

Foraging distances and potentiality in forest pest insect control: an example with two candidate ants (Hymenoptera: Formicidae)

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Abstract

Ants have been suggested to protect forests against insect defoliators. Here, the association between colony size and foraging distances of two common Eurasian multinest-breeding, mound-building ant species, *Formica aquilonia* YARROW, 1955 and *Formica exsecta* NYLANDER, 1846, are compared, and the results are discussed in the context of the species' potential to protect trees from insect defoliators. The distance to the most distant foraging tree was over 100 m in a large nest of *F. aquilonia*, whereas always less than 10 m in *F. exsecta*. Foraging distance increased with an increase in colony size in *F. aquilonia*, but not in *F. exsecta*. Nest mounds were clearly larger in *F. aquilonia*, but the foraging distance differences were not due to nest size differences. Foraging distance was larger in *F. aquilonia* even when the effect of colony size was controlled for statistically. The smaller foraging range of *F. exsecta* could be compensated by its ability to form dense nest populations, but in Fennoscandian boreal forests it lives in temporarily open habitats and disappears before canopy closure. Therefore it may have a more limited use against insect defoliators than *F. aquilonia*. *Formica aquilonia* instead, like other polydomous members of the *Formica rufa* LINNAEUS, 1761 group, also lives inside older forests and has large foraging areas and wide-spread multi-nest colonies. Thus it may have greater potential to protect trees against defoliator insects during the lifespan of a forest.

Key words: Foraging range, forest pest control, *Formica aquilonia*, *Formica exsecta*, spatial scale, Finland.

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Introduction

Ants live in perennial colonies that in most cases are located in the same place for many years, and they forage relatively close to their nest due to wingless workers. Thus their predation effect is constant over several years and is concentrated near the nest (e.g., NIEMELÄ & LAINE 1986, HÖLDOBLER & WILSON 1990). Most ant species tend aphids for carbohydrate and predate other arthropods on trees for protein. Owing to their predatory habits, ants have been suggested to be useful against forest pests such as insect defoliators (WAY & KHOO 1992; but see ADLUNG 1966). The foraging behaviour of ants may have large ecological effects and also economical importance, which is why it is important to study their potential to control defoliating insects. However, important ant species must thrive in shaded forests, and must have realistic potential to control large areas. Even the most aggressive predator ant may be poor in defoliator control if it has effects only on a limited spatial scale.

The radius of foraging area varies between species irrespective of the similar size of workers of different species (e.g., for *Formica* species see SAVOLAINEN & VEPSÄLÄINEN 1988). The radius of the foraging area may reach up to 100 m in large nests of the *Formica rufa* LINNAEUS, 1761 group species (SAVOLAINEN & VEPSÄLÄINEN 1988, ROSENGREN & SUNDSTRÖM 1991, VEPSÄLÄINEN & SAVOLAINEN 1994). In another *Formica* species of a slightly smaller body-

size (COLLINGWOOD 1979), the mound-building ant *Formica exsecta* NYLANDER, 1846, the radius of the foraging area is mostly less than ten metres (SAVOLAINEN & VEPSÄLÄINEN 1988). Colonies in *F. exsecta* are, however, smaller than those of the *F. rufa* group; thus it is not clear whether the smaller foraging areas are only due to the smaller colony sizes. If so, *F. exsecta* may have the same effect on defoliating insects when it occurs in high nest densities (SEIFERT 2007). Nest densities may reach 20 mounds per ha in *Formica aquilonia* YARROW, 1955, but *F. exsecta* may reach 430 mounds per ha (SEIFERT 2007). Both species live in the same geographical zones (PUNTTILA & KILPELÄINEN 2009) and have similar diets (SEIFERT 2007).

