenetic species benefit from the lack of density-dependent population control whereas the opposite is true for sexual species.

Keywords Oribatida · Parthenogenesis · Temporal fluctuations · Temperate forests

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Introduction

Understanding the reasons for the evolution and maintenance of sexual reproduction and its dominance in the animal kingdom for long poses a challenge for ecologists and evolutionary biologists (e.g., Weismann 1889; Fisher 1930; Muller 1964; Maynard Smith 1968; Hamilton 1980; Bell 1982; Scheu and Drossel 2007). Despite the "twofold costs of sex" due to producing males, sexual reproduction is widespread with about 99.9 % of animal species reproducing sexually (White 1978; Bell 1982).

A number of ecological and evolutionary theories have been proposed to explain how sexual reproduction outweighs this twofold disadvantage. The Red Queen Hypothesis postulates a coevolutionary arms race between host and parasites or predator and prey (Jaenike 1978; Hamilton 1980). It states that species have to evolve continuously to survive in a temporally changing environment conferring sexuality an advantage over asexuality. The Tangled Bank Hypothesis attributes the prevalence of sexual taxa to their ability to produce genetically diverse offspring able to occupy a larger variety of niches in spatially structured environments as compared to genetically more uniform offspring produced by parthenogenetic reproduction (Maynard Smith 1971; Bell 1982). Building on the latter, the 'Structured Resource Theory of Sexual Reproduction' (SRTS) assumes that sexual taxa outcompete asexual ones in habitats where resources are in short supply or are difficult to access (Scheu and Drossel 2007). In contrast, asexual taxa prevail in environments where resources are easily available, little structured or replenish quickly. Additionally, asexuals dominate in habitats where death rates are so high that available resources are not fully exploited. Hence, the SRTS predicts that sexual species prevail at conditions where density-dependent factors predominate (e.g., predation, resource competition, parasites), whereas asexual species are favoured if density-independent factors prevail, such as desiccation, frost or flooding. This implies that temporal fluctuations should be more pronounced in parthenogenetic than in sexual species; this hypothesis, however, has never been tested until today.

Testing the different theories on the advantage of sexual reproduction is difficult, in part as they are making similar predictions (Bell 1982), but also due to the scarcity of taxa that include closely related parthenogenetic and sexual species. Moreover, parthenogenetically reproducing species tend to form singular terminal offshoots in phylogenetic trees, whereas clusters of species rarely occur. The few existing clusters of species reproducing parthenogenetically often exhibit very different ecological characteristics to those reproducing sexually and do not allow straightforward comparisons. For example, the parthenogenetically reproducing bdelloid rotifers live very different to the (predominantly) sexually reproducing monogonont rotifers and are difficult to compare in respect to forces regulating their populations (Segers 2008).

A promising group allowing straightforward comparison of sexually and parthenogenetically reproducing species of similar ecology are oribatid mites (Oribatida, Acari; Maraun et al. 2003a; Heethoff et al. 2007; Schaefer et al. 2010). Oribatid mites are a diverse cosmopolitan taxon often numerically dominating soil animal communities (Walter and Proctor 2013). To date more than 10,000 species have been described of which approximately 8–9 % reproduce via thelytokous parthenogenesis scattered across phylogenetic distinct groups (Norton and Palmer 1991; Palmer and Norton 1991). Additionally, sexual and asexual species co-occur in the same habitat and therefore their population dynamics can be compared.

Parthenogenetically reproducing oribatid mite species are not evenly distributed over different ecosystems but dominate in freshwater, in agricultural systems and in acidic habitats such as peat bogs or boreal forest soils (Karg 1967; Norton and Sillman 1985; Beckmann 1988; Behan-Pelletier 1989; Behan-Pelletier and Bissett 1994), whereas they rarely occur on the bark of trees (Erdmann et al. 2006) or in montane tropical forest soils (Illig et al. 2010). The incidence of parthenogenesis is generally high in forest soils, but it markedly differs between forest types (e.g., coniferous vs. deciduous), suggesting that environmental conditions and niches differ in these ecosystems (Erdmann et al. 2012; Maraun et al. 2012). On a larger scale, regional factors may also affect the reproductive mode of soil animals due to differences in climate, landscape history and pedogenic processes, e.g. different parent rock, which affect the pH of the respective systems (Maraun et al. 2012; Zaitsev et al. 2013).

Recently, evidence supporting the SRTS has been provided in showing that the proportion of parthenogenetic individuals correlates with overall oribatid mite density indicating that ample resources favour asexual reproduction (Maraun et al. 2012). Further, in tropical as well as temperate regions sexual oribatid mite taxa have been shown to dominate at higher altitudes (Maraun et al. 2013; Fischer et al. 2014). Since resource quality (as indicated by high litter C/N ratio) decreases with increasing altitude (Wilcke et al. 2008) this supports the hypothesis that poor accessibility of resources promotes sexual reproduction.

We investigated if community structure and the relative density (dominance) of parthenogenetic individuals differ between regions of different climate, between forest types (beech vs. coniferous) and between years (2008 vs. 2011). We further analysed if temporal fluctuations differ between sexual and parthenogenetic taxa of oribatid mites. We hypothesized that population fluctuations in parthenogenetic species exceed those of sexual species, since the former flourish if populations are controlled by density-independent factors. We further hypothesized that forest type and region affect the dominance of parthenogenetic species with the dominance of parthenogenetic species increasing with forest disturbance and in regions with harsher abiotic conditions.

Materials and methods

Study sites

The study was carried out in three regions of Germany at the experimental forest sites of the "Biodiversity Exploratories", an integrative ecosystem research project (M. Fischer et al. 2010). The three regions included (1) the Schorfheide-Chorin (3–140 m a.s.l.), situated in the lowlands of North-east Germany and characterized by a young glacial landscape with sandy soils and many wetlands, (2) the Hainich-Dün (285–550 m a.s.l.), located in the hilly lands of central Germany featuring large unfragmented beech forests, and (3) the Schwäbische Alb (460–860 m a.s.l.), located in the low mountain ranges of South-west Germany. Mean annual precipitation in the Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb are 500–600, 500–800 and 700–1000 mm with mean annual temperatures of 8.0–8.5, 6.5–8.0 and 6.0–7.0 °C, respectively. Soils mainly comprise Cambisols and Luvisols in the Schorfheide-Chorin and Hainich-Dün, and Cambisols and Leptosols in the Schwäbische Alb. Bedrock is glacial till in the Schorfheide-Chorin, Triassic limestone in the Hainich-Dün and Jurassic shell limestone in the Schwäbische Alb. Soil pH ranges from 3.00 ± 0.19 to 4.51 ± 0.72 to 4.59 ± 0.67 in the Schorfheide-Chorin, the Schwäbische Alb and the Hainich-Dün, respectively. For more details on the study sites see M. Fischer et al. (2010).

