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Ecological Spotlights on Mites (Acari) in Norwegian Conifer Forests: A Review

Sigmund Hågvar

Abstract

Long-term studies on mites in Norwegian coniferous forests are summarized. In podzol soil with raw humus, mite densities could pass 1 million per m², with 48 species of Oribatida and 12 species of Mesostigmata. Field and laboratory experiments with liming and artificial acid rain showed that soil pH affected the structure of the mite community. Certain species of mites and springtails typical for acid soils did, however, show preference for a higher pH in monoculture. We hypothesized that competition could be a strong regulating factor in microarthropod communities. Several oribatid species were flexible regarding soil type, vegetation, substrate, and decomposition stage. The genus *Carabodes* showed examples on specialists: two species were grazers on *Cladonia* lichens in dry pine forests, while three were decomposers in dead polypore fungi. Another three oribatid species from different genera were unique in excavating spruce needles, producing slowly decomposing excrements, and probably contributing to stable, carbon-storing humus. In microcosms, predatory Gamasina mites were seen to regulate microarthropod numbers. Mites were able to adjust both their vertical and horizontal distribution in soil according to environmental change. A local and temporary burst of fungal activity could rapidly attract opportunistic fungal feeders. Several mites were active under snow, often feeding. Some even penetrated into the snow layer.

Keywords: Acari, coniferous forest, ecology, mites, Norway, Oribatida, review, soil pH

1. Introduction

Nowhere else, in nature, organisms are so densely packed as in soil. Combined with a huge number of species, “biodiversity in the dark” has fascinated biologists for long. In concert, soil organisms play a key role in terrestrial ecosystems, being of fundamental importance for plant growth, sustainable crop production, and biogeochemical cycling of nutrients. At the same time, soil biodiversity is vulnerable to human disturbance of different kinds. There is a critical need for understanding soil processes, how soil organisms respond to global change, and to take measures for long-term protection of soil biodiversity [1].

Mites (Acari) represent one of the species rich and abundant soil animal groups. Oribatid mites alone cover five feeding guilds, including the ability to digest chitin [2], and they represent four trophic levels in the decomposition process [3].

Another mite group, Mesostigmata, contains a multitude of predator species which control other microarthropod populations, both in the soil and in vegetation [4, 5]. Forest habitats, especially old forests with a well-developed litter layer, tend to have a high mite density, often with a species-rich fauna of oribatids [6–8].

Norwegian coniferous forests represent the western outpost of the Eurasian taiga. This giant forest belt, which is dominated by Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus silvestris* L.), typically contains a well-developed raw humus layer which represents a considerable global carbon storage. The slowly decomposing needles, cones, and other litter items in the forest floor create a fungus rich and sometimes deep, humus world, in which several mite groups thrive, including many oribatid species.

The present review is a synthesis of mite studies in coniferous forest soils of Southern Norway, published over a 40-year period [9–26]. In the 1970s, extensive studies on soil microarthropods were initiated as part of a large project, “Effects of acid precipitation on forest and soil,” and certain subjects were followed up long after the project was ended. In addition to summing up field and laboratory experiments with liming and artificial acid rain, spotlights will be given on the following topics: density and species numbers of mites, their horizontal and vertical distribution, effects of different pH, vegetation types, soils and substrates, succession in the mite fauna during decomposition, whether mites can influence the humification process, how species within one genus may differ in habitat use, an experiment on the predatory effect of Gamasina mites, and mite activity beneath and within snow.

2. Material and methods

2.1 Study areas

2.1.1 Main study area: Nordmoen

This was a spruce forest with *Vaccinium myrtillus* L. vegetation, situated on a flat plain of glaciofluvial sandy deposits, about 45 km N of Oslo. On clearcut areas, *Deschampsia flexuosa* (L.) dominated. The soil was a stone-free iron podzol with a 3 cm thick organic layer and a correspondingly bleached layer below. Experiments with artificial acidification and liming and decomposition experiments with litter bags were performed here, partly in a young spruce stand, and partly on a clearcut area [14].

2.1.2 Two study areas covering the range of coniferous forest types: Ås (A) and Skrukkelia (B)

Two study areas were chosen for soil sampling in natural forest, each area with a gradient in vegetation types from the poorest pine forest to the richest spruce forest [15, 27]. Area A near Ås, about 30 km south of Oslo, had a cover of marine sediments. In area B in Skrukkelia, NW of lake Hurdalssjøen and about 60 km north of Oslo, the soil was mainly morainic deposits. In both study areas, spruce forest with *Vaccinium myrtillus* dominated. Listed after increasing soil fertility based on plant associations, the vegetation types were short named as follows:

1. *Cladonia* sp.: pine forest on iron podzol soil, with a dense cover of *Cladonia* lichens. Due to a thin soil layer, conditions were dry, and trees grew slowly (**Figure 1**).

2. *Calluna vulgaris*: pine forest with less *Cladonia*, and a field layer dominated by *Calluna vulgaris* (L.) Hull. The soil was shallow peat in area A and iron podzol in area B.
3. *Vaccinium sp.*: pine forest on iron podzol soil, with a dense cover of *Vaccinium myrtillus* or *Vaccinium vitis-idaea* L., but also containing some *Cladonia* lichens.
4. *Vaccinium myrtillus*: spruce forest with *Vaccinium myrtillus*. Brown earth-like soil in area A and iron podzol in area B.
5. *Small ferns*: spruce forest with small ferns, *Dryopteris phegopteris* (L.) C. Chr. and *Dryopteris linnaeana* C. Chr. Brown earth in area A and iron podzol in area B.
6. *Small herbs*: spruce forest on brown earth, with small herbs like *Carex digitata* L., *Melampyrum silvaticum* L., and *Fragaria vesca* L.
7. *Tall herbs*: spruce forest on brown earth, with tall herbs like *Filipendula ulmaria* (L.) Maxim., *Athyrium filix-femina* (L.) Roth., and *Aconitum septentrionale* Koelle.

2.1.3 Study area for mites in decomposing sporocarps

Dead sporocarps of different wood-living polypore fungi were sampled in an old spruce forest in the Østmarka area, about 20 km east of Oslo [24, 25].

