

The red wood ant *Formica aquilonia* (Hymenoptera : Formicidae) may affect both local species richness and composition at multiple trophic levels in a boreal forest ecosystem

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In temperate forests, red wood ants (*Formica aquilonia*) are considered ecosystem engineers affecting ecosystem properties and functions. Possible effects of *F. aquilonia* ants on species communities of invertebrates and plants were studied in the pine-dominated Geitaknottane forest reserve, Norway. Species richness of carabids, lichens and epiphytes (tree-living lichens and bryophytes) was negatively affected by ant mound density. Species of all groups, except for lichens and snails, were affected either positively or negatively by ant presence. Food availability and interference competition are plausible explanations of decreased species richness and negative species associations in carabids; while collecting, foraging and changed chemical environment may explain decreased species richness in lichens and epiphytes. Thirteen out of 15 plant and invertebrate species were weakly associated with ant mound density. Associations of only two species (*Carabus violaceus* and *Drusilla canaliculata*) were negative, while *Pella humeralis* and *Agroeca proxima* were associated positively and very strongly with ant mounds. Positive associations with ants of those invertebrates may be a response to excessive abundance of food and chemical mimicry.

Introduction

Ants are some of the most successful organisms on Earth. The red wood ants, *Formica* (*Formica*) *sensu lato* are abundant in European forests, and their stable and high population levels make the ants a very important component of the forest ecosystem (Gößwald 1989–1990, Domisch *et*

al. 2005, 2009, Sorvari & Hakkarainen 2005, Ohashi *et al.* 2007, Finér *et al.* 2013). In boreal forests, ants are thought to regulate other invertebrates, including pest species, and protect other groups of insects such as aphids against parasites and predators (Moya-Laraño & Wise 2007, Kilpeläinen *et al.* 2009, Johansson & Gibb 2012, Maňák *et al.* 2016).

Ants in the forest ecosystem are versatile (Folgarait 1998). For example, their voracity can greatly affect primary production and prey biomass (Petal 1978, Moya-Laraño & Wise 2007, Domisch *et al.* 2009, Kilpeläinen *et al.* 2009). They have also been shown to be positively associated with a wide array of other organisms, such as vascular plants, myrmecophilous arthropods, fungi and microorganisms (e.g., Weber 1972, Päivinen *et al.* 2002, Härkönen & Sorvari 2014, Parmentier *et al.* 2014, Duff *et al.* 2016, Maksimova *et al.* 2016). Ants living in mounds can be important for the development of a rhizosphere-related fauna and may also be important for the establishment of plants because mounds can create mycorrhizal-enriched patches (McIveen & Cole 1976, Allen *et al.* 1989, Friese & Allen 1993, McGinley *et al.* 1994). Some authors (e.g., Lyford 1963, Gotwald 1986) suggested that ants are just as important for soil rotation as earthworms, and contribute substantially and directly to the movement of subterranean soil (Whitford *et al.* 1986, Paton *et al.* 1995, Laakso 1999) as well as regulate cycling of carbon and other nutrients in forest ecosystems (Frouz *et al.* 2005, Ohashi *et al.* 2007, Jurgensen *et al.* 2008, Domisch *et al.* 2009, Finér *et al.* 2013, King 2016). Ants may be significant dispersers of plant propagules (Wilson 1992, Heinken 2004, Heinken *et al.* 2007, Rudolphi 2009, Türke *et al.* 2012) but may also harvest lichens and their propagules (Lorentsson & Mattson 1999, Heinken *et al.* 2007).

Ants are very important for the vitality of forests because they control other invertebrate species, including pests (Adlung 1966, Petal 1978, Sudd & Lodhi 1981, Halaj *et al.* 1997, Folgarait 1998, Gibb 2003, Punttila *et al.* 2004, Moya-Laraño & Wise 2007, Kilpeläinen *et al.* 2009, Mestre *et al.* 2013, Maňák *et al.* 2013; but see also Maňák *et al.* 2015). They, however, have the potential to both reduce and increase invertebrate population levels, in particular that of the aphids (Wellenstein 1954, Adlung 1966). As shown by Wellenstein (1952), Sudd and Lodhi (1981) and Weseloh (1995), the fraction of invertebrates in the diet of ants is not particularly great for them to be considered a pest reducing agent. In addition, although ants protect aphids from which they harvest honeydew, numbers of individuals

in species from which they do not harvest honeydew can also increase. This may be because they prey upon parasitoids or other general predators (Bartlett 1961).