Sampling design, extraction and determination of soil animals

Within each region, four different forest types were selected: managed young and old beech (*Fagus sylvatica*) forests with an average tree age of 30 (young beech) and 70 (old beech) years, respectively, unmanaged beech forests taken out of management for at least 60 years (natural beech), with mature trees being 120–150 years old, and old managed coniferous forests (coniferous) with an average tree age of 70 years (*Pinus sylvestris* in Schorfheide-Chorin and *Picea abies* in Hainich-Dün and Schwäbische Alb). All managed forests were planted as age class forests. The forest types were replicated four times in each of the three regions resulting in a total of 48 forest plots.

Soil samples were taken from April to May in 2008 and 2011. At each date, two soil samples per plot were taken from a 5 m^2 subplot using a soil corer (Ø 5 cm); as we focus on temporal variability, those samples were pooled for statistical analysis. Soil animals were extracted by heat (Macfadyen 1961) and subsequently transferred into 70 % ethanol. Oribatid mites were determined to species level, except for Brachychthoniidae, *Suctobelbella* and *Phthiracarus*, which were determined to family or genus level, using the key of Weigmann (2006). Juvenile oribatid mites were counted but not determined. Data on the reproductive mode of oribatid mite species were taken from Palmer and Norton (1991), Norton et al. (1993), Cianciolo and Norton (2006), Domes et al. (2007) and B. M. Fischer et al. (2010). We classified oribatid mite species on the basis of known information on their ecology into the subgroups Enarthronota, Desmonomata, Phthiracaroidea, Tectocepheidae, sexual Oppiidae, parthenogenetic Oppiidae, Suctobelbidae, Poronota and 'Others' (including all oribatid mites not included to any of the groups above). Species of the respective groups share similar life history characteristics and are therefore assumed to respond in a similar way to changing environmental factors (Maraun and Scheu 2000; Norton and Behan-Pelletier 2009).

Statistical analysis

Oribatid mite density, diversity and the proportion of parthenogenetic individuals and taxonomical subgroups were analysed by repeated measures analysis of variance (ANOVA) with the fixed factors region (Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin) and forest type (coniferous, young beech, old beech, natural beech), and time (2008, 2011) as a repeated factor using R version 2.14.1 (R Development Core Team 2011). Data on oribatid mite density were log-transformed to improve homoscedasticity.

To investigate the fluctuations of oribatid mite communities, the density of sexual and parthenogenetic species, and also for Enarthronota, Desmonomata, Phthiracaroidea, Tectocepheidae, sexual Oppiidae, parthenogenetic Oppiidae, Suctobelbidae, Poronota and 'Others' of the dataset of 2008 were subtracted from those of 2011 for each of the 48 plots. Algebraic signs were ignored since only the difference between the two years was of relevance for this study, i.e. all values were positive. These differences were then expressed as percentage of the mean of the respective group or taxon, i.e. sexual versus parthenogenetic species, and of the respective taxonomical groups. These percentages were analysed by three-factorial analysis of variance (ANOVA) with the fixed factors region (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb), forest type (young beech, old beech, natural beech, coniferous) and reproductive mode (sex, parthenogenesis) or taxonomic group (Enarthronota, Desmonomata, Phthiracaroidea, Tectocepheidae, sexual Oppiidae, parthenogenetic Oppiidae, Suctobelbidae, Poronota, Others).

The relationship between oribatid mite communities and the factors region, forest type and time was analysed by principal components analysis (PCA) with species occurring in more than five samples using CANOCO 5 (Microcomputer Power, Ithaca, NY, USA; Šmilauer and Lepš 2014). No rotation was used for the PCA. Subsequently, the coordinates 1–4 of the PCA were used in STATISTICA 11 (Statsoft, Tulsa, OK, USA) for Discriminant Function Analyses (DFA) to inspect differences between treatment levels.

Results

Total density and diversity

Oribatid mite densities were similar in 2008 and 2011 in the Hainich-Dün and in the Schwäbische Alb, but in the Schorfheide-Chorin significantly lower in 2011 than in 2008 (region × time interaction; Fig. 1a; Table 1). Generally, oribatid mite densities were higher in coniferous forests (89,967 ± 68,877 ind./m^2) than in the three beech forests

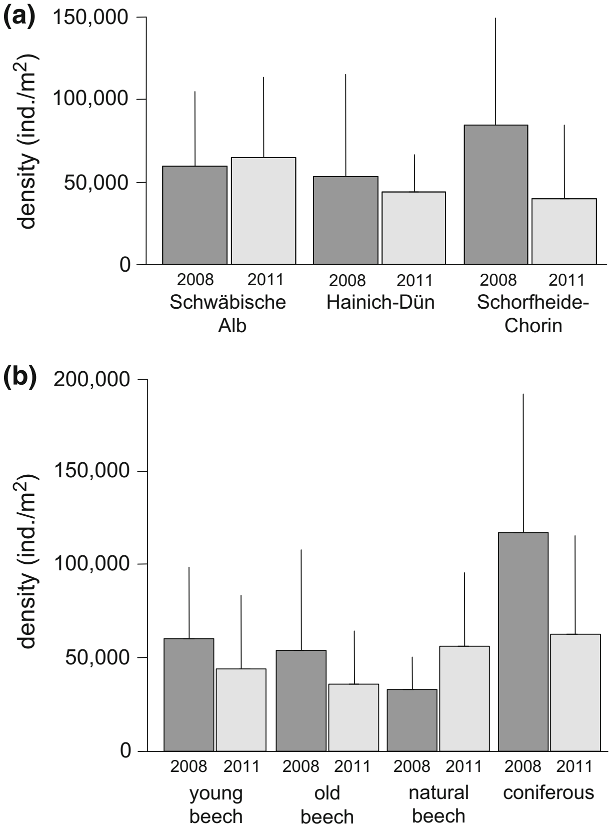

Fig. 1 Oribatid mite densities (±SD) in 2008 and 2011 in **a** three regions in Germany (Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin) and **b** the four management types, young managed beech forest (young beech), old managed beech forest (old beech), unmanaged natural beech forest (natural beech) and coniferous forest (coniferous)

