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Original Research Article

Drought, windthrow and forest operations strongly affect oribatid mite communities in different microhabitats

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ABSTRACT

Climate change is enhancing the annual mean temperature and the risk for droughts and natural disasters. Hot and dry summers not only have a negative impact on forest performance, but also affect fundamental ecosystem processes such as litter decomposition and nutrient cycling and the organisms involved. Oribatid mites are sexually or parthenogenetically reproducing soil-living microarthropods substantially involved in these processes. We compare oribatid mite communities (abundance, species richness, effective Shannon diversity and life-history parameters such as sex ratio, gravidity, number of eggs) in four microhabitats (litter, dead wood, moss and bare soil) before (2016) and after a sequence of disturbance events (2020). These disturbances include the severe drought of 2018/2019 in Germany, a single summer storm event in August 2019, and subsequent forest operations in spring 2020. Abundance and species richness were reduced up to 87% in all microhabitats and so was the effective Shannon diversity in moss (65%). Communities in moss were most affected, while effects were buffered in litter. In litter and moss, sexual species suffered slightly more than parthenogenetic species. Life history parameters were largely unaffected. In bare soil, microarthropods were almost absent. Our study demonstrates that consequences of climate change – drought, windthrow, necessary forest operations – are not restricted to above-ground systems but also strongly affect soil-living microarthropod communities. If natural and human-introduced disturbances remain in the long-term, severe consequences for forest soil arthropods must be expected. Since life-history parameters were unaffected, species probably recover over time if climate becomes more moderate in the short-term.

1. Introduction

The stability of an ecosystem includes its ability, after a disturbance, to recover essential ecosystem services such as decomposition, nutrient mobilisation and soil formation (Ives and Carpenter, 2017). With increasing species diversity, ecosystems become more stable in time as environments change (Ives and Carpenter, 2017; Duffy, 2009; Elmquist et al., 2010). However, both human-mediated and natural influences directly or indirectly shape the complex interactions among living organisms and their environment in almost all ecosystems (Elmqvist et al., 2010). Global climate change – somehow promoted by humans – has become a prominent topic during recent decades (Rossati, 2017) and a tremendous loss of species diversity may be only several years away (Warren et al., 2018). While climate change is a subtle process, it enhances the frequency and intensity of natural disasters such as droughts, bushfires and thunderstorms. As the single-event risk increases and the resistance of ecosystems decreases due to species losses, these events cause

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massive damage, affecting organisms on all trophic levels (Sarewitz et al., 2003; Pielke et al., 2005).

Due to the increasing annual mean temperature, more frequent and longer-lasting droughts have been observed worldwide (IPCC, 2018; Lüttger and Feike, 2018; Heisig and Samini, 2020), which results in many costly and cascading effects (Wens et al., 2019). In Central Europe, an extremely hot and dry summer occurred in 2018, with unusually high temperatures lasting until 2019 (Heisig and Samini, 2020; de Brito et al., 2020). This drought lowered the groundwater level and reduced soil moisture, causing spotty and irregular die-offs of certain tree species (Heisig and Samini, 2020).

Reductions of species diversity due to human land use or climate change have been reported for numerous animal groups (Brook

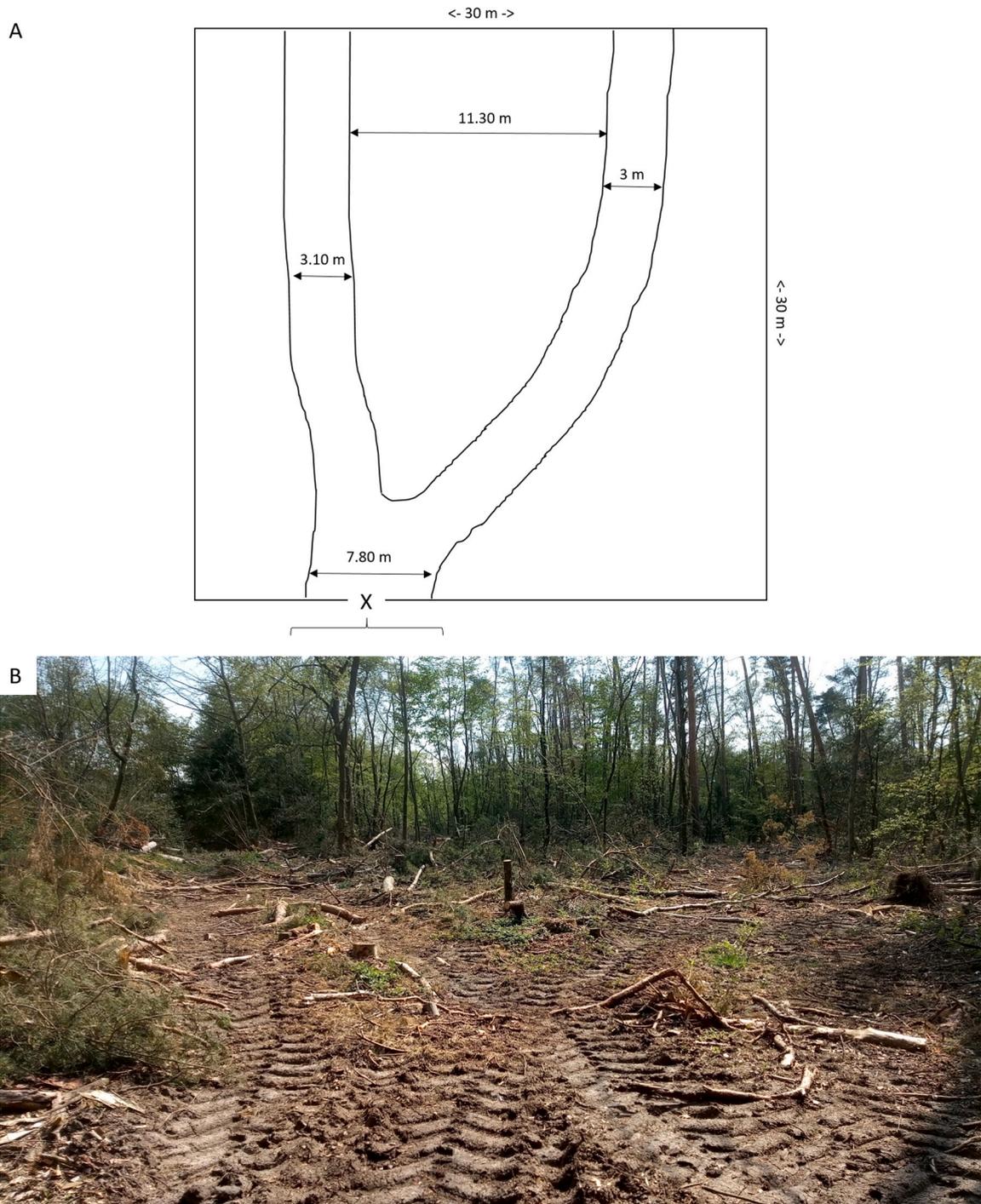


Fig. 1. Experimental plot overview (A) and lanes of bare soil introduced by large forest harvesters (B).

