

RESEARCH ARTICLE

Mites of the genus *Carabodes* (Acari, Oribatida) in Norwegian coniferous forests: occurrence in different soils, vegetation types and polypore hosts

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Oribatid mites (Acari) represent a considerable part of the biodiversity in Fennoscandian forests, but our knowledge about their habitat requirements is limited. We studied 10 *Carabodes* species in the forest floor of seven coniferous forest types, and in dead fruiting bodies (sporocarps) of 6 species of wood-living polypore fungi in southern Norway. The most common *Carabodes* species in soil were rare in sporocarps, and vice versa. The density of several ground-living species was significantly influenced by vegetation type and soil type. *Carabodes willmanni* and *C. subarcticus* were considered as lichen feeders on the ground, and occurred abundantly in *Cladonia*-rich pine forests. Three species, *C. femoralis*, *C. areolatus* and *C. reticulatus*, seem to be sporocarp specialists. Their relative numbers were rather similar in dead sporocarps of five different fungal species, including annual and perennial sporocarps, soft and hard. This was in contrast to beetles from the same sporocarps, which in a previous study proved to be strongly host-specific. Although being tolerant to different fungal species, the association of certain *Carabodes* species to dead sporocarps could make them vulnerable in forests with little dead wood and few sporocarps.

Keywords: biodiversity; *Carabodes*; conifer forest; dead wood; polypore fungi; soil; sporocarp

Introduction

In recent years, there has been increasing focus on the conservation of European forest biodiversity, both regarding the need for protected areas, and measurements taken during forestry operations (Kraus & Krumm 2013). The importance of dead wood and associated microhabitats for species diversity was highlighted by Stokland et al. (2012), with a main focus on Fennoscandian forest types. However, the diverse group of mites (Acari) has rarely been included in studies of saproxylic communities. Polish studies have shown that dead, fallen spruce or beech logs represent habitat islands for a specialized community of Oribatida mites. Many species found in sporocarps (fruiting bodies of wood-decaying macrofungi) and other microhabitats of dead wood were absent from the forest soil (Skubala & Sokolowska 2006; Skubala & Duras 2008; Skubala & Maslak 2010; Skubala & Marzec 2013). Similarly, decomposing aspen logs in Québec revealed a distinct oribatid community, different from surrounding soil (Déchène & Buddle 2010). Also Finnish studies have concluded that various microhabitats in coarse woody debris support a unique mite community, but sporocarps were not included here (Siira-Pietikäinen et al. 2008; Huhta et al. 2012).

In a review paper on species richness, host specificity and rarity of insects in sporocarps, Komonen (2003) considered sporocarps to be hotspots of insect diversity in Fennoscandian boreal forests. This might also be the case for specialized mites. In Canada, Matthewman and Pielou (1971) listed more than 180 arthropod species, including 30 species of mites, extracted from living and dead sporocarps of *Fomes fomentarius* (L.) Fr. Mites were the most frequently occurring and probably the most numerous arthropods. Since species depending on patchy and temporary habitats like sporocarps may be vulnerable, it is due time to include mites in Fennoscandian studies of sporocarp communities.

Oribatida is a species-rich group of mites, and many of them are typical forest inhabitants. Their main function is as decomposers. Gjelstrup (1978) reported 215 oribatid species from Denmark, Mehl (1979) listed 244 from Norway, Lundqvist (1987) 263 from Sweden and Niemi et al. (1997) 309 species from Finland. *Carabodes* is a morphologically characteristic genus of Oribatida mites. They are burrowers during ontogeny, and only adults can be collected effectively using funnels or traps. In Fennoscandian forests, *Carabodes* species have been found both in forest soil, in dead wood, in sporocarps of polypore fungi (often called fruiting bodies or carpophores) and in

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lichens growing on soil or on trees (e.g. Forsslund 1944; Sellnick & Forsslund 1953; Niemi et al. 1997; Hågvar & Steen 2013). Forsslund (1944) gave density data for several *Carabodes* species in the litter and humus layer of different spruce (*Picea abies* (L.) Karst.) forest types in northern Sweden, but not for pine (*Pinus silvestris* L.) forest soils. Scattered supplementary data from Sweden were given by Sellnick and Forsslund (1953). Niemi et al. (1997) summarized the known distribution of each *Carabodes* species in Finland, and referred to several field studies which together give a fragmentary picture of their occurrence in various forests soils and vegetation types. However, the habitat flexibility for each *Carabodes* species is still insufficiently known.

This study is a continuation of Hågvar and Steen (2013) who recorded 10 *Carabodes* species in decomposing sporocarps of the red-banded polypore fungus *Fomitopsis pinicola* (Swartz:Fr.) Karst. in Norwegian spruce forest. The purpose is to learn more about which forest microhabitats the various *Carabodes* species use, and to discuss their habitat use and flexibility in the light of other Fennoscandian studies. Are certain species sporocarp specialists, which might be vulnerable to forestry? In which polypore species do the different species live? Are sporocarp-living species also found in the forest floor, and in that case within which vegetation types or soil types? First, we present abundance data per m² of the soil-living *Carabodes* fauna, comparing all major vegetation types and soil types of coniferous forest in southern Norway. Second, we compare the occurrence of *Carabodes* species in dead sporocarps of the red-banded polypore fungus *Fomitopsis pinicola* in four different sites with similar forest environment. Third, we compare host specificity of *Carabodes* species between dead sporocarps of different polypore species within the same forest area of similar forest environment. The last approach also allowed us to compare host specificity of *Carabodes* species with that of different sporocarp-living beetles which were extracted from the same sporocarp material (Økland 1995). We hypothesized that flying beetles guided by fungal odour could be more host selective than non-flying and slow-moving mites.