Table 1 F and *P* values of repeated measures ANOVA with the factors region and forest type, and time as repeated factor on the number of species (mean per sample), the proportion of parthenogenetic individuals (parth. %), densities of total Oribatida (ind./m^2) and dominances of subgroups (% of total oribatid mites)

	df	Species		Parth. %		Oribatida total		Enarthronota		Phthiracaroidea		Desmonomata	
		F	P	F	P	F	P	F	P	F	P	F	P
Between subject effects													
Region	2	**7.30**	**0.0022**	**17.62**	**<0.0001**	0.57	0.57	**5.13**	**0.011**	1.18	0.32	**14.00**	**<0.0001**
Forest type	3	**3.53**	**0.024**	2.62	0.066	**3.15**	**0.037**	**8.23**	**0.0003**	0.53	0.66	0.20	0.89
Region × forest type	6	**8.68**	**<0.0001**	0.29	0.94	2.16	0.070	1.37	0.25	**3.02**	**0.017**	0.55	0.77
Within subject effects													
Time	1	3.27	0.079	**6.10**	**0.018**	**5.71**	**0.022**	1.72	0.20	1.84	0.18	**11.29**	**0.0019**
Time × region	2	**6.13**	**0.0051**	0.53	0.59	**6.65**	**0.0035**	0.61	0.55	0.38	0.69	2.64	0.085
Time × forest type	3	0.70	0.56	0.44	0.72	**3.28**	**0.032**	1.08	0.37	0.98	0.42	1.35	0.27
Time × region × forest type	6	0.66	0.68	1.26	0.30	0.53	0.78	0.80	0.58	0.99	0.45	1.67	0.16

	Tectocepheidae		Suctobelbidae		Parth. Oppiidae		Sexual Oppiidae		Poronota		Others	
	F	P	F	P	F	P	F	P	F	P	F	P
Between subject effects												
Region	1.32	0.28	2.17	0.13	**7.56**	**0.0018**	**32.02**	**<0.0001**	0.59	0.56	1.73	0.19
Forest type	**5.66**	**0.0028**	**3.47**	**0.026**	1.11	0.36	1.96	0.14	0.29	0.84	0.32	0.81
Region × forest type	1.75	0.14	1.47	0.22	1.26	0.30	0.86	0.53	0.74	0.55	1.10	0.38
Within subject effects												
Time	0.09	0.76	**5.86**	**0.021**	0.26	0.62	0.68	0.42	**6.00**	**0.019**	0.01	0.94
Time × region	0.03	0.97	**3.68**	**0.035**	0.07	0.93	0.60	0.56	1.52	0.23	**3.36**	**0.046**
Time × forest type	0.93	0.44	0.15	0.93	0.20	0.90	0.20	0.89	1.19	0.33	0.82	0.49
Time × region × forest type	0.51	0.79	1.48	0.21	0.71	0.64	0.51	0.80	1.21	0.32	0.93	0.48

Significant results ($p < 0.05$) are given in bold

(51,855 ± 39,195, 44,767 ± 43,085 and 44,678 ± 32,070 ind./m^2 in young, old and natural beech forests, respectively) with differences being most pronounced in the Schwäbische Alb. Moreover, oribatid mite densities decreased in young and old beech forests and in coniferous forests but increased in natural beech forests from 2008 to 2011 (forest × type time interaction; Fig. 1b).

Overall, 116 species of oribatid mites were recorded, 98 at each sampling date. Total species number decreased from Schwäbische Alb (87) to Schorfheide-Chorin (68) to Hainich-Dün (61) with on average 85 species in young beech, 82 in coniferous, 69 in natural and 63 in old beech forests.

Average species number per sample was lower in 2011 than in 2008 in the Hainich-Dün (16.8 ± 4.4 and 19 ± 4.8, respectively) and in the Schorfheide-Chorin (13.3 ± 5.0 and 18.1 ± 4.7, respectively) but higher in the Schwäbische Alb (20.3 ± 5.0 and 17.9 ± 4.5, respectively; region × time interaction, Table 1). Average species number per sample was higher in coniferous than in beech forests in the Schwäbische Alb (23.9 ± 3.5 %, 16 ± 2.7, 16.3 ± 3.8 and 20.3 ± 4.8 % in coniferous and young, old and natural beech forests, respectively) and Schorfheide-Chorin (19.1 ± 4.9, 17.5 ± 6.0, 13.9 ± 4.6 % and 12.3 ± 3.7 in coniferous and young, old and natural beech forests, respectively), whereas in the Hainich-Dün the number of species was higher in beech as compared to coniferous forests (13.9 ± 3.4, 21.5 ± 5.0, 17.4 ± 3.6 and 18.8 ± 3.6 in coniferous and young, old and natural beech forests, respectively; region × forest type interaction).

Dominance of taxonomic groups

Variation with time

Dominance of most taxonomic groups did not vary significantly between the two sampling dates except for Poronota and Desmonomata which were more dominant in 2011 (17.0 ± 15.5 and 6.9 ± 8.8 %, respectively) than in 2008 (11.2 ± 8.0 and 3.6 ± 5.5 %, respectively; Table 1), and Suctobelbidae which were less dominant in the Schorfheide-Chorin in 2011 (12.8 ± 9.1 %) than in 2008 (25.0 ± 13.3 %; time × region interaction).

