# Comparison of ant-associated beetle communities inhabiting mounds of forest-dwelling ants in forests and forest clearings

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## Abstract

Red wood ant nests contain a highly diverse community of invertebrates, which is largely due to their abundant resources and regulated microclimatic conditions. However, clear felling causes nest mounds to lose surface layer moisture thus disrupting their inner stability. To study the effects of clear felling on ant-associated beetles (myrmecophile and non-myrmecophile), 41 nests of *Formica aquilonia* located on three clear fells and adjacent mature forest stands were sampled, and the beetle communities between these habitats were compared. We investigated how habitat type, nest surface moisture content, nest volume, and isolation affect the community composition, species richness and abundance of beetles. Beetle community composition or species richness did not markedly differ between clearings and forests, although total abundance was higher in forests. Also, total species richness and abundance, and myrmecophile abundance increased with increasing moisture content. Overall, nests with similar moisture content and volume had similar species compositions. Nest volume correlated negatively with myrmecophile species richness. Nest isolation was not related to species richness or abundance. The lower abundances in clearings could be problematic in the long-term, since small populations are more likely of becoming extinct. To ensure the survival of ants and their associates, small-scale clearings should be preferred.

**Keywords:** Formicidae, myrmecophiles, humidity, species richness, clear felling

## Introduction

The effects of clear felling and other forest management practices on animal populations and communities have received much interest (e.g., Heliövaara and Väisänen 1984; Niemelä 1997). Felling of trees and subsequent soil management together with the changing microclimate bring about considerable changes in the forest-dwelling fauna (Heliövaara and Väisänen 1984; Niemelä 1997).

Red wood ants (*Formica rufa* group) are dominant species in Eurasian boreal forests (e.g., Rosengren and Pamilo 1983) where they may be beneficial for forestry through predation of various pest species (Way and Khoo 1992). Furthermore, they build large and long-lived nest mounds consisting of forest litter, soil particles, and resin, thus changing soil structure and nutrient distribution (Frouz and Jilková 2008). Their nests also support a highly diverse group of invertebrates, some of which, the so called myrmecophiles, are dependent on the ants (e.g., Robinson et al. 2016). The nest mounds are relatively stable environments with temperature and humidity conditions regulated to be optimal by the ants (Hölldobler and Wilson 1990). These characteristics together with ample resources (e.g., prey and other organic matter) are considered as the main contributing factors to the formation of the associate fauna.

Effects of clear felling on wood ants are clearly negative, as evidenced by reduced reproduction and offspring growth as well as increased nest abandonment rate

(Sorvari and Hakkarainen 2005, 2007, 2009). These are caused not only by the loss of a large part of the ants' food resources (especially aphid-containing trees) ( Rosengren et al. 1979), but also by the drastic changes on abiotic conditions, i.e., increased solar radiation and wind, more extreme temperature conditions, and changed moisture conditions, which in turn disrupt the inner functions of their nest mounds (Sorvari et al. 2016). Nest mounds of *Formica aquilonia* Yarrow 1955 were recently found to be significantly drier in clear fell areas than in forests (Sorvari et al. 2016). This is likely behind the less stable inner temperatures observed in clear fell nests (Sorvari and Hakkarainen 2009), since dry nests generally have more variable temperatures than moist nests (Frouz and Finer 2007). Nest mounds are developed over years, even decades, and shaped to suit the surrounding habitat. Nests that are built in shaded forests with a humid microclimate and shelter from wind are typically high and steep sloped, whereas nests in more open and windy areas are flatter (Martin 1975; Sorvari et al. 2016). Well-functioning nests of *Formica polyctena* Förster 1850 usually have a moist surface layer acting as a barrier against cooling winds and a dry insulating warm core (Elo et al. 2017) where the conditions are optimal for the development of ant pupae (Hölldobler and Wilson 1990). As the heat generated by the ants' activity rises towards the cooler surface, condensation occurs, thus creating the moist layer. Drying of the surface layer after clear felling disrupts the thermoregulatory ability of the nest mound, and thus also the development of ant brood.

It has, however, remained unclear whether the changes caused by clear felling influence the invertebrate assemblage within the nest mounds. Since insects and other invertebrates are ectotherms, temperature and humidity play an important role in their growth and development (Ratte 1984; Chown and Nicolson 2004). Moisture is one of the main abiotic factors structuring soil invertebrate communities and might thus determine the quality of ant nest mounds for the associate species as well (Giller, 1996). Moisture may have direct effects through desiccation and indirect effects through changes in food resources and microhabitat modifications (e.g., Setälä et al. 1995; Pflug and Wolters 2001).