In general, ant density is high close to the nests and decreases with increasing distance (Niemelä & Laine 1986, Domisch *et al.* 2009). On a somewhat larger scale, ant density may be particularly high in some areas due to clustering of mounds (Kilpeläinen *et al.* 2008). There are relatively few studies documenting the effect of ants on other organisms. Gibb (2003) found no impact on arthropod communities in an exclusion experiment with the dominant *Iridomyrmex purpureus* in Australia except that other ant species became more abundant when *I. purpureus* was excluded. Neuvonen *et al.* (2012) in Finland and Galle *et al.* (2014) in Hungary found that forest stand type is more important than ant abundance for the assemblage of ground-dwelling arthropods, and that other arthropods are more or less insensitive to ant abundance. Moya-Laraño and Wise (2007) found positive relations between ant density and Collembola at the expense of spider densities in the USA, while Zhang *et al.* (2012) observed a significant increase in ground-dwelling arthropods in large plots with reduced ant density in a study carried out in China. Mestre *et al.* (2013) documented a negative relation between ant abundance and spiders in Spain, though the association became detectable not earlier than after five years. In addition, chemical cues used by ants appeared to have an effect on spiders by increasing their dispersal activity (Mestre *et al.* 2014). In England and Russia, respectively, Dorosheva and Reznikova (2006) and Hawes *et al.* (2013) discovered that *Formica* ants and predatory ground beetles avoid competition. Except for epigeic species (Heinken *et al.* 2007), the knowledge on the extent of impact of ants on lichen and bryophyte communities is very sparse. The studies on the effects of ants on snails are also limited, ambiguous, and concentrate principally on how invasive tropical species affect native snail populations rather than on ecosystems in equilibrium. Uchida *et al.* (2016) found a significant negative effect of *Pheidole megacephala* on achatinellid snails in Japan, and Yusa (2001) a reduction in egg masses of *Pomacea canaliculata*

being preyed upon by *Solenopsis geminata* in the Philippines, while O'Loughlin and Green (2015) found a positive relationship between *Anoplolepis gracilipes* and land snails on the Christmas Island. Thus, the overall picture is not consistent for snails, and showing relatively small effects within short time scales.

We studied relationships between local density of red wood ant mounds in a boreal forest, and species richness and composition of several groups of plants and animals (vascular plants, lichens, bryophytes, spiders, carabids, staphylinids and snails). As studies show that *F. aquilonia* affects stronger canopy than forest-floor communities (Lenoir 2003, Punttila *et al.* 2004), we aimed to quantify this by investigating the effects also on the species of the forest floor. Consequently, our hypotheses were: (1) ant mound density negatively affects predatory arthropods because of a dietary overlap with ants, (2) the effect of ants on abundance of myrmecophilous arthropods is positive, and (3) there is no effect of ant mound density on the species richness of lichens, bryophytes, vascular plants and snails.

Material and methods

Species survey

The study was carried out in a 1.47 km² area in Kvam, Hordaland County (5°53'E, 60°05'N, 120–340 m a.s.l.) in western Norway (for details see Gjerde *et al.* 2005), as part of a forest biodiversity research project (Gjerde *et al.* 2007). The study area is located in the southern boreal zone (mean annual precipitation and temperature are 2300 mm and 7.2 °C, respectively). Seventy-two percent of the area is covered by a Scots pine (*Pinus sylvestris*) forest, while 13% by broad-leaved forest (*Ulmus glabra*–*Tilia cordata* and *Alnus*–*Fraxinus excelsior*) and northern deciduous forest (*Betula*–*Corylus avellana*). The area is within the Geitaknottane forest reserve, and less than 0.5% of the forest is younger than 80 years.

The entire study area was (20 years ago) divided into a grid of 147 cells, 100 × 100 m each (Fig. 1), with 50 × 50 m sample plots situated in the southeastern corner of each cell. Within this area, sample plots (65 in total), and

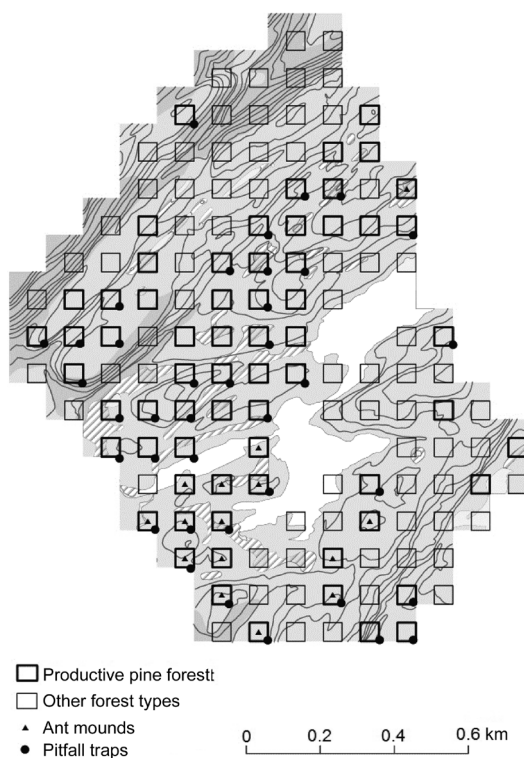


Fig. 1. Study area. Pitfall traps were placed throughout the area in 38 of the 65 plots. The white area in the middle is a lake.

neighbouring areas within 10-m distance of the plots, in a productive pine forest (i.e., part of the pine forest whose annual yield capacity per hectare is at least 1 m³ of wood) were surveyed for red wood ant (*Formica* spp.) mounds in 1998, and for vascular plants, bryophytes, macrolichens (*sensu* Krog *et al.* 1994) and snails in 1997. In a subset of plots in the productive pine forest ($n = 38$), ground-living invertebrate predators (Araneae, Carabidae, and Staphylinidae) were caught using pitfall traps between the end of April and the end of November in 1997 and 1998. The traps were emptied four times during each year. There were eight traps (65 mm in diameter) in each sample plot; they were filled to 1/3 with 4% formaldehyde. Vascular plants were surveyed on all substrates, whereas macrolichens and bryophytes on logs, rocks, slabs, bare soil, and on trees, snags, and rock walls below 2 m. Macrolichens and bryophytes growing on trees were classified as epiphytes. Snails were collected by sifting through ground

litter. Six ground-litter samples were collected from each sample plot, and care was taken to sample different microhabitats (below rock walls, around stones, stumps and logs, crevices and other aggregations of litter).

