Specialization of oribatid mites to forest microhabitats—the enigmatic role of litter

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Abstract. The degree of ecological specialization influences the biological performance of species in their natural environment and affects the coexistence of different taxa. However, on a small scale, the diversity of microarthropods that coexist in forest soils and leaf litter seems inordinately high, a situation known as the “enigma of soil animal species diversity”. Since recent studies point to the importance of small-scale heterogeneity to explain this phenomenon, we use interaction networks between microhabitats and their inhabitants to resolve and quantify the community structure (species composition, richness, and diversity) of oribatid mites (Oribatida) in five discrete, patchy substrates—dead wood, lichens, mosses, sod, and tree bark—and in the general leaf litter. Since oribatid mites are ubiquitous in all these microhabitats in temperate forests, the analysis of their community structure in the light of generalization and specialization might help us understand the ecological role of litter. We investigated whether litter acts as a specific microhabitat with the intrinsic characteristics that enable the “enigmatic” high diversity of oribatid mites (Habitat-Hypothesis), if litter acts as a source from which oribatid mite species more or less randomly invade different associated microhabitat-patches (Source-Hypothesis), or if litter only connects patchily distributed microhabitats with specific species compositions (Connector-Hypothesis). In total, 25,162 adult oribatid mite individuals were analyzed, most belonging to the derived group Brachypylina. Species richness, density, and diversity differed among microhabitats with highest values found in mosses and dead wood and lowest on tree bark. In general, specialization of oribatid mite species was low—highest on tree bark and in grass sod—but differed slightly among oribatid mite taxa (Enarthronota, Mixonomata, Nothriana, Brachypylina). The Connector- and Habitat-Hypotheses can explain the distribution of most oribatid mite species but the Source-Hypothesis explains the distribution patterns for only a few species.

Key words: enigma of soil biodiversity; microhabitats; oribatid mites; specialization.

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INTRODUCTION

Ecological specialization is a complex process influenced by biological mechanisms, evolutionary patterns, biological performance, and interactions among communities, species, populations, or individuals (Devictor et al. 2010, Poisot et al. 2011, 2012, Vamosi et al. 2015). The degree of specialization differs among animal taxa, and can be considered from different aspects, so that a species may be generalized on some axes but specialized on others (Devictor et al. 2010). The biological performance of species probably depends on their degree of specialization since specialists with a narrow niche are more prone to extinction than generalists, and specialists are more negatively affected if environmental conditions change (McKinney and Lockwood 1999).
Mechanisms influencing ecological specialization and the assembly of animal communities are numerous and can be explained by neutral and niche differentiation theories (HilleRisLambers et al. 2012, Kraft et al. 2015). Stochastic processes, dispersal limitations, temporal effects, resource partitioning, biotic interactions (e.g., natural enemies), and environmental filtering create spatial patterns in species distribution, strongly depending on spatial scales (Chase and Leibold 2003, Adler et al. 2013, Gao et al. 2014, Maaß et al. 2015). Since many studies show complex combinations and interactions among several of these factors, defining the underlying significant processes is often complicated. Furthermore, it is not always obvious whether coexisting mechanisms (environmental filtering or biotic interactions) may be sequential steps or interact dynamically (Kraft et al. 2015, Maaß et al. 2015).

Microhabitats in forest soils (different soil layers and the litter system) seem to provide rather stable conditions for their inhabitants and an unexpectedly great diversity of soil and litter microarthropods can coexist on a small scale; this phenomenon has become famous as the “enigma of soil animal species diversity” (Anderson 1975, Nielsen et al. 2010). Nielsen et al. (2010) provided direct evidence that small-scale heterogeneity in soil is important for species richness of intermediate-sized soil fauna (Mesostigmata, Oribatida, Collembola, Nematoda). In temperate forests, heterogeneity in soil is greatest within the continuous leaf litter, but is augmented by different patchy microhabitats on or emerging from the forest floor, such as lichens, mosses, dead wood, fungi, and the bark of trees (Aoki 1967).

Each of these microhabitats has distinct traits, consisting of abiotic factors (e.g., moisture, habitat fragmentation) and biotic interactions, which enable the establishment of specific animal (and plant) communities.

Forest soils are continuous and—slightly depending on the soil layer—relatively stable microhabitats having narrow fluctuation of ecological conditions (e.g., moisture, temperature; Maraun and Scheu 2000). The faunal composition depends on forest type and layer thickness. For example, in litter both the density and diversity of oribatid mites are higher in recalcitrant, persistent litter than in rapidly decomposing litter of high nutrient quality; this suggests that litter thickness and therefore microhabitat structural complexity are of major importance (Heethoff et al. 2009, Eissfeller et al. 2013).

Tree bark is one of multiple microhabitats found in tree canopies (others include twigs, branches and leaves, suspended soils in branch crotches and crusts of lichens and mosses; Behan-Pelletier and Winchester 1998, Behan-Pelletier and Walter 2000) and it provides substrate for a variety of microarthropods. However, the harsh environmental conditions, such as exposure to sun, wind, and predators, require specific adaptations (Nicolai 1986).

In forests, lichens and mosses grow on bare soil, stones, or organic surfaces such as living trees and dead wood, and they are important for soil fertility through their role in mineral transfer (Seyd and Seaward 1984, Root et al. 2007, Neher et al. 2009). Lichens seem to be inhabited by highly specialized species due to their specific environmental conditions and small size (Seyd and Seaward 1984). In contrast, mosses are biotopes for many microarthropod species due to their high surface–volume relation and the presence of different food resources such as fungi, algae and bacteria (Frahm 2001).

Dead wood, including portions of standing trees and decaying wood on the ground, is an important component of natural temperate zone forests. Primeval forests comprise up to 30% dead wood, contrasting strongly with the 1–3% in managed temperate forests (Müller-Using and Bartsch 2003, Jonsson et al. 2005). This microhabitat has an important impact on forest animal communities: about 600 fungi and 1,300 beetle species participate in its decomposition, but it is also a preferred biotope for other insects as well as for mites (Ehnström 2001, Huhta et al. 2012, Bluhm et al. 2015). Because of its dark surface and low thermal conductivity, in combination with a constant high water content, dead wood provides unique microclimatic conditions (Lachat et al. 2012).