2.1.4 Study areas for mite activity under and within snow

Activity under snow was studied in an old spruce forest with *Vaccinium myrtillus* vegetation near Veggli in Numedal valley, about 150 km NW of Oslo. Here, at 850 m above the sea level, a snow cover of 1–2 m is common [23]. In the main study area, Nordmoen, mite activity was studied both under and within snow [11].

2.2 Methods for field studies

2.2.1 Soil sampling

Each vegetation type in areas A and B was sampled twice, in autumn 1977 and in spring 1978. Using a soil corer of 10 cm², 20 soil cores were taken both



Figure 1.
The poorest coniferous forest type: slow-growing pines on a thin soil layer dominated by *Cladonia* lichens. Certain drought-tolerant, lichen-feeding mites were abundant here. Photo: S. Hågvar.

during spring and autumn in each vegetation type. The cores were divided into 0–3 and 3–6 cm depth. In the main study area at Nordmoen, the same sampling method was used. Here, a clearcut area with 0.5 m high *Picea abies* seedlings was chosen for intense studies. Eight random replicates were established, each 4 × 4 m. Density of mites per replicate was based on 10 soil cores, each 5.3 cm² and 6 cm deep.

2.2.2 Artificial acidification and liming

Lime was applied as crushed CaCO₃ (3000 kg CaO ha⁻¹), and 50 mm of artificial acid rain was applied monthly by adding sulfuric acid to ground water (**Figure 2**). Treatments were no watering, pH 6 (control), pH 4, pH 3, pH 2.5, and pH 2. The natural pH in the organic layer (upper 3 cm) was 3.9. Liming increased pH about 2 units, and the strongest acid reduced pH about 0.5 units. Only application of acid rain with pH 3 or stronger lowered the pH in the organic layer [14].

2.2.3 Litter bag studies on succession

The clearcut area in the main study area was used to study the mite succession during decomposition of spruce needles [19] and birch leaves [12, 13]. Cylindrical litter bags, 3 cm high and with a diameter of 3.4 cm, were filled with 4.2 g (dry weight) of naturally shed spruce needles. The litter bags were then inserted into holes made in the raw humus layer, which had a corresponding depth. This is not a natural position of the litter, but it allowed to study the preference among mites for different decomposition phases. While the litter bags stood in this fixed position, in contact with various depth levels of the organic horizon, all species had a continuous access to the needles. With a mesh size of 0.6 mm, migration to and from the bags was easy for all microarthropods.

Succession in decomposing birch leaves was studied in a similar way in the same site. Cylindrical litter bags with a mesh size of 1 mm, 3 cm high and with a diameter of 6.5 cm, were each filled with 6.85 g (dry weight) of naturally shed birch leaves. These bags also received artificial rain of pH 6, 4, 3, and 2.

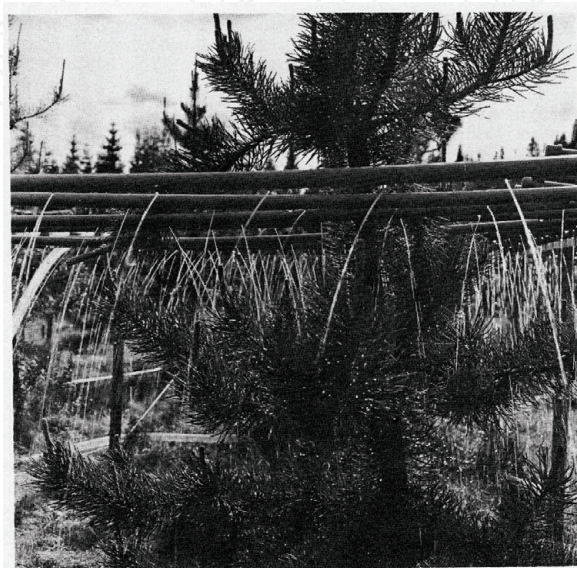


Figure 2.
Artificial acid rain is applied on a 4 × 4 m experimental plot with small pine trees.

2.2.4 Mites living inside decomposing spruce needles

In the main study area at Nordmoen, naturally shed spruce needles were sampled on snow and dried. Later, needles were stuck into fine-meshed nylon strips, which were placed on the ground of a 10–20 m high spruce stand. Gradually, needles were covered by new litter in a natural way. Strips with needles were recovered after 4, 12, 16, 24, 35, 38, 40, and 52 months [22].

2.2.5 Sporocarp sampling and extraction

Dead sporocarps were brought to the laboratory, carefully fragmented, and mites were extracted in funnels, using heat from a light bulb [24, 25].

2.2.6 Sampling mites active under snow

Specially designed pitfall traps were used [23]. The mechanism allowed sampling without disturbing the subnivean air space near the traps.

2.3 Methods for laboratory studies

2.3.1 A “preference” experiment

This was a greenhouse experiment, where forest soil was kept in large plastic boxes [10]. Microarthropods (and microflora as well) had the opportunity to colonize sterilized soil (raw humus, poor mull, and rich mull) which had been adjusted to three different pH levels. Cylindrical litter bags with a mesh size of 1 mm, 3 cm high and with a diameter of 6.5 cm, were used. The design can be characterized as a preference experiment, where also the ability to reproduce during the four-month period influenced the establishment of each species.

2.3.2 Microcosm studies

Small microcosms were used, consisting of a cylindrical, open litter bag which was inserted into a lidded plastic container. The litter bag was 3 cm high, 3.4 cm in diameter, and made from a nylon cloth with 0.6 mm mesh size. Holes drilled in the plastic container were covered with nylon cloth of 5- μ m mesh size. Before adding microarthropods to sterilized soil, microflora was introduced partly by soil water sieved through 5- μ m pores and partly by allowing soil fungi to grow in through corresponding pores for 1–2 months. Then animals were added, either from monocultures or from ordinary soil samples [17]. Raw humus adjusted to different pH levels was used in the microcosms. About 25 microcosms were extracted after 3, 6, and 12 months, respectively. This setup allowed for studying the effect of soil pH on population growth in monocultures of selected species. An interesting by-product was the effect of predatory Gamasina mites, which survived in some microcosms, but went extinct in others [21].

3. Results and discussion

3.1 The coniferous forest floor: a high density and species rich habitat for mites

Podzol soil with vegetation type 4 in the main study area contained 48 species of Oribatida and 12 species of Mesostigmata (**Table 1**). The density of mites was high.