The surveys of ant mounds, plants and lichens were considered to be more or less exhaustive inventories, whereas the surveys of invertebrate groups should be considered comparable samples from existing species communities. The invertebrate material was deposited in the Zoological Museum, University of Bergen.

Species abundance

For sampled invertebrates (snails, spiders, and beetles), the number of specimens caught in traps or by sifting was used as a proxy for abundance. The material from all the eight pitfall traps in the same sample plot was pooled. Abundances of lichens, bryophytes and vascular plants (qualitative) were classified as follows: 0 = absent, 1 = singular (1 recorded individual or unit), 2 = rare (2–3 recorded units for bryophytes, 2–5 for lichens), 3 = frequent (10 recorded units for bryophytes, 6–20 for lichens), and 4 = abundant (> 10 recorded units for bryophytes and > 20 for lichens). Ant density was expressed as the number of mounds within a plot. A mound that was closer than 10 m to the plot border was included in the analyses as 0.5 mound.

Analyses

The sample plot data were used for the analyses of relationships between number of ant mounds, and diversities and abundances of other species groups. Because all ant mounds except one were found in a pine forest of the *Calluna vulgaris*–*Vaccinium uliginosum* vegetation type (Fremstad 1997) in the southern part of the study area (Fig. 1), we also carried out a separate analysis for sample plots dominated by this vegetation type, which included 45 plots for vascular plants, bryophytes, macrolichens and snails, and 27 plots for invertebrates caught in pitfalls.

We used univariate General Linear Modelling (GLM) to detect relationships between

arthropods (pitfall trap data) as well as plants and lichens and number of ant mounds. Because earlier studies indicated a positive correlation between productivity of vegetation types and species richness (Gjerde *et al.* 2005), GLM was also carried out separately using the data from sample plots in *C. vulgaris*–*V. uliginosum* woodland (Fremstad 1997). To fulfil the assumption of homoscedasticity, abundances of vascular plants were ln-transformed.

The effects of ant mound density on species and individual numbers were evaluated with Spearman's rank-order correlation analysis.

In order to associate particular species or higher taxa with density of mounds, Canonical Variate Analysis (CVA) was carried out on a full data set, and the *C. vulgaris*–*V. uliginosum* plot data. CVA is a multivariate technique with only one environmental variable and is also called linear discriminant analysis. Thus, we used ant mound density as the only "environmental" variable. Species present in only one sampling plot were excluded from the analyses. No down-weighting or transformation of species data was considered necessary. For the invertebrate species, positive or negative associations with ants based on CVA species scores were considered significant when the fraction fit of total variation along the first CVA axis was ≥ 0.2 , provided the mean number of individuals per plot was ≥ 3 .

GLM and Spearman's rank-order correlation were performed in SPSS ver. 20 (IBM Corp. 2011), while the CVA analyses were carried out in CANOCO ver. 4.5 (ter Braak & Smilauer 1997–2009).

Results

During the experiment we caught in pitfall traps 3156 individuals of Carabidae, 7144 of Staphylinidae, 2443 of Gastropoda and 7309 of Araneae (305 species in total), while 451 species of bryophytes, lichens and vascular plants were recorded (cf. Table 1).

Ant mounds were found in 15 (8 of those sampled pitfall traps) of the 65 plots searched for ants, and all investigated mounds were inhabited by *F. aquilonia*. There were 0–4.5 mounds per plot. We found a decrease in the number of

lichen species (Spearman's $r = -0.58$, $n = 15$, $p < 0.03$), as well as Gastropoda species ($r = -0.84$, $n = 8$, $p < 0.01$) and individuals ($r = -0.79$, $n = 8$, $p < 0.02$) with increasing number of mounds in a plot. Species numbers of Araneae increased with increasing number of mounds in a plot ($r = 0.73$, $n = 8$, $p < 0.04$).

Species richness

According to GLM, the number of carabid species was negatively associated with ant mound density (Table 2), also when only the *C. vulgaris*–*V. uliginosum* vegetation sample plots were considered. Results for other groups were insignificant (Table 2).

Regarding plants, species richness of lichens and that of epiphytes were negatively associated with ant mound density, also when only the *C. vulgaris*–*V. uliginosum* vegetation sample plots ($n = 48$) were considered (cf. Table 2).

Species composition

When using the entire data set (65 plots), snails and lichens were the only groups whose species numbers were not affected by ant mound density (non-significant CVA-ordination results, cf. Table 3, Figs. 2 and 3). When only the *C. vulgaris*–*V. uliginosum* vegetation sample plots were considered, the effect of ant mound density on bryophytes and vascular plants became non-significant.

At the species level, however, there were significant responses to ant mound density. Associations of two species, the myrmecophilous staphylinid *Pella humeralis* (Fig. 4) and the liocranid spider *Agroeca proxima* (Fig. 5), with ant mounds were strong and positive, while the staphylinid *Drusilla canaliculata* (Fig. 4) was associated with ant mounds negatively and rather weakly.

Associations of most species with ant mounds were stronger in the *C. vulgaris*–*V.*

Table 1. Numbers of species and individuals of invertebrates, and abundance classes for plants (cf. chapter 'Species abundance'). All = 65 sample plots in productive pine forest, *Vacc.-Call.* = *Vaccinium*–*Calluna* sample plots.