Material and methods

Soil sampling

Two study areas were chosen for soil sampling, each containing a gradient in vegetation types from the poorest pine forest to the richest spruce forest. In area I in Skrukkelia, NW of lake Hurdalsjøen and about 60 km north of Oslo (middle boreal region, 60°27'N, 10°50'E), the soil was mainly morenic deposits. Area II near Ås, about 30 km south of Oslo (boreonemoral region, 59°40' N, 10°47'E), had a cover of marine sediments. In both study areas, spruce forest with *Vaccinium myrtillus* L. dominated. Listed after increasing soil fertility based on

plant associations (Dahl et al. 1967), the vegetation types were short-named as follows:

- (1) *Cladonia* sp.: Pine forest on iron podzol soil, with a dense cover of *Cladonia*-species (Association Cladonia-Pinetum).
- (2) *Calluna vulgaris*: Pine forest with less *Cladonia*, and a field layer dominated by *Calluna vulgaris* (L.) Hull. (Association Barbilophozio-Pinetum). The soil was iron podzol in area I and shallow peat in area II.
- (3) *Vaccinium* sp.: Pine forest on iron podzol soil, with a dense cover of *Vaccinium myrtillus* L. or *Vaccinium vitis-idaea* L., but also containing some *Cladonia* lichens (Association Vaccinio-Pinetum).
- (4) *Vaccinium myrtillus*: Spruce forest with *Vaccinium myrtillus* (Association Eu-Piceetum Myrtillus). Iron podzol in area I, and brown earth-like soil in area II.
- (5) *Small ferns*: Spruce forest with small ferns (*Dryopteris phegopteris* (L.) C. Chr. and *Dryopteris linnaeana* C. Chr.) (Association Eu-Piceetum Dryopteris). Iron podzol in area I and brown earth in area II.
- (6) *Small herbs*: Spruce forest on brown earth, with small herbs like *Carex digitata* L., *Melampyrum silvaticum* L. and *Fragaria vesca* L. (Association Melico-Piceetum, typical subassociation).
- (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 (Association Melico-Piceetum, *Athyrium* subassociation).

Each vegetation type was sampled twice, in autumn 1977 and in spring 1978. Using a soil corer of 10 cm², 20 soil cores down to 12 cm depth were taken both during spring and autumn in a given vegetation type. The cores were divided into four depth levels of 3 cm. Data below 6 cm depth have been omitted in the tables, as only a very few specimens of *C. willmanni* and *C. labyrinthicus* were recorded there. In area II, an unusually rich soil in spruce forest has not been included in the present Tables. It was a small clear-cut area with young *Fraxinus excelsior* L., which was devoid of *Carabodes*, except for a very few *C. labyrinthicus*. Detailed data on vegetation, soils, sampling and extraction were given by Hågvar (1982). Totally, 5573 adult *Carabodes* specimens were extracted from soil.

Sampling and extraction of sporocarps

The material of dead sporocarps was collected mid-April 1992 in spruce forest, within or close to Østmarka nature reserve, about 15 km southeast of Oslo (boreonemoral region, 59°51'N, 11°2'E, see Økland 1995). The actual

sporocarps were rather intact in shape, and therefore in relatively early phases of decomposition, corresponding to phase III in Graves (1960). According to Hågvar and Steen (2013), the *Carabodes* fauna in dead sporocarps of *F. pinicola* showed greatest changes in late decomposition stages. While old spruce forest dominated, several deciduous trees occurred, mainly *Betula verrucosa* Ehrh., *B. pubescens* Ehrh., *Populus tremula* L., *Salix caprea* L., *Sorbus aucuparia* L., *Alnus incana* (L.) Moench and *Prunus padus* L. The reserve has a general high density of dead wood. Thirty dead sporocarps were randomly collected of each of the following fungus species within the reserve (locality Tappenberg): *Fomitopsis pinicola*, *Trametes* sp., *Phellinus tremulae* (Bondartsev) Bondartsev & P. N. Borisov and *Inonotus radiatus* (Sowerby) P. Karst. Thirty dead sporocarps of *Fomes fomentarius* were collected in similar forest environments 6 km N of the reserve (locality Østby).

Additional material of the very common species *Fomitopsis pinicola* was sampled to compare the mite fauna in four different localities. Therefore, thirty dead sporocarps were sampled also from each of three similar old spruce forest sites 4–6 km N of the reserve: Østby, Styggvann and Losby west. Finally, 13 dead sporocarps were sampled of the more rare species *Pycnoporus cinnaberinus* (Jacq.) P. Karst. within the Østmarka reserve (Tappenberg).