In the upper 6-cm soil, the mean numbers per m², based on eight replicates, were: Prostigmata (Actinedida) 490,000, Oribatida 220,000, and Astigmata (Acaridida) 10,000. The total mite density was 720,000 per m². The highest total density in one replicate amounted to 1.2 million mites per m² [14].

Comparable data exist from Finland and Sweden. In southern and central parts of Finland, mites were studied in four coniferous forest sites [28]. The localities corresponded to vegetation types 2 and 4 in the present study. The densities of oribatids, 186,000–351,000 per m², were in the same order of magnitude as in

Oribatida	Oribatida (continued)
<i>Adoristes poppei</i> (Oudemans)	<i>Oppia subpectinata</i> Willmann
<i>Autogneta parva</i> Forsslund	<i>Oppia unicarinata</i> (Paoli)
<i>Autogneta trågårdhi</i> Forsslund	<i>Oppia nova</i> (Oudemans)
<i>Belba</i> cf. <i>compta</i> Kulczynski	<i>Oribatula tibialis</i> (Nicolet)
<i>Brachychochthonius zelandensis</i> (Sellnick)	<i>Palaeacarus</i> sp.
<i>Caleremaeus monolipes</i> (Michael)	<i>Parachipteria</i> cf. <i>willmanni</i> (V. D. Hammen)
<i>Camisia biurus</i> (C. L. Koch)	<i>Paraleius</i> cf. <i>leontonycha</i> (Berlese)
<i>Camisia</i> cf. <i>lapponica</i> Trägårdh	<i>Paulonothrus longisetosus</i> (Willmann)
<i>Camisia spinifer</i> (C. L. Koch)	<i>Pergalumna nervosus</i> (Berlese)
<i>Carabodes femoralis</i> (Nicolet)	<i>Phthiracarus</i> sp.
<i>Carabodes forsslundi</i> Sellnick	<i>Platynothrus peltifer</i> (C. L. Koch)
<i>Carabodes labyrinthicus</i> (Michael)	<i>Porobelba spinosa</i> (Sellnick)
<i>Carabodes marginatus</i> (Michael)	<i>Scheloribates laevigatus</i> (C. L. Koch)
<i>Carabodes subarcticus</i> Trägårdh	<i>Steganacarus</i> sp.
<i>Cepheus cepheiformis</i> (Nicolet)	<i>Suctobelba subcornigera</i> (Forsslund)
<i>Ceratozetes</i> sp.	<i>Tectocepheus velatus</i> (Michael)
<i>Chamobates incisus</i> (V. D. Hammen)	<i>Zygoribatula</i> cf. <i>trigonella</i> Bulanova & Zachvatkina
<i>Chamobatidae</i> sp.	Mesostigmata
<i>Eueremaeus silvestris</i> (Forsslund)	<i>Eviphis ostrinus</i> (Koch)
<i>Eupelops duplex</i> (Berlese)	<i>Gamasellus montanus</i> (Willmann)
<i>Eupelops geminus</i> (Berlese)	<i>Hypoaspis forcipata</i> Willmann
<i>Euphthiracaridae</i>	<i>Leioseius bicolor</i> Berlese
<i>Hemileius initialis</i> Berlese	<i>Parazerkon sarekensis</i> Willmann
<i>Hypochthonius rufulus</i> C. L. Koch	<i>Pergamasus</i> cf. <i>lapponicus</i> Trägårdh
<i>Liacarus</i> cf. <i>coracinus</i> (C. L. Koch)	<i>Pergamasus parrunciger</i> Bhattacharyya
<i>Licneremaeus licnophorus</i> (Michael)	<i>Pergamasus robustus</i> Oudemans
<i>Nanhermannia</i> cf. <i>forsslundi</i> Karppinen	<i>Prozercon kochi</i> Sellnick
<i>Nothrus silvestris</i> Nicolet	<i>Trachytes</i> sp.
<i>Oppia</i> cf. <i>translamellata</i> (Willmann)	<i>Veigaia cerva</i> (Kramer)
<i>Oppia obsoleta</i> (Paoli)	<i>Veigaia nemorensis</i> C. L. Koch
<i>Oppia ornata</i> (Oudemans)	

Table 1.
In the clearcut area of the main study site Nordmoen, 48 species/taxa of Oribatida were recorded, and 12 of Mesostigmata.

the present study for vegetation type 4. However, their Prostigmata densities, 34,000–80,000 per m², were only about one tenth of ours. As much as 62 oribatid taxa were recorded in a Finnish spruce site with vegetation type 4. In another Finnish study of spruce forest soil, 35 taxa of oribatids were recorded and a relatively low density, only 70,000 oribatids per m² [29].

In an old Swedish pine forest of vegetation type 1–2, 52 oribatid species were recorded and very high densities [30]. As much as 425,000 oribatids per m² were found, which surpasses both the Norwegian and Finnish densities mentioned above. Prostigmata numbers (210,000 per m²) were between Norwegian and Finnish numbers, and total mite numbers (684,000 per m²) approached the high Norwegian number of 720,000. We can conclude that Nordic coniferous forest soils with raw humus have a very rich mite fauna, both in oribatid species and in total mite numbers.

3.2 Horizontal and vertical distribution

The main study area had very homogeneous soil conditions over a large area. It was a flat plain with stone-free, sandy soil, without visible variations in moisture conditions or vegetation. Still, as shown in **Table 2**, the horizontal distribution of many species showed considerable local variations [14, 15].

In another experiment, litter bags with birch leaves were placed in the humus layer of four random blocks. The mite fauna which colonized the litter varied significantly between blocks [12]. The Astigmata species *Tyrophagus* cf. *fungivorus* (Oudemans) colonized heavily in Blocks 1 and 2, while *Oppia ornata* occurred mainly in the other two. Actinedida mites were especially numerous in litter bags of Block 4, while the same litter bags had the lowest number of *Autogneta trågårdhi*. Block 1 had high numbers of *Oribatula tibialis*, while *Chamobates incisus* had its highest numbers in Blocks 2 and 3 (**Table 3**).