Finally, temperate forests also include grassy patches of different size. While a specific microarthropod community characterizes more extensive grasslands, meadows, or fields (Curry and Momen 1988, Ivan 2006), the sod community in forest grassy patches has a below-ground fauna that may be more similar to that of other forest microhabitats due to proximity effects.
Oribatid mites (Oribatida, Acari, Arachnida) —comprising 11,000 described species (Subías 2004, 2014)—are ubiquitous but unevenly distributed in all forest microhabitats (e.g., Aoki 1967, Hammer 1972, Wunderle 1992). While best known as an important component of soil communities, occupying all layers of litter and soil, they are also abundant in various insular microhabitats on the forest floor and in the canopy. These include epiphytic and epilithic lichens and mosses, fungal sporophores, tree bark, twigs and dead wood, grasses, and shrubs (Aoki 1967, Hammer 1972, Seyd and Seaward 1984, Wunderle 1992, Behan-Pelletier 1999, Sovik et al. 2003, Root et al. 2007, Siira-Pietikäinen et al. 2008). The ubiquity of oribatid mites in forest microhabitats, in combination with known specific adaptations to microhabitat conditions, enables the analysis of their community structure in the light of generalization or specialization of inhabiting species. Knowing the small-scale distribution and specificity of oribatid mite communities might help us understand the ecological role of litter and may help explain the “enigmatic high diversity”.

Here, we use tools borrowed from network analysis to illustrate the distribution of oribatid mite species among microhabitats and to quantify their specificity and exclusiveness. We particularly tried to understand the connectivity between the contiguous leaf litter and the more patchy, insular forest microhabitats. Our main aim was to investigate three hypotheses on the role of litter in overall faunal dynamics: (1) Litter acts as a specific microhabitat having intrinsic characteristics that enable the “enigmatic” high diversity of oribatid mites (Habitat-Hypothesis, HH). (2) Litter acts as a diversity source from which oribatid mite species more or less randomly invade different associated microhabitat-patches (Source-Hypothesis, SH). (3) Litter only connect patchily distributed microhabitats that have more specialized species compositions (Connector-Hypothesis, CH).

We compared these hypotheses by analyzing oribatid mite communities in the general leaf litter and in five discrete, patchy substrates—dead wood, lichens, mosses, sod, and tree bark—replicated in three German forests. We used the specialization indices $d'$ at species/microhabitat level and $H_2'$ at network level, respectively, to quantify the microhabitat partitioning among the mite species (Blüthgen et al. 2006) and to compare this pattern against a null model of random distribution. We expected that the five patchy microhabitats, which are generally either ephemeral or subjected to rapidly changing environmental conditions, would have more exclusive mite communities (higher $d'$) than the relatively stable litter. For the Source-Hypothesis, we expected interaction networks to show large litter plots in a central position with a $d'$-value close to zero and a high number of connections (Fig. 1a); the Connector-Hypothesis would be supported by small central litter plots, but with a high number of connections and a $d'$-value close to zero (Fig. 1b); and the Habitat-Hypothesis would be supported if the interaction network shows all microhabitats to be of similar size and randomly distributed, with $d'$ being $>0$ (Fig. 1c).

**Materials and Methods**

**Sample locations**

In November 2014, samples of different microhabitats were taken at three different forests in Hesse, Germany: Groß-Gerau (GG, N49°65.978′/E8°29.741′), Raunheim (RH, N50°00.911′/E8°29.172′), and Rüsselsheim (RU, N49°58.372′/E8°28.479′). Microhabitats included leaf litter, grass sod, the bark of different tree species, dead wood, lichens, and mosses. Forests were characterized by the forest management plan of the forestry Groß-Gerau as follows:

The state forest of Groß-Gerau (GG) (Abt 63 B2), located about 15 km northwest of Darmstadt, has a total area of 1.8 ha lying 89–90 m above sea level; the climate is moderate subcontinental and wet, and the environment is eutrophic. Parent rock is high flood loam with carbon, covered with sandy loam and loamy sand. The stand age of oak (*Quercus robur*) and ash trees (*Fraxinus excelsior*) is about 31 yr, the stand age of cherry (*Prunus sp.*) and linden trees (*Tilia sp.*) is about 30 yr.

The urban forest of Raunheim (RH) (Abt 39A 1), located about 30 km northeast of Darmstadt, has a total area of 12.9 ha lying 95–96 m above sea level; the climate is moderate subcontinental, and the environment is mesotrophic. Parent rock is pumice stone covered with sand and loamy sand. The forest is dominated by approximately
Fig. 1. (a) Litter as Source-Hypothesis: if litter is the main microhabitat for oribatid mite species and functions as the source of fauna for surrounding and attached microhabitats (dead wood, lichens, mosses, tree bark), interaction networks should show large litter plots in a central position with a $d'$-value close to zero and high numbers of connections. (b) Litter as Connector-Hypothesis: if litter functions as a connector corridor between other microhabitats (dead wood, lichens, mosses, tree bark), litter plots are small and in a central position of an interaction network, but have a high number of connections and a $d'$-value close to zero. (c) Litter as Habitat-Hypothesis: if litter is just another microhabitat for oribatid mites, equally favored as dead wood, lichens, mosses, and tree bark, all microhabitat plots in an interaction network are of similar size and randomly distributed with $d'$ being >0. Width of connecting line indicates species abundances.
122-yr-old beech (Fagus sylvatica) and 185-yr-old pine (Pinus sylvestris).

The state forest of Rüsselsheim (RU) (Abt 124.1), located about 25 km northeast of Darmstadt, has a total area of 8.1 ha lying 90 m above sea level; the climate is moderate subcontinental and fresh, and the environment is mesotrophic. The substrate is moderately sloped and soil is completely sandy. The stand age of pine trees is about 55 yr and the age of neophytic black cherry (Prunus padus) varies between 5 and 20 yr.