Group	Species		Individuals		Top 3 species (individuals)	
	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>
Invertebrates						
Carabidae	29	22	3156	2166	<i>Carabus violaceus</i> (918) <i>Pterostichus diligens</i> (481) <i>Trechus secalis</i> (272)	<i>C. violaceus</i> (660) <i>P. diligens</i> (444) <i>T. secalis</i> (159)
Gastropoda	25	18	2443	1883	<i>Columella aspera</i> (735) <i>Nesovitrea hammonis</i> (476) <i>Punctum pygmaeum</i> (465)	<i>C. aspera</i> (530) <i>N. hammonis</i> (390) <i>P. pygmaeum</i> (351)
Staphylinidae	126	64	7144	4994	<i>Pella humeralis</i> (2454) <i>Drusilla canaliculata</i> (1429) <i>Olophrum piceum</i> (536)	<i>P. humeralis</i> (1990) <i>D. canaliculata</i> (1016) <i>O. piceum</i> (389)
Araneae	125	88	7309	5152	<i>Tenuiphantes alacris</i> (1138) <i>Centromerus arcanus</i> (441) <i>Agyneta cauta</i> (404)	<i>T. alacris</i> (699) <i>C. arcanus</i> (264) <i>Alopecosa taeniata</i> (242)
Plants						
Bryophyta	167	146	1–2	0–1	<i>Hypnum cupressiforme</i> (3–4) <i>Frullania tamarisci</i> (3–4) <i>Diplophyllum albicans</i> (3–4)	<i>Frullania tamarisci</i> (3–4) <i>H. cupressiforme</i> (3–4) <i>Fissidens dubius</i> (3–4)
Vascular plants	225	166	0–1	0–1	<i>Pinus sylvestris</i> (3–4) <i>Molinia caerulea</i> (3–4) <i>Juniperus communis</i> (3–4)	<i>P. sylvestris</i> (3–4) <i>M. caerulea</i> (3–4) <i>J. communis</i> (3–4)
Lichens	59	39	0–1	0–1	<i>Hypogymnia physodes</i> (3–4) <i>Platismatia glauca</i> (3–4) <i>Pseudevernia furfuracea</i> (3–4)	<i>H. physodes</i> (3–4) <i>P. glauca</i> (3–4) <i>P. furfuracea</i> (3–4)

uliginosum sample plots than when all plots were included in the analysis (Tables 4 and 5). For example, *Carabus violaceus* was negatively associated with ants (fit = 0.22) when only the data from *C. vulgaris*–*V. uliginosum* sample plots were included in the analysis but not (fit = 0.16) when the whole data set used (Table 4).

Discussion

Species richness

Presence of ants had a negative effect on species richness of Carabidae, lichens and bryophytes

(Table 2). As *F. aquilonia* aggressively defends its nest, food sources and foraging areas (Hölldobler & Wilson 1990), one would expect a stronger negative effect of ants on all invertebrate groups. However, red wood ants seem to forage mostly in tree canopies (rather than on the ground), where their effect on many prey species is detectable (Lenoir 2003, Punttila et al. 2004). Ants remaining on the ground mostly guard the mound, gather nest material or scout for other resources.

There is little information on the effects of ants on epiphytic cryptogams (lichens and bryophytes). Based on their studies of *Cladonia* lichens, Heinken et al. (2007) concluded that red wood ants may help maintain the diversity of epi-

Table 2. Associations with number of ant mounds (GLM analysis). All = 65 sample plots in productive forest, *Vacc.-Call.* = *Vaccinium*–*Calluna* sample plots. Data for vascular plants were ln-transformed.

Group	Adjusted R^2		Type III SS		MS		F		p	
	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>
Invertebrates										
Carabidae	0.50	0.44	240.70	186.05	60.18	46.51	10.10	6.15	<0.001	0.002
Gastropoda	-0.01	-0.03	38.69	40.05	9.67	10.01	0.89	0.81	0.483	0.532
Staphylinidae	0.04	0.004	318.89	222.80	79.72	55.70	1.43	1.03	0.246	0.416
Araneae	-0.05	-0.10	147.24	118.49	37.06	29.62	0.60	0.41	0.663	0.803
Plants										
Bryophyta	0.06	0.10	3820.68	3549.17	545.81	507.03	1.54	1.70	0.174	0.136
Vascular plants	-0.03	-0.04	0.44	1178.08	0.06	168.30	0.74	0.77	0.639	0.612
Epiphytes	0.18	0.23	782.18	736.07	111.74	105.15	2.96	2.99	0.010	0.013
Lichens	0.21	0.25	187.60	143.46	26.80	20.49	3.44	3.23	0.004	0.008

Table 3. Canonical Variate Analysis (CVA) results for the full data set (65 sample plots in productive forest) and the data set of *Vaccinium*–*Calluna* (*Vacc.-Call.*) sample plots when all species present in only one sampling plot were removed. Eigenvalue 1 = explanatory power of CVA axis 1, Cum. var. 1 = cumulative variation (%) of CVA axis 1, F and p = results of the Monte Carlo permutation test.