The mound-building wood ant *F. aquilonia* is the most common and dominant species among the wood ants of the *F. rufa* group (subgenus *Formica* s. str.) in boreal coniferous and mixed forests (COLLINGWOOD 1979, ROSENGREN & PAMILO 1983, ROSENGREN & al. 1993). Colonies are polygynous (several hundred queens per each nest) and usually polydomous (multiple nest federations) (COLLINGWOOD 1979, ROSENGREN & PAMILO 1983, ROSENGREN & al. 1993). *Formica exsecta*, a member of the subgenus *Coptoformica*, is also a common mound-building ant in the boreal forest zone, and has a relatively similar colony structure to that of *F. aquilonia* (see ROSENGREN & PAMILO 1983). Although young colonies are commonly monodomous (single colo-

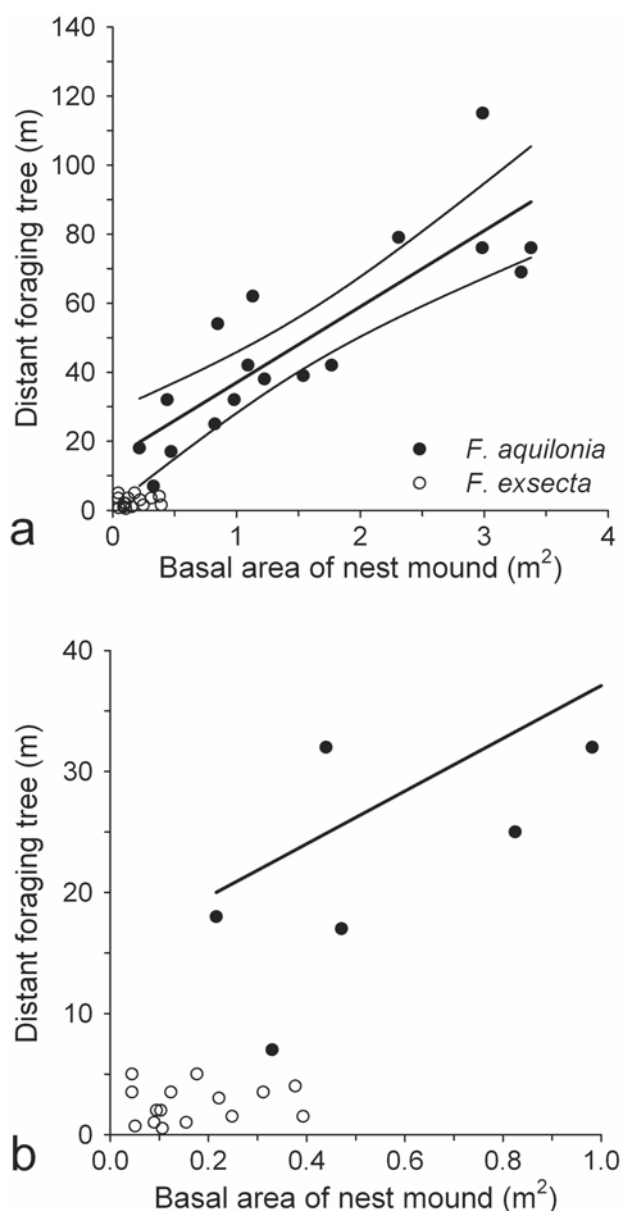


Fig. 1: Relationships between basal area of nest mound (i.e., colony size) and distance of the most distant tree used for foraging in *F. exsecta* and *F. aquilonia*. (a) Full-scale figure with fitted regression line \pm 95% CI for *F. aquilonia* (adj. $R^2 = 0.70$, $y = 22.006 * x + 14.985$) and (b) enlarged part more clearly showing the distribution of *F. exsecta* observations.

nies), colonies tend to develop towards polydomous associations (SEIFERT 2000). In Fennoscandian boreal forests *F. exsecta* lives in open or temporarily open habitats, whereas *F. aquilonia* lives inside forests and along forest edges (COLLINGWOOD 1979, ROSENGREN & PAMILO 1983, SEIFERT 2000, PUNTTILA & KILPELÄINEN 2009).

Nest mounds are built mostly using conifer needles, small twigs, resin and excavated soil in *F. aquilonia*, whereas *F. exsecta* mostly uses finely cut pieces of herbs (mainly grasses) and excavated soil. The nests of *F. aquilonia* are usually larger than those of *F. exsecta*. The diameter of a large *F. aquilonia* nest can be 3 m whereas a maximum of

1.5 m is reported for *F. exsecta*. The worker populations estimated for nests of these sizes are a million for *F. aquilonia* and 300,000 for *F. exsecta* (ROSENGREN & al. 1987, SEIFERT 2000).