**Sampling procedure**

Samples of the bark of oak (five replicates for GG, two replicates for RH and RU), beech (five replicates for GG and RH), birch (Betula pendula, five replicates for GG and RU), and pine (five replicates for RH and RU) were obtained by brushing 25 × 25 cm of the bark surface. The collected particulate material (approximately 85 g dry weight) was transferred directly into 75% ethanol in the field. Samples of other microhabitats were taken from the respective substrate and collected in plastic bags. Those of sod, dead wood, and litter had a surface area of 25 × 25 cm, while those of lichens and of mosses (growing on soil or dead wood) were 10 × 10 cm (five replicates each, but only four for the sod at GG). Microarthropods were extracted from these samples for 24 h using a modified Kempson heat extractor (Kempson et al. 1963) and stored in 75% ethanol. Samples (except tree bark) were weighed before and after extraction to determine their water content. Sampled lichens included Cladonia coniocraea and Cladonia fimbriata, mosses included Mnium undulatum, Polytrichum cf formosum, Amblystegium varium, Brachythecium sp., Dicranella sp., and Eurhynchium sp.

Adult oribatid mites (juveniles were not included in this study) were determined to species-, genus-, or family-level under a stereomicroscope using the key of Weigmann (2006). Taxonomic classification was adapted from Weigmann (2006), Norton and Behan-Pelletier (2009), Schatz et al. (2011), and Subías (2014).

**Statistical analysis**

Numbers of individuals were standardized relative to the sample dry weight (Ind/kgDW) and \( \log(x + 1) \) transformed to obtain homoscedasticity. Differences in species richness, density, and diversity were analyzed by two-way analysis of variance (ANOVA) with location (GG, RH, RU) and microhabitat (tree bark, sod, dead wood, lichens, litter, mosses) as fixed factors using PAST 3.05 (Hammer et al. 2001). Samples from the bark of different tree species were pooled prior to analyses since oribatid mite densities were extremely low and specialization of oribatid mites to tree species was also low (\( H_2^2 = 0.366; \) Appendix S1); samples of moss species were also pooled, since networks were similar among moss species, showing low specialization (\( H_2^2 = 0.288; \) Appendix S1). Species richness (total number of species) and Shannon indices for species diversity were calculated using PAST 3.05; Shannon indices \( (x) \) were transferred to true diversities by \( \exp(x) \) following Jost (2006), which reduces the sensitivity to common and rare species.

Afterwards, samples of the various microhabitats were pooled over all three forests (GG, RH, RU), since there were no significant differences among locations. We used separately calculated location values (GG, RH, RU) for calculating means of individuals per kilogram dry weight, species richness, and species diversity, respectively. Microhabitat values (species richness, species density, and species diversity) were analyzed by univariate ANOVA, Welch F-, Kruskal–Wallis, Tukey-, or Mann–Whitney U tests, depending on the structure of data, in PAST 3.05; all combined analyses comprise six microhabitats (tree bark, sod, dead wood, lichens, litter, mosses) with 28, 13, 15, 15, 15, and 30 replicates, respectively.

**Microhabitat specificity**

Network analysis allowed us to examine the specialization of oribatid mite species to different microhabitats in a manner analogous to consumer–resource interactions. Networks were illustrated and analyzed with the “bipartite” package (Dormann et al. 2008) in R (R Development Core Team 2011). The “interaction strength” in the network of a given mite species on a specific microhabitat (tree bark, sod, dead wood, lichens, litter, mosses) is defined as its standardized density (number of individuals per kilogram dry weight of the substrate). We constructed a network for each
location (GG, RH, RU), and a pooled network for all locations including all microhabitats. Furthermore, networks for oribatid mite subgroups (Enarthronota, Mixonomata, Nothrina, and Brachypylylina) were analyzed. Within network analyses, Phthiracaridae (excluding Steganacarus) and Euphthiracaridae and species of the genera Steganacarus (belonging to Phthiracaridae), Carabodes (Brachypylylina), Chamobates (Brachypylylina), and Tectocepheus (Brachypylylina) were combined for greater lucidity within graphs.

**Source- vs. connector- vs. habitat-hypothesis**

Following Blüthgen et al. (2006), microhabitat specialization was characterized by the diversity of microhabitats used by each taxon, by the specialization indices $d'$ at taxon and microhabitat levels, and by $H_2'$ at network level. The diversity of habitats in which each taxon is detected ($e^{F_2}$, a commonly used generalization measure) that increases with the total number of observations per taxon (a sampling bias), but $d'$ and $H_2'$ are independent of the observation totals. Both $d'$ and $H_2'$ describe the microhabitat selectivity of a species compared with that of the other species. That is, $d'$ of a given mite species increases with the exclusiveness of habitats that it inhabits, compared to all other species in the community; $d'$ of a microhabitat increases with the exclusiveness of its mite community (B-diversity) compared with the other microhabitats; and $H_2'$ expresses the overall degree of microhabitat partitioning at the community level. All three indices are weighted by the species’ abundance, and $H_2'$ is particularly sensitive to the microhabitat complementarity across the most abundant species. The variability in $d'$ and $H_2'$ was shown as the standard deviation across the three locations (GG, RH, RU). Values above 0.5 are considered to be high, below 0.5 to be low.