Variation between regions

Overall, Oppiidae represented the most abundant taxon of oribatid mites in each of the three regions, but their dominance was significantly lower in the Schorfheide-Chorin (26.8 ± 23.1 %) than in the Hainich-Dün (40.6 ± 15.4 %) and the Schwäbische Alb (44.9 ± 18.8 %; Table 1). The dominance of sexually reproducing Oppiidae was significantly lower (1.4 ± 2.9, 27.7 ± 15.6 and 34.1 ± 19.8 %, respectively) and that of parthenogenetically reproducing Oppiidae was significantly higher in the Schorfheide-Chorin than in the Hainich-Dün and Schwäbische Alb (25.5 ± 23.4, 12.9 ± 12.1 and 10.9 ± 9.6 %, respectively). The dominance of Enarthronota significantly increased from the Schwäbische Alb (3.7 ± 4.7 %) to the Schorfheide-Chorin (8.6 ± 9.4 %) and the Hainich-Dün (12.1 ± 15.5 %), whereas proportions of Desmonomata were significantly higher in Schorfheide-Chorin (11.0 ± 9.5 %) than in the Schwäbische Alb (2.1 ± 4.3 %) and Hainich-Dün (2.7 ± 3.6 %).

Variations with forest type

The dominance of Oppiidae was significantly lower in coniferous (25.6 ± 17.4 %) as compared to the three beech forests (39.2 ± 18.1, 40.3 ± 19.6 and 44.7 ± 23.0 % in young, old and natural beech forests, respectively), and this was mainly due to sexual species (14.0 ± 16.4, 23.1 ± 20.7, 21.8 ± 21.4 and 25.4 ± 21.7 % in coniferous and young, old and natural beech forests, respectively; Table 1). In contrast, the dominance of Enarthronota (17.1 ± 17.1, 6.8 ± 7.8, 5.7 ± 6.2 and 2.9 ± 3.1 % in coniferous and young, old and natural beech forests, respectively) and Tectocepheidae (7.2 ± 8.2, 1.7 ± 2.9, 1.1 ± 2.8 and 2.6 ± 5.8 % in coniferous and young, old and natural beech forests, respectively) was considerably higher in coniferous as compared to the three beech forests. The dominance of Suctobelbidae also differed between forest types and decreased from coniferous (20.9 ± 9.8 %) to young (18.9 ± 10.1 %) to old (14.9 ± 9.8 %) to natural beech forests (13.6 ± 12.4 %). Also, the dominance of Phthiracaroidea differed between forest types, but this varied between regions; in the Schwäbische Alb it was highest in old beech forests (7.2 ± 5.2 %, 13.5 ± 10.8 %, 23.3 ± 10.4 % and 7.1 ± 7.9 % in coniferous and young, old and natural beech forests, respectively), in the Hainich-Dün in natural beech forests (6.1 ± 8.8, 9.9 ± 7.2, 7.5 ± 7.7, 16.6 ± 12.3 % in coniferous and young, old and natural beech forests, respectively) and in the Schorfheide-Chorin in coniferous forests (13.4 ± 17.4, 6.2 ± 6.2, 6.9 ± 6.8 and 8.9 ± 4.6 % in coniferous and young, old and natural beech forests, respectively; region × forest type interaction).

Variations with reproductive mode

The percentage of parthenogenetic individuals was significantly higher in Schorfheide-Chorin than in Hainich-Dün and Schwäbische Alb (Fig. 2a; Table 1), and significantly lower in 2011 than in 2008 (53.6 ± 23.2 and 62.3 ± 21.5 %, respectively). Further, the percentage of parthenogenetic individuals significantly differed between forest types with a higher percentage in coniferous forests than in the three beech forests (Fig. 2b).

Temporal fluctuations

Temporal fluctuations did not significantly differ between the taxonomic groups ($F_{8,324} = 1.39$, $P = 0.20$), but were significantly higher in parthenogenetic (98.0 ± 100.7 %) than in sexual species (61.1 ± 55 %; $F_{1,72} = 4.61$, $P = 0.035$). Further, temporal fluctuations of oribatid mites were positively correlated with the percentage of parthenogenetic individuals (linear regression; $r^2 = 0.18$, t value = 3.17, $F_{1,46} = 10.02$, $P = 0.0028$).

Variations in community structure

Oribatid mite communities differed significantly between each of the three regions (DFA: Wilk's Lambda = 0.20, $F_{18,180} = 27.95$; Mahalanobis Distance between Schorfheide-Chorin and Schwäbische Alb: 13.38, $F_{4,90} = 51.78$, between Schorfheide-Chorin and Hainich-Dün: 8.81, $F_{4,90} = 34.12$, and between Hainich-Dün and Schwäbische Alb: 3.24, $F_{4,90} = 12.55$, all $P < 0.0001$; Fig. 3).

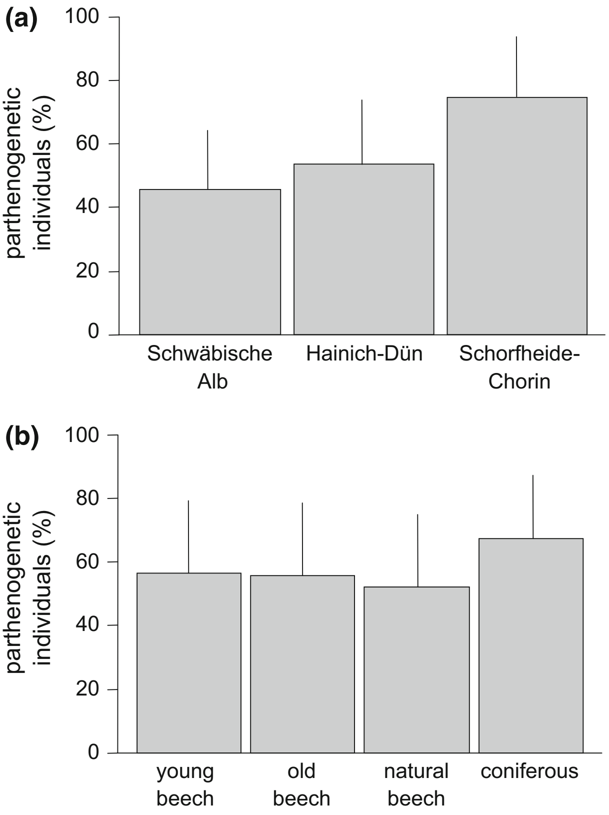

Fig. 2 Relative density (% of total ± SD) of parthenogenetic species in **a** three regions in Germany (Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin), and **b** the four forest types, young managed beech forest (young beech), old managed beech forest (old beech), unmanaged natural beech forest (natural beech) and coniferous forest (coniferous)

Oribatid mite communities also significantly differed between the forest types separating coniferous from the three beech forests (DFA: Wilk's Lambda $= 0.43$, $F_{12,235} = 7.47$; Mahalanobis Distance between coniferous and young beech: 4.65, $F_{4,89} = 13.49$, coniferous and old beech: 6.40, $F_{4,89} = 18.56$, and between coniferous and natural beech: 8.49, $F_{4,89} = 24.63$, all $P < 0.0001$).

