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

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8

Draft

9 Abstract

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

28

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

30

31 Introduction

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

37

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

50

51 Effects of clear felling on wood ants are clearly negative, as evidenced by reduced
52 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.

73

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

83

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

93

94 **Materials and methods**

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

101

102 The field work was carried out near the city of Kuopio in central Finland (WGS84:
103 62°52': 27°29') on three clear fell – forest pairs in September 2014 (on 5th, 7th and 8th).
104 On each site, the clear fell area and forest stand were side by side. The distance
105 between the sites varied between 3.9 km and 6.5 km. The forests were dominated by
106 Norway spruce (*Picea abies*) mixed with Scotts pine (*Pinus sylvestris*) and birches
107 (*Betula pendula*, *B. pubescens*) with bilberry (*Vaccinium myrtillus*) dominating the
108 scrub layer. The clear felling occurred one to three years before the study.

109

110 In total, 41 nest mounds of *F. aquilonia* were sampled: seven nests per each clear fell
111 and forest site, except in one forest where only six suitable nests were found. As
112 selection criteria, we used the minimum basal diameter of 0.70 m as well as the
113 occurrence of a seemingly vital *F. aquilonia* colony, i.e., the deserted or semi-deserted
114 and young (small) post-harvesting nests were not used. From each nest, 0.5 l of nest
115 material was collected just beneath the moisture layer (10-15 cm from the top) and

116 sieved while in the field (2 mm mesh size). The beetles were extracted from the
117 sieved material with the Berlese-funnel technique in room temperature for five days.
118 Beetles were identified on species level using identification keys (Freude et al. 1971,
119 1974, 2012) and comparisons to the beetle collections of the Zoological Museum at
120 the University of Turku (ZMUT), Finland.
121
122 The nest surface moisture was measured gravimetrically from a nest material sample
123 taken from the surface layer (depth 0-10 cm) near the top of the mound
124 simultaneously when sampling the beetles; further details and findings were already
125 reported in Sorvari et al. (2016). The height and basal diameter of nest mounds were
126 measured, and the above ground volume of the nest mounds was quantified using
127 the equation for a half ellipsoid: $V = (4/3\pi abc)/2$, where a and b are the radiuses and c
128 the height of the nest (i.e. the lengths of the semi-axes of the ellipsoid). Distance to
129 the nearest neighbouring nest was calculated using nest coordinates; the coordinates
130 were recorded for all study nests and one non-study nest, as in all but one case the
131 nearest neighbour was another study nest.

132

133 *Statistics*

134 To visualize the beetle community compositions, we used principal coordinate
135 analysis (PCoA) based on Bray-Curtis dissimilarity, which considers species
136 abundances (Legendre and Legendre 1998). This was done both using the full dataset
137 and separately for myrmecophilous species. Since a couple of species were much

138 more abundant in some nests compared to the other species, a square root
139 transformation was done on the data first. Simple and partial Mantel tests based on
140 Pearson's correlation were used to test for correlations of faunal distance with
141 environmental and geographic distance. A simple measure of environmental distance
142 was obtained by using two variables of nest mound characteristics (moisture and nest
143 volume). First, a principal component analysis (PCA) of the environmental variables
144 was performed, after which Euclidean distances were computed for the first principal
145 components (Oksanen 2015). The significance of correlations was determined with a
146 permutation test using 999 permutations. These analyses were performed with the R
147 software using the vegan package (Oksanen et al. 2017; R Core Team 2017).

148

149 The GLIMMIX procedure of the statistical software SAS 9.3 was used to study the
150 species richness and abundance of i) all beetle species and ii) myrmecophiles in the
151 nests of *F. aquilonia*. Poisson error distribution, suitable for count data, was employed
152 with log link function. Nest surface moisture content and habitat type were the main
153 fixed effects, while nest mound volume and distance to the nearest neighbouring nest
154 were used as covariates. However, since moisture content was associated with
155 habitat type, being lower in clear fells ($F_{1,37} = 132.66$, $P < 0.0001$; see Sorvari et al.
156 2016), and nearest neighbour distance was correlated with moisture (Pearson's $r = -$
157 0.34 , $P = 0.03$) and volume (Spearman's $\rho = 0.35$, $P = 0.025$), habitat type and distance
158 were tested in a separate model. Initially, site (clear fell - forest pair) was used as
159 random factor in the models with Kenward-Roger approximation for degrees of

160 freedom. However, with species richness models, the use of Kenward-Roger
161 approximation caused problems (Den DF of the fixed effects was equal to 1), so it was
162 removed and site was included as fixed effect instead of random. Since site was not
163 even close to significant it was dropped from the models. Also, the models without
164 site had smaller AIC values, indicating better model fit (Akaike, 1974). The structure of
165 the initial and final models with AIC value comparison can be seen in supplementary
166 Table S1¹.