The distribution of mite species across microhabitats was compared against a null model with fixed marginal totals, as suggested by Patefield (1981) for contingency tables (implemented in R as “r2dtable” and commonly applied in interaction network analyses). Here, we used the raw data (integers), i.e., unstandardized number of individuals per habitat, not transformed to densities. The fixation of marginal totals assures that each habitat receives the same number of mite individuals as actually observed in the site, and that each mite species has the same total number of individuals as collected. The null model algorithm randomly distributes the individual mites, assuming that habitat preferences do not differ among mites. For the observed mite distribution, $H_{2,\text{obs}}'$ was obtained and compared against 10,000 randomizations, each yielding an individual $H_{2,\text{null}}'$. The proportion of randomizations yielding a $H_{2,\text{null}}' \geq H_{2,\text{obs}}'$ defines the significance level, hence $P < 0.001$ if none of the randomized $H_{2,\text{null}}'$ was equal or higher than $H_{2,\text{obs}}'$ (Blüthgen et al. 2006). $H_{2,\text{obs}}'$ was similar but not the same as for the matrices with standardized densities (those transferred to kg dry weight). We performed a null model analysis for each location and for the litter microhabitat in particular.

**RESULTS**

In total, 25,162 adult oribatid mite individuals were collected. Individuals were assigned to 72 species, eight genera (Carabodes, Ceratotelites, Chamobates, Eupelops, Galumna, Microtritia, Scheloribates, Steganacarus) and four families: Brachychthoniidae, Euphthiracaridae (excluding Microtritia), Phthiracaridae (excluding Steganacarus and Phthiracaridae laevigatus), and Suctobelbidae (Table 1). In general, Brachypylylina were most abundant (69 taxa with 23,168 individuals), followed by Mixonomata (six taxa with 894 individuals), Enarthronota (four taxa with 869 individuals), and Nothrina (five taxa with 231 individuals; Table 1). No species from the infraorders Paleosomata or Parhyposomata were found.

Species richness was similar among locations (Groß-Gerau (GG), Raunheim (RH), and Rüsselsheim (RU)) but significantly differed among microhabitats (two-way ANOVA: location: $F_{2,99} = 0.342, P = 0.711$; microhabitat: $F_{5,99} = 27.86, P < 0.001$; interaction: $F_{10,99} = 2.56, P = 0.009$). Species richness was highest in mosses ($n = 76$) and lowest on tree bark ($n = 20$; Table 2, Fig. 2).

Density (total number of Ind/kgDW) also was similar among locations while differing significantly among microhabitats (two-way ANOVA: location: $F_{2,99} = 0.225, P = 0.799$; microhabitat: $F_{5,99} = 28.44, P < 0.001$; interaction: $F_{10,99} = 1.861, P = 0.06$). Density was highest in mosses and
Table 1. Species list of adult oribatid mites including percentages of females (%♀), total number of individuals, and d’-values. Species in bold reproduce by sexuality. SD, standard deviation.

| Species                        | %♀  | Total | d’  | SD d’ |
|--------------------------------|-----|-------|-----|-------|
| **Enarthronota**               |     |       |     |       |
| Brachychthoniidae (unidentified)|     |       |     |       |
| Eniochthonius minutissimus     | 0.157| 674   | 0.156| 0.157 |
| Hypochthonius rufulus          | 0.138| 100   | 0.138| 0.216 |
| Mesoplophora cf pulchra       | 0.007| 100   | 0.007| 0.012 |
| Mixonomata                     |     |       |     |       |
| Phthiracaridae (unidentified)  |     |       |     |       |
| Phthiracarus laevigatus        | 0.206| 719   | 0.206| 0.077 |
| Steganacarus sp. Ewing, 1917   | 0.077| 15    | 0.077| 0.014 |
| Steganacarus carinatus Koch, 1841 | 0.195| 2    | 0.195| 0.212 |
| Eupthiracaridae (unidentified) |     |       |     |       |
| Microtritida sp. Märkel, 1964  |     |       |     |       |
| Nothrina                       |     |       |     |       |
| Malacothenus gracilis Purvis, 1982 |     | 3    | 0.138| 0.240 |
| Notrus silvestris (Koch 1839)  |     | 107   | 0.138| 0.240 |
| Camisia spinifer Koch, 1836    |     | 32    | 0.138| 0.240 |
| Platythiracarus pelifer (Koch 1839) | 0.129| 107  | 0.129| 0.195 |
| Nantherrmannia nana (Nicolet, 1855) | 0.037| 13   | 0.037| 0.037 |
| Brachypylina                    |     |       |     |       |
| Hermannia convexa (Koch, 1840) |     |       |     |       |
| Damaeus gracilipes (Kulczynski 1902) | 0.161| 80.00| 0.161| 0.65  |
| Metabelba pulvorostra Strenzke, 1953 | 0.132| 82.79| 0.132| 0.421 |
| Porolodes farinosus (Koch, 1840)|     | 61    | 0.218| 0.308 |
| Cepheus cepheiformes (Nicolet 1855) | 0.383| 74.63| 0.383| 0.383 |
| Cepheus dentatus (Michael 1888) | 0.138| 66.67| 0.138| 0.240 |
| Zetorches falzoni Coggi, 1898   | 0.065| 80.00| 0.065| 0.065 |
| Cultroribula bicultrata (Berlese 1905) | 0.077| 92.56| 0.077| 0.065 |
| Gustavia microcephala (Nicolet, 1855) | 0.138| 72.41| 0.138| 0.240 |
| Adoristes ovatus (Koch 1839)    | 0.153| 72.24| 0.153| 0.212 |
| Xenillus tegrocranus (Hermann, 1804) | 0.421| 82.79| 0.421| 0.132 |
| Comarnus oblongus (Koch 1935)   | 0.000| 59.81| 0.000| 0.000 |
| Autognota longilamellata (Michael 1885) | 0.383| 74.63| 0.383| 0.383 |
| Conchognotia dalearctica Forsslund, 1947 | 0.161| 66.67| 0.161| 0.161 |
| Banksinoma lanceolata (Michael 1885) | 0.240| 54.55| 0.240| 0.240 |
| Multioppia laniseta (Moritz 1966) | 0.413| 77.00| 0.413| 0.413 |
| Micropia minus (Paoli 1908)     | 0.248| 96.83| 0.248| 0.248 |
| Mediothrix subsectinata (Oudemans 1900) | 0.162| 65.44| 0.162| 0.162 |
| Berninilla sigma (Strenzke, 1951) | 0.256| 61.81| 0.256| 0.256 |
| Dissorhina ornata (Oudemans 1900) | 0.179| 69.76| 0.179| 0.179 |
| Oppiella falcata (Paoli, 1908)   | 0.147| 60.47| 0.147| 0.147 |
| Oppiella minutissima (Sellnick, 1950) | 0.147| 99.1| 0.147| 0.147 |
| Oppiella nova (Oudemans 1902)    | 0.286†| 99.1| 0.286†| 0.286† |
| Quadroppia quadrinarina (Michael 1885) | 0.128| 97.9| 0.128| 0.128 |
| Suctobelbidae (unidentified)    |       | 2477  | 0.137| 0.137 |
| Carabodes sp. (Koch, 1835)      | 0.076| 5714  | 0.076| 0.076 |
| Carabodes areolatus (Berlese 1916) | 4     | 84.62| 4     | 4     |
| Carabodes coriaceus (Koch 1835) | 0.138| 84.62| 0.138| 0.216 |
| Carabodes femoralis (Nicolet 1835) | 0.127| 59.09| 0.127| 0.127 |
| Carabodes labyrintheticus (Michael 1879) | 0.127| 59.09| 0.127| 0.127 |
| Carabodes marginitus (Michael, 1884) | 0.127| 59.09| 0.127| 0.127 |
| Carabodes ornatus (Storkan 1925) | 0.127| 75.00| 0.127| 0.127 |
| Carabodes reticulatus (Berlese 1913) | 0.076| 75.41| 0.076| 0.076 |
| Achipteria coleoptrata (Linné 1758) | 0.076| 75.41| 0.076| 0.076 |
lichens (20.805 ± 11.237 and 33.501 ± 22.263 Ind/kgDW, respectively), and lowest on tree bark (79 ± 37 Ind/kgDW) and in sod (138 ± 82 Ind/kgDW; Table 2, Fig. 3).