Oribatid mite communities did not differ between 2008 and 2011 (DFA: Wilk's Lambda $= 0.95$, $F_{4,91} = 1.13$, $P = 0.35$).

Discussion

Density, species richness and community structure

Oribatid mite densities did not differ between the three regions studied and ranged between 49,000 and 62,000 ind./m^2 (averaged over all forest types), being in the range typically recorded from soils of mesophilic forests of the temperate zone (Maraun et al. 2003b;

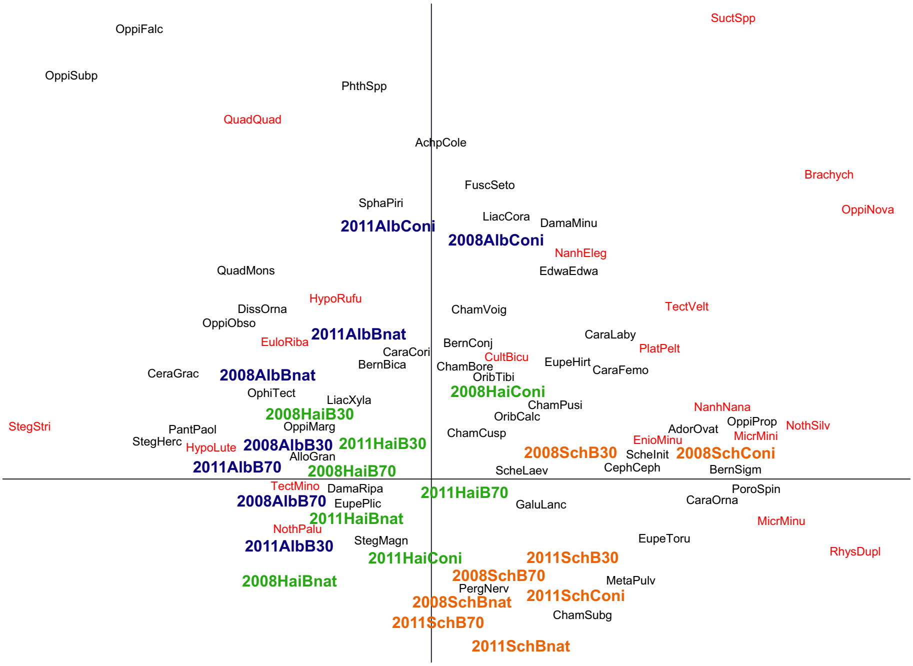

Fig. 3 Principal components analysis (PCA) of oribatid mite species in different forest types in three regions in Germany in 2008 and 2011. Length of gradient 2.7; eigenvalues of 0.23 and 0.20 for the first and second axis, respectively. *Alb* Schwäbische Alb, *Hai* Hainich-Dün, *Sch* Schorfheide-Chorin, *B30* young managed beech forest, *B70* old managed beech forest, *Bnat* unmanaged natural beech forest, *Coni* coniferous forest. Parthenogenetic species are marked *red*. For full names of species and their abbreviations see Table 2

Maraun and Scheu 2000). Remarkably, oribatid mite communities of the Hainich-Dün and Schwäbische Alb were dominated by Oppiidae, especially sexual species such as *Oppiella falcata*, *Berniniella bicarinata*, *Berniniella conjuncta*, *Dissorhina ornata*, *Oppiella obsoleta*, *Quadroppia monstruosa* which were rare or absent in the Schorfheide-Chorin. In contrast, parthenogenetic Oppiidae, e.g. *Oppiella nova* and *Microppia minus,* dominated in the Schorfheide-Chorin. Also, the parthenogenetic Desmonomata species *Nanhermannia nana*, *Nothrus silvestris* and *Platynothrus peltifer* were more abundant in the Schorfheide-Chorin than in the other regions.

Oribatid mite densities were generally higher in coniferous than in the beech forests, a pattern recorded previously (Lindo and Visser 2004; Sylvain and Buddle 2010; Walter and Proctor 2013). Differences in community structure between forest types were less pronounced than between regions and mainly separated coniferous forests from the three beech forests. *Suctobelbella* spp., *Tectocepheus velatus* and Brachychthoniidae dominated in coniferous forests whereas species of Oppiidae, Poronota and Phthiracaroidea were more abundant in beech forests. Similar patterns were reported earlier (Maraun and Scheu 2000). Oribatid mite community structure was surprisingly constant between 2008 and 2011, indicating low species turnover in time and suggesting that soil animal communities are remarkably stable. However, mainly due to the decline of the predominantly parthenogenetic Suctobelbidae oribatid mite density significantly varied between the two sampling dates in the Schorfheide-Chorin.

Table 2 Name of oribatid mite species, abbreviations used in Fig. 3, reproductive mode (*Sex* sexual, *Parth* parthenogenetic), and densities (ind./m^2 ± SD; averaged over time and forest type) in the three study regions