et al., 2003; Thomas et al., 2004; Dickmann et al., 2007; Fonesca, 200; Pereiro et al., 2010). Recently, many studies focused on the decline of insect species that are involved in above-ground ecosystem services (Bouget and Duelli, 2004; Chisté et al., 2016; Seibold et al., 2019). Only a few studies have focused on soil fauna, even though they are essential for ecosystem functioning (Sullivan and Ozman-Sullivan, 2020). Oribatid mites, one of the microarthropod components of this fauna, comprise about 11,000 described sexual and parthenogenetic species worldwide, with high local diversity and density in numerous ecosystems and microhabitats (Wallwork, 1983; Schatz and Behan-Pelletier, 2008; Norton and Behan-Pelletier, 2009; Subías, 2020). They contribute importantly to different ecosystem processes. Many species feed directly on organic material, so are substantially involved in litter decomposition and nutrient cycling; their effect on soil porosity influences aeration, infiltration and the distribution of organic matter (Bird et al., 2004). Their direct and indirect interactions with the soil microbial community promotes nutrient availability and plant growth (Seastedt, 1984; Marshall, 2000).

Oribatid mite communities are affected by forest type (Bluhm et al., 2016), abiotic conditions such as soil pH and soil moisture (Erdmann et al., 2012), land-use intensification (Wehner et al., 2021) and soil compaction (Battigelli et al., 2004). Since climate change impacts such features we can expect soil-living oribatid mites to be somehow affected. Furthermore, oribatid mites are present not only in the continuous forest litter system, but also in patchy, epigeal surface microhabitats such as mosses, lichens and dead wood (Frahm, 2001; Huhta et al., 2012; Wehner et al., 2016). Even without external influences, these microhabitats are characterized by different environmental conditions such as microclimate, pore structure and food availability (Lachat et al., 2012; Thakur et al., 2020). While many oribatid mite species are equally distributed among these microhabitats, community fluctuations during seasons are most pronounced in moss and least in litter (Wehner et al., 2018). Litter is assumed to buffer effects on temperature and humidity, while mosses are vulnerable to desiccation at high temperatures (Frahm, 2001; Nielsen et al., 2010).

Here, we investigated the accumulated effects of three disturbance events on the oribatid mite community in a temperate forest in Germany, by comparing data from 2016 and 2020. The events included the drought of 2018/2019, a single summer storm event in August 2019, and subsequent forest operation procedures at the beginning of 2020. We compared total abundance, species richness and diversity among four microhabitats: moss, dead wood, litter and newly-bared soil exposed by large mechanical harvesters. We focused on differences in the responses of sexually and parthenogenetically reproducing species and also compared life-history parameters (sex ratios, gravidity and egg numbers per gravid female) that might indicate the potential for recovery after disturbance. We expected oribatid mite communities to be negatively affected by the natural drought and summer storm as well as the human-introduced soil disturbances. We further expected changes to be less pronounced in the continuous litter habitat than in moss or dead wood since microsite complexity could allow litter to function as refugium.

2. Material and methods

2.1. Location and sampling

In 2016 and 2020, samples were taken in a 900 m² study site in State Forest 2043 A in Mörfelden-Walldorf, Southwest Germany (N49° 58' 30.8424/E8° 33' 1.0332; 96 m a.s.l.). The oak-mixed forest is moderate subcontinental and mesotrophic, the topsoil is flat and covered with sand. Seasonality in oribatid mite communities at this site in 2016 has already been discussed (Wehner et al., 2018). In 2018 and 2019, the site suffered from dry and hot summers (see 2.2.). A single summer storm event on 19 August 2019 caused windthrow losses in the tree community. Subsequent forest operations at the beginning of 2020 used large mechanical harvesters and introduced several trails of bare soil with deep tire imprints that did not exist in 2016 (Fig. 1).

From April to September, we sampled moss, dead wood and litter in 2016 and 2020, but also the newly present bare soil in the trails in 2020 (ten replicates per microhabitat, resulting in 180 total samples in 2016 and 240 total samples in 2020). Samples of moss (including *Mnium undulatum*, *Polytrichum cf. formosum*, *Amblystegium varium*, *Brachythecium* sp., *Dicranella* sp. and *Eurhynchium* sp., depending on sampling date), prostrate dead wood of different decaying stages and litter material were taken haphazardly at the beginning of each month.

Individual samples were taken according to substrate: bare soil was taken with soil corer with 5 cm Ø; litter was removed by hand (about 20 cm × 20 cm) including the sub-litter organic matter; pieces of dead wood (about 10 cm × 10 cm) were snapped from prostrate larger pieces on the forest floor; and sections of moss patches (including a mixture of different species) were collected to reach a sample size of at least 5 g wet weight. Samples were stored in plastic bags and transferred to the laboratory. Microarthropods were extracted for 48 h using a modified Kempson heat extractor (Kempson et al., 1963) and stored in 75% ethanol. Dry weight of each sample after extraction was used to standardize the number of individuals as ind/kg dry weight following (Wehner et al., 2018; Skubala, 2016). Adult oribatid mites were determined to species, genus or family level under a microscope using the key of Weigmann (Weigmann, 2006). Taxonomic classification was adopted from (Norton and Behan-Pelletier, 2009; Weigmann, 2006; Schatz et al., 2011). Adult species were sexed if possible and numbers of eggs were counted; the mode of reproduction was inferred from sex ratios and literature (Cianciolo and Norton, 2006; Norton and Palmer, 1991).