Wood ants (*F. aquilonia* and other members of the *F. rufa* group) are commonly thought to be useful against defoliator insects (e.g., WHITTAKER 1991). A recent study also proposed that *F. exsecta* could be useful against defoliators (LINSTEDT & al. 2006). The aim of this study was to find out (1) whether foraging distances are associated with colony size in *F. aquilonia* and *F. exsecta*, and (2) whether the association differs between the two species.

Material and methods

The distance to the most distant tree used for foraging (preying or collecting aphid honeydew) was measured to the nearest 1 m (or to the nearest 0.1 m for the shortest distances) in 17 *F. aquilonia* and 15 *F. exsecta* nests in central Finland, near the town of Jyväskylä (62° 15' N, 25° 45' E). Ants also hunt insect prey in trees that are mainly used for collecting aphid honeydew of (J. Sorvari, unpubl.). For independent samples, each nest was at the periphery of a different polydomous colony. The distance between studied colonies and other members of the same polydomous colony was about 5 - 10 m in *F. exsecta* and about 70 - 100 m in *F. aquilonia*. The study was conducted in spruce-dominated forests (*F. aquilonia*) and semi-open mixed forest saplings close to spruce-dominated forests (*F. exsecta*). In the study area nest densities of *F. aquilonia* colonies were about 5 per ha and about 100 per ha in *F. exsecta*. The area of polydomous colonies of *F. exsecta* were however quite small, the largest being 0.2 ha, while the polydomous colonies of *F. aquilonia* easily reached over 2 ha. The species were identified using the key of COLLINGWOOD (1979).

Counting all the ants in each colony would have been impractical to estimate colony sizes, so the basal area of nest mounds was used as an estimate of colony size. The basal diameter and basal area of nest mounds has been shown to correlate positively with the worker population inhabiting the nest mound in mound-building *Formica* ants of both subgenus *Formica* s. str. and *Coptoformica* (SEIFERT 1991, LIAUTARD & al. 2003) as well as in other *Formica* species (DESLIPPE & SAVOLAINEN 1994). The shape of the nest mound base of the study species varied from circular (especially so in *F. aquilonia*) to ellipsoid (especially so in *F. exsecta*). Thus the maximum (a) and minimum (b) basal diameter was measured, and the basal area of the nest mound (in m²) was calculated using the equation of an ellipse: $\pi * (a * b) / 4$ (DESLIPPE & SAVOLAINEN 1994, SORVARI & HAKKARAINEN 2005, 2007). Basal area, instead of volume, was used because I did not excavate the nests to see how deep they penetrated.

Nest sizes were compared with t-tests (Satterthwaite method where variances were unequal). The relationship between nest mound size and foraging distance was first analysed with a linear regression analysis (species separately). Differences in residual distance (residual from the regression between nest mound area and foraging distance, both species pooled) between species was analyzed with t-tests (Satterthwaite method where variances were unequal). The analyses were made by using procedures Reg and Ttest in SAS 9.1 statistical software (SAS Institute Inc., Cary, NC, USA).

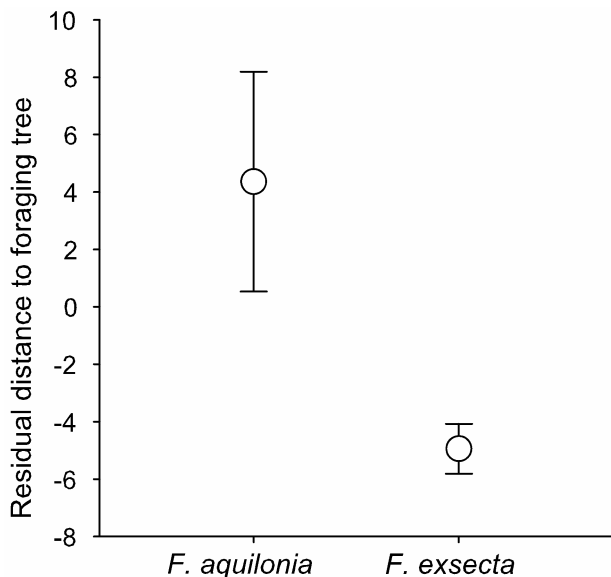


Fig. 2: Relative distances (mean \pm SE) to the most distant tree used for foraging in *F. aquilonia* and *F. exsecta*. Negative value means shorter foraging distance than predicted by nest size.