Species name	Abbreviation in Fig. 3	Reproductive mode	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Enarthronota					
Brachychthoniidae	Brachych	Parth	1958 ± 4067	5338 ± 13962	4496 ± 8609
Hypochthoniidae					
Hypochthonius luteus Oudemans	HypoLute	Parth	80 ± 368	119 ± 330	0 ± 0
Hypochthonius rufulus C.L. Koch	HypoRufu	Parth	302 ± 416	279 ± 486	103 ± 241
Eniochthoniidae					
Eniochthonius minutissimus (Berlese)	EnioMinu	Parth	24 ± 75	382 ± 2161	605 ± 1577
Mixonomata					
Eulohmanniidae					
Eulohmannia ribagai (Berlese)	EuloRiba	Parth	183 ± 506	183 ± 721	0 ± 0
Euphthiracaridae					
Microtritia minima (Berlese)	MicrMini	Parth	0 ± 0	0 ± 0	3810 ± 18581
Rhysotritia duplicata (Grandjean)	RhysDupl	Parth	40 ± 225	0 ± 0	987 ± 1684
Phthiracaridae					
Phthiracarus spp. Perty	PhthSpp	Sex	2109 ± 2067	454 ± 540	525 ± 593
Steganacarus magnus (Nicolet)	StegMagn	Sex	80 ± 246	271 ± 360	151 ± 266
Steganacarus striculus (C.L. Koch)	StegStri	Parth	1687 ± 2094	1592 ± 1794	64 ± 224
Steganacarus herculeanus Willmann	StegHerc	Sex	430 ± 569	0 ± 0	8 ± 45
Desmonomata					
Nothridae					
Nothrus palustris C.L. Koch	NothPalu	Parth	40 ± 94	119 ± 242	0 ± 0
Nothrus silvestris Nicolet	NothSilv	Parth	382 ± 1014	231 ± 648	1806 ± 2716
Camisiidae					
Camisia segnis (Hermann)	–	Parth	8 ± 45	0 ± 0	0 ± 0

Table 2 continued

Species name	Abbreviation in Fig. 3	Reproductive mode	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Platynothrus peltifer (C.L. Koch)	PlatPelt	Parth	318 ± 448	302 ± 511	629 ± 865
Nanhermanniidae					
Nanhermannia elegantula Berlese	NanhEleg	Parth	127 ± 419	0 ± 0	16 ± 90
Nanhermannia nana (Nicolet)	NanhNana	Parth	414 ± 1893	72 ± 318	660 ± 961
Brachypylina					
Hermanniidae					
Hermannia gibba (C.L. Koch)	–	Sex	8 ± 45	24 ± 135	0 ± 0
Hermanniellidae					
Hermanniella punctulata Berlese	–	Sex	40 ± 184	0 ± 0	0 ± 0
Damaeidae					
Belba corynopus (Hermann)	–	Sex	0 ± 0	8 ± 45	0 ± 0
Damaeobelba minutissima (Sellnick)	DamaMinu	Parth	143 ± 382	0 ± 0	0 ± 0
Damaeus auritus C.L. Koch	–	Sex	0 ± 0	0 ± 0	16 ± 90
Damaeus onustus C.L.Koch	–	Sex	8 ± 45	8 ± 45	0 ± 0
Damaeus riparius Nicolet	DamaRipa	Sex	151 ± 258	191 ± 354	215 ± 415
Epidamaeus setiger (Kulczynski)	–	Sex	24 ± 99	0 ± 0	0 ± 0
Metabelba propexa (Kulczynski)	–	Sex	8 ± 45	0 ± 0	0 ± 0
Metabelba pulverosa Strenzke	MetaPulv	Sex	0 ± 0	40 ± 114	143 ± 274
Porobelba spinosa (Sellnick)	PoroSpin	Sex	0 ± 0	8 ± 45	143 ± 303
Cepheidae					
Cepheus cepheiformes (Nicolet)	CephCeph	Sex	8 ± 45	0 ± 0	95 ± 265
Tritegeus bisulcatus Grandjean	–	Sex	0 ± 0	32 ± 141	0 ± 0
Microzetidae					
Microzetes septentrionalis (Kunst)	–	Sex	16 ± 63	0 ± 0	0 ± 0

Table 2 continued

Species name	Abbreviation in Fig. 3	Reproductive mode	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Ameridae					
Amerus polonicus Kulczynski	–	Sex	72 ± 405	8 ± 45	0 ± 0
Damaeolidae					
Fosseremus laciniatus (Berlese)	–	Parth	0 ± 0	143 ± 765	0 ± 0
Hungarobelbidae					
Hungarobelba pyrenaica	–	Sex	24 ± 135	0 ± 0	0 ± 0
Ctenobelbidae					
Ctenobelba pectinigera (Berlese)	–	Sex	8 ± 45	0 ± 0	0 ± 0
Eremaeidae					
Eremaeus hepaticus C.L. Koch	–	Sex	8 ± 45	0 ± 0	0 ± 0
Astegistidae					
Cultroribula bicultrata (Berlese)	CultBicu	Parth	16 ± 63	56 ± 168	40 ± 184
Liacaridae					
Adoristis ovatus (C.L.Koch)	AdorOvat	Sex	88 ± 271	16 ± 90	358 ± 833
Liacarus coracinus (C.L. Koch)	LiacCora	Sex	48 ± 120	0 ± 0	0 ± 0
Liacarus nitens (Gervais)	–	Sex	8 ± 45	0 ± 0	0 ± 0
Liacarus subterraneus (C.L. Koch)	–	Sex	16 ± 63	0 ± 0	0 ± 0
Liacarus xylariae (Schrank)	LiacXyla	Sex	16 ± 63	32 ± 107	0 ± 0
Xenillus tegeocranus (Hermann)	–	Sex	24 ± 99	8 ± 45	8 ± 45
Carabodidae					
Carabodes coriaceus C.L. Koch	CaraCori	Sex	56 ± 125	0 ± 0	16 ± 63
Carabodes femoralis (Nicolet)	CaraFemo	Sex	24 ± 75	0 ± 0	40 ± 114
Carabodes labyrinthicus (Michael)	CaraLaby	Sex	32 ± 86	16 ± 63	56 ± 141
Carabodes ornatus Storkan	CaraOrna	Sex	24 ± 75	0 ± 0	294 ± 644