The study of vertical distribution in mites was restricted to the upper 6 cm. *Carabodes* species only rarely occurred in the 3–6 cm layer and were to a large degree

Species	Group	Densities
<i>Parazercon sarekensis</i>	M	1.7–5.2
<i>Veigaia nemorensis</i>	M	0.1–1.7
<i>Tectocephus velatus</i>	O	20–110
<i>Nothrus silvestris</i>	O	2–95
<i>Brachychochthonius zelawaiensis</i>	O	2–100
<i>Oppia obsoleta</i>	O	0–5.5
<i>Oppia nova</i>	O	0–4.5
<i>Paulonothrus longisetosus</i>	O	0–3.7
Brachychthoniidae	O	20–200
Total Oribatida		80–360
Astigmata (Acaridida)		3–30
Prostigmata (Actinedida)		230–850
Total Acari		400–1200

Table 2.
Lowest and highest density of various mites (1000 per m²) in eight random study plots (each 4 × 4 m) on a flat and homogeneous forest area. O = Oribatida and M = Mesostigmata. Mite density in a given plot was the mean of 10 soil cores, 6 cm deep and with a surface area of 5.3 cm².

Species	Sample No	Block numbers				Significance
		B 1	B 2	B 3	B 4	
<i>Tyrophagus cf. fungivorus</i>	I	533.5	735.8	13.5	2.3	B3 & B4 < B1 & B2
<i>Oppia ornata</i>	III	0	0	21.7	6.3	B3 > B1, B2 & B4
Prostigmata (Actinedida)	II	46.8	77.5	211.0	343.8	B4 > B1 & B2
<i>Autogneta trågårdhi</i>	I	56.6	45.1	55.8	21.4	
<i>Oribatula tibialis</i>	II	208.5	92.7	44.9	28.6	B1 > B2, B3 & B4
<i>Chamobates incisus</i>	II	0	2.0	4.6	0.6	B3 > B1 & B4

Table 3.
Examples of how the number of mites per litter bag with birch leaves may vary between four blocks in a flat and apparently homogeneous forest floor [12].

living in close connection with *Cladonia* lichens on the surface [25]. In the main study area, there was no sharp change in the mite fauna between the organic layer (0–3 cm) and the bleached mineral layer (3–6 cm). For instance, the large *Nothrus silvestris* was equally abundant in the two layers. However, the addition of strong doses of lime or artificial acid rain was apparently stressful for several mites, forcing animals to deeper layers. After treatment, the following oribatids moved significantly deeper, shifting from living mainly in the organic layer, to live mainly in the mineral layer: *Nothrus silvestris*, *Suctobelba* sp., *Brachychochthonius zelawaiensis*, and total oribatids. However, Prostigmata mites showed a shift upwards in the soil profile [14]. A frequent natural stress factor in soil is drought. In a Finnish forest, *Nothrus silvestris* was seen to migrate into deeper layers during warm periods [31].

In the comparative study between different vegetation types and soils, all the six selected mites showed variations in depth distribution, not only between habitats, but also between seasons [15]. On the average, the following percentages of the populations occurred in the upper 3 cm compared to 3–6 cm depth: 85% in *Tectocepheus velatus*, 65% in *Parazercon sarekensis*, 60% in *Schwiebea cf. cavernicola* Vitzthum, 54% in *Brachychochthonius zelawaiensis*, 52% in *Nothrus silvestris*, and 51% in *Schwiebea cf. nova* (Oudemans). The somewhat deeper distribution of *Nothrus silvestris* compared to *Tectocepheus velatus* has been confirmed by other studies [32–34].

3.3 Effect of ground vegetation and soil type

Eight mite species were studied systematically with respect to vegetation types and soil characteristics [15, 25]. Five belonged to the oribatids, two belonged to Acaridida, and one to Mesostigmata (Table 4). Most species preferred poor and acidic podzol soils with raw humus (up to vegetation type 4), but *S. cf. cavernicola* had the highest density in a poor brown earth (type 6). None of the eight species were abundant in the richest soil, a brown earth with mull humus (type 7). The non-*Carabodes* species in Table 4 were tested for correlation between population size and soil chemical parameters. Soil pH, and the accompanying parameters base saturation and calcium content, turned out to be the strongest explanatory factor.

Some other *Carabodes* species were so rare in all soils that they have been excluded from Table 4, but further mentioned under the next point.

Comparable data from Finland and Sweden confirm that *Nothrus silvestris* and *Tectocepheus velatus* occur in many different plant communities of coniferous forest, but typically in acid raw humus, and with low densities in richer soils [31, 33, 35, 36]. Although preferences exist, it has been concluded on a general basis that many oribatid species are able to persist in a wide range of humus forms and vegetation types [37].

Species	Group	Vegetation type						
		1	2	3	4	5	6	7
<i>Carabodes subarcticus</i>	Oribatida	15.2	0.5	2.5			0.02	
<i>Carabodes willmanni</i>	Oribatida	37.1	43.1	4.7				
<i>Parazercon sarekensis</i>	Mesostigmata	3.4	1.5	1.8	4.0	2.9	1.3	
<i>Tectocephus velatus</i>	Oribatida	175.3	66.8	99.1	47.2	7.4	11.5	0.7
<i>Brachychochthonius zelawaiensis</i>	Oribatida	0.9	1.5	27.7	38.8	12.2	1.6	0.5
<i>Nothrus silvestris</i>	Oribatida	1.8	3.5	14.8	22.0	3.7	7.3	1.9
<i>Schwiebea cf. cavernicola</i>	Acaridida	0.7	1.3	7.1	4.0	7.8	11.3	2.6
<i>Schwiebea cf. nova</i>	Acaridida	0.4	0.9	1.8	12.2	3.4	0.4	0.5

Numbers are mean value from two localities, each sampled during spring and autumn. Vegetation types 1–7 are described in Material and Methods. Soil fertility increased from left to right. For complete vegetation data, see [27].

Table 4.
Abundance (1000 per m² in the upper 6 cm soil layer) of some common mite species in seven different vegetation types in coniferous forest.

3.4 Carabodes: a genus with different life forms

The combined study of mites in different coniferous forest types and mites in decomposing polypore fungi illustrated that closely related species within a genus (*Carabodes*) can fill quite different niches in the forest ecosystem [25]. The most common *Carabodes* species in soil were rare in sporocarps and vice versa. The first two species in **Table 5** were considered *Cladonia*-feeders on the ground and were able to live in a dry forest floor. The third species on the list is also a lichen-feeder, which often climbs tree stems. Then, we have three fungal feeders which decompose dead sporocarps and may achieve high densities in these patchy and temporary habitats. Their relative numbers were rather similar in dead sporocarps of five different fungal species, including annual and perennial sporocarps, soft and hard. Although being tolerant to different fungal species, these specialists were considered vulnerable in forests with little dead wood and few sporocarps [25]. The five lower species have been found in low numbers, both in sporocarps, in dead wood, and in soil. They are either generalists or have unknown preferences.