Species diversity varied among locations and microhabitats (two-way ANOVA: location: \( F_{2,99} = 0.419, P = 0.018 \); habitat: \( F_{5,99} = 16.66, P < 0.0001 \); interaction: \( F_{10,99} = 1.934, P = 0.049 \)). Mean species diversity in microhabitats ranged from 5.57 ± 2.4 on tree bark and 5.59 ± 4.31 in lichens to 15.32 ± 6.45 in mosses and 19.51 ± 4.93 in dead wood (ANOVA: \( F_{5,12} = 5.089, P = 0.01 \); Table 2, Fig. 4).

**Microhabitat specificity**

Enarthronota (Brachychthoniidae, *Eniochthonius minutissimus*, *Hypochthonius rufulus*, and *Mesoplophora pulchra*) were associated with dead wood, litter, lichens, and mosses with a low degree of species-specific microhabitat partitioning (\( H^2 = 0.207 ± 0.190 \)); they were absent from sod and tree bark (Fig. 5a). Highest densities

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Table 1. Continued

| Species | %♀ | Total | d' | SD d' |
|---------|----|-------|----|-------|
| *Achipteria nitens* (Nicolet 1855) | 74.01 | 333 | 0.236 | 0.088 |
| *Ophidiotrichus tectus* (Michael 1884) | 60.00 | 5 | 0.269 |
| *Oribatella calcarata* (Koch 1835) | 45.45 | 16 | 0.310 | 0.319 |
| *Oribatella quadricornuta* (Michael, 1880) | 55.67 | 107 | 0.000 | 0.000 |
| *Ceratozetes* sp. Berlese, 1908 | 80.00 | 18 | 0.151 | 0.094 |
| *Trichoribates norus* (Sellnick, 1928) | 61.29 | 117 | 0.190 | 0.214 |
| *Chamobates* sp. Hull, 1926 | 45.45 | 21 | 0.048 | 0.042† |
| *Chamobates cuspidatus* (Michael 1884) | 47.01 | 558 | |
| *Minunthozetes seminifus* (Koch, 1841) | 62.75 | 55 | 0.333 | 0.466 |
| *Punctoribates punctum* (Koch, 1839) | 60.8 | 134 | 0.122 | 0.110 |
| *Oribatula tibialis* (Nicolet 1855) | 69.83 | 188 | 0.054 | 0.092 |
| *Zygoribatula exilis* (Nicolet 1855) | 57.41 | 1459 | 0.099 | 0.072 |
| *Phauoplia pilosa* (Koch, 1841) | 76.92 | 126 | 0.224 | 0.201 |
| *Dometorina plantivaga* (Berlese, 1895) | 68.03 | 139 | 0.207 | 0.122 |
| *Liebstadia similis* (Michael, 1888) | 51.16 | 45 | 0.103 | 0.169† |
| *Scheloribates ascenden* (Weigmann & Wunderle 1990) | 55.56 | 20 | |
| *Scheloribates latipes* (Koch, 1844) | 53.09 | 198 | |
| *Scheloribates pallidulus* (Koch 1840) | 51.53 | 213 | |
| *Galumna* sp. Hyden, 1826 | 61.22 | 11 | 0.120 | 0.207† |
| *Galumna lanceata* (Oudemans 1900) | 61.29 | 327 | |
| *Galumna obvia* (Berlese, 1914) | 60.12 | 204 | 0.189 | 0.315 |
| *Pergalumna nervosa* (Berlese 1906) | 70.59 | 96 | 0.465 | 0.193 |
| *Cymbaeremaeus cymba* (Nicolet 1855) | 51.16 | 45 | 0.253 |
| *Micreremus brevipes* (Michael 1888) | 76.92 | 126 | 0.224 | 0.201 |
| *Scutovertex minutus* (Koch, 1836) | 61.29 | 95 | |
| *Eupelops sp. Ewing, 1917* | 60.12 | 327 | |
| *Eupelops cf occultus* (Koch, 1835) | 90.00 | 10 | 0.071 | 0.123† |
| *Eupelops plicatus* (Koch 1836) | 73.58 | 136 | |
| *Eupelops cf torulosus* (Koch, 1839) | 4 | |
| *Peloptus phaenotus* (Koch, 1844) | 71.88 | 85 | 0.096 | 0.084 |
| *Tectocepheus minor* (Berlese, 1903) | 99.23 | 543 | |
| *Tectocepheus sarekensis* (Tragardh, 1910) | 99.54 | 3128 | |
| *Tectocepheus velatus* (Michael 1880) | 25,162 | |

Total number of species: 72
Total number of genera: 8
Total number of families: 4
† Values refer to combined genus.
were found in lichens and mosses, especially due to Brachychthoniidae and *E. minutissimus*. *Mesoplophora pulchra*, an uncommon species of which only two individuals were found—for the first time in Hesse—was associated only with dead wood.