In this study, we compare the community composition, species richness and abundance of ant-associated beetles in clear fell and forest nests of red wood ant *F. aquilonia.* Beetles were chosen as a study group, since they are one of the most diverse groups of ant associates (Hölldobler and Wilson 1990). Our aim was to find out i) whether species composition, species richness and abundance differ between clear fells and forests, ii) whether species composition is structured by nest mound characteristics and geographic location, and iii) whether species richness and abundance were associated with mound characteristics (i.e. moisture and nest volume) and nearest neighbour distance.

## Materials and methods

The studied nest mounds belonged to the highly polygynous (several queens per nest) and polydomous (multi-nest colonies) red wood ant *Formica aquilonia*, a member of the *F. rufa* group and the most common wood ant in the boreal coniferous forests ( Punttila and Kilpeläinen 2009). Though *F. aquilonia* predominantly inhabits interiors of mature forests, it can also be found from forest edges (Punttila 1996; Punttila and Kilpeläinen 2009).

The field work was carried out near the city of Kuopio in central Finland (WGS84: 62°52’: 27°29’) on three clear fell – forest pairs in September 2014 (on 5th, 7th and 8th). On each site, the clear fell area and forest stand were side by side. The distance between the sites varied between 3.9 km and 6.5 km. The forests were dominated by Norway spruce (*Picea abies*) mixed with Scotts pine (*Pinus sylvestris*) and birches (*Betula pendula, B. pubescens*) with bilberry (*Vaccinium myrtillus*) dominating the scrub layer. The clear felling occurred one to three years before the study.

In total, 41 nest mounds of *F. aquilonia* were sampled: seven nests per each clear fell and forest site, except in one forest where only six suitable nests were found. As selection criteria, we used the minimum basal diameter of 0.70 m as well as the occurrence of a seemingly vital *F. aquilonia* colony, i.e., the deserted or semi-deserted and young (small) post-harvesting nests were not used. From each nest, 0.5 l of nest material was collected just beneath the moisture layer (10-15 cm from the top) and sieved while in the field (2 mm mesh size). The beetles were extracted from the sieved material with the Berlese-funnel technique in room temperature for five days. Beetles were identified on species level using identification keys (Freude et al. 1971, 1974, 2012) and comparisons to the beetle collections of the Zoological Museum at the University of Turku (ZMUT), Finland.

The nest surface moisture was measured gravimetrically from a nest material sample taken from the surface layer (depth 0-10 cm) near the top of the mound simultaneously when sampling the beetles; further details and findings were already reported in Sorvari et al. (2016). The height and basal diameter of nest mounds were measured, and the above ground volume of the nest mounds was quantified using the equation for a half ellipsoid: $V = (4/3\pi abc)/2$, where a and b are the radiuses and c the height of the nest (i.e. the lengths of the semi-axes of the ellipsoid). Distance to the nearest neighbouring nest was calculated using nest coordinates; the coordinates were recorded for all study nests and one non-study nest, as in all but one case the nearest neighbour was another study nest.

### *Statistics*

To visualize the beetle community compositions, we used principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity, which considers species abundances (Legendre and Legendre 1998). This was done both using the full dataset and separately for myrmecophilous species. Since a couple of species were much more abundant in some nests compared to the other species, a square root transformation was done on the data first. Simple and partial Mantel tests based on Pearson's correlation were used to test for correlations of faunal distance with environmental and geographic distance. A simple measure of environmental distance was obtained by using two variables of nest mound characteristics (moisture and nest volume). First, a principal component analysis (PCA) of the environmental variables was performed, after which Euclidean distances were computed for the first principal components (Oksanen 2015). The significance of correlations was determined with a permutation test using 999 permutations. These analyses were performed with the R software using the vegan package (Oksanen et al. 2017; R Core Team 2017).

The GLIMMIX procedure of the statistical software SAS 9.3 was used to study the species richness and abundance of i) all beetle species and ii) myrmecophiles in the nests of *F. aquilonia*. Poisson error distribution, suitable for count data, was employed with log link function. Nest surface moisture content and habitat type were the main fixed effects, while nest mound volume and distance to the nearest neighbouring nest were used as covariates. However, since moisture content was associated with habitat type, being lower in clear fells ($F_{1,37} = 132.66$, $P < 0.0001$; see Sorvari et al. 2016), and nearest neighbour distance was correlated with moisture (Pearson's $r = -0.34$, $P = 0.03$) and volume (Spearman's $\rho = 0.35$, $P = 0.025$), habitat type and distance were tested in a separate model. Initially, site (clear fell - forest pair) was used as random factor in the models with Kenward-Roger approximation for degrees of freedom. However, with species richness models, the use of Kenward-Roger approximation caused problems (Den DF of the fixed effects was equal to 1), so it was removed and site was included as fixed effect instead of random. Since site was not even close to significant it was dropped from the models. Also, the models without site had smaller AIC values, indicating better model fit (Akaike, 1974). The structure of the initial and final models with AIC value comparison can be seen in supplementary Table S1[1].