3.5 Effect of soil acidity on mites—natural and manipulated

3.5.1 General results

Three approaches were used to test whether soil pH was an important environmental factor for mites. First, a “preference experiment” was arranged in the laboratory [10]. Here, mites were allowed to colonize soils adjusted to different pH levels. Second, we studied responses to artificial pH changes in soil through liming and artificial acid rain, both in the field and in the laboratory [13, 14]. Third, mites were sampled in natural soils of varying pH, to check if there were species that occurred mainly at certain pH levels [15].

Table 6 gives the most consistent results from the first two approaches. Clear responses were found in three oribatid species, in total Oribatida, and in the Acaridida species *Schwiebea cf. nova*. Raised pH due to liming reduced densities of these taxa, while acidification usually led to higher densities. The third approach from natural soils of different pH supported the pattern: species which increased

Species	In sporocarps	In dead wood	In soil	Remark
<i>C. willmanni</i> Bernini	(+)		++++	<i>Cladonia</i> -feeder on the ground
<i>C. subarcticus</i> Trägårdh	(+)	+	++	<i>Cladonia</i> -feeder on the ground?
<i>C. labyrinthicus</i> (Michael)	+(+)	+	+(+)	Lichen-feeder, common on tree stems
<i>C. femoralis</i> (Nicolet)	++++	++	+	Polypore specialist
<i>C. areolatus</i> Berlese	+++	++	(+)	Polypore specialist
<i>C. reticulatus</i> Berlese	+++	+		Polypore specialist
<i>C. marginatus</i> (Michael)	(+)	+	+	
<i>C. forsslundi</i> Sellnick	+	+	+	
<i>C. rugosior</i> Berlese	+	+	(+)	
<i>C. tenuis</i> Forsslund	+	+	(+)	
<i>C. coriaceus</i> Koch	+	+	(+)	
Very high abundance is subjectively indicated by ++++ and very low abundance by (+). Short remarks are given for some species.				

Table 5.
Simplified overview on the occurrence of various *Carabodes* species in different forest habitats, compiled from several sources. From [25].

Species	Effect of liming		Effect of acidification			
	Colonization experiment [10]	Field experiment [14]	Colonization experiment [10]	Field experiment [14]	Birch leaves [13]	
					Field	Green-house
<i>Nothrus silvestris</i>	—	—	+			
<i>Tectocepheus velatus</i>	—	—	+	+	+	+
<i>Brachychochthonius zelawaiensis</i>	—	—	+		+	—
<i>Total Oribatida</i>		—	+	+	+	
<i>Schwiebea</i> cf. <i>nova</i>	—		+			+

Table 6.
Significant effects of liming and acidification on mite densities. Compiled from several studies.

in numbers during artificial acidification were often numerous in naturally acid soils [15]. It was concluded that soil pH was a highly relevant environmental factor for certain mites. Among them was the rather large oribatid species *Nothrus silvestris* (Figure 3).

In field experiments with application of artificial rain, the structure of the mite community changed in a characteristic way. Figure 4 shows how the dominance structure was influenced by liming and application of “rain” with pH 2.5 and 2. Watering with pH 6 was considered as control. The dominance of Oribatida increased with increased acidification. Changes were mainly due to reactions in the sensitive species from Table 6.

Finnish [38] and Swedish [39] experiments conformed well with these data, as well as other studies referred to in [14].

Soil acidity is, of course, only one of many factors that modify the abundance of these species, and the relation is not absolute. Even if the pH level is favorable, other limiting factors, for instance drought, may depress populations. The



Figure 3.
Nothrus silvestris is an oribatid species that is typical for acid raw humus and declined after liming. Photo by courtesy of SNSB—Zoologische Staatssammlung München.

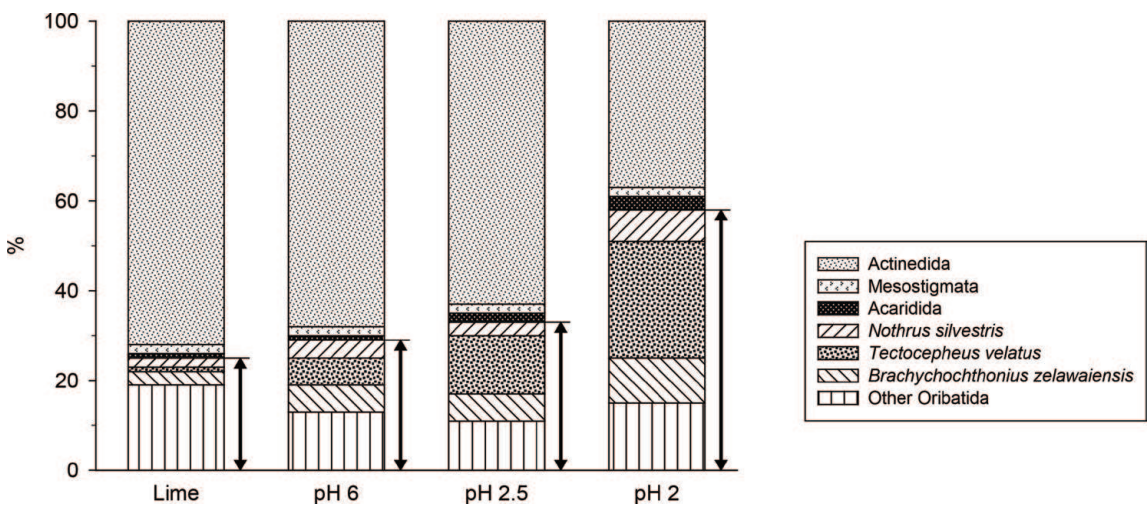


Figure 4.
Effect of liming and acidification (the two most extreme treatments, pH 2.5 and 2) on the relative dominance among mites. Watering with pH 6 was considered as “control.” The dominance of Oribatida mites, indicated by double arrows, increased with increased acidification [14]. Actinedida = Prostigmata and Acaridida = Astigmata.

experiments support the following conclusion: a high abundance in certain species can only be achieved within a certain pH interval (and only if other factors are not limiting), while within another pH interval, high abundance cannot be achieved. In soils of the latter pH interval, the acidity level (or correlated factors) seems to be limiting [16].