In April 2020, the barren trails introduced by forest harvesters were free of plants, but were colonized with herbaceous plants such as bryony, blackberry or common peony during the summer. In September 2020, we recorded the vegetation of the sampling area, which then included shrub species (Appendix 2). Within the study plot, 71 living trees were present, belonging to eight tree species (Appendix 3). The tree community mainly consisted of *Fagus sylvatica* (25%), *Quercus robur* (19%) and *Carpinus betulus* (14%). While being only a minor part of the tree community, *Tilia cordata*, *Pinus sylvestris*, *Taxus baccata* and *Corylus avellana* showed the highest amount of dead parts (twigs and branches; Appendix 3).

Dead wood on the forest floor (classified as stumps or lying dead wood (LDW)) was assigned to a tree species if possible, length and

circumferences (or diameter for stumps) were measured and the grade of decay was classified as either (1) fresh, (2) starting decaying, bark starting to peel, (3) decaying, soft inside, hard outside or (4) strongly decayed, wood completely softened. The total amount of dead wood (including stumps and LDW) on the forest floor was about 9 m³, dominated by pine (5 m³) and undefined dead wood (2 m³; Appendix 4). About three-fourths of the dead wood (74%) was either fresh or at the beginning of decay; only about 4% was strongly decayed (Appendix 4).

2.2. Climate

Climate data (mean temperature and mean precipitation per month from 2016 to 2020) were obtained from the nearest weather station in Offenbach (wetterkontor.de). Deviations from the longtime mean are based on the years 1981–2010 (Appendix 5).

Although the mean temperature from April to September was highest in 2018 (2016: 17.0 ± 4.1 °C, 2017: 16.6 ± 4.3 °C, 2018: 19.1 ± 3.4 °C, 2019: 17.3 ± 4.5 °C, 2020: 15.8 ± 4.9 °C), it did not differ significantly among years ($F_{1,23} = 0.261$ $p = 0.615$; Appendix 6A). On the other hand, total precipitation differed significantly among years ($F_{1,23} = 4.291$ $p = 0.049$, Appendix 6B) being highest in 2017 and lowest in 2018 (2016: 60.0 ± 32.6 liters per square meter (l/sqm), 2017: 63.5 ± 38.1 l/sqm, 2018: 28.4 ± 13.9 l/

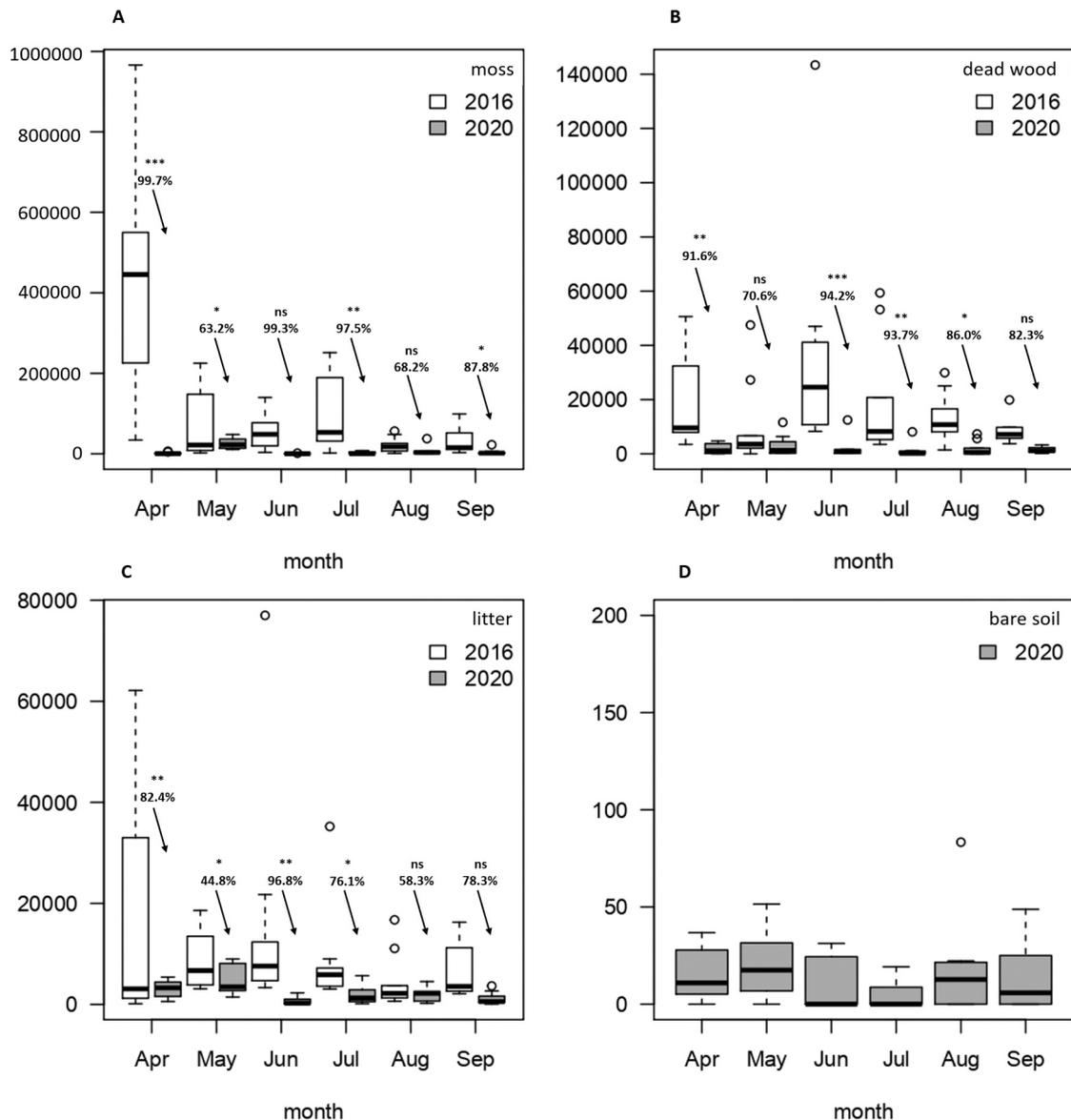


Fig. 2. Comparison of oribatid mite abundances [individuals per kg dry weight] between 2016 (white) and 2020 (grey) from April to September in (A) moss, (B) dead wood, (C) litter and (D) bare soil (not present in 2016). Note the different scales. Abbreviations: ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 1

Statistical values comparing months between 2016 and 2020 for (A) total abundance, (B) species richness and (C) effective Shannon diversity in the microhabitats dead wood, litter and moss. Significant values are given in bold.