Group	Number of species		Number of plots		Eigenvalue 1		Cum. var. 1		F		p	
	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>
Invertebrates	215	193	38	27	0.39	0.37	12.6	12.5	5.20	3.57	0.001	0.001
Plants	394	356	65	48	0.03	0.04	2.3	2.9	1.47	1.38	0.021	0.025
Invertebrates												
Araneae	92	89	38	27	0.17	0.18	6.5	7.1	2.51	1.92	0.012	0.043
Carabidae	23	23	38	27	0.18	0.20	8.3	9.5	3.27	2.64	0.009	0.037
Gastropoda	20	19	38	27	0.04	0.04	2.5	3.8	0.94	0.99	0.411	0.400
Staphylinidae	84	65	38	27	0.52	0.46	16.8	16.1	7.25	4.81	0.001	0.002
Plants												
Epiphytes	58	58	65	48	0.02	0.02	2.5	3.3	1.59	1.58	0.046	0.042
Lichens	50	40	65	48	0.05	0.05	2.3	3.1	1.46	1.49	0.112	0.108
Bryophyta	146	146	65	48	0.02	0.02	2.4	2.5	1.56	1.18	0.020	0.160
Vascular plants	193	167	65	48	0.04	0.04	2.3	2.5	1.45	1.16	0.042	0.190

geic bryophytes and lichens in temperate conifer forests. *Cladonia* spp. were not included in the lichen inventory study, and we discovered a negative association of epiphytic lichens with presence of ants (Table 2) possibly because ants use those lichens (Lorentsson & Mattson 1999, Heinken *et al.* 2007) for mound material.

Overall, diversities of vascular-plant and invertebrate species on the forest floor were little affected by red wood ants, which confirms the findings of earlier studies on ground-dwelling fauna and flora (e.g. Laakso 1999, Laakso & Setälä 2000, Dauber *et al.* 2003, Lenoir 2003, Lenoir *et al.* 2003, Neuvonen *et al.* 2012).

Effects of ants on bryophytes and lichens have to date been poorly studied, hence the negative relationship between ants and epiphytic species richness found here should be further studied.

Species composition

Carabidae

Päivinen *et al.* (2002) listed the ant-associated beetles in Denmark and Fennoscandia. *Dyschirius*

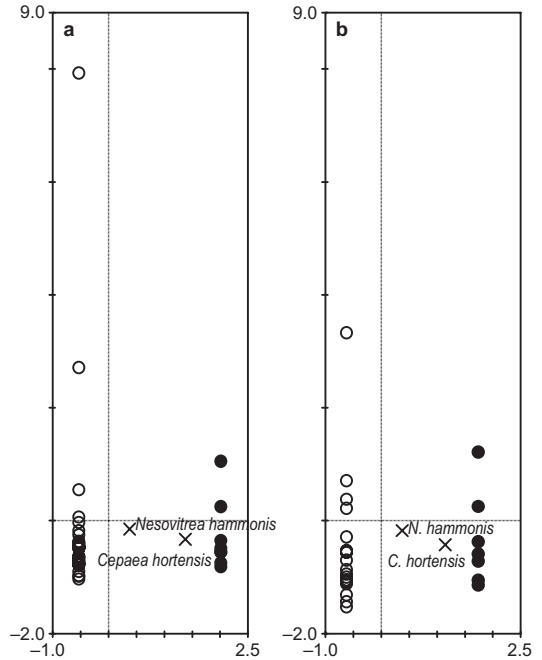


Fig. 2. CVA ordinations for Gastropoda (cf. Table 3): (a) sample plots in productive forest ($n = 38$), and (b) *Vaccinium-Calluna* sample plots ($n = 27$). Circles = plots without ant mounds, dots = plots with ant mounds.

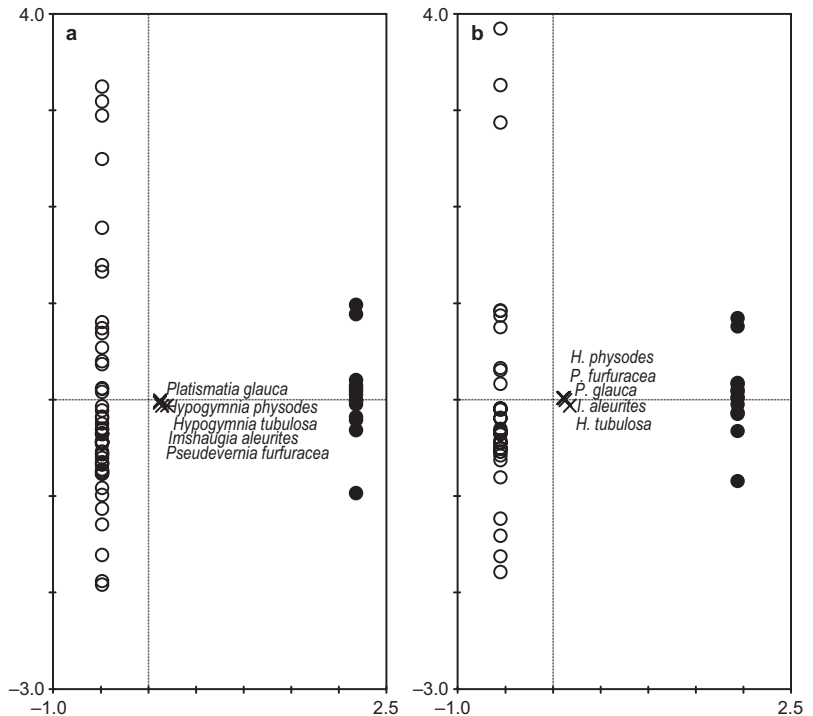


Fig. 3. CVA ordinations for lichens (cf. Table 3): (a) 65 sample plots in productive forest, and (b) *Vaccinium-Calluna* sample plots ($n = 48$). Circles = plots without ant mounds, dots = plots with ant mounds.