3.5.2 Is competition a key factor?

Relations between abundance of mites and soil acidity are difficult to explain. Soil pH is a measure of the H^+ activity of the soil solution. This parameter may have a direct importance for the water-living part of the soil fauna (such as Protozoa and Rotifera), and to other groups living in contact with the soil solution, as Nematoda [40, 41]. Both Enchytraeidae and Lumbricidae prefer relatively high moisture in the soil [42]. The survival of the Enchytraeidae species *Cognettia sphagnetorum* Vejdovsky decreased rapidly when the animals were submerged in diluted sulfuric acid of pH below 4 [9]. Many Enchytraeidae species show distinct relations to soil pH, both in experiments and in the field [10, 39, 43, 44]. The dependence of Lumbricidae species upon soil pH is well documented [45–47].

Microarthropods, on the other hand, have a hydrophobic cuticula and are restricted to the air-filled pore spaces of the soil. The relations described are probably indirect. Several possibilities have been discussed [16]: changes in ground vegetation due to artificial acid rain, direct effects of lime or sulfuric acid, various factors correlated to soil pH, changed predation pressure, availability of fungal hyphae as food, or fecundity. After having refuted several hypotheses, the following laboratory experiment pointed toward competition as a possible explanation [18].

Some microcosms were added a full soil fauna, while others were monocultures of selected species. The acidophilic Acaridid mite *Schwiebea* cf. *nova* (later named *S. cf. lebruni* Fain) thrived in monocultures. Starting with 30 specimens, populations increased to around 2000. Surprisingly, population growth in monoculture was lowest in the most acid soil. In the “full fauna” microcosms, however, the species revealed its typical acidophilic character and achieved the highest populations in the most acid soil. Quite parallel results were achieved for the acidophilic springtail *Mesaphorura yosii* (Rusek) [18]. These species have an optimum at a high pH when being alone. However, by some reason, they seem to be good competitors at low pH. They were winners both in natural soils with a low pH and in various experiments with artificial acid rain. Also the acidophilic oribatid *Nothrus silvestris* reproduced best in limed soil when alone [18].

For Collembola, other laboratory studies on population growth, with or without other species present, have illustrated that competition occurs [48, 49]. In most cases, the presence of another species reduced population growth. The most common mechanism was disturbance during oviposition. A classic study about competition among oribatid mites was performed in microcosms with natural soil. Two species with overlapping niches, *Hermaniella granulata* (Nicolet) and *Nothrus silvestris*, were first bred in monocultures. When put together, both species underwent significant shifts in their use of space and food. Their vertical distribution changed so that *Hermaniella* moved upwards into the litter layers, while the *Nothrus* population increased in the deeper fermentation layer [50].

Competition may attain many forms, and the topic is not easy to disentangle. However, since species live so densely packed in soil, one can imagine that disturbance or limited space or food may have an influence. If competition is a key factor regulating population size in soil, a general study of competition in microarthropods might be rewarding. Although a species may have its set of preferences, the key quality may be its ability to compete under suboptimal conditions.

3.6 The effect of predatory Mesostigmata mites

While the function of soil mites is often focused on their role in decomposition, predatory Mesostigmata mites have the potential to control the density of little sclerotized prey of various taxa. The evolution of strongly sclerotized bodies in many oribatid species obviously has an antipredator role.

The microcosm experiment described above illustrated the predatory effect of large Gamasina mites. At the start, 96% of the cultures contained predatory Gamasina mites, mainly *Veigaia nemorensis*. This percentage was reduced to 73% after 3 months, 62% after 6 months, and 50% after 12 months. The local extinction of these predators often resulted in very high densities of springtails or mites. For instance, after 1 year, the number of *Schwiebea* mites in certain predator-free microcosms could amount to several hundred, while predator-containing cultures usually had numbers below 30. Also for springtails, the highest populations were recorded in cultures where predatory Gamasina mites had gone extinct [21].

From the literature, another laboratory experiment illustrated well this top-down control of microarthropods. The addition of predatory mites to isolated soil cores containing a natural microarthropod fauna reduced the density of small and less sclerotized oribatids, as well as Collembola and Protura [5].

In agroecosystems, edaphic Mesostigmata have been shown to be important predators of Collembola and Nematoda, and those living on plants may efficiently control pests like spider mites [4].

3.7 Succession in the mite community during decomposition of spruce needles and birch leaves

In the main study area at Nordmoen, the clearcut area was used for litter bag studies, as described above. Litter bags with birch leaves were placed out in July 1975. There were four samplings: September 1975, April 1976, September 1976, and November 1978. The number of leaf-containing litter bags harvested at each sampling was 32, 68, 128, and 78, respectively.

Litter bags with spruce needles were placed out in September 1977, and samplings were made after 7 weeks, 8 months, 1 year, 2 years, 5 years, and 10 years. All samplings, except for the second one, were taken at the same time of the year. There were four replication sites, and 5–15 litter bags were harvested from each replication at a given sampling. Detailed results were given for birch leaves [12] and for needles [19]. Here, the main trends shall be presented and compared.

In both litter types, a gradual change in the mite community was observed during the decomposition process. However, the succession pattern differed in spruce needles and birch leaves. It means that mites in the surrounding soil were selective about which litter they colonized, at which rate, and at which decomposition stage. For instance, two oribatid species which were common in the soil, *Tectocepheus velatus* and *Nothrus silvestris*, never became abundant in litter bags. On the other hand, certain low-density species in soil could achieve very high densities in the bags. In such cases, a high density was only seen in one of the litter types. Examples in spruce needle bags were high density of *Eremaeus* sp. after 1 year, *Steganacarus* sp. after 5 years, and *Oppiella nova* after 10 years.

A considerable number of spruce needles were decomposed from the inside by certain specialized oribatid mites [22, 26]. Smaller, deeper-living species became abundant after 5–10 years, when the needles had been more or less fragmented. The fragmentation created new microhabitats and perhaps allowed for a more intense microfloral colonization.