With abundance models, overdispersion was encountered when using Poisson. To correct this, we used generalized Poisson distribution instead (log link function) with maximum likelihood estimation based on Laplace approximation. Generalized Poisson is similar to the more commonly used negative binomial distribution, i.e., they usually seem to fit equally well; however, generalized Poisson distribution fits better with data having long right tails as was the case here (Joe and Zhu 2005).

Occurrence (presence-absence) of the most prevalent myrmecophiles (those found in at least ten nests) was studied in relation to habitat type. Only one species, *Monotoma conicicollis* Aubé 1837, showed a significant difference in nest occupancy between habitats, being more common in forest nests ($F_{1,39} = 8.07$, $P = 0.007$). The abundance of this species was further studied in relation to moisture content and volume. Since the congeneric species, *Monotoma angusticollis* (Gyllenhal 1827) was

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[1] Supplementary material

found only in forest (in four nests), also another model with the pooled abundances of both species was made. Binomial distribution with logit link function was used for the occurrence models and Poisson distribution with log link function for abundance models. Kenward-Roger approximation was used for degrees of freedom.

## Results

In total, 32 beetle species (1123 individuals) of which 17 were myrmecophilous (815 individuals) were identified (Table S2[2]). Most species (59 %) were found both in forest and clear fell nests. The two most common species were myrmecophiles *Ptenidium formicetorum* and *Ptilium myrmecophilum* (Ptiliidae) with 306 individuals in 28 nests and 248 individuals in 30 nests respectively. Most non-myrmecophilous species (N = 8) were found only as singletons in this study. However, a few non-myrmecophilous species were very common (*Acrotrichis montandonii*: 105 individuals in 22 nests, *Euplectus signatus*: 119 individuals in 17 nests, and *Oligota muensteri*: 55 individuals in 10 nests), and they are regularly associated with ants (Päivinen et al. 2002).

The ordination diagrams of the PCoA did not reveal any clearly separable clusters and no polarization into clear fell and forest nests (Fig. 1). In both ordinations, most nests on forest site 1 appeared to have quite similar species compositions, while nests on other sites were less aggregated (Fig. 1). Dissimilarity of the species composition was

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[2] Supplementary material

correlated with environmental distances, that is, species composition was more similar in nests sharing similar moisture content and nest volume (all species: $r_M$ = 0.239, $P$ = 0.009; myrmecophiles: $r_M$ = 0.257, $P$ = 0.004). Partial Mantel tests showed that environmental distance correlated with faunal distances even after considering the effect of geographical distance (all species: $r_M$ = 0.221, $P$ = 0.011; myrmecophiles: $r_M$ = 0.263, $P$ = 0.003). Species composition was weakly structured along a spatial gradient when all species were considered ($r_M$ = 0.103, $P$ = 0.006), but when environmental distance was taken into account there was no correlation ($r_M$ = 0.043, $P$ = 0.111). In the case of myrmecophiles, there was no correlation with geographic distance ($r_M$ = 0.021, $P$ = 0.245).

The total number of species found in clear fells was higher than that in forests (31 and 20 respectively; Table 1), though on average forest nests had slightly more species (Table 1). However, there was no significant difference in species richness between habitat types (all species: $F_{1, 36}$ = 0.83, $P$ = 0.367; myrmecophiles: $F_{1, 36}$ = 0.67, $P$ = 0.419). Total abundance of beetles was significantly higher in forest nests than in clear fell nests (all species: $F_{1, 36}$ = 4.43, $P$ = 0.042; Fig. 2), while there was no difference in myrmecophile abundances ($F_{1, 36}$ = 1.9, $P$ = 0.177).

Distance to the nearest neighbouring nest varied between 11 and 82 metres (mean = 34 m, SD = 17.6). The nearest neighbour for each studied nest happened to be within the same habitat type. Distance was not associated with species richness (all species:

$F_{1,36} = 0.36$, $P = 0.553$; myrmecophiles: $F_{1,36} = 0.47$, $P = 0.498$) or abundance (all species: $F_{1,36} = 0.03$, $P = 0.853$; myrmecophiles: $F_{1,36} = 0.1$, $P = 0.756$).