Euphthiracaridae and Phthiracaridae (Mixonomata) inhabited all microhabitats except tree bark, among which they were not notably partitioned (*H_*^2 = 0.171 ± 0.085); they were the most abundant generalists in litter and mosses and were only rarely found in sod. Of *Steganacarus* (Phthiracaridae) and *Microtritia* (Euphthiracaridae), only a few individuals were found in dead wood and mosses (Fig. 5b).

*Nothrina* (*Camisia spinifer, Malaconothrus gracilis, Nanhemnania nana, Nothrus silvestris*, and *Platynothrus peltifer*) were present in all microhabitats except tree bark, but showed a strong partitioning across species (*H_*^2 = 0.710 ± 0.004). *Nothrus silvestris* was the most abundant, comprising half of the nothrine individuals on lichens and a great part in litter. The litter habitat was dominated by *P. peltifer*, which also occurred

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**Table 2.** Species richness, numbers of individuals per kilogram dry weight (Ind/kgDW), and Shannon diversity for the microhabitats tree bark, sod, dead wood, litter, lichens, and mosses. SD, standard deviation.

| Microhabitat   | Tree bark | Sod | Dead wood | Litter | Lichen | Moss |
|---------------|-----------|-----|-----------|--------|--------|------|
| Species richness | Total     | 20  | 61        | 66     | 50     | 54   | 76   |
| Ind/kgDW      | Total     | 78.49 | 137.75 | 975.84 | 1929.16 | 33,501.57 | 20,805.14 |
|               | SD        | 36.86 | 82.37   | 598.40 | 1976.18 | 22,263.76 | 11,237.66 |
| Shannon diversity | Total     | 5.57 | 13.31    | 19.51  | 13.22  | 5.59  | 15.32 |
|               | SD        | 2.40  | 1.89     | 4.93   | 3.80   | 4.31  | 6.45  |

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![Graph showing species richness, numbers of individuals per kilogram dry weight (Ind/kgDW), and Shannon diversity for the microhabitats tree bark, sod, dead wood, litter, lichens, and mosses. SD, standard deviation.](https://www.esajournals.org/doi/10.1890/16-0133.1)
in mosses. *Camisia spinifer* was highly abundant on lichens, but only rarely present in dead wood, litter, mosses, and sod. Sod was mainly inhabited by *M. gracilis* and *P. peltifer* (Fig. 5c).

The interaction network of Brachypylina comprised of 52 taxa that were present in all microhabitats, with an intermediate level of species-specific preferences ($H^2_{uni} = 0.441 \pm 0.207$). Although all 18 species inhabiting tree bark were members of Brachypylina, their density there was low. Highest densities but low values of specialization were found in lichen, especially due to *Carabodes* and *Tectocephus*, and in mosses due to *Tectocephus*, *Suctobelbidae*, and *Z. exilis*. Compared to lichens and mosses, density was low in sod, dead wood, and litter, but with a high connectivity within the network (Fig. 5d).

In general, specialization of oribatid mite species was low; 18 species had a $d'$ value $< 0.1$, 16 showed a $d'$ between 0.1 and 0.2, and 14 taxa had a $d'$ of 0.2–0.3 (Table 1). Higher specialization was found in the genus *Carabodes* ($d' = 0.319 \pm 0.286$), *Oribatella calcarata* ($d' = 0.310 \pm 0.319$), and *Minunthozetes semirufus* ($d' = 0.333 \pm 0.466$); the only species with a $d'$ value greater than 0.4 was *Cymberemaus cymba* ($d' = 0.465 \pm 0.193$, Table 1). Community structure of oribatid mites, as indicated by the percentage of the dominant species, differed among microhabitats (Fig. 6). In sod (*Liebstadia similis* 11.6%), dead wood (*Zygoribatula exilis* 16%), litter (*Phthiracaridae* 24.6%), and mosses (*Z. exilis* 13.3%) this was below 25%, whereas tree bark was strongly dominated by *Cymberemaus cymba* (40.6%) and lichens by the genus *Carabodes* (72%).

**Source- vs. connector- vs. habitat-hypothesis**

In the ecological network of all microhabitats with 66 oribatid mite taxa in total, microhabitat specificity of the entire mite community was pronounced, as revealed by a network specialization level of $H^2_{obs} = 0.457 \pm 0.195$ (Fig. 7). A comparison with null models (assuming a random distribution of mite individuals across the microhabitats) revealed that oribatid mite species were highly significantly partitioned across different microhabitats (null models for each the three regions: all $H^2_{obs} >> H^2_{null}$, $P < 0.001$; App. 3–5).
Tree bark had the most exclusive mite community \( (d' = 0.513 \pm 0.248) \), followed by sod \( (d' = 0.337 \pm 0.291) \) and mosses \( (0.355 \pm 0.370) \), and lowest specificity was found for dead wood habitats \( (d' = 0.174 \pm 0.170; \text{Table 2}) \), followed by litter \( (d' = 0.274 \pm 0.281) \) and lichens \( (d' = 0.275 \pm 0.128) \). While sod and dead wood had low oribatid mite densities, their network was characterized by a high connectivity (51 and 66 taxa, respectively). Densities and diversities in litter were intermediate, while both lichens and mosses were characterized by high density and species diversity (Fig. 7, Table 2).