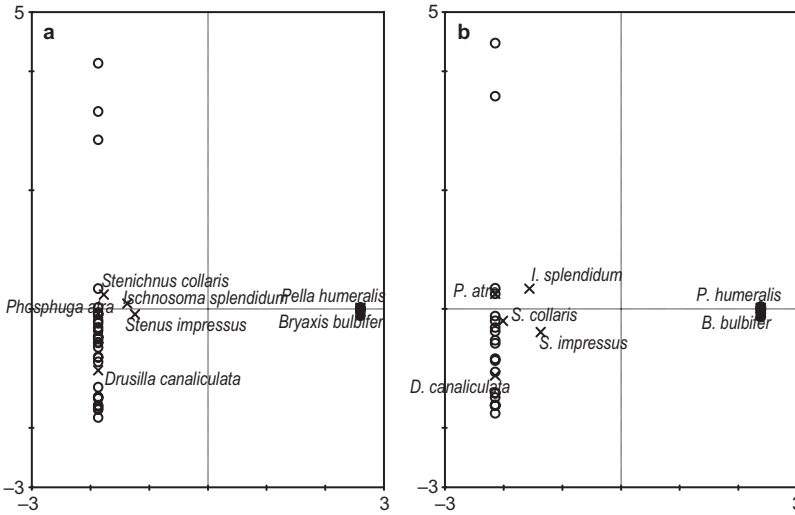


Fig. 4. CVA ordinations for Staphylinidae (cf. Table 3): (a) sample plots in productive forest ($n = 38$), and (b) *Vaccinium-Calluna* sample plots ($n = 27$). Circles = plots without ant mounds, dots = plots with ant mounds.

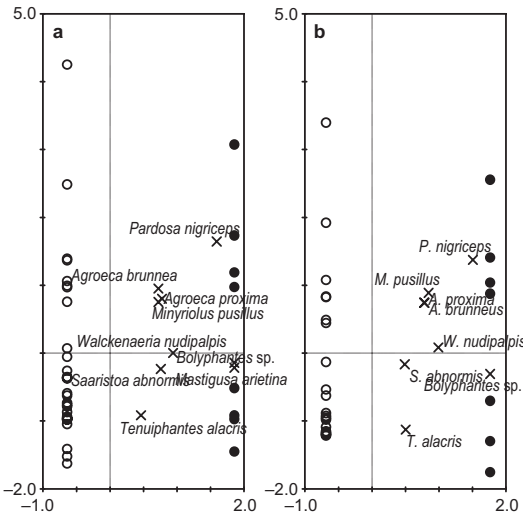


Fig. 5. CVA ordinations for Araneae (cf. Table 3): (a) sample plots in productive forest ($n = 38$), and (b) *Vaccinium-Calluna* sample plots ($n = 27$). Circles = plots without ant mounds, dots = plots with ant mounds.

globosus, one of the three carabid species mentioned by them, was also encountered in our study, but only two individuals were caught. Being a hygrophilous species and heathland pioneer (Bargmann *et al.* 2016), its occasional presence around ant mounds can be expected. A common feature of ant-Carabidae relationships is interference competition (*sensu* Hawes *et al.* 2013), where dietary overlap, not predation, results in exclusion of one group. Due to their social organization, red wood ants are more

numerous than carabids in the vicinity of mounds, so even though the former can kill the latter and *vice versa*, carabids are always outnumbered by ants. Even though Hawes *et al.* (2013) carried out their experiment on *Abax parallelepipedus* and *Pterostichus madidus* in a *F. rufa* dominated environment, it is likely that interference competition also occurs between *F. aquilonia* and the most abundant carabid in this study, *Carabus violaceus*, even though *C. violaceus* has a broader diet than for example *C. coriaceus* (Larochele 1990).

Staphylinidae

According to Päivinen *et al.* (2002), *Drusilla canaliculata*, *Oxypoda vittata*, *Pella cognata* and *P. humeralis* are myrmecophilous species. Only *D. canaliculata* and *P. humeralis* were abundant in our material, and our results confirmed a positive association of *P. humeralis* with *F. aquilonia*, while an association of *D. canaliculata* with *F. aquilonia* was negative. Stoeffler *et al.* (2011) reported *D. canaliculata* as non-myrmecophilous and free-living, but commonly found together with ants. *Drusilla canaliculata* has chemical defence mechanisms against ant attacks, but the probability of surviving such attacks is comparably lower than that of *Pella* species (Stoeffler *et al.* 2011). Also, taking the size of the species into consideration (approx. length 5 mm), *D. canaliculata* is more likely to live together with ants of the

genera *Myrmica* or *Lasius* rather than the larger *Formica* (e.g. Hölldobler *et al.* 1981) which poses a greater threat to *D. canaliculata* due to its poorer developed chemical mimicry as compared with that of *P. humeralis*.