The moisture content of the ant nest surface layer varied from 6.1 % to 52.5 % in clear fells (mean = 20.5 %, SD = 13.0, N = 21) and from 34.2 % to 67.2 % in forests (mean = 55.3 %, SD = 9.3, N = 20). Total species richness of beetles increased with increasing surface moisture content (Table 2, Fig. 3), while no association was found with the species richness of myrmecophiles (Table 2). There was a significant positive correlation between beetle abundance and nest surface moisture content (Table 2, Fig. 4 a-b). Abundance of *Monotoma* increased with increasing moisture content (Table 2, Fig. 4 c). Nest volume was not significantly associated with beetle abundance or total species richness, though with myrmecophile species richness there was a significant negative correlation (Table 2, Fig. 5).

## Discussion

We identified 17 myrmecophilous beetle species, including three red wood ant specialists, and 15 non-myrmecophilous beetle species in the 41 studied nests of *F. aquilonia*. The species richness was similar to that reported in previous studies; Päivinen et al. (2004) found 16 myrmecophilous beetle species in 49 mounds of *F. aquilonia* in central Finland, Härkönen and Sorvari (2014) reported 17 myrmecophilous beetles in 12 *F. polyctena* mounds in SW Finland, and Parmentier et al. (2015) found 13 myrmecophilous beetles in 83 nest mounds (29 *F. rufa,* 54 *F.*

*polyctena*) in Belgium. Päivinen et al. (2004) collected samples in late spring, since according to their field observations, adults of most myrmecophilous beetle species are only found in the nests during spring. However, as demonstrated by our data, just as diverse myrmecophile beetle community appears to be present in early autumn. Most of the observed myrmecophilous species have several hosts of *Formica* and *Lasius* ants, but three species (*M. conicicollis, M. angusticollis* and *Spavius glaber*) are wood ant specialists (Päivinen et al. 2002). Most non-myrmecophilous species in this study have been found from ant nests before (Päivinen et al. 2002). Some of these species, such as *Acrotrichis montandonii, Oligota muensteri*, *Euplectus signatus,* and *E. karstenii,* are regularly associated with ants (Päivinen et al. 2002) and might thus be classified as facultative myrmecophiles.

There was no clear difference in community composition between the felled and non-felled habitat types. Mostly, the same species were found in both clear fell and forest nests. All singleton species (N = 9) were found from clear fells, and apart from one, they were all non-myrmecophilous. Some of them could be new (post-felling) colonists. Similar nests (in terms of moisture content and size) had more similar species compositions. Geographic location, on the other hand, did not structure species composition.

Moisture is one of the most important variables influencing the distribution, abundance, and life cycles of insects and other soil organisms (e.g., Giller 1996;

Chown and Nicolson 2004; Tsiafouli et al. 2005). Dry soils often have lower diversity and abundance of soil animals (Tsiafouli et al. 2005), and our results are partly in accordance with this general pattern. Total beetle species richness as well as both total and myrmecophile abundance increased with increasing nest surface layer moisture content. On the other hand, myrmecophile species richness was not associated with moisture. Parmentier et al. (2015) also found no association between moisture content in the central core of *F. polyctena* and *F. rufa* nests and the species richness or community composition of myrmecophiles, even though the moisture content varied considerably between the nests (5 – 67 %).

The nest mound surface moisture content was significantly lower in clear fells compared to forests (see results in a companion study of these same nest mounds Sorvari et al. 2016). Yet, we found no significant difference in species richness between the habitat types, although forest nests had slightly more species on average. However, while myrmecophile abundance did not differ between habitat types, total abundance was higher in forest nests. It might take longer than a couple of years for clear felling to have an effect on the beetle assemblage. Moisture was measured only from one place at the top of the nest mound. However, the surface layer closer to the ground could retain more moisture than the top of the nest. Thus, beetles could stay in the nests, especially if they are not very sensitive to the increased temperature variations.

Of the ten most common myrmecophiles, only one species showed a clear difference in occurrence between habitat types. *M. conicicollis* was significantly more common in forest nests than in clear fell nests, while the less prevalent congeneric *M. angusticollis* was only found in forest. As stated before, these two myrmecophiles are also wood ant specialists. This could indicate that they are more vulnerable to disturbances occurring to the ant colony than the more generalist species, which may also be associated with *Lasius* ants and are thus accustomed to more variable conditions. The abundance of *Monotoma* increased with increasing moisture content. In laboratory experiments, both *Monotoma* species were found to feed on ant brood (eggs and larvae) and ants' prey items (Parmentier et al. 2016a, 2016b). They are also thought to be fungivores, and according to stable isotope analysis, seem to occupy slightly different niches (e.g., feeding on different types of fungi)(Parmentier et al. 2016a). The high humidity and temperature conditions within the nest mounds together with a constant input of new organic material give rise to an abundant and functionally specialised decomposer community of fungi and bacteria, which creates the basis for multi-level food webs (Jílková et al. 2015; Laakso and Setälä 1998). Drying of the nest mounds may hence decrease the growth of these microbes thus reducing the food resources of fungivores and bacterivores such as earthworms, springtails, oribatid mites, and also beetles such as *Monotoma* (Laakso and Setälä 1998).