Table 2 continued

Species name	Abbreviation in Fig. 3	Reproductive mode	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Carabodes subarcticus Trägardh	–	Sex	0 ± 0	0 ± 0	16 ± 63
Oppiidae					
Berniniella bicarinata (Paoli)	BernBica	Sex	1775 ± 9095	191 ± 488	8 ± 45
Berniniella conjuncta (Strenzke)	BernConj	Sex	159 ± 810	40 ± 184	0 ± 0
Berniniella dungeri Schwalbe	–	Sex	8 ± 45	0 ± 0	0 ± 0
Berniniella sigma (Strenzke)	BernSigm	Sex	0 ± 0	0 ± 0	175 ± 601
Dissorhina ornata (Oudemans)	DissOrna	Sex	470 ± 735	1178 ± 1434	263 ± 1350
Microppia minus (Paoli)	MicrMinu	Parth	239 ± 946	836 ± 3325	6220 ± 24371
Neotrichoppia confinis (Paoli)	–	Parth	8 ± 45	358 ± 1980	0 ± 0
Oppiella acuminata (Strenzke)	–	Sex	8 ± 45	0 ± 0	16 ± 90
Oppiella falcata (Paoli)	OppiFalc	Sex	7162 ± 6786	1504 ± 2210	0 ± 0
Oppiella fallax (Paoli)	–	Sex	8 ± 45	0 ± 0	8 ± 45
Oppiella marginedentata (Strenzke)	OppiMarg	Sex	0 ± 0	247 ± 635	8 ± 45
Oppiella nova (Oudemans)	OppiNova	Parth	3661 ± 5969	3945 ± 11006	8101 ± 13841
Oppiella obsoleta (Paoli)	OppiObso	Sex	374 ± 776	668 ± 963	0 ± 0
Oppiella propinqua Mahunka and Mahunka-Papp	OppiProp	Parth	0 ± 0	0 ± 0	119 ± 330
Oppiella subpectinata (Oudemans)	OppiSubp	Sex	6215 ± 7688	4050 ± 2881	151 ± 578
Quadroppia monstruosa Hammer	QuadMons	Sex	557 ± 1106	438 ± 1145	0 ± 0
Quadroppia quadricarinata (Michael)	QuadQuad	Parth	1838 ± 2675	1011 ± 1060	167 ± 417
Suctobelbidae					
Allosuctobelba grandis (Paoli)	AlloGran	Parth	8 ± 45	32 ± 107	0 ± 0
Suctobelba altvateri Moritz	–	Parth	0 ± 0	127 ± 553	0 ± 0
Suctobelba trigona (Michael)	–	Parth	103 ± 288	0 ± 0	0 ± 0
Suctobelbella spp. Jacot	SuctSpp	Parth	10224 ± 12593	5338 ± 8899	8021 ± 8670

Table 2 continued

Species name	Abbreviation in Fig. 3	Reproductive mode	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Thyrisomidae					
Pantelozetes paolii (Oudemans)	PantPaol	Sex	366 ± 533	167 ± 422	0 ± 0
Autognetidae					
Autogneta longilamellata (Michael)	–	Sex	8 ± 45	0 ± 0	8 ± 45
Conchogneta dalecarlica (Forsslund)	–	Sex	0 ± 0	0 ± 0	8 ± 45
Tectocepheidae					
Tectocepheus minor Berlese	TectMino	Parth	8 ± 45	318 ± 669	0 ± 0
Tectocepheus velatus (Michael)	TectVela	Parth	1735 ± 5044	485 ± 988	1416 ± 3052
Cymbaeremaeidae					
Cymbaeremaeus cymba (Nicolet)	–	Sex	8 ± 45	0 ± 0	0 ± 0
Micreremidae					
Micreremus brevipes (Michael)	–	Sex	0 ± 0	0 ± 0	16 ± 63
Micreremus gracilior Willmann	–	Sex	0 ± 0	0 ± 0	16 ± 63
Licneremaeidae					
Licneremaeus licnophorus (Michael)	–	Sex	0 ± 0	0 ± 0	8 ± 45
Phenopelopidae					
Eupelops hirtus (Berlese)	EupeHirt	Sex	24 ± 75	0 ± 0	40 ± 114
Eupelops plicatus (C.L. Koch)	EupePlic	Sex	24 ± 75	119 ± 183	32 ± 107
Eupelops torulosus (C.L. Koch)	EupeToru	Sex	0 ± 0	0 ± 0	103 ± 213
Achipteriidae					
Achipteria coleoptrata (L.)	AchiCole	Sex	2228 ± 2551	947 ± 1051	660 ± 705
Achipteria nitens (Nicolet)	–	Sex	24 ± 99	72 ± 405	0 ± 0
Parachipteria punctata (Nicolet)	–	Sex	247 ± 993	0 ± 0	0 ± 0
Parachipteria willmanni van der Hammen	–	Sex	16 ± 90	0 ± 0	0 ± 0

Table 2 continued

Species name	Abbreviation in Fig. 3	Reproductive mode	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Oribatellidae					
Ophidiotrichus tectus (Michael)	OphiTect	Sex	24 ± 75	16 ± 63	0 ± 0
Oribatella calcarata (C.L. Koch)	OribCalc	Sex	16 ± 63	103 ± 371	48 ± 120
Oribatulidae					
Oribatula tibialis (Nicolet)	OribTibi	Sex	40 ± 131	175 ± 326	159 ± 512
Scheloribatidae					
Liebstadia humerata Sellnick	–	Sex	0 ± 0	8 ± 45	16 ± 63
Liebstadia similis (Michael)	–	Sex	0 ± 0	80 ± 285	0 ± 0
Scheloribates ascendens Weigmann & Wunderle	–	Sex	0 ± 0	0 ± 0	16 ± 63
Scheloribates laevigatus (C.L. Koch)	ScheLaev	Sex	0 ± 0	64 ± 224	32 ± 107
Scheloribates initialis (Berlese)	ScheInit	Sex	24 ± 75	24 ± 75	111 ± 296
Ceratozetidae					
Ceratozetes gracilis (Michael)	CeraGrac	Parth	493 ± 751	279 ± 635	16 ± 90
Ceratozetes minimus Sellnick	–	Sex	0 ± 0	0 ± 0	8 ± 45
Edwardzetes edwardsi (Nicolet)	EdwaEdwa	Sex	56 ± 168	8 ± 45	0 ± 0
Fuscozetes setosus (C.L. Koch)	FuscSeto	Sex	390 ± 972	0 ± 0	0 ± 0
Jugatala angulata (C.L. Koch)	–	Sex	8 ± 45	0 ± 0	0 ± 0
Melanozetes mollicomus (C.L. Koch)	–	Sex	32 ± 107	0 ± 0	0 ± 0
Sphaerozetes piriformes (Nicolet)	SphaPiri	Sex	103 ± 273	0 ± 0	0 ± 0
Trichoribates novus (Sellnick)	–	Sex	8 ± 45	8 ± 45	0 ± 0
Chamobatidae					
Chamobates borealis (Trägardh)	ChamBore	Sex	302 ± 622	183 ± 373	167 ± 780
Chamobates cuspidatus (Michael)	ChamCusp	Sex	103 ± 347	470 ± 718	239 ± 640
Chamobates pusillus (Berlese)	ChamPusi	Sex	64 ± 242	0 ± 0	40 ± 131
Chamobates subglobulus (Oudemans)	ChamSubg	Sex	0 ± 0	0 ± 0	143 ± 289