Araneae

Associations of all spider species whose response to presence of ants was significant, were positive (Table 4). Several studies showed that ants and spiders mutually benefit from each other and apparently do not compete or prey upon each other (e.g. Gibb 2003, Lenoir *et al.* 2003, Moya-Laraño & Wise 2007, Schuch *et al.* 2008, Neuvonen *et al.* 2012), while in other studies the opposite was found, and relationships often

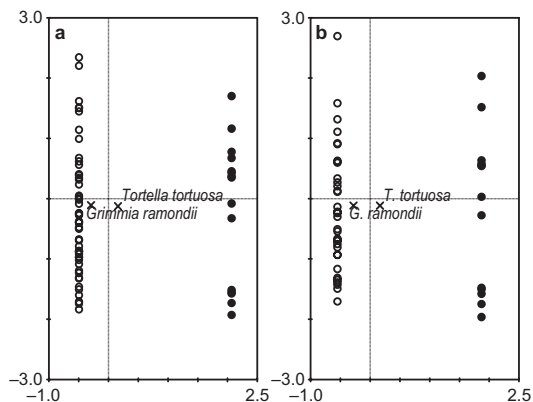


Fig. 6. CVA ordinations for Bryophyta (cf. Table 3): (a) sample plots in productive forest ($n = 65$), and (b) *Vaccinium-Calluna* sample plots ($n = 48$). Circles = plots without ant mounds, dots = plots with ant mounds.

Table 4. Associations (Assoc.) of invertebrate species with presence of ant mounds calculated with all plot data (65 sample plots in productive forest) and the data of *Vaccinium-Calluna* (*Vacc.-Call.*) sample plots. Fit > 0.20 with CVA axis 1 indicates a strong negative or positive association with ant mound presence. Cf. also Figs. 2–5.

Group	Species	Indiv.		Number of plots		Fit		Assoc.
		All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	
Linyphiidae	<i>Saaristoia abnormis</i>	75	50	23	16	0.33	0.20	Positive
Liocranidae	<i>Agroeca proxima</i>	134	117	23	17	0.48	0.57	Positive
	<i>Agroeca brunnea</i>	44	40	19	16	0.15	0.20	Positive
Lycosidae	<i>Pardosa nigriceps</i>	38	38	7	7	0.24	0.29	Positive
Gnaphosidae	<i>Zelotes clivicola</i>	76	70	15	13	0.24	0.33	Positive
Carabidae	<i>Carabus violaceus</i>	918	660	31	21	0.16	0.22	Negative
Gastropoda	<i>Nesovitrea hammonis</i>	476	390	36	26	0.20	0.24	Positive
Staphylinidae	<i>Drusilla canaliculata</i>	1429	1016	28	19	0.25	0.25	Negative
	<i>Pella humeralis</i>	2454	1990	8	7	0.64	0.56	Positive

Table 5. Associations (Assoc.) of plant species with presence of ant mounds calculated with all plot data (65 sample plots in productive forest) and the data of *Vaccinium-Calluna* (*Vacc.-Call.*) sample plots. Fit > 0.20 with CVA axis 1 indicates a strong negative or positive association with ant mound presence. Cf. also Figs. 6 and 7. For abundance classes cf. chapter ‘Species abundance’.

Group	Species	Abundance		Number of plots		Fit		Assoc.
		All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	All	<i>Vacc.-Call.</i>	
Lichens	<i>Hypogymnia physodes</i>	3–4	3–4	65	48	0.29	0.27	Positive
	<i>Hypogymnia tubulosa</i>	2–3	2–3	63	48	0.29	0.33	Positive
	<i>Imshaugia aleurites</i>	3–4	3–4	64	48	0.24	0.24	Positive
	<i>Platismatia glauca</i>	3–4	3–4	64	48	0.24	0.24	Positive
	<i>Pseudevernia furfuracea</i>	3–4	3–4	65	48	0.25	0.30	Positive
Juncaceae	<i>Juncus bulbosus</i>	0–1	0–1	12	11	0.24	0.19	Positive

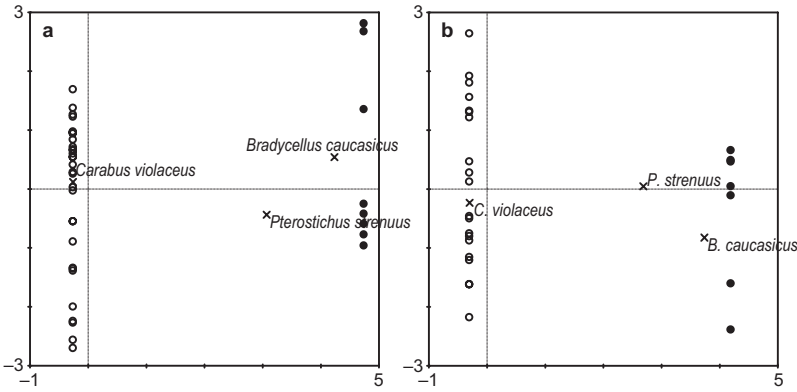


Fig. 7. CVA ordinations for Carabidae (cf. Table 3): (a) sample plots in productive forest ($n = 38$), and (b) *Vaccinium-Caluna* sample plots ($n = 27$). Circles = plots without ant mounds, dots = plots with ant mounds

depended on the taxonomic resolution (Halaj *et al.* 1997, Lenoir 2003, Sanders & Platner 2007, Mihorski 2011, Mestre *et al.* 2013).