In addition to the *Monotoma* species, the non-myrmecophilous rove beetles *E. signatus* (Pselaphinae) and *O. muensteri* (Aleocharinae) were also more common in forests than in clear fells. Pselaphinae species are predatory, feeding on mites, springtails, worms and symphylans (Sabella and Mifsud 2016). They are typically associated with forest litter and debris, but can be found in any habitat as long as there is sufficient humidity for their prey to exist (Sabella and Mifsud 2016). The feeding habits of *Oligota* are poorly known, though at least some species prey on mites (Frank et al. 1992). Elo et al. (2017) found that the species richness and abundance of ant associated oribatid mites, which predominantly occupy the nest mound surface layer, was significantly positively correlated with the mound surface moisture content.

Like in our previous study (Härkönen and Sorvari 2014), and in contrast to Päivinen et al. (2004), nest volume was negatively associated with myrmecophile species richness, while total species richness and abundance were not significantly affected. However, since an equal amount of nest material was collected from each nest, this gives indication of beetle density rather than population size. Had we looked through the whole nest or adjusted the sampling to be proportional to nest size, we would likely have found that larger nests harbour more species. Samples were also taken from the same depth, regardless of the nest height. In large nests, myrmecophiles could be more aggregated deeper in the nest. Nevertheless, large, high-profiled nests are more prone to drying after clear felling than small nests (Sorvari et al. 2016). The steep-sloped forest nests are not well-suited to open areas, and especially larger nests may be more vulnerable to the increased wind conditions in clear fells, whereas smaller nests could be more sheltered by the undergrowth. Thus, assemblages within large nest mounds might be more affected by clear felling than assemblages within smaller nests.

Red wood ant diet consists mostly of honey-dew, aphids, and other arthropods collected from trees (Rosengren and Sundström 1991; Punttila et al. 2004). When excluded experimentally from trees, wood ants search for new trees further away instead of increasing predation on the forest floor (Lenoir 2003). Normally, large colonies may have enhanced capabilities to exploit food resources due to larger worker populations (Wagner and Gordon 1999). However, in clear fells, the environment may not provide sufficient resources for large colonies causing a large part of the worker force to starve. This will in turn further reduce the colony’s ability to control the abiotic conditions within the nest.

In contrast to previous studies (Päivinen et al. 2004; Härkönen and Sorvari 2014; Parmentier et al. 2015), nearest neighbour distance had no effect on species richness or abundance of beetles, although the distances varied considerably (11-82 m). While the variable conditions surrounding and within the nests in clear fells might be confounding factors in this case, nearest neighbour distance may not be the most accurate measure for isolation. For instance, for the occurrence of the guest ant

*Formicoxenus nitidulus,* inter-nest distance as such was not important, but rather the nest density (Härkönen and Sorvari 2017). The degree to which a nest mound is effectively isolated depends on the dispersal ability of the species of interest and the location of the nest in relation to all the other nests in the area, not just the closest one. However, using e.g. nest density would require a more extensive recording of coordinate information than was done here.

Although we studied a large number of nests, they were from only three clear fell – forest pairs. This small number of true replicates somewhat limits generalization of the results. While this limitation is partly avoided with the pairwise study set up, more studies in a wider geographical area would give more generalizable results.

In conclusion, although total and myrmecophile species richness was not greatly affected by clear felling, and only the total species richness was lower in dry nests, the reduced population sizes in dry nests could be a problem in the long run. After all, small populations have a higher risk of becoming extinct (Hanski 1999). Furthermore, some species may be more vulnerable than others either directly due to the changed physical conditions or indirectly through changes in food availability. We investigated only the short-term effects of clear felling on the associate community in active nest mounds. However, nests in clear fells have a high probability of being abandoned (Sorvari and Hakkarainen 2007), in which case the myrmecophiles will inevitably suffer. On the other hand, the surviving nests might receive immigrants escaping from the deserted nests, which could help keep the populations viable. How the community in the surviving nests develops in the long term requires further study. At any rate, since nests in clear fell areas have a better chance to survive when they are located close to the forest edge (Sorvari 2013), smaller-scale clearings are preferable to ensure the continued survival of red wood ants and their associates.