While colonization of needle litter was slow, and no species or group achieved its maximum abundance within 8 months, colonization of birch leaves was much faster. Here, certain mites, which had a low density in the surrounding soil, appeared very numerous already after 7 weeks. Examples were three oribatid mites: *Oribatula tibialis*, *Eupelops duplex*, and *Autogneta trågårdhi*, and one Acaridida (Astigmata): *Tyrophagus* cf. *fungivorus*. Studies of the gut contents of these four species revealed a mixture of fungal spores and hyphae, and some guts contained mainly spores. This indicated an intense grazing, probably due to a temporal “flush” of fungal activity. The same was seen for certain springtail species [12]. It is, of course, important for soil microarthropods to detect such spatial and temporal food sources, and it is reasonable to assume that animals were attracted from surroundings by smell. Also other studies have documented a rapid migration of microarthropods into decomposing deciduous leaves [51–53]. Such species can be characterized as mobile opportunists. An abundant food source may allow a high number of species and specimens to coexist in a substrate with a low structural diversity. The body of *Eupelops duplex*, but also other species, was often covered by

fungal spores or hyphae, promoting the spread of microflora to all parts of the litter. The study also indicated that several species did not reproduce in the substrate, but only visited it during the adult stage for feeding purpose.

Table 2 shows that litter-dwelling pioneer mites in birch litter had a very uneven horizontal distribution, within 20–50 m. It meant that the succession pattern in the early decomposition phase varied widely, even within an apparently homogeneous forest floor. In later decomposition stages, however, the microarthropod community was less variable and more predictable.

In both litter types, large, surface-living species were among the early colonizers, while smaller, usually deeper-living species, took over the dominance in later decomposition stages. Since the litter bags had continuously contact with the whole organic layer in the actual soil, the succession studies confirmed that deeper-living, and often small species, preferred a more decomposed material.

While this experiment demonstrated that species often had different preferences for litter type or decomposition stage, it also showed that many species had wide tolerances and could survive, sometimes in low densities, under rather different circumstances. In an English study of oribatid mites in decomposing leaves of beech and chestnut, the 12 most abundant species were present in the litter bags throughout the 20-month study period. During this time, species were able to remain by changing their feeding habits [51]. Another example of high tolerance among oribatid species to different decomposition stages of leaf litter is from Central Amazonas. During the one-year long study, there was no successional changes in the species composition [54].

Few decomposition studies last long enough to describe the late stages of the microarthropod succession. For instance, in a study of root litter decomposition, it was found that oribatid mites showed a preference for the late stages of decomposition [55]. A general challenge in litter bag studies is how to simulate natural conditions. And even if natural conditions are achieved, the result may only have local value. Anyhow, due to a high species number and an ecological flexibility in many species, mites do in several ways contribute in transforming litter to humus. This is exemplified in the next chapter.

3.8 From litter to humus: can mites influence the process and the products?

Juveniles of certain specialized mites excavated cavities in about 40% of newly fallen spruce needles. Their activity reduced the decomposition rate of the actual needles, at least temporarily, probably because their excrements decomposed slowly [22, 26]. The adult mites, which hatched after about 2 years, attacked other needles from the outside and fragmented these (**Figure 5**). Their “inert” excrement pellets

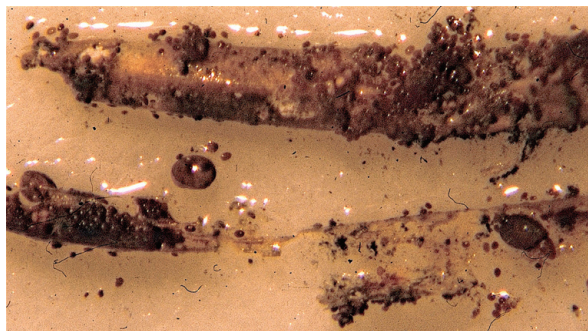


Figure 5.

Two spruce needles that have been fragmented by adult “box mites” (*Steganacarus cf. striculus*) kept in culture. Two ellipsoide-shaped animals are seen. Excrement pellets are numerous. Photo: S. Hågvar.

may contribute to a stable humus layer and perhaps to carbon sequestration [26]. Also other studies have pointed to the fact that fecal pellets of oribatids decompose slowly and may contribute significantly to humus production [56, 57]. Even pine needles can be tunneled by phthiracarid mites [57].

Individual spruce needles may show quite different decomposition patterns, even if situated close to each other in soil. While some are heavily transformed to excrement pellets, others remain morphologically intact for years. Needles which happen to come in close contact with fine roots may be rapidly “dissolved.” These “individual fates” of needles may explain the heterogeneous structure of deep humus [26].

3.9 Mite activity beneath and within snow

Norwegian coniferous forest is covered by snow for several months each year. When the snow layer exceeds about 20 cm, the temperature at the soil surface stabilizes around 0°C [58]. At this temperature, several surface-living invertebrates are active in the subnivean air space and even feeding [23]. Among these are several species of springtails and mites. During two winters, pitfall traps were operated under 30–150 cm snow in a high altitude spruce forest with bilberry vegetation in Southern Norway. Traps were emptied and replaced at least monthly during the snow-covered period from October/November to April/May.

Twelve taxa of Oribatida were trapped and 10 of Mesostigmata. A number of Prostigmata were also taken (Table 7). The Oribatida material was dominated by one species, *Platynothrus capillatus*. All developmental stages of this species were active under snow, and fungal hyphae and spores in their guts proved winter feeding. It was assumed that they were grazing on certain fungi known to decompose litter beneath snow (snow molds) [23]. Also other species of Oribatida, as well as some Prostigmata, had visible gut content.

In the main study area at Nordmoen, microarthropod activity both beneath and within snow was studied [11]. Most surface-living springtails were winter active and even migrated up into the snow layers. Among mites, four predacious Mesostigmata mites and one oribatid species (*Adoristes poppei* Oudemans) were taken in small numbers in pitfall traps, together with numerous Prostigmata. Mites were also found within the snow layers: some Prostigmata, seven taxa of predacious Mesostigmata, and six taxa of oribatids, of which *Adoristes poppei* was the most numerous. It was suggested that microarthropods went into snow to escape possible harmful water logging or ice formation in late winter [11].