In order to reduce the effect of local conditions, the material used for comparing mites in different fungal species was collected within a small area in the reserve, close to lake Tappenberg. For *F. pinicola*, which was sampled in four different localities, we therefore used only the “Tappenberg” site in this comparison. However, for *F. fomentarius*, we had to use the only site where it was sampled, the nearby locality Østby with a similar forest environment.

Mites were collected in rearing traps with long-term drying, in the same way as insects were extracted (Økland 1995). Each sporocarp was placed in a plastic funnel enclosed in black textile, and with a collecting vial with ethylene glycol below. The traps were situated in an outdoor cage house with a natural climate from 1 May to 30 August. Totally, 6699 adult *Carabodes* specimens were extracted from sporocarps.

Taxonomy

We used names according to Fauna Europaea (<http://www.faunaeur.org/index.php>). The species which is named *Carabodes forsslundi* Sellnick, 1953 in the present paper was initially named *Carabodes ornatus* Storckan, 1925 by Forsslund (1944). However, Sellnick and Forsslund (1953) decided that it was a misidentification, and Sellnick proposed the name *C. forsslundi* for the species. Rajsiki (1968), however, concluded that they were indeed the same species, so *C. forsslundi* became a junior synonym. The

literature is mixed in the usage, and both names are considered as valid by Fauna Europaea. Since *C. forsslundi* was used in our earlier paper on *Carabodes* species in sporocarps (Hågvar & Steen 2013), we use this name also here. *C. willmanni* Bernini 1975 was wrongly named *C. minusculus* Berlese, 1923 by Sellnick and Forsslund (1953) and also by several Finnish studies before the catalogue of Finnish oribatids was compiled by Niemi et al. (1997). *C. rugosior* Berlese, 1916 is now a separate species, but was considered as a variety of *C. femoralis* by Sellnick and Forsslund (1953), as well as in certain early Finnish studies (Niemi et al. 1997). *Carabodes rugosior* tends to be a rare species. While *C. rugosior* and *C. femoralis* have been separated in our present soil material (Tables 1–2) and in our previous sporocarp study (Hågvar & Steen 2013), *C. femoralis* in the present sporocarp data might include a few overlooked *C. rugosior* (Table 4).

Statistics

The variation in mite numbers across vegetation types and soil types was tested by the Kruskal–Wallis rank sum test, using the `kruskal.test` in R (R Development Core Team 2012). Since very few individuals were found deeper than 3 cm (Tables 1–2), the test was based on 0–3 cm depth. Due to local variation in *Carabodes* density within a given vegetation type, we took into consideration the variation between single soil core samples. The 40 soil cores from each vegetation type and local area (20 in spring and 20 in autumn) were used as replicates. Ideally, our study should also have included samples from more than two study areas to ensure samples that are optimally representative of each vegetation type in southern Norway. Since this was not feasible due to resource demands, we used two study areas that were situated rather far apart, one below and one above the marine limit, but containing corresponding vegetation types. The four most abundant species in soil were tested: *C. willmanni*, *C. subarcticus*, *C. labyrinthicus* and *C. marginatus*. The remaining species were too sparsely represented to be tested.

The number of individuals of each mite species extracted per sporocarp of *Fomitopsis pinicola* was compared across sites within 2–8 km distance (Østby, Losby west, Tappenberg, Styggvann) by variance analysis. Variance analysis was also used to compare across fungal species, comparing both the mean number per sporocarp for each mite species, and the percentage of individuals constituted by the respective mite species in each sporocarp (so-called “dominance”). All of the variance analyses were performed by non-parametric methods, Kruskal–Wallis rank sum test (Corder and Foreman 2009), because these types of data usually are not expected to be normal-distributed. All statistics and graphic presentations, including variance analyses and

Table 1. Density (in thousands per m²) of *Carabodes* species in pine forest soils based on different vegetation types (see text).

Vegetation type		1. <i>Cladonia</i> sp.				2. <i>Calluna vulgaris</i>				3. <i>Vaccinium</i> sp.			
Soil type		Iron podzol				Iron podzol/shallow peat				Iron podzol			
Study area		Area I		Area II		Area I		Area II		Area I		Area II	
Spring–autumn	Depth (cm)	s	a	s	a	s	a	s	a	s	a	s	a
<i>Carabodes willmanni</i>	0–3	16.85	23.70	32.75	34.80	42.95	39.65	8.05	8.65			2.42	4.60
Bernini, 1975	3–6	1.13		8.33	2.29	0.10	1.20	0.80	0.60			0.10	0.05
<i>Carabodes subarcticus</i>	0–3	15.15	5.05	0.35	0.30	0.50	0.40	0.05	0.10	2.20	2.40	0.11	0.60
Trägårdh, 1902	3–6								0.10	0.10	0.06		
<i>Carabodes labyrinthicus</i>	0–3	2.00	0.65	0.75	0.45	0.10	0.15	0.15	0.10	0.30	0.50	0.21	0.40
(Michael, 1879)	3–6						0.05	0.05				0.10	
<i>Carabodes marginatus</i>	0–3	0.90	0.10	0.05	0.05	0.35	0.20			0.80		0.37	0.15
(Michael, 1884)	3–6												
<i>Carabodes forsslundi</i>	0–3							0.20			0.05	0.74	1.35
Sellnick, 1953	3–6												0.10
<i>Carabodes femoralis</i>	0–3												
(Nicolet, 1855)	3–6											0.05	
<i>Carabodes rugosior</i>	0–3		0.05			0.10				0.05	0.10		
Berlese, 1916	3–6												
<i>Carabodes tenuis</i>	0–3												
Forsslund, 1953	3–6												
<i>Carabodes areolatus</i>	0–3											0.05	
Berlese, 1916	3–6												