## Acknowledgements

The study was funded by Jenny and Antti Wihuri Foundation. A previous version of this paper was published as part of a doctoral thesis by S.K. Härkönen in the Annales-series of the University of Turku (2017, Annales Universitatis Turkuensis, AII 338).

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**Table 1.** Number of myrmecophilous, non-myrmecophilous, and all beetle species and individuals found in the nests of red wood ant *Formica aquilonia* in clear fells and forests with the mean number of species and individuals (± SD) found per nest.

| | | Myrmecophiles | | Non-myrmecophiles | | All species | |
|---|---|---|---|---|---|---|---|
| | | N | mean ± SD | N | mean ± SD | N | mean ± SD |
| Species | Clear fell | 16 | 3.7 ± 2.6 | 15 | 1.7 ± 1.3 | 31 | 5.5 ± 3.3 |
| | Forest | 14 | 4.4 ± 2.0 | 6 | 1.9 ± 1.2 | 20 | 6.3 ± 2.5 |
| | Total | 17 | 4.1 ± 2.3 | 15 | 1.6 ± 1.1 | 32 | 5.9 ± 3.0 |
| Individuals | Clear fell | 447 | 21.3 ± 32.4 | 114 | 5.4 ± 12.1 | 561 | 26.7 ± 43.0 |
| | Forest | 346 | 17.3 ± 14.2 | 216 | 10.8 ± 9.1 | 562 | 28.1 ± 21.9 |
| | Total | 793 | 19.3 ± 25.0 | 330 | 7.5 ± 9.7 | 1123 | 27.4 ± 33.9 |

**Table 2.** The effect of nest surface moisture content and nest mound volume on the species richness and abundance of all beetles and myrmecophilous beetles in the nests of red wood ant *Formica aquilonia*.

| | Distribution | Explanatory variable | DF | F | P |
|---|---|---|---|---|---|
| Species richness | | | | | |
| Total | Poisson | Moisture | 1, 38 | 4.77 | 0.035 |
| | | Nest volume | 1, 38 | 3.52 | 0.068 |
| Myrmecophiles | Poisson | Moisture | 1, 38 | 2.51 | 0.121 |
| | | Nest volume | 1, 38 | 5.26 | 0.027 |
| Abundance | | | | | |
| Total | GP | Moisture | 1, 36 | 9.82 | 0.003 |
| | | Nest volume | 1, 36 | 1.1 | 0.301 |
| Myrmecophiles | GP | Moisture | 1, 36 | 5.25 | 0.028 |
| | | Nest volume | 1, 36 | 3.37 | 0.075 |
| *M. conicicollis* | Poisson | Moisture | 1, 38 | 9.87 | 0.003 |
| | | Nest volume | 1, 38 | 0.04 | 0.838 |
| pooled *Monotoma* | Poisson | Moisture | 1, 38 | 16.53 | 0.0002 |
| | | Nest volume | 1, 38 | 0.31 | 0.580 |

Note: GP = Generalized Poisson

**Fig. 1.** PCoA ordination diagrams based on Bray-Curtis dissimilarity index visualising beetle species composition in *Formica aquilonia* nests for (a) all species and (b) myrmecophiles. Filled symbols refer to forest nests and open symbols indicate clear fell nests (site 1 = triangle, site 2 = circle, site 3 = square).

**Fig. 2.** The estimated marginal means (± 95 % CL) of beetle abundance in clear fell and forest nests of *Formica aquilonia*.

**Fig. 3.** The species richness of ant-associated beetles (all species) in relation to the mound surface layer moisture content (%) of *Formica aquilonia* nest mounds. Lines represent predicted values (mean ± 95 % CL) and symbols represent observed values in clear fell nests (open) and forest nests (filled).

**Fig. 4.** The abundance of ant-associated beetles in relation to the surface layer moisture content (%) of *Formica aquilonia* nest mounds: (a) all species, (b) myrmecophiles, and (c) pooled *Monotoma* (i.e. *M. conicicollis* and *M. angusticollis*). Lines represent predicted values (mean ± 95 % CL) and symbols represent observed values in clear fell nests (open) and forest nests (filled). Note the break in the y-axis in (a) and (b).

**Fig. 5.** The species richness of myrmecophilous beetles in relation to the volume (l) of *Formica aquilonia* nest mounds. Lines represent predicted values (mean ± 95 % CL) and symbols represent observed values in clear fell nests (open) and forest nests (filled).

Fig. 1.