A - Total abundance moss - GLM with quasi-poisson distribution					B - Species richness moss - LMM with type III Anova and F-test					C - Effective Shannon diversity moss - LMM with type III Anova and F-test				
	df	sum sq	F	p		df	sum sq	F	p		df	sum sq	F	p
year	1	54971356	149.08	< 0.001	year	1	1411.8	114.84	< 0.001	year	1	7.14	28.27	< 0.001
month	5	1013310	5.06	0.0003	month	5	1510.0	8.30	< 0.001	month	5	5.10	4.04	0.002
year*month	5	1011669	5.05	0.0003	year*month	5	510.6	8.31	< 0.001	year*month	5	5.11	4.05	0.002
residuals	107	4285969			residuals	107	1314.9			residuals	107	27.04		
dead wood - GLM with quasi-poisson distribution					dead wood - LMM with type III Anova and F-test					dead wood - LMM with type III Anova and F-test				
	df	sum sq	F	p		df	sum sq	F	p		df	sum sq	F	p
year	1	186681	16.22	0.001	year	1	237.3	11.56	0.0009	year	1	0.92	3.31	0.072
month	5	34629	0.60	0.699	month	5	254.7	2.48	0.036	month	5	2.03	1.46	0.208
year*month	5	35540	0.60	0.700	year*month	5	254.6	2.48	0.036	year*month	5	2.04	1.47	0.280
residuals	104	1196932			residuals	104	2135.7			residuals	107	28.90		
litter - LMM with type III Anova and F-test					litter - LMM with type III Anova and F-test					litter - LMM with type III Anova and F-test				
	df	sum sq	F	p		df	sum sq	F	p		df	sum sq	F	p
year	3	70531	9.50	0.003	year	1	182.9	11.20	< 0.001	year	1	0.45	2.32	0.131
month	5	61062	1.65	0.155	month	5	866.2	10.61	< 0.001	month	5	2.18	2.27	0.053
year*month	15	61019	1.64	0.155	year*month	5	866.9	10.62	< 0.001	year*month	5	2.18	2.27	0.053
residuals	212	749690			residuals	101	1649.2			residuals	101	19.39		

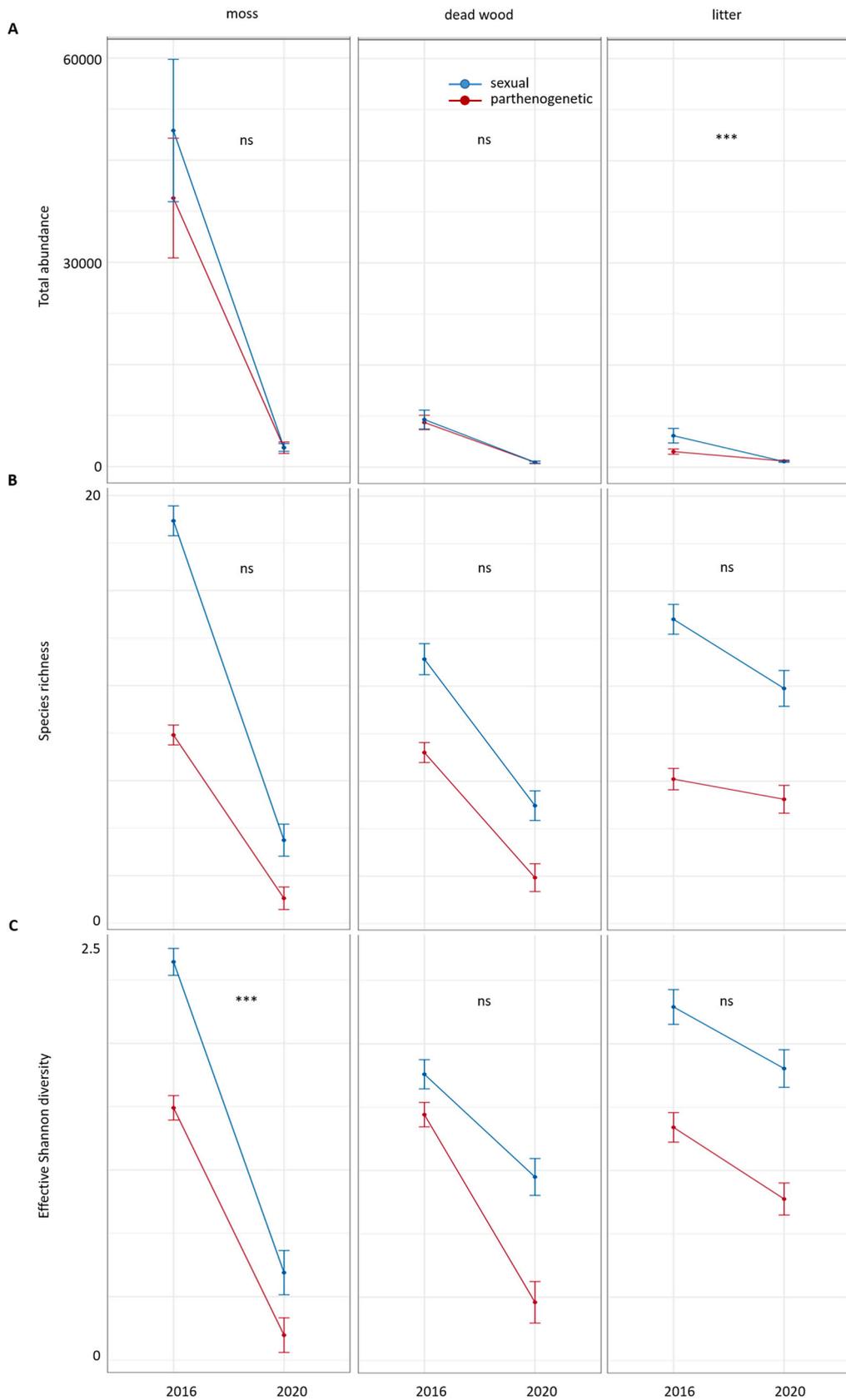
Abbreviations: df = degrees of freedom, sum sq = sum of squares, GLM = general linearized model, LMM = linearized mixed model. Significant values are given in bold.

Table 2

Statistical values comparing the mode of reproduction (sexual vs parthenogenetic) between 2016 and 2020 for (A) total abundance, (B) species richness and (C) effective Shannon diversity in the microhabitats dead wood, litter and moss. Significant values are given in bold.