Note: Within both study areas (Area I and Area II), sampling was made both in spring (s) and autumn (a).

box plots, were carried out with the software R Development Core Team (2012).

Results

Ten *Carabodes* species were recorded, nine in soils (Tables 1–2) and eight in sporocarps (Table 4). Seven species were found in both soil and sporocarps, but *C. reticulatus* only in sporocarps, and *C. rugosior* and *C. tenuis* only in soil. The tables also illustrate that the three most common species in sporocarps were rare or absent in soil, while the two most abundant species in soils were rare in sporocarps. *Carabodes* mites were mainly found in the uppermost 3 cm soil layer.

Carabodes species in coniferous forest soils with different vegetation

Table 1 shows the density of each *Carabodes* species in various vegetation types and soils in pine forest, and Table 2 correspondingly in spruce forest. The abundance of *Carabodes* mites in soils was generally low, but with several thousands per m² for certain species in pine forest. The density of a given species was usually in a similar order of magnitude in spring and autumn within a given site. In the four most abundant species, the number of individuals varied significantly across vegetation types and soil types (Table 3). For *C. marginatus*

and *C. subarcticus*, the abundance was higher in “Iron podzol” than in the other soil types ($H = 11.9$, $p = 0.0005653$, and $H = 66.8$, $p = 3.01E-16$, respectively). This was also the case for *C. willmanni* ($H = 106.8$ and $p < 2.2E-16$), but for this species even between “Brown earth” and the other soil types ($H = 139.5$, $p < 2.2E-16$). For *C. labyrinthicus*, “Shallow peat” had a significantly lower abundance than the other soil types ($H = 5.2$, $p = 0.023$).

C. willmanni was absent from spruce forests, but numerous in pine forest with *Cladonia* or *Calluna/Cladonia*-dominated vegetation, showing densities between 9000 and 43,000 per m² ($H = 247.3$ and $p < 2.2E-16$ for pine compared to spruce). *C. subarcticus* had a similar distribution, with up to 15,000 per m² in *Cladonia*-dominated vegetation ($H = 105.6$ and $p < 2.2E-16$ for pine compared to spruce). *C. labyrinthicus* was found in low numbers in all vegetation types, but passed 2000 per m² in *Cladonia* and *Vaccinium myrtillus* vegetation (pine compared to spruce not significant). This species appeared more abundantly in “Cladonia”, “Vaccinium”, “V. myrtillus” and “Tall herbs” than in the other vegetation types ($H = 29.7$ and $p = 5.115E-08$). *C. marginatus* was likewise a generalist, always rare, but with a certain preference for pine forest ($H = 14.0$ and $p = 0.00018$ for pine compared to spruce). The five remaining species in Tables 1–2 were always rare without any clear preference, except for a possible *Vaccinium*-maximum in *C. forsslundi*.

Table 2. Density (in thousands per m²) of *Carabodes* species in spruce forest soils based on different vegetation types (see text).

Vegetation type		4. <i>Vaccinium myrtillus</i>				5. Small ferns				6. Small herbs				7. Tall herbs			
Soil type		Iron podzol/brown earth				Iron podzol/brown earth				Brown earth				Brown earth			
Study area		Area I		Area II		Area I		Area II		Area I		Area II		Area I		Area II	
Spring–autumn	Depth (cm)	s	a	s	a	s	a	s	a	s	a	s	a	s	a	s	a
<i>C. willmanni</i>	0–3																
	3–6																
<i>C. subarcticus</i>	0–3											0.02					
	3–6																
<i>C. labyrinthicus</i>	0–3	0.15	0.21	2.65	1.30	0.05	0.20	0.30	0.15			0.45	1.00	0.05	0.10	1.30	0.80
	3–6				0.25							0.02	0.05				
<i>C. marginatus</i>	0–3						0.05		0.05	0.05		0.02					
	3–6																
<i>C. forsslundi</i>	0–3			0.05							0.05						
	3–6																
<i>C. femoralis</i>	0–3								0.05			0.02	0.42			0.05	
	3–6																
<i>C. rugosior</i>	0–3	0.25				0.05				0.10							
	3–6																
<i>C. tenuis</i>	0–3	0.05				0.05											
	3–6																
<i>C. areolatus</i>	0–3																
	3–6																

Note: Within both study areas (Area I and Area II), sampling was made both in spring (s) and autumn (a).