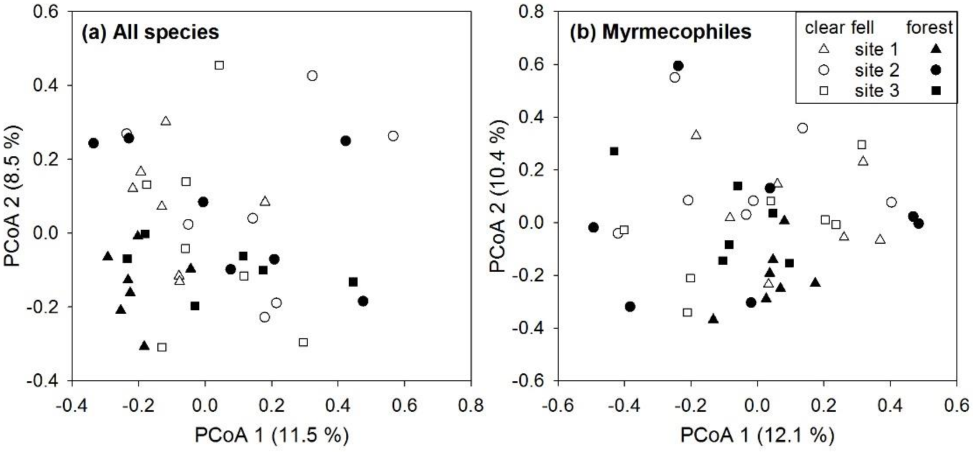

(a) All species
PCoA 1 (11.5 %)
PCoA 2 (8.5 %)
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
(b) Myrmecophiles
PCoA 1 (12.1 %)
PCoA 2 (10.4 %)
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
clear fell
forest
site 1
site 2
site 3

Fig. 2.

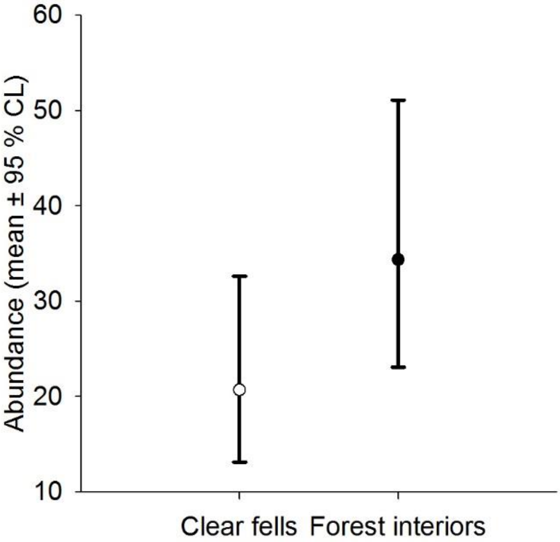

Abundance (mean ± 95 % CL)
60
50
40
30
20
10
Clear fells
Forest interiors

Fig. 3.

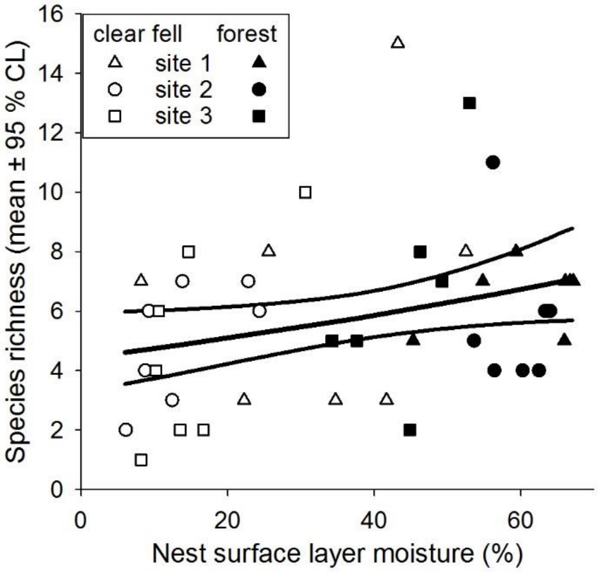

clear fell
forest
site 1
site 2
site 3
Species richness (mean ± 95 % CL)
16
14
12
10
8
6
4
2
0
0
20
40
60
Nest surface layer moisture (%)

Fig. 4.