A - Total abundance GLMM with zero-altered gamma distribution, month as random factor and type III Anova				B - Species richness GLMM with poisson distribution, month as random factor and type III Anova				C - Effective Shannon diversity LMM with month as random factor and type III Anova			
	df	Chi ²	p		df	Chi ²	p		df	Chi ²	p
year	1	81.203	< 0.001	year	1	70.519	< 0.001	year	1	64.117	< 0.001
reproduction	1	0.084	0.772	reproduction	1	24.380	< 0.001	reproduction	1	6.521	0.011
microhabitat	2	132.649	< 0.001	microhabitat	2	5.235	0.073	microhabitat	2	23.482	< 0.001
year*reproduction	1	0.000	0.998	year*reproduction	1	2.784	0.095	year*reproduction	1	6.546	0.011
year*microhabitat	2	17.231	0.0002	year*microhabitat	2	62.010	< 0.001	year*microhabitat	2	23.518	< 0.001
reproduction*microhabitat	2	5.466	0.065	reproduction*microhabitat	2	10.080	0.006	reproduction*microhabitat	2	12.892	0.002
year*reproduction*microhabitat	2	3.341	0.188	year*reproduction*microhabitat	2	3.947	0.139	year*reproduction*microhabitat	2	12.886	0.002
intercept	1	1738.952	< 0.001	intercept	1	555.841	< 0.001	intercept	1	64.409	< 0.001
moss - GLMM with zero-altered gamma distribution, month as random factor and type III Anova				moss - GLMM with poisson distribution, month as random factor and type III Anova				moss - LMM with month as random factor and type III Anova			
	df	Chi ²	p		df	Chi ²	p		df	Chi ²	p
year	1	58.318	< 0.001	year	1	111.154	< 0.001	year	1	106.250	< 0.001
reproduction	1	0.448	0.503	reproduction	1	102.157	< 0.001	reproduction	1	46.687	< 0.001
year*reproduction	1	0.015	0.902	year*reproduction	1	0.170	0.680	year*reproduction	1	7.157	< 0.001
intercept	1	937.428	< 0.001	intercept	1	409.490	< 0.001	intercept	1	203.013	< 0.001
dead wood - GLMM with zero-altered gamma distribution, month as random factor and type III Anova				dead wood - GLMM with poisson distribution, month as random factor and type III Anova				dead wood - LMM with month as random factor and type III Anova			
	df	Chi ²	p		df	Chi ²	p		df	Chi ²	p
year	1	66.680	< 0.001	year	1	69.867	< 0.001	year	1	64.715	< 0.001
reproduction	1	0.028	0.867	reproduction	1	24.406	< 0.001	reproduction	1	3.015	< 0.001
year*reproduction	1	9.221	0.354	year*reproduction	1	2.787	0.095	year*reproduction	1	6.625	0.082
intercept	1	2362.201	< 0.001	intercept	1	455.625	< 0.001	intercept	1	261.200	< 0.001
litter - GLMM with zero-altered gamma distribution, month as random factor and type III Anova				litter - GLMM with poisson distribution, month as random factor and type III Anova				litter - LM with type III Anova			
	df	Chi ²	p		df	Chi ²	p		df	Chi ²	p
year	1	24.972	< 0.001	year	1	2.283	0.131	year	1	8.978	0.003
reproduction	1	12.609	0.0003	reproduction	1	64.725	< 0.001	reproduction	1	24.311	< 0.001
year*reproduction	1	9.221	0.0002	year*reproduction	1	0.997	0.318	year*reproduction	1	0.088	0.767
intercept	1	2048.760	< 0.001	intercept	1	522.522	< 0.001	intercept	1	294.777	< 0.001

Abbreviations: df = degrees of freedom, GLMM = general linearized mixed model, LMM = linearized mixed model, LM = linearized model. Significant values are given in bold.



(caption on next page)

Fig. 3. Comparison of (A) oribatid mite abundance [individuals per kg dry weight], (B) species richness and (C) Shannon diversity in moss, dead wood and litter between 2016 and 2020 in sexual (blue) and parthenogenetic (red) species. Abbreviations: ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sqm, 2019: 49.8 ± 13.0 l/sqm, 2020: 32.6 ± 12.5 l/sqm).

2.3. Statistical analysis

All statistical analyses were performed with R 3.5.2 (R Core Team, 2018). Normal distribution, homogeneity of variances and fitting of models were tested by Shapiro test, Levene test and goodness-of-fit-test, respectively. To ensure normal distribution of model