Table 3. Non-parametric test of variance in number of mite individuals across seven vegetation types and three soil types.

Species	Vegetation types			Soil types		
	H	df	p	H	df	p
<i>C. willmanni</i>	353.2	6	3.2E-73	139.6	2	4.8E-31
<i>C. subarcticus</i>	137.6	6	3.2E-27	68.0	2	1.7E-15
<i>C. labyrinthicus</i>	45.3	6	4.0E-8	15.6	2	0.00042
<i>C. marginatus</i>	17.4	6	0.008	12.0	2	0.0024

Note: The method used is Kruskal–Wallis rank sum test.

H = Kruskal–Wallis chi-squared, df = degrees of freedom, p = p-value.

Carabodes species in dead sporocarps

Eight *Carabodes* species were extracted from the various dead sporocarps (Table 4). Except for *Pycnoporus cinnabarinus* with only 2 species resulting from 13 sporocarps, the other fungus species harboured 5–8 species. Four species were numerous enough to be tested: *C. reticulatus*, *C. areolatus*, *C. femoralis* and *C. labyrinthicus*, but variations in mite numbers between individual sporocarps could be very high (Figures 1–2). A significantly higher number of *C. femoralis* were extracted from *Fomes fomentarius* compared to other sporocarps (Figure 1; $p = 0.0015$). We also tested whether the dominance in numbers between different *Carabodes* species was influenced by the fungal species. However, no significant effects of fungal species were found on the structure of the *Carabodes* community.

Among *F. pinicola* sporocarps, there was no significant difference in *Carabodes* numbers between sites (Figure 2), but a near to significance-value for *C. femoralis* ($p = 0.07$).

Discussion

The influence of vegetation types in the forest floor

Our data confirm Forsslund's (1944) conclusion that *Carabodes* mites are living mainly in the litter and upper humus layer, including the thin mat of lichens and mosses. Also, the general low densities of *Carabodes* species in all vegetation types of spruce forest (Table 2) is in accordance with his studies. However, the forest floor of Norwegian pine stands could have rather high densities of certain species, especially where *Cladonia* lichens were common. *C. willmanni*, which showed densities between 18,000 and 41,000 per m² in the two poorest pine forests (Table 1), is known from France to be a typical *Cladonia* feeder (Bellido 1979, 1989), thriving even in open, dry heathland. Also in Sweden, Sellnick and Forsslund (1953) pointed to *Cladonia* vegetation as preferred habitat for this species. Even *C. subarcticus*, which showed a high density in certain pine forest with *Cladonia* vegetation in area I (Table 1), may be a lichen feeder. Its occurrence in pine forest and/or *Cladonia* vegetation has been confirmed both from Sweden (Sellnick & Forsslund 1953) and Finland (Huhta et al. 1986; Karppinen 1962). *C. marginatus* was never

Table 4. Mean number of *Carabodes* individuals per sporocarp, extracted from dead sporocarps of (A) *Fomitopsis pinicola* in four localities A1-4 and mean values, (B) *Fomes fomentarius*, (C) *Phellinus tremulae*, (D) *Trametes* sp., (E) *Inonotus radiatus* and (F) *Pycnoporus cinnabarinus*.

	A.1	A.2	A.3	A.4	A.mean	B	C	D	E	F
Polypore species:	<i>Fomit. pinic.</i>	<i>Fomit. pinic.</i>	<i>Fomit. pinic.</i>	<i>Fomit. pinic.</i>	<i>Fomit. pinic.</i>	<i>Fomes fomen.</i>	<i>Phell. tremu.</i>	<i>Tram. sp.</i>	<i>Inono. radia.</i>	<i>Pycno. cinna.</i>
Life cycle of polypore species:	Perennial	Perennial	Perennial	Perennial	Perennial	Perennial	Perennial	Annual	Annual	Annual
Context of polypore species:	Hard	Hard	Hard	Hard	Hard	Hard	Very hard	Rather soft	Soft	Soft
<i>C. reticulatus</i>	18.3	3.7	13.6	3.9	9.9	17.7	35.5	2.6	17.2	
<i>C. areolatus</i>	12.9	5.3	18.1	1.7	9.5	5.1	4.2	3.1	12.7	0.2
<i>C. femoralis</i>	7.6	1.8	2.9	1.5	3.5	16.4	0.1	0.5	0.9	
<i>C. labyrinthicus</i>	1.5	2.3	3.0	1.6	2.1	1.6	1.4	1.1	1.7	0.2
<i>C. subarcticus</i>	0.2	0.03		0.2	0.1	0.3	0.1	0.1	0.1	
<i>C. marginatus</i>	0.3	0.03	0.1	0.1	0.1			0.2		
<i>C. forsslundi</i>				0.03	0.01					
<i>C. willmanni</i>				0.03	0.01					
Total number of specimens	1223	392	1130	273	755	1230	1236	229	980	6
Number of species	6	6	5	8	6	5	5	6	5	2
% sporocarps with <i>Carabodes</i>	100	100	97	83	95	97	97	70	97	38

Note: Each sampling category consisted of 30 sporocarps, except for only 13 of *Pycnoporus cinnabarinus*. A1 = Losbywest, A2 = Styggvann, A3 = Tappenberg, A4 = Østby.