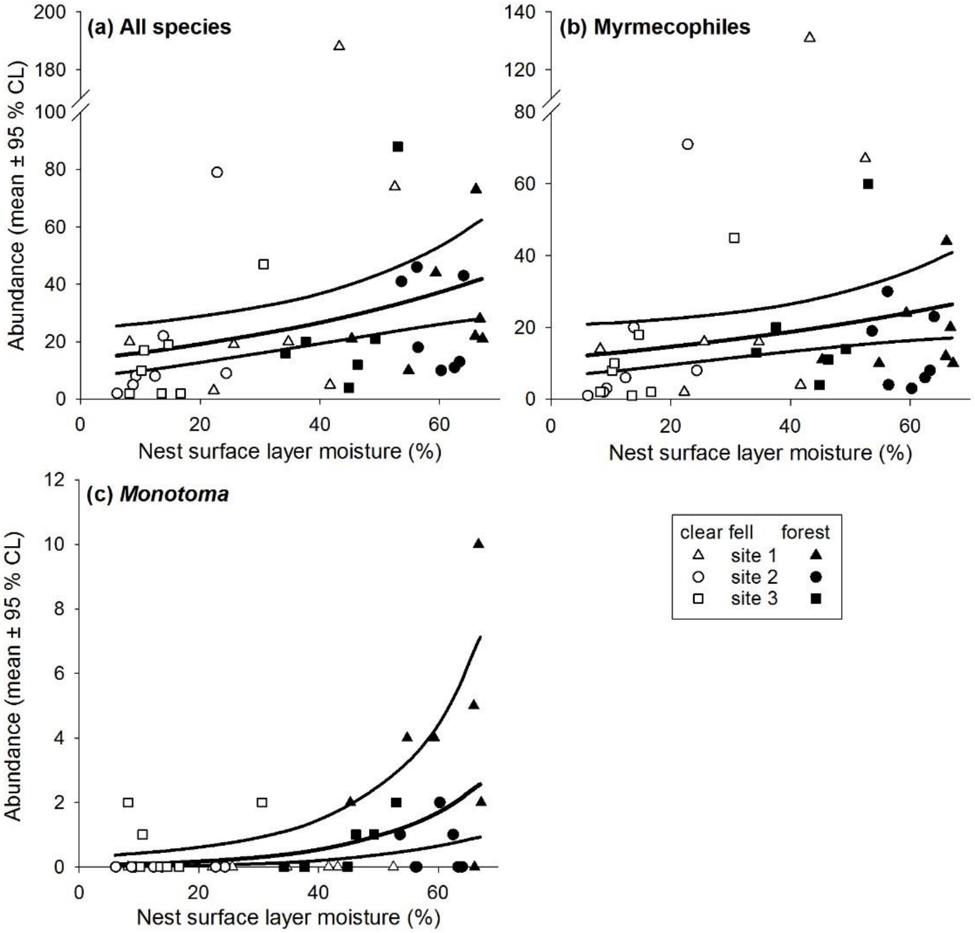
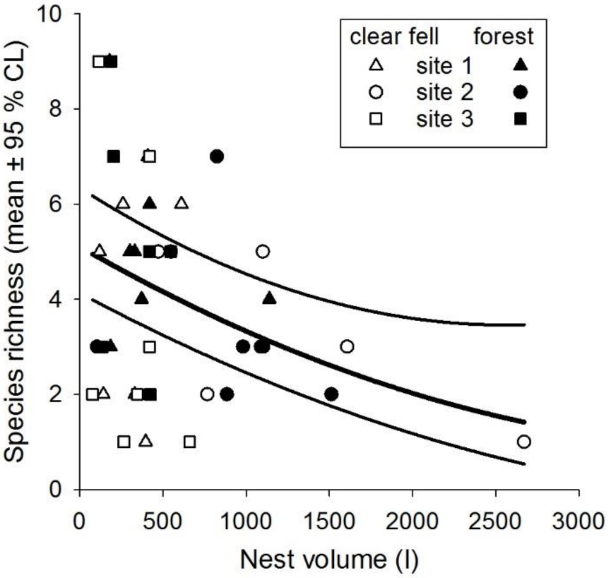

(a) All species
Abundance (mean ± 95 % CL)
0
20
40
60
80
100
180
200
Nest surface layer moisture (%)
0
20
40
60
(b) Myrmecophiles
0
20
40
60
80
120
140
Nest surface layer moisture (%)
0
20
40
60
(c) Monotoma
Abundance (mean ± 95 % CL)
0
2
4
6
8
10
12
Nest surface layer moisture (%)
0
20
40
60
clear fell
forest
site 1
site 2
site 3

Fig. 5.



Species richness (mean ± 95 % CL)
10
8
6
4
2
0
0
500
1000
1500
2000
2500
3000
Nest volume (l)
clear fell
forest
△ site 1 ▲
○ site 2 ●
□ site 3 ■