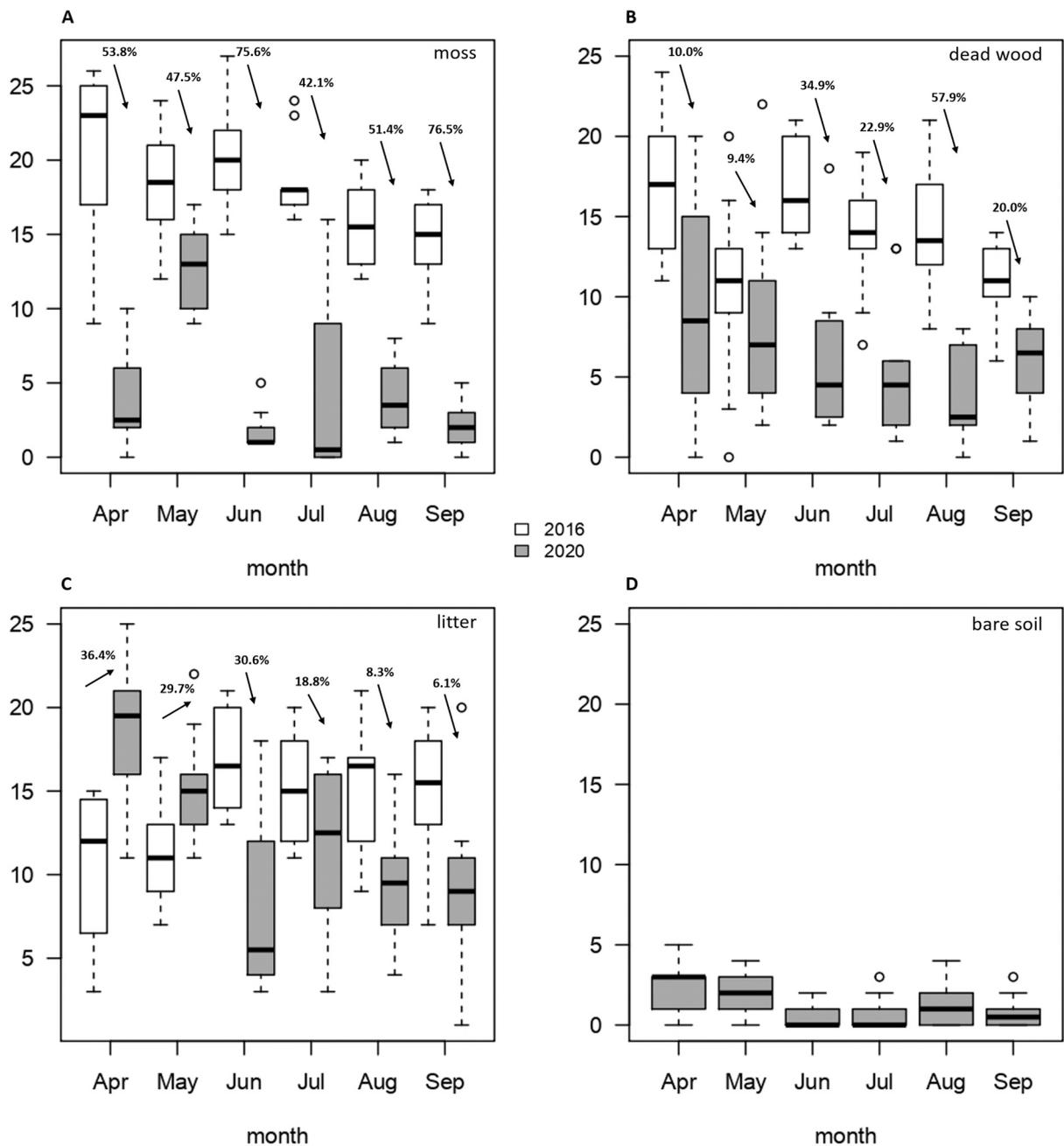


Fig. 4. Comparison of species richness between 2016 (white) and 2020 (grey) from April to September in (A) moss, (B) dead wood, (C) litter and (D) soil (not present in 2016). Abbreviations: ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

residuals, we used general linearized mixed models (GLMM) with either Poisson or negative binomial error distribution depending on data structure. Statistical significances were tested for with type III ANOVA and Chi² or F-test, respectively.

We characterized oribatid mite assemblages by abundance (ind/kg dry weight), species richness (N, mean number of species per sample) and effective Shannon diversity (e^H) (Jost, 2006). To determine general changes over time, these parameters were analyzed as response variables with year (2016 and 2020), month and their interaction as explanatory factors.

We further analyzed whether changes in abundance, richness and diversity between the two years differ between microhabitats (litter, deadwood, moss and bare soil) or reproductive mode (sexual vs. parthenogenetic species) using year, mode of reproduction and microhabitat as well as their two-way and three-way interactions as fixed effects and month as a random factor. Since microhabitat showed a significant effect on all parameters, we also calculated separate models per microhabitat including only the interaction between year and reproductive mode.

Changes in life-history parameters (proportion of females, gravidity of females and number of eggs per gravid female (square root transformed)) between the two years were analyzed using year, month and mode of reproduction as well as their two-way and three-way interactions as response variables with species included as a random factor.