167

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

174

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

¹ Supplementary material

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

185

186 Results

187 In total, 32 beetle species (1123 individuals) of which 17 were myrmecophilous (815
188 individuals) were identified (Table S2²). Most species (59 %) were found both in forest
189 and clear fell nests. The two most common species were myrmecophiles *Ptenidium*
190 *formicetorum* and *Ptilium myrmecophilum* (Ptiliidae) with 306 individuals in 28 nests
191 and 248 individuals in 30 nests respectively. Most non-myrmecophilous species (N =
192 8) were found only as singletons in this study. However, a few non-myrmecophilous
193 species were very common (*Acrotrichis montandonii*: 105 individuals in 22 nests,
194 *Euplectus signatus*: 119 individuals in 17 nests, and *Oligota muensteri*: 55 individuals
195 in 10 nests), and they are regularly associated with ants (Päivinen et al. 2002).

196

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

² Supplementary material

202 similar in nests sharing similar moisture content and nest volume (all species: $r_M =$
203 0.239, $P = 0.009$; myrmecophiles: $r_M = 0.257$, $P = 0.004$). Partial Mantel tests showed
204 that environmental distance correlated with faunal distances even after considering
205 the effect of geographical distance (all species: $r_M = 0.221$, $P = 0.011$; myrmecophiles:
206 $r_M = 0.263$, $P = 0.003$). Species composition was weakly structured along a spatial
207 gradient when all species were considered ($r_M = 0.103$, $P = 0.006$), but when
208 environmental distance was taken into account there was no correlation ($r_M = 0.043$,
209 $P = 0.111$). In the case of myrmecophiles, there was no correlation with geographic
210 distance ($r_M = 0.021$, $P = 0.245$).
211
212 The total number of species found in clear fells was higher than that in forests (31 and
213 20 respectively; Table 1), though on average forest nests had slightly more species
214 (Table 1). However, there was no significant difference in species richness between
215 habitat types (all species: $F_{1,36} = 0.83$, $P = 0.367$; myrmecophiles: $F_{1,36} = 0.67$, $P =$
216 0.419). Total abundance of beetles was significantly higher in forest nests than in clear
217 fell nests (all species: $F_{1,36} = 4.43$, $P = 0.042$; Fig. 2), while there was no difference in
218 myrmecophile abundances ($F_{1,36} = 1.9$, $P = 0.177$).
219
220 Distance to the nearest neighbouring nest varied between 11 and 82 metres (mean =
221 34 m, SD = 17.6). The nearest neighbour for each studied nest happened to be within
222 the same habitat type. Distance was not associated with species richness (all species:

223 $F_{1,36} = 0.36, P = 0.553$; myrmecophiles: $F_{1,36} = 0.47, P = 0.498$) or abundance (all
224 species: $F_{1,36} = 0.03, P = 0.853$; myrmecophiles: $F_{1,36} = 0.1, P = 0.756$).
225
226 The moisture content of the ant nest surface layer varied from 6.1 % to 52.5 % in clear
227 fells (mean = 20.5 %, SD = 13.0, N = 21) and from 34.2 % to 67.2 % in forests (mean =
228 55.3 %, SD = 9.3, N = 20). Total species richness of beetles increased with increasing
229 surface moisture content (Table 2, Fig. 3), while no association was found with the
230 species richness of myrmecophiles (Table 2). There was a significant positive
231 correlation between beetle abundance and nest surface moisture content (Table 2,
232 Fig. 4 a-b). Abundance of *Monotoma* increased with increasing moisture content
233 (Table 2, Fig. 4 c). Nest volume was not significantly associated with beetle
234 abundance or total species richness, though with myrmecophile species richness
235 there was a significant negative correlation (Table 2, Fig. 5).
236

237 Discussion

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

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

256
257 There was no clear difference in community composition between the felled and non-
258 felled habitat types. Mostly, the same species were found in both clear fell and forest
259 nests. All singleton species (N = 9) were found from clear fells, and apart from one,
260 they were all non-myrmecophilous. Some of them could be new (post-felling)
261 colonists. Similar nests (in terms of moisture content and size) had more similar
262 species compositions. Geographic location, on the other hand, did not structure
263 species composition.