Results

The basal areas of the studied nest mounds ranged from 0.22 to 3.38 m² in *F. aquilonia* and from 0.04 to 0.39 m² in *F. exsecta*. The basal areas of the nest mounds of *F. aquilonia* were larger than those of *F. exsecta* (*F. aquilonia*: 1.52 m² \pm SE 0.26, *F. exsecta*: 0.17 m² \pm SE 0.03; t-test: d.f. = 16.4, $t = 5.12$, $P < 0.0001$).

The distance to the most distant foraging tree was about 100 m in large nests of *F. aquilonia*, whereas always less than 10 m in *F. exsecta* (Fig. 1). The distance of the most distant foraging tree increased with increasing nest mound size in *F. aquilonia*, whereas such an association was not found in *F. exsecta* (linear regressions: *F. aquilonia*, $n = 17$, $t = 6.21$, $P < 0.0001$; *F. exsecta*, $n = 15$, $t = 0.39$, $P = 0.71$; Fig. 1). The most distant tree used for foraging was often inside the forest in *F. aquilonia*, but a younger lone standing tree in *F. exsecta*. The relative distance (free from the effect of colony size) to the most distant tree used for foraging differed between species, being longer in *F. aquilonia* compared to *F. exsecta* (t-test: d.f. = 17.6, $t = 2.37$, $P = 0.03$; Fig. 2).

Discussion

Foraging distances of ants have been shown to differ between species (e.g., SAVOLAINEN & VEPSÄLÄINEN 1988, EGUCHI & al. 2004). The foraging distances in this study were up to 100 m in large nests of *F. aquilonia* and always less than 10 m in *F. exsecta*. This is very similar to the distances reported for *F. rufa* group wood ants and *Coptoformica* species in previous studies (e.g., SAVOLAINEN & VEPSÄLÄINEN 1988, DESLIPPE & SAVOLAINEN 1995). Colony size has been shown to affect foraging distances in the ant *Rhytidoponera metallica* (SMITH, 1858) (see THOMAS & FRAMENAU 2005) and in the honey bee *Apis mellifera* LINNAEUS, 1758 (see WOLF & SCHMID-HEMPPEL 1990, ECKERT & al. 1994). In this study an increasing distance to the most distant foraging tree was associated with increased

nest size (basal area of nest mound) in *F. aquilonia*, whereas such an association was not found with *F. exsecta*. The trees used by *F. aquilonia* were mature spruce and birch, and saplings of spruce, birch and pine in *F. exsecta*. The basal area of nest mounds was generally larger in *F. aquilonia* than in *F. exsecta*. However, after statistically ruling out the effect of nest size, the relative foraging distances were still larger in *F. aquilonia*. Large workers have been shown to travel further away from the nest than small workers in wood ants (ROSENGREN & SUNDSTRÖM 1987), but not in all ant species (FERSTER & TRANIELLO 1995). Worker size has been shown to increase with increased nest size in *F. aquilonia* (see SORVARI & HAKKARAINEN in press), but this phenomenon is not known in *F. exsecta*. Mean worker body size is slightly larger in *F. aquilonia* than in *F. exsecta* (*F. aquilonia*: 4.0 - 8.5 mm, *F. exsecta*: 4.5 - 7.5 mm) (COLLINGWOOD 1979, SEIFERT 2007), but this is unlikely to be the sole cause of different foraging distances.

Both of the species use a somewhat similar nest multiplication strategy, the so-called "step-by-step"-dispersal sensu ROSENGREN & PAMILO (1983). A mature colony of *F. aquilonia* needs a foraging area with a radius of 30 - 50 m (e.g., NIEMELÄ & LAINE 1986). Thus, a "step" length should be twice the required foraging radius, i.e., approximately 60 - 100 m. *Formica exsecta* instead has much smaller foraging areas and uses only one or few trees for foraging. Thus the "steps" are much shorter, less than 20 m, usually only a few metres. The difference in foraging distances between the species is likely related to nest-budding behaviour and the "step" length. Foraging range increased with the colony age in *Pogonomyrmex barbatus* (GORDON 1995). The positive relationship between nest size and foraging distances in *F. aquilonia* is probably due to it being not necessary for the few individuals of a young colony to travel far away from the nest. In *F. exsecta* foraging distance probably does not grow because of frequent short-distance nest budding.