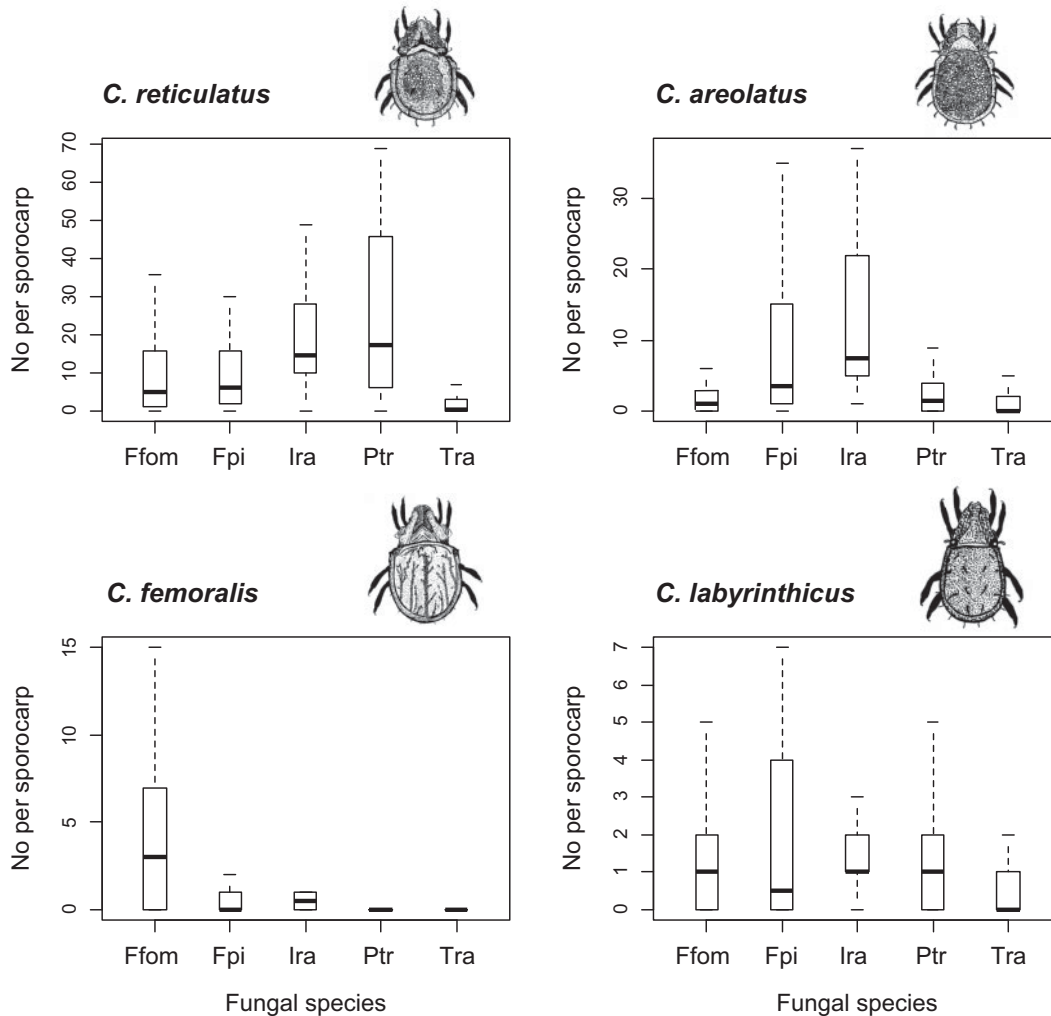


Figure 1. For each of the four most abundant *Carabodes* species, numbers per sporocarp is shown in five different fungus species. Ffom = *Fomes fomentarius*, Fpi = *Fomitopsis pinicola*, Ira = *Inonotus radiatus*, Ptr = *Phellinus tremulae*, and Tra = *Trametes* sp. Difference between fungal species was significant only for *C. femoralis*, which had highest abundance in *Fomes fomentarius*. The central lines of the box-and-whiskers plot show the median, the box indicates lower and upper quartiles, and the whiskers show the largest and smallest observations that fall within a distance of 1.5 times the box size from the nearest quartile.

abundant in the Norwegian forest soils. It could also be a lichen feeder since pine forests had highest numbers. Swedish and Finnish studies confirm not only its tolerance for different forest types but also its possible preference for pine forest with lichens (Sellnick & Forsslund 1953; Karppinen 1962; Huhta et al. 1986).

Also *C. labyrinthicus*, which was found in low numbers in all vegetation types, is considered to be a lichen feeder, but a generalist which typically inhabits epiphytic lichens growing on tree stems (Forsslund 1944; Wunderle 1991, 1992; Maraun et al. 2011). The few individuals that were found in soil may have fallen from trees, or they could be in dispersal. The species has been recorded in various vegetation types in Finland, including pine forest and/or *Cladonia* vegetation (Karppinen 1962, 1972, 1977; Huhta et al. 1986). It also lives in alpine heathland (Solhøy 1975; Solhøy & Koponen 1981).