264
265 Moisture is one of the most important variables influencing the distribution,
266 abundance, and life cycles of insects and other soil organisms (e.g., Giller 1996;

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

276

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

288

289 Of the ten most common myrmecophiles, only one species showed a clear difference
290 in occurrence between habitat types. *M. conicicollis* was significantly more common
291 in forest nests than in clear fell nests, while the less prevalent congeneric *M.*
292 *angusticollis* was only found in forest. As stated before, these two myrmecophiles are
293 also wood ant specialists. This could indicate that they are more vulnerable to
294 disturbances occurring to the ant colony than the more generalist species, which may
295 also be associated with *Lasius* ants and are thus accustomed to more variable
296 conditions. The abundance of *Monotoma* increased with increasing moisture content.
297 In laboratory experiments, both *Monotoma* species were found to feed on ant brood
298 (eggs and larvae) and ants' prey items (Parmentier et al. 2016a, 2016b). They are also
299 thought to be fungivores, and according to stable isotope analysis, seem to occupy
300 slightly different niches (e.g., feeding on different types of fungi)(Parmentier et al.
301 2016a). The high humidity and temperature conditions within the nest mounds
302 together with a constant input of new organic material give rise to an abundant and
303 functionally specialised decomposer community of fungi and bacteria, which creates
304 the basis for multi-level food webs (Jílková et al. 2015; Laakso and Setälä 1998).
305 Drying of the nest mounds may hence decrease the growth of these microbes thus
306 reducing the food resources of fungivores and bacterivores such as earthworms,
307 springtails, oribatid mites, and also beetles such as *Monotoma* (Laakso and Setälä
308 1998).
309

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

321

322 Like in our previous study (Härkönen and Sorvari 2014), and in contrast to Päivinen et
323 al. (2004), nest volume was negatively associated with myrmecophile species
324 richness, while total species richness and abundance were not significantly affected.
325 However, since an equal amount of nest material was collected from each nest, this
326 gives indication of beetle density rather than population size. Had we looked through
327 the whole nest or adjusted the sampling to be proportional to nest size, we would
328 likely have found that larger nests harbour more species. Samples were also taken
329 from the same depth, regardless of the nest height. In large nests, myrmecophiles
330 could be more aggregated deeper in the nest. Nevertheless, large, high-profiled nests
331 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.

337

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.

347

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

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

360

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

365

366 In conclusion, although total and myrmecophile species richness was not greatly
367 affected by clear felling, and only the total species richness was lower in dry nests, the
368 reduced population sizes in dry nests could be a problem in the long run. After all,
369 small populations have a higher risk of becoming extinct (Hanski 1999). Furthermore,
370 some species may be more vulnerable than others either directly due to the changed
371 physical conditions or indirectly through changes in food availability. We investigated
372 only the short-term effects of clear felling on the associate community in active nest
373 mounds. However, nests in clear fells have a high probability of being abandoned
374 (Sorvari and Hakkarainen 2007), in which case the myrmecophiles will inevitably
375 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.

381

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386

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Draft

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 ($\pm$ SD) found per nest.

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

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531 **Table 2.** The effect of nest surface moisture content and nest mound volume on the
 532 species richness and abundance of all beetles and myrmecophilous beetles in the
 533 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
<i>M. conicicollis</i>	Poisson	Moisture	1, 38	9.87	0.003
		Nest volume	1, 38	0.04	0.838
pooled <i>Monotoma</i>	Poisson	Moisture	1, 38	16.53	0.0002
		Nest volume	1, 38	0.31	0.580

Note: GP = Generalized Poisson

534

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

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

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

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

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

555 Fig. 1.

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558 Fig. 2.

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561 Fig. 3.

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564 Fig. 4.

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567 Fig. 5.

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