Overall, analysis of the entire oribatid mite community did not unequivocally confirm any of our initial hypotheses regarding the role of litter in faunal dynamics (SH, CH, HH; Fig. 1). The \( d' \) value of litter was higher than zero and null model analyses revealed a distribution that significantly differs from chance in all three locations (null models for each location: all \( H^2_{\text{obs}} >> H^2_{\text{null}} \), \( P < 0.001; \text{App. 6} \)). However, the oribatid mite densities in litter were low, indicating that the litter microhabitat functions as a connector among insular microhabitats rather than as an oribatid mite source. However, dead wood showed an even smaller \( d' \) value in combination with low densities.

At the subgroup level, members of Enarthronota, Mixonomata, and Nothrina did not use litter as a source or connector, but seemed to equally inhabit all microhabitats, as indicated by similar \( d' \) values, with most being \( d' = 0 \) (Fig. 5a–c). In contrast, the distribution of species of Brachypylina completely matched the Connector-Hypothesis: the litter microhabitat appeared in the center of the ecological network with \( d' \) being close to zero and with low total densities, while most individuals were found in other microhabitats, with increasing \( d' \) values to the edges (Fig. 5d).

**Discussion**

Oribatid mite communities in the three German forests (Groß-Gerau, Raunheim, and Rüsselsheim) differed neither in species richness nor in individual densities and only slightly in species diversity. Therefore, when different microhabitats were combined, the
Fig. 5. Mite—microhabitat network based on numbers of individuals per kilogram dry weight for oribatid mite subgroups (a) Enarthronota ($H^2_2$ value: $0.207 \pm 0.190$), (b) Mixonomata ($H^2_2$ value: $0.171 \pm 0.085$), (c) Nothrina ($H^2_2$ value: $0.710 \pm 0.004$), and (d) Brachypylina ($H^2_2$ value: $0.441 \pm 0.207$). See Table 1 for full species names.
type of forest was of minor importance for oribatid mite densities and only slightly influenced oribatid mite community structure, consistent with previous studies (Rajski 1967, Migge et al. 1998, Maraun and Scheu 2000).

In contrast, densities, species richness, and species diversity differed significantly among microhabitats, indicating a close correlation of microhabitats and the dominance of oribatid mite subgroups.

Fig. 6. Percentages of the most abundant oribatid mite species in sod, tree bark, dead wood, litter, lichens, and mosses. Note different scales!
Fig. 7. Mite—microhabitat network based on numbers of individuals per kilogram dry weight for the microhabitats sod, tree bark, dead wood, litter, lichens, and mosses for 66 oribatid mite taxa. $H^2$ value: $0.457 ± 0.195$. See Table 1 for full species names.
**Microhabitat specificity**

Oribatid mite communities differed strongly among forest microhabitats. Species of Enarthronota and Mixonomata appeared to be abundant generalists in all microhabitats except tree bark and sod, with densities highest in mosses and litter, respectively (Fig. 5a, b). For enarthronote species, especially *Hypochthonius rufulus*, litter was the main habitat.

Older studies on Mixonomata in a beech forest in the Northern Black Forest (Berg 1991) showed a complex distribution of different species. While *Phthiracarus piger* (*Phthiracaridae*) appeared as typical generalist, *P. crinitus* (*Phthiracaridae*) spent its whole life on rotten wood and *Rhysotritia duplicata* (*Euphthiracaridae*) inhabited both litter and rotten wood. Analysis is complicated by the fact that juveniles of Phthiracaridae and Euphthiracaridae (not investigated in our study) burrowed in woody substrates until they disperse as adults (Forsslund 1938). For such species, it is difficult to determine if an adult mite was collected while it searched for a substrate suitable for oviposition, or if it had already found it. For these and other groups that are endophages within particular substrates, further studies that include developmental stages should increase the degree of specialization detectable in ecological network studies.

Of Nothrina, only a few species were represented, which agrees with other studies in temperate forests (e.g., Wunderle 1992, Domes et al. 2007, Wehner et al. 2014). Tree-dwelling species (e.g., species of *Camisia*; Olszanowski et al. 2002) were not found, and densities on dead wood were low compared to those in mosses, litter, and lichens. The most dominant species were *Platy nothrus peltifer* in mosses and litter and *Nothrus silvestris* in lichens.

Except for litter and mosses, microhabitats were dominated by species of Brachypylina (Fig. 6); this was particularly true for tree bark, though highest densities were found in mosses and lichens. However, this taxon comprises a vast diversity of groups that differ considerably in their basic biology and ecology (Travé 1963, Norton 1990, Weigmann 2006).

In general, specialization of oribatid mite species was low with $d'$ values often below 0.3. Highest specialization was seen in the brachypylene species *Cymbereinaeus cymba*, which was mainly found on tree bark and in litter. The genus *Carabodes* (collectively) and the species *Minunthozetes semirufus* and *Oribatella calcarata* had $d'$ values of ~0.3. The highest numbers of *Carabodes* were observed in lichens, in which the juveniles of certain species burrowed (Bellido 1979), but they were found in all microhabitats and appear to use them as connecting paths. *Minunthozetes semirufus* and *O. calcarata* were most abundant in moss samples and the former was absent (tree bark, litter, lichens) or extremely rare (sod, dead wood) in the other microhabitats. Most oribatid mite species were present in all microhabitats (usually except tree bark) but with differing densities. For example, *Zygoribatula exilis* was among the dominant species in all microhabitats except sod and thus showed a low specificity ($d' = 0.099$).