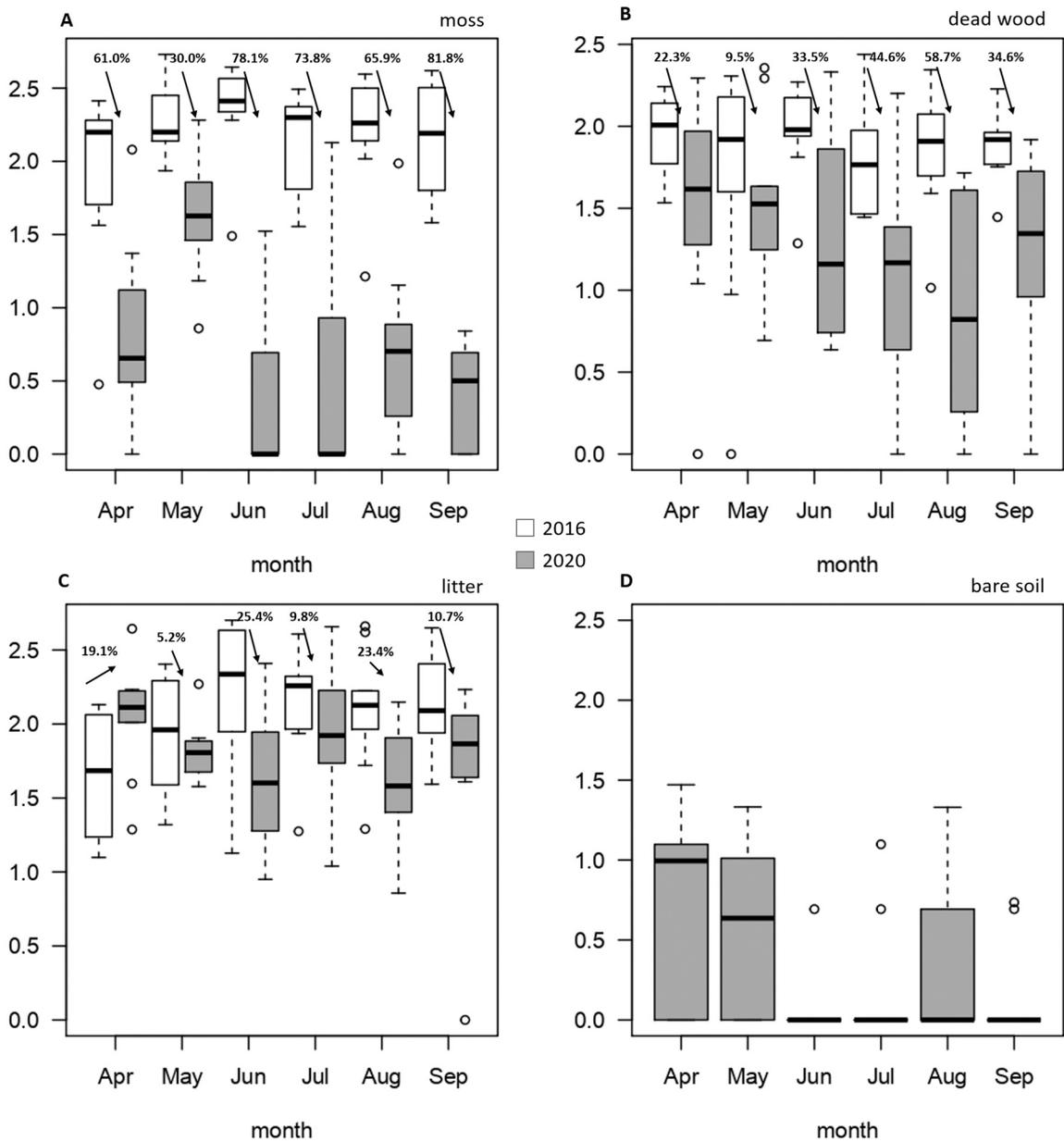


Fig. 5. Comparison of Shannon diversity between 2016 (white) and 2020 (grey) from April to September in (A) moss, (B) dead wood, (C) litter and (D) soil (not present in 2016). Abbreviations: ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Total abundance was analyzed using GLMM with a zero-altered gamma distribution with zeros being considered with a binomial model containing only the intercept. For species richness, we used GLMM with Poisson distribution and for the effective Shannon diversity linear mixed models (LMM). Gravidity of females and numbers of eggs per gravid female were analyzed using GLMM with Poisson distribution; sex ratio (proportion of females) was analyzed using LMM.

3. Results

In total, we collected 56,069 adult oribatid mite individuals belonging to 54 identified species, with others identified only to genus (*Carabodes*, *Galumna*, *Tectocephus*, *Steganacarus*) or family (Brachychthoniidae, Phthiracaridae, Suctobelbidae; Appendix 7). Nine species present in 2016 were missing in 2020 (*Camisia spinifer*, *Ceratozetes gracilis*, *Chamobates borealis*, *Cosmochthonius lanatus*, *Euzetes globulus*, *Liacarus subterraneus*, *Liebstadia longior*, *Pantelozetes paolii*, *Peloptulus phaenotus*) and two species were newly encountered (*Micreremeus brevipes*, *Odontocephus elongatus*) in 2020. Among the 61 taxa, 15 reproduce by parthenogenesis and 46 are sexual (Appendix 7).

The total abundance of oribatid mites showed a significant reduction between the years 2016 and 2020 for all microhabitats (dead wood: $p = 0.001$, litter: $p = 0.003$, moss: $p < 0.001$) and was equally strong in all months with the exception of a significantly stronger reduction in April compared to the other months in moss (Fig. 2A–C, Table 1A). In moss, the total abundance was reduced by 85.9% on average and ranged from 63.2% in May to 99.7% in April (Fig. 2A). In dead wood, total abundance was reduced by 86.4% on average and ranged from 70.6% in May to 94.2% in June (Fig. 2B). The lowest reduction was found in litter (69.5% on average), ranging from 44.8% in May to 96.8% in June (Fig. 2C). The overall decline in abundance between 2016 and 2020 differed in strength between the microhabitats (year*microhabitat $p = 0.001$, Table 2A) with the strongest reduction seen in moss (Fig. 3A) There was no general interaction between mode of reproduction, microhabitat and years (year*reproduction*microhabitat $p = 0.188$, Table 2A), but the abundance of sexual oribatid mite species declined more strongly between years than those of parthenogens in the litter microhabitat (Fig. 3A, Table 2A). In bare soil, for which we have data only for 2020, few oribatid mite individuals were present (Fig. 2D), which also was true for other soil microarthropods such as gamasid and uropodid mites and collembolans.

Similarly, species richness declined from 2016 to 2020 in all microhabitats (dead wood: $p = 0.0009$, litter: $p < 0.001$, moss: $p < 0.001$) but differed significantly in strength or direction between months for litter (year*month $p < 0.001$) and moss (year*month $p < 0.001$) microhabitat (Fig. 4A–C, Table 1B). Species richness declined by 57.8% on average in moss (Fig. 4A), 29.1% in dead wood (Fig. 4B) and 15.9% in litter (Fig. 4C). In litter, species richness in April and May was higher in 2020 as compared to 2016. The overall decline in species richness between 2016 and 2020 differed in strength between the microhabitats (year*microhabitat $p < 0.001$, Table 2B) with the strongest reduction again seen in moss (Fig. 3B). In all microhabitats, species richness of sexual and parthenogenetic species was affected equally (Fig. 3B, Table 2B).

The effective Shannon diversity differed significantly between 2016 and 2020 only in moss (dead wood: $p = 0.072$, litter: $p = 0.131$, moss: $p < 0.001$, Table 1C, Fig. 5A–C) and no significant difference in effects between months was found. However, if the general change between 2016 and 2020 is considered together with the effect of microhabitat and mode of reproduction (with month included only as random effect), all three microhabitats show a significant reduction in diversity (Table 2C). In moss, the effective Shannon diversity of sexual species was more affected than that of parthenogens (Fig. 3C, Table 2C).

Overall, the ratio between males and females did not differ between 2016 and 2020 (year: $\text{Chi}^2 = 0.015$, $df = 1$, $p = 0.902$), but differences between sexual and parthenogenetic species were naturally highly significant (mode of reproduction: $\text{Chi}^2 = 29.792$, $df = 1$, $p < 0.001$). The proportion of females was always 100% in parthenogenetic species and 58.9% on average in sexuals. The proportion of females in sexual species collected in dead wood averaged 0.613 ± 0.38 in 2016 and 0.620 ± 0.38 in 2020; it was lowest in litter (respectively 0.590 ± 0.37 and 0.561 ± 0.38) and highest in moss (respectively 0.663 ± 0.34 and 0.612 ± 0.36). Parthenogenetic species almost always comprised all-female populations (ranging from 0.982 ± 0.13 in litter in 2016 to 1.00 in litter in 2020) and rare spanandric males were found only in *Oppiella nova* and *Tectocephus* spp. (Appendix 8).

Gravidity, given as the proportion of gravid females, was constant between years in litter (year: $\text{Chi}^2 = 0.253$, $df = 1$, $p = 0.614$) and dead wood (year: $\text{Chi}^2 = 0.066$, $df = 1$, $p = 0.797$). In moss, the proportion of gravid females varied between years during the season depending on the mode of reproduction (year*microhabitat*mode of reproduction: $\text{Chi}^2 = 15.269$ $df = 5$ $p = 0.009$, Appendix 9). Among parthenogenetic species only 25.6% of females were gravid, in sexuals about 50% of females were gravid.