Having sorted out these four species as documented or possible lichen feeders, the remaining species in Tables 1–2 are generally rare in forest soils. As shown below, three of them are, however, typical inhabitants of special substrates as dead sporocarps or dead wood.

The importance of dead sporocarps and dead wood

Hågvar and Steen (2013) documented that three species were common in dead sporocarps of *Fomitopsis pinicola*, with some changes in relative dominance during a five-year-long decomposition process: *C. femoralis*, *C. areolatus* and *C. reticulatus*. The present study not only confirms their high numbers in decomposing *F. pinicola* sporocarps, but also shows that they are numerous in dead sporocarps of several other fungi (Table 4). We consider them as specialists in dead sporocarps, but with a wide tolerance for both soft and hard sporocarps, as well as for annual and

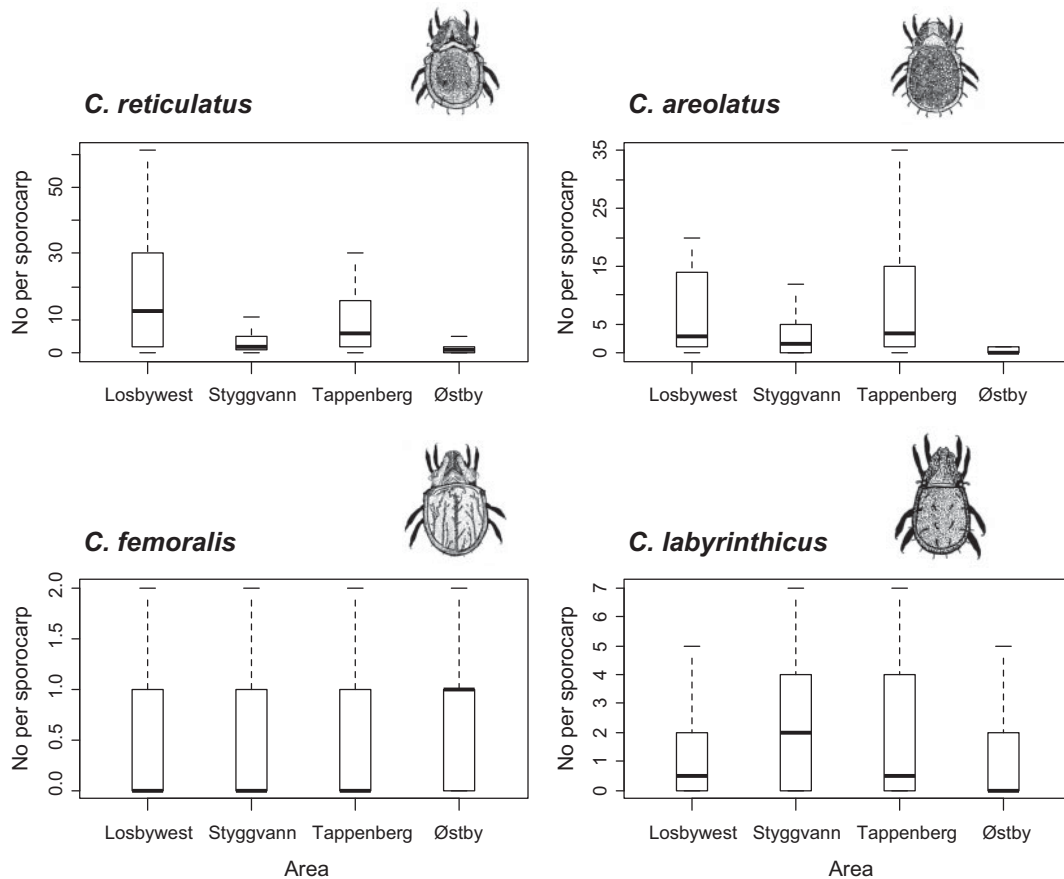


Figure 2. Number of *Carabodes* mites extracted from dead sporocarps of *Fomitopsis pinicola*, sampled in four different areas in Østmarka near Oslo. Only data for the four most abundant species are shown. There were no significant differences between sampling areas. The central lines of the box-and-whiskers plot show the median, the box indicates lower and upper quartiles, and the whiskers show the largest and smallest observations that fall within a distance of 1.5 times the box size from the nearest quartile.

perennial fungi. These mites also have in common that they often inhabit decomposing wood, especially *C. femoralis* and *C. areolatus* (Sellnick & Forsslund 1953; Wunderle 1992; Skubala & Duras 2008). According to OConnor (1984), fungus-feeding *Carabodes* species probably disperse to polypore fruiting bodies from bark crevices and subcortical microhabitats in decaying logs. Having colonized dead sporocarps, their populations increase strongly. *Carabodes reticulatus* was absent in the forest soil study, and the two others were very rare (Tables 1–2). Maybe the few specimens crawling in the forest floor of these species are migrating animals in search of dead wood and sporocarps.