Contradicting patterns indicate that spiders do not respond to presence of ants as a group; autoecological studies or analyses at least at the family level or functional feeding group are needed to extract consistent information, as shown by e.g. Sudd and Lodhi (1981), Lenoir *et al.* (2003), Sanders and Platner (2007) and Mihorski (2011). Species of Liocranidae, Gnaphosidae and Lycosidae are active hunters. In our study, those groups were represented by *Agroeca proxima*, *A. brunnea*, *Pardosa nigriceps* and *Zelotes clivicola*, which all showed positive associations with presence of ants. There are numerous examples that free-living spiders profit from ant presence and abundance (e.g., Halaj *et al.* 1997, Moya-Laraño & Wise 2007, Platner *et al.* 2012, Davey *et al.* 2013, Mestre *et al.* 2013) and our results corroborate those findings. As biomass of Collembola in some studies was found to correspond with ant abundance (Moya-Laraño & Wise 1997), and that intraguild predation seems limited between ants and hunting spiders (Halaj *et al.* 1997), a plausible explanation of the positive associations between hunting spiders and ants is that they, both being major predators on Collembola, occur in higher numbers in areas where the prey is abundant as well.

Gastropoda

Nesovitrea hammonis were weakly and positively associated with ant mound density. The species

profits from high concentrations of exchangeable ions of calcium and nitrogen (Wareborn 1992, Hermida *et al.* 1996), and appears to be indifferent to pH (Ondina *et al.* 2004). The effects of concentration of those elements vary with ant species but they seem to be more pronounced within and close to ant mounds of some ant species than in their surroundings (e.g. Petal 1978, but see Frouz *et al.* 2008, Jílková *et al.* 2011). Additionally, overall organic content increases close to ant mounds (Jílková *et al.* 2011) and being saprophagous, the snails may have access to increased amounts of food there, provided they are not attacked by ants. An alternative but not exclusive explanation to *N. hammonis* being more abundant in the vicinity of *F. aquilonia* mounds is to avoid predation from *Carabus violaceus*. Our study showed that *C. violaceus* was negatively associated with ant presence, and being a voracious predator on most snails (e.g. Paill 2000), it is likely that the predation pressure is lower near the mounds.

Other abundant gastropods, *Columella aspera* and *Punctum pygmaeum*, were found not to be associated with the *Formica* ants even though one could expect them to also profit from increased levels of exchangeable ions. However, according to Ondina *et al.* (2004), both species are negatively affected by high levels of calcium and positively by high N/C ratio.

Lichens and bryophytes

All species associations (CVA fit > 0.2) with ants were positive (Table 5) despite the rather coarse

and indiscriminate 0–4 scale of relative abundance. Lorentsson and Mattsson (1999) observed *Formica cunicularia* workers harvesting soredia of *Ramalina* sp. or *Hypogymnia physodes*. In our study, *H. physodes* was very abundant and positively associated with ants (Table 5). This may be due to sensitivity of CVA and is most likely an artefact because the species was highly abundant everywhere. Nonetheless, we have no evidence that ants segregate among species but they rather harvest whatever is available as there is a positive correlation between lichen and bryophyte species composition in the mound material and their composition and abundance in the vicinity of the mound (Heinken *et al.* 2007). Despite the limitations stemming from the method species abundances were scored, our results corroborate those of Heinken *et al.* (2007) in that the most abundant species were also positively associated with ant presence.

Conclusions

Currently it is acknowledged that in European temperate forests ants affect the arthropod forest-floor species community to a lesser extent than their abundance could suggest (Laakso 1999, Laakso & Setälä 2000, Lenoir *et al.* 2003, Domisch *et al.* 2009, Neuvonen *et al.* 2012). Predation of ants on arthropods plays a minor role as honeydew is by far the most important food source for ants, normally constituting over 80% of the diet (Domisch *et al.* 2009). However, as abundant ant larvae require nitrogen, which is very limited in honeydew, there is always a need for animal prey. Diptera is apparently the most important arthropod group preyed upon by ants while the proportions of Coleoptera and Araneae are comparably small (Domisch *et al.* 2009). Our results regarding species of beetles and spiders corroborate those observations as there were mostly no associations between numbers of individuals of some species and ant mound density, and if an association was found it was predominantly positive. Laakso (1999) and Laakso and Setälä (2000) found that predatory meso- and macrofauna were significantly reduced in experimental plots with high densities of *F. aquilonia* ants. Our results in part support their observa-

tions as Carabidae treated as a group were negatively associated with ant mound density while no association was found in case of spiders and staphylinids (Table 2).

Carabidae was the only invertebrate group being negatively associated with ant mound density and this effect was shown for the most abundant carabid species, *Carabus violaceus*. The second most common arthropod in the our data, *Drusilla canaliculata*, was also negatively affected by mound density of *Formica aquilonia*. Its known association with ants does not include *Formica* but smaller genera of *Myrmica* and *Lasius*. Thus, our hypothesis 1 is confirmed with the exception of spiders. The most common species, the myrmecophilous *Pella humeralis*, was strongly associated with ants as all specimens were sampled in plots with ant mounds present, which confirms hypothesis 2. Finally, the species richness of lichens and epiphytes was negatively affected by ant mound density, which was probably due to their inability to regenerate when being harvested by ants for mound building material or a result of chemical changes in the vicinity of mounds. As such, our hypothesis 3 was not confirmed.

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