The number of eggs per gravid female was constant between years (year: $\text{Chi}^2 = 0.633$, $df = 1$, $p = 0.426$). In moss and litter, the number of eggs depended on the mode of reproduction: sexual species carried about twice as many eggs as parthenogens (on average 4.88 vs 2.0, Appendix 10).

4. Discussion

We compared the oribatid mite communities in different microhabitats (bare soil, dead wood, litter, moss) before (2016) and after (2020) a spate of disturbances. The sequence of natural (drought, thunderstorm) and human-introduced (forest operations) disturbance events had a strong negative impact on below-ground oribatid mite communities. Overall abundance and species richness were reduced in all studied microhabitats (dead wood, moss, litter) and the effective Shannon diversity was reduced in moss. As expected, the oribatid mite community living in moss was most strongly affected, followed by that in dead wood; the litter community appeared to be least affected. In moss, the diversity of sexual species suffered more than that of parthenogens. Life history parameters such as the proportion of females, gravidity, and the number of eggs per gravid female remained largely unaffected by the combined disturbances in all microhabitats. The highly compacted bare-soil lanes of harvester trails supported the least abundant and diverse community.

High temperatures during the German drought in 2018/2019 lowered the groundwater level and deprived the forests of soil moisture (Heisig and Samini, 2020), a decisive factor influencing oribatid mite communities. Many oribatid mite species require elevated humidity and are susceptible to drought (Lindberg et al., 2002; Lindo, 2003; Lindberg and Bengtsson, 2005; Gergócs and Hufnagel, 2009). Several studies have shown that species richness and abundance decrease during drought. Developmental stages in particular can be more sensitive to drought, and larger mites may not be able to move deeper into moister but more finely-grained underlying soil (Lindberg et al., 2002; Lindberg and Bengtsson, 2005; Tsiafouli et al., 2005). However, microhabitats differ in their ability to buffer drought consequences (Nielsen et al., 2010; Huhta, 1976). Small moss patches are extremely vulnerable to desiccation, while litter and dead wood have greater water-holding capacity and desiccation tolerances (Frahm, 2001; Nielsen et al., 2010).

In general, litter is probably the most stable microhabitat for oribatid mites, functioning as refugium and connector pathway for many species that are more specialized to microhabitats such as dead wood and moss (Wehner et al., 2016). Since windthrow gaps of the canopy enhance the light level of the forest, sun-exposed dead wood and moss suffer more from desiccation during high summer temperatures than does litter (Bouget and Duelli, 2004). Understorey vegetation and the soil pore-space system can probably retain a moist microclimate in heterogeneous microsites in litter on the forest floor (Bouget and Duelli, 2004; Lindo, 2003; Huhta, 1976; Battigelli, 2000).

Oribatid mite abundance is often high in dead wood (Huhta et al., 2012), but it can vary greatly depending on the stage of decomposition. Abundance in our study was rather low, but only 4% of the dead wood on the forest floor showed pronounced decay. Probably wood-inhabiting oribatid mites will recover at this site as decay of freshly cut timber progresses.

In addition to drought, soil compaction is known to have short-term impacts on oribatid mite communities (Battigelli et al., 2004; Lindo, 2003; Siepel, 1994), but harvesting methods differ greatly in their effects. In a Canadian boreal spruce forest, whole-tree harvesting and forest floor removal caused an abundance reduction of up to 93%, whereas reduction was only 20% with stem-only harvesting (Battigelli et al., 2004). In the present study, abundance declined up to 86% in dead wood and moss, and about 70% in litter, which probably is a combined effect of drought, windthrow and subsequent forest operations. While abundance was strongly affected, diversity parameters (richness, effective Shannon diversity) were less reduced indicating a non-selective removal of individuals and that many oribatid mite species are equally sensitive to disturbance. Again, the litter microhabitat was less affected than dead wood and moss.

The highly compacted soil in the lanes introduced by large mechanical harvesters showed extremely low oribatid mite abundance and very low diversity. Probably, this was due to the strong reduction of food (organic matter and microbial biomass) and structural degradation (loss of the soil pore system and buffering litter layer with heterogeneous microsites having a range of specific microclimates) on which oribatid mites strongly depend (Seastedt and Crossley, 1981). Other soil microarthropods were similarly affected: gamasid and uropodid mites, as well as collembolans, were absent or found in very low numbers in bare soil. The understorey vegetation forming during the 2020 growing season had not yet compensated for operational impacts by the end of the study.

Beside direct effects of drought and habitat destruction, oribatid mites may also suffer from a reduction of food sources. Oribatid mites consume various kinds of resources and therefore are an important part of the soil food web (Lebrun and van Straalen, 1995; Behan-Pelletier, 1999; Schneider et al., 2004). Beside feeding on a variety of fungi, they are also associated with fine-root and microbial biomass (Lindo, 2003; Schneider and Maraun, 2005). As a consequence of drought, biomass and diversity of fungi and microbes may also drop (Gergócs and Hufnagel, 2009), having also negative impacts on the abundances of oribatid mites.

Sullivan and Ozman-Sullivan (Sullivan and Ozman-Sullivan, 2020) linked the maintenance of mite diversity to plant diversity and habitat complexity. They concluded that since habitat destruction and degradation continue on a large scale and climate change is worsening the effects of other drivers, about 15% of mite species are likely to have become extinct by now (Sullivan and Ozman-Sullivan, 2020). In the present study, about 18% of the species found in 2016 did not appear in 2020 samples. Presumably, these species have not become locally extinct, but hopefully will reinvade from less-disturbed surroundings in the future. Furthermore, in 2020 the reproductive life-history parameters - gravidity and number of eggs per gravid female - of both sexual and parthenogenetic oribatid mite species had not changed from pre-disturbance sampling in 2016. Thus, a successful recovery in disturbed microhabitats can be expected.

In summary, climate change influences not only above-ground animal communities, but also soil-living microarthropods such as oribatid mites. Drought, windthrow and forest operations significantly reduced oribatid mite abundance and their diversity, which has negative impacts on all ecosystem processes in which these animals are involved. If these natural and human-introduced disturbances persist in the long-term, severe consequences must be expected for soil-living arthropods. However, if - in the short-term - the climate becomes more moderate again, oribatid mite communities may recover over time since the litter system can buffer a certain amount of disturbance and life-history parameters of species seem largely unaffected so far.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01757](https://doi.org/10.1016/j.gecco.2021.e01757).

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