The tree bark community showed the highest specialization, and the species seem to possess several adaptations for the arboreal life such as a capitate sensillus or cuticular structures resistant to desiccation (Maraun et al. 2009). All species found on tree bark belonged to Brachypylina (*Cymbereinaeus cymba, Dometorina plantivaga, Zygoribatula exilis, Eupelops sp.*, *Oribatula quadricularia, Poroliodes farinosus, and Oribatula tibialis*). This is consistent with the review of Behan-Pelletier and Walter (2000), who listed species in at least 110 genera (51 families) known to live in arboreal microhabitats, 91% being members of Brachypylina. However, oribatid mite species richness on tree bark seems generally low, ranging from 35 species on *Pinus sylvestris* in Poland (Seniczak et al. 1996) and 36 species on *Picea sitchensis* in British Columbia (Behan-Pelletier and Winchester 1998), to 64 species on *Fagus sylvatica* in Germany (Wunderle 1992).

Specialization was also high in mosses and grass sod, and in mosses oribatid mites were numerous and diverse (Fig. 7). The association of oribatid mites and mosses has long been known (they are commonly termed “moss mites”) and seems evolutionary old, with many taxa adapted to use them for food, shelter, or environmental constant habitat (McNamara and Seldon 1993, Glime 2013). Few oribatid mite species feed directly on moss material; most species consume fungi, algae, and bacteria present within the moss (Wolf and Rockett 1984, Smrz 2010). A further advantage attraction may be that mosses provide suitable habitat at times when other substrates are inhospitable (Glime 2013). In special cases,
the association of moss and oribatid mites even can be almost symbiotic; e.g., Scutovertex minutus can serve as sperm vectors, and mosses only 2–4 cm apart fail to reproduce without their arthropod fauna (Cronberg et al. 2006, Milius 2006).

In grass sod, Enarthronota were absent and abundances of Mixonomata (Phthiracaridae and Euphthiracaridae) and Nothrina (Canisia spinifer, Malacocephalus gracilis, and Platynothrus peltifer) were low. Species with highest densities belonged to Brachypylina (e.g., Liebstadia similis, O. nova, Trychobrates novus, Eupelops plicatus, M. subpectinata, A. coleoptrata, P. punctum, Peloptulus phaenotus, and T. velatus).

Lichens showed highest species richness and individual densities but species diversity was relatively low, indicating that the oribatid mite community was dominated by few but abundant taxa such as Carabodes, Tectocepheus, and Suctobelbidae (Fig. 7). This agrees with the review of Seyd and Seaward (1984) who found that lichen-associated oribatid mite taxa included 27% of the families and 12% of the genera known at that time, including Carabodes, Domerotina, Oribatula, and Phauloppia. In our study, members of Carabodes strongly dominated the lichen habitat (72% of individuals); the next most numerous species (T. velatus, Suctobelbidae, T. sarekensis, Z. exilis) each contributed less than 10%. Probably, many oribatid mite species use lichens as food resources since it seems easy for oribatid mites to feed on fungi in lichens once they have penetrated the surface (Glime 2013).

On the other hand, low species densities but high species richness and diversity characterized dead wood microhabitats, which was used by species of all oribatid mite groups encountered in the study, with the brachypyline species Z. exilis, Chamobates cuspidatus, T. velatus, Multioppia laniseta, and Galumna lanceata being most numerous. In agreement with this low level of specialization, past studies on dead wood communities found only a few specialist oribatid mites, suggesting that this is a transitory rather than a specific habitat (Bluhm et al. 2015). However, dead wood material may possess specific microconditions and since dead wood material is often replete with decomposer fungi and bacteria, and externally covered with mosses and lichens, oribatid mites may use it as a feeding location, with the community being mixed with moss and lichen specialists. On the other hand, dead wood is a typical substrate for specialized, burrowing juveniles of certain families, including especially Phthiracaridae, Euphthiracaridae, Carabodidae, and Liacaridae; since only adults were included in this study, results could differ when juvenile life stages are included.

Source- vs. connector- vs. habitat-hypothesis

The mechanisms that mediate the community assembly and coexistence of oribatid mite species in different forest microhabitats need further investigation. Recent studies on soil microarthropods provide evidence that environmental filtering plays a major role in structuring oribatid mite communities (Maaß et al. 2015), while resource-based niche partitioning and biotic interactions are of minor importance (Gao et al. 2014, Maaß et al. 2015). In contrast to our expectations based on current literature, litter microhabitats did not show highest species richness and densities in our study. Species richness was similar to that of sod and lichens and densities of individuals were only intermediate. However, species diversity was high, indicating that the abundances of the 50 species found in litter were similar. This is also supported by a low specialization value (mean $d' = 0.274$). As in dead wood, species of all oribatid mite groups were found in litter, with Brachypylina being most abundant. For species of Enarthronota, especially Hypochthonius rufulus, and the nothrine Platynothrus peltifer, densities were highest in litter.

These results—low specialization, low density, and high diversity—suggest that litter functions as an oribatid mite “pool” and as a transitional substrate for species dispersing to specific microhabitats. Regarding our initial hypotheses (Fig. 1), we conclude that litter does not fit the Source-Hypothesis since densities are rather low. In contrast, litter may simply function as a specific microhabitat for some groups of oribatid mites (Habitat-Hypothesis), including a few litter specialists (e.g., H. rufulus) and many generalists (e.g., C. cuspidatus) which is consistent with a level of community exclusiveness ($d'$) that significantly differs from zero (null model). For species that are not abundant in litter but show high densities in other habitats (e.g., Z. exilis, Suctobelbidae, Carabodes, and Tectocepheus), the Connector-Hypothesis seems most suitable.
Conclusions

Attempts to unravel the “enigma of soil animal diversity” usually focus on biotic and abiotic characteristics of litter (and soil). We conclude that studying litter alone is not sufficient to understand the composition of oribatid mite communities. We tested if litter is, as it is commonly conceived, a source for oribatid mite communities in other microhabitats (SH), or a transitional habitat connecting microhabitats with a more specialized community (CH), or simply one microhabitat among others, characterized by its own community (HH). The answer is that all three roles might contribute to the distribution of mites, and their relative importance varies across the taxa/species in question. However, in contrast to common opinion, the Source-Hypothesis is supported for very few species, while the Connector- and Habitat-Hypotheses can explain the distribution of most oribatid mite species.

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