In Poland, Skubala and Duras (2008) found that 49 oribatid species in dead beech logs, representing nearly half of the combined species from logs and soil, were obligate members of the intra-log community. This community contained specialists preferring certain microhabitats like bark, sapwood, epiphytic vegetation or sporocarps. Even the position on the log (upper part or sides of the fallen stem) could be important. Similar conclusions were drawn from oribatids in dead spruce logs (Skubala & Sokolowska 2006; Skubala & Maslak

2010). Correspondingly, Siira-Pietikäinen et al. (2008) and Huhta et al. (2012) demonstrated the importance of coarse woody debris for oribatids and other mites in Finnish forests. European studies can be summarized in this way: (1) Decomposing logs contain an oribatid fauna which is different from the forest floor. (2) The saproxylic oribatid community is influenced by the decomposition stage and the various microhabitats on the log. (3) A specialized oribatid community establish in decomposing sporocarps. The genus *Carabodes* illustrates these points. The possible “hot spot function” of sporocarps for mites in general remains to be studied in Fennoscandian forests.

Rare Carabodes species in coniferous forest

Three other species were generally rare in Norwegian forest soils: *C. forsslundi*, *C. rugosior* and *C. tenuis*. They are not typical sporocarp inhabitants, as the present material only contained one specimen of *C. forsslundi*, and in the sporocarps studied by Hågvar and Steen (2013) their dominance was only 1–2%. However, they have a certain affinity to dead wood (Sellnick & Forsslund 1953; Skubala & Duras 2008).

Table 5. Simplified overview on the occurrence of various *Carabodes* species in different forest habitats, compiled from several sources (see text).

Species	In sporocarps	In dead wood	In Soil	Remark
<i>C. willmanni</i>	(+)		++++	Cladonia-feeder on the ground
<i>C. subarcticus</i>	(+)	+	++	Cladonia-feeder on the ground?
<i>C. labyrinthicus</i>	+(+)	+	+(+)	Lichen-feeder, common on tree stems
<i>C. femoralis</i>	++++	++	+	Polypore specialist
<i>C. areolatus</i>	+++	++	(+)	Polypore specialist
<i>C. reticulatus</i>	+++	+		Polypore specialist
<i>C. marginatus</i>	(+)	+	+	
<i>C. forsslundi</i>	+	+	+	
<i>C. rugosior</i>	+	+	(+)	
<i>C. tenuis</i>	+	+	(+)	

Note: Very high abundance is subjectively indicated by +++, and very low abundance by (+). Short remarks are given for some species.

Conclusion about use of different habitats

Table 5 sums up schematically the main conclusions about habitat use for each species, based on a combination of the present study and literature. The most clear distinction is between lichen feeders (partly on the ground and partly on trees), and those living mainly in sporocarps or dead wood.

Host preferences of *Carabodes* mites compared to sporocarp-living insects

Insects extracted from the same sporocarp material was studied by Økland (1995). In contrast to the present mite species, several sporocarp-living beetles proved to have a strong preference for certain fungal species. Both beetle larvae and *Carabodes* nymphs are burrowers within the sporocarp and have to overcome two obstacles: the hardness of the sporocarp and their chemical defence. Preferences among beetles have often been related to hardness and hyphal structure (Paviour-Smith 1960; Lawrence 1973; Orledge & Reynolds 2005), but Jonsell and Nordlander (2004) showed that beetle preferences are well related to phylogenetic and chemical relatedness of the fungi.

For insects, flight and attraction by odour are means for finding preferred sporocarp species. Orledge and Reynolds (2005) identified six holarctic host-use groups of Cisidae beetles, which could be explained by characteristic, emitted volatiles within each fungal group. Jonsell and Nordlander (1995) showed that two characteristic beetles in dead sporocarps of *F. pinicola*, *Cis glabratus* Mellié, 1848 and *Cis quadridens* Mellié, 1848, were attracted by chopped, dying fragments. However, slow and non-flying *Carabodes* mites cannot select hosts easily, and seem to have developed a high tolerance for substrate hardness and chemical defence. We suggest that *Carabodes* species found in decaying sporocarps are primarily living in decomposing wood where fungal food is limited, but they use the opportunity to multiply efficiently in

energy-rich sporocarps if these are available. Whether they are able to orientate towards sporocarps by odour, and stay in a “waiting position” until the sporocarp dies, remains unknown.

Conclusions

The most common *Carabodes* species in soil were rare in sporocarps, and vice versa. Species with very low densities in the forest floor could be animals in dispersal, seeking an appropriate new substrate. The lichen-feeding species *C. willmanni*, however, had high densities in *Cladonia*-rich pine forests, and also *C. subarcticus* showed a corresponding tendency. Three species were abundant in dead sporocarps and were considered sporocarp specialists: *C. femoralis*, *C. areolatus* and *C. reticulatus*. Although accepting several polypore fungal species, they can probably be vulnerable to lack of dead wood substrate containing sporocarps. Sporocarps are often considered to be hotspots of insect diversity, but this may also be the case for mites. Both oribatids and other mite groups should be closer studied in sporocarps and other saproxylic microhabitats of Fennoscandia. Breeding experiments would help to understand microhabitat selection.

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