Formica exsecta and other members of the *Coptoformica* group are aggressive and predaceous. Therefore one could think that they could be useful for biological control against folivorous insects in forests (LINSTEDT & al. 2006). However, the foraging distance in *F. exsecta* is very short and does not increase much as the colony grows. Dense nest populations might protect trees from folivores in younger forest succession stages, but in Fennoscandian boreal forests *F. exsecta* disappears before canopy closure because its colonies cannot live in shaded forests (SEIFERT 2000). *Formica exsecta* may make bud nests more frequently than *F. aquilonia*, but *F. exsecta* may not have time to form dense multi-nest colonies covering large areas in growing forests. Multi-nest colonies of *F. exsecta* still normally cover a smaller combined foraging area than one medium-sized *F. rufa* group wood ant nest (e.g., *F. aquilonia*). A North-American species, *F. exsectoides*, closely related to *F. exsecta*, is reported to actively prevent future increase of habitat shadiness by damaging tree saplings with its sharp mandibles (ANDREWS 1928). *Formica exsecta* has also sharp mandibles (e.g., SEIFERT 2000) and may potentially harm saplings in similar ways, but this has not yet been studied.

Formica aquilonia and other polydomous members of the *F. rufa* group live in both forest edges and, despite shadiness, forest interiors (COLLINGWOOD 1979, ROSENGREN & PAMILO 1983). They have large foraging areas, and thus

may have greater potential to protect trees against defoliating insects, especially in older succession stages of forests. *Formica aquilonia* and its relatives in the *F. rufa* group have been shown to be effective against defoliating insects (WHITTAKER 1991, NIEMELÄ & LAINE 1986, KARHU 1998, KARHU & NEUVONEN 1998, PUNTTILA & al. 2004). Individual predatory behaviour may be similar between *F. aquilonia* and *F. exsecta*, but at the scale of forests *F. aquilonia* is likely more useful against defoliators because of its long-distance foraging and nest dispersion in forest interiors.

Foraging distance is not the sole measure of the effect of ant species as forest protection agents. An ant species that has long foraging distances, but is selective in choosing sites for preying, is likely to have less of a protective effect than a species, which has shorter foraging distances but completely eradicates defoliators in the circular area. Both of the study species seem to have more or less circular foraging areas, thus not differing in that respect (J. Sorvari, unpubl.). Vegetation structure can affect foraging distances. For example dense vegetation may cause shorter foraging distances in *Pogonomyrmex occidentalis* (CRESSON, 1865) (see USNICK 2000). Paths of *F. aquilonia* are often well cleared, whereas not so in *F. exsecta*. Therefore it is easier for *F. aquilonia* than *F. exsecta* to travel far away from nest.

In conclusion, the two species complete each other as defoliator control agents. *Formica exsecta* preys in younger succession stage forests, while *F. aquilonia* preys in older succession stage forests.

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Zusammenfassung

Ameisen sind wiederholt zur biologischen Kontrolle von blattfressenden Forstinsekten vorgeschlagen worden. Hier werden die Beziehungen von Koloniegröße und Fouragierdistanz bei zwei häufigen, eurasischen, Hügel bauenden Ameisenarten mit polydomen Kolonien, *Formica aquilonia* YARROW, 1955 und *Formica exsecta* NYLANDER, 1846, miteinander verglichen. Die Ergebnisse werden im Zusammenhang mit dem Potenzial der beiden Arten diskutiert, Bäume vor blattfressenden Forstinsekten zu schützen. Die Distanz zu dem am weitesten entfernten Fouragierbaum war bei einem großen Nest von *F. aquilonia* über 100 m, wohingegen sie bei *F. exsecta* immer geringer als 10 m war. Bei *F. aquilonia* stieg die Fouragierdistanz mit der Koloniegröße an, bei *F. exsecta* aber nicht. Die