Table 2 continued

Species name	Abbreviation in Fig. 3	Reproductive mode	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Chamobates voigtsi (Oudemans)	ChamVoig	Sex	1130 ± 1500	1194 ± 1233	732 ± 759
Euzetidae					
Euzetes globulus (Nicolet)	–	Sex	0 ± 0	0 ± 0	64 ± 274
Mycobatidae					
Minunthozetes pseudofusiger (Schweizer)	–	Sex	0 ± 0	40 ± 225	0 ± 0
Galumnidae					
Acrogalumna longipluma (Berlese)	–	Sex	0 ± 0	0 ± 0	24 ± 135
Galumna alata (Hermann)	–	Sex	0 ± 0	0 ± 0	16 ± 90
Galumna lanceata Oudemans	GaluLanc	Sex	16 ± 63	0 ± 0	48 ± 136
Galumna tarsipennata Oudemans	–	Sex	0 ± 0	0 ± 0	8 ± 45
Pergalumna nervosa (Berlese)	PergNerv	Sex	0 ± 0	0 ± 0	72 ± 174
Pilogalumna crassiclava (Berlese)	–	Sex	8 ± 45	0 ± 0	16 ± 90
Pilogalumna tenuiclava (Berlese)	–	Sex	8 ± 45	0 ± 0	0 ± 0

Parthenogenesis and temporal fluctuations

The relative abundance of parthenogenetic individuals varied significantly between forest types. Coniferous forests favoured parthenogenetic species presumably due to higher amounts of organic material accumulating on the forest floor as compared to beech forests. Higher amounts of organic material promote fungal growth resulting in increased resource availability (Blair et al. 1994). Accumulation of litter might be a consequence of low numbers of macrodecomposers such as earthworms due to lower pH of coniferous forest soils (Maraun and Scheu 2000). According to SRTS, higher amounts of resources, mediated by the absence or reduction of macrofauna activity, favours parthenogenetic reproduction. Generally, primary decomposers, in particular parthenogenetic species, such as *Platynothrus peltifer*, *Nanhermannia nana*, *Nothrus palustris*, *Tectocepheus velatus*, dominate in acidic coniferous forests, whereas sexual species dominate in tropical, subtropical and base-rich forests (Maraun et al. 2012; Fischer et al. 2014; Mumladze et al. 2015).

Furthermore, the dominance of parthenogenetic species varied significantly with region; densities in the Schorfheide-Chorin markedly exceeded those of the other two regions. A number of factors might be responsible for the more favourable conditions for parthenogenetic species in the Schorfheide-Chorin. On one hand, similar to coniferous forests, the sandy soils of the Schorfheide-Chorin are of low pH (M. Fischer et al. 2010) which is associated with thick organic layers and low earthworm density (Klarner 2013). This indicates that, similar to coniferous forests, high amounts of resources favour parthenogenetic species. Additionally, the continental climate of the Schorfheide-Chorin with low precipitation and dry summers, likely is associated with high mortality due to density-independent factors, supporting the prediction of the SRTS that abiotic forcing favours parthenogenetic species. On the other hand, increasing elevation from north (Schorfheide-Chorin) to south (Schwäbische Alb) coincided with an increase in parthenogenetic species which is in agreement with studies investigating altitudinal gradients (Maraun et al. 2013; Fischer et al. 2014). It has been demonstrated that resource quality declines with altitude (Wilcke et al. 2008), thereby increasing resource control of detritivore species (Maraun et al. 2013). Again, this is consistent with the prediction of the SRTS that the advantage of sexual reproduction increases with increasing resource control, i.e. density-dependent factors. However, historical factors also may have contributed to the increased dominance of parthenogenetic species in the Schorfheide-Chorin, since, as compared to the Hainich-Dün and Schwäbische Alb, the Schorfheide-Chorin was more heavily glaciated and this may have favoured parthenogenetic species (Zaitsev et al. 2013). Parthenogenetically reproducing species vigorously invade new habitats due to faster reproduction and the ability to successfully colonize new habitats by single individuals, and therefore often dominate at early stages, but are replaced by sexually reproducing species at later stages of succession (Ryabinin and Pan'kov 1987; Norton and Palmer 1991). Since colonization of new habitats by oribatid mite communities is slow due to low dispersal ability (Lehmitz et al. 2011) and long generation times, establishment of climax communities in even small areas may take decades (Hågvar et al. 2009; Farská et al. 2014). Accordingly, the oribatid mite community of formerly glaciated regions such as the Schorfheide-Chorin still may not have reached its ultimate composition.

Temporal fluctuations of parthenogenetic species exceeded those of sexuals, supporting our hypothesis that parthenogenetic species are more heavily exposed to density-independent population control. Fluctuations in both parthenogenetic and sexual species were most pronounced in the Schorfheide-Chorin, presumably due to harsher climatic conditions in this region. Similar results were found when analysing mortality and recovery rates of parthenogenetic and sexual species in a drought experiment in Sweden (Lindberg and Bengtsson 2005). Oribatid mites were more sensitive to desiccation when reproducing via parthenogenesis but recovered more quickly reflecting stronger population variations in time in parthenogenetic species.

Conclusion

Overall, the results suggest that the structure of oribatid mite communities of forests in temperate regions varies significantly in space, but is rather stable in time. Temporal fluctuations in population density were more pronounced in parthenogenetic as compared to sexual species suggesting that the latter are more heavily controlled by density-dependent factors presumably predominantly by resource availability and quality. In contrast, parthenogenetic species are more heavily affected by density-independent factors, such as frost in winter and drought in summer, and flourish at sites where resources are plentiful and easily available such as coniferous forests and regions with more acidic soils and thick organic layers supporting the prediction of the SRTS.

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