3.10 Remarks on ecological flexibility and vulnerability

Several mite species showed a high tolerance for different plant communities, soils, humus types, litter type, and succession phase. Both birch leaves and spruce needles in litter bags were colonized by a high number of oribatid species. Several of them occurred in both substrates, although colonization was much slower in needle litter. Birch leaves represented an uncommon substrate at the actual site, but probably offered a flush of fungal food. Furthermore, at least some individuals of most species participated in various decomposition phases, where the substrate underwent significant changes. Except for pH, mites seemed to have few strong relations to soil chemical parameters [15].

Each mite species continually adjusts its vertical position, as far as narrow pores allow, to optimize its survival, food access, and reproductive ability. Such changes were seen also in the horizontal distribution. A more fixed vertical or horizontal position of each species could reduce interspecific competition but would be a disadvantage as soon as adverse or favorable conditions developed in certain layers or sites.

ORIBATIDA	Stage	Number trapped	Gut contents observed?
<i>Camisia biurus</i>	Ad	3	No
	T	2	Yes
	P	3	No
	L	2	No
<i>Carabodes labyrinthicus</i>	Ad	2	Yes
<i>Carabodes marginatus</i>	Ad	1	No
<i>Carabodes</i> sp.	T	1	No
<i>Chamobates pusillus</i> (Berlese)	Ad	1	No
<i>Eobrachychthonius borealis</i> Forsslund	Ad	3	Yes
<i>Oppiella neerlandica</i> (Oudemans)	Ad	12	Yes
<i>Oppiella</i> sp.	Ad	1	Yes
<i>Oribatella calcarata</i> (C.L. Koch)	Ad	1	No
	D	7	Yes
	P	5	Yes
<i>Platynothrus capillatus</i> (Berlese)	Ad	10	Yes
	T	9	Yes
	D	14	Yes
	P	8	Yes
	L	2	Yes
<i>Steganacarus</i> sp.	Ad	1	Yes
<i>Belba</i> sp.?	Ad	2	No
	T/juv	5	Yes
MESOSTIGMATA			
<i>Mixozercon serlachii</i> Lehtinen		1	
<i>Zercon curiosus</i> Trägårdh		1	
<i>Zercon colligans</i> Berlese		2	
<i>Holoparasitus</i> sp.		1	
<i>Lysigamasus lapponicus</i> (Trägårdh)		4	
<i>Vulgarogamasus kraepelini</i> (Berlese)		14	
<i>Veigaia nemorensis</i>		6	
<i>Trachytes aegrota</i> (C.L. Koch)		2	
<i>Urodiaspis tecta</i> (Kramer)		1	
<i>Uropodina</i> sp., nymph		2	
PROSTIGMATA (ACTINEDIDA)		115	Yes
TOTAL		244	
Numbers per 12 functioning traps. Only periods with a continuous snow cover are included. Ad = adults, T = tritonymphs, D = deuteronymphs, P = protonymphs, and L= larvae.			

Table 7.
Mites (Acari) caught in pitfall traps under snow during two winter seasons in a high altitude spruce forest, central South Norway. Modified from [23].

The present documentation [12] showing that many springtails and mites change their food habits through the different successional stages is in good accordance with other observations [51].

Within both springtail and mite communities, it is a general pattern that most species are relatively rare. A high tolerance for various habitat or nutritional factors, often combined with asexual reproduction, may keep species going on in low numbers. However, when special conditions are created locally, rare species may act as opportunists and flourish temporarily. They also represent an important resource if the ecosystem has to adapt to a new situation, for instance due to climate change.

Although single species may show tolerance to different environmental conditions, the mite community as a whole can be vulnerable to various types of human disturbance. For instance, in New York, the diversity of oribatid mites decreased along a gradient of land use types in the order from forests, via abandoned fields and willow, to corn [7]. A European review on mites as indicators of soil biodiversity and land use monitoring illustrated how sensitive mite communities can be to various types of soil disturbance [59]. Changes in the dominance structure of mite communities were suggested to be an “early warning criterion” for stressed mite communities. The author concluded that residual natural and semi-natural habitats (such as old woodlands, riparian ecosystems, old hedges, and grasslands) with species-rich mite communities found in rural and urban landscapes should be preserved as refuges for dispersion of soil fauna.

4. Conclusions: spotlights in short

Coniferous forests are rich in mites: a podzol soil with acid raw humus may contain more than a million mites per m². This includes a species-rich oribatid fauna.

Flexible vertical and horizontal distribution: mites can adjust both their depth in the soil profile and their horizontal distribution, either to escape stress or to aggregate in a patchy and temporary food source.

Opportunism as a successful strategy: several litter-dwelling mite species rapidly colonized birch leaves in an early decomposition phase, in order to feed on a temporary and patchy flush of fungal hyphae and spores.

Substrate flexibility: decomposition of spruce needles and birch leaves followed quite different succession patterns, but several mite species participated in both. Closely related species may differ widely in habitat choice and life forms: this was exemplified in the genus *Carabodes*.

Predacious Gamasina mites matter: microcosm studies showed high population growth of certain mites and springtails if predatory Gamasina mites went extinct.

Oribatids matter in the decomposition process from litter to humus: specialized oribatids excavate spruce needles and produce slowly decomposable excrements.

Soil acidity matters: colonization experiments and population studies in monocultures showed that soil pH affected population size in certain species. This led to predictable changes in the community structure of mites.

Successful competition under suboptimal conditions: surprisingly, certain mites common in acid soils thrived best in less acid soil when being alone (in monoculture). However, in acid soil, they were good competitors.

Mites are winter active: several mites are active under snow, often feeding. Some even penetrate into the snow layer.

5. Final remarks

There is an increasing awareness for preserving the huge biodiversity of soils [1, 60, 61]. Fragmentation and various management practices of forests may affect even these tiny animals. Some microarthropod species are confined to local soil types, for instance under dry or wet conditions. Furthermore, a forest contains various microhabitats in addition to soils. Examples are moss or lichen vegetation on certain trees, suspended soils in birds' nests, mold in old, hollow trees, decomposing wood, or fruiting bodies of various fungi. To preserve the species, diversity of microarthropods may demand a relatively large forest area, covering a variety of vegetation types, soils, humus types, and microhabitats.

Due to their long life span, low fecundity, slow development, and low dispersion ability, oribatid mites have been suggested as suitable indicators of soil biodiversity and land use monitoring. In this respect, there is a need to develop standardized procedures for sampling and data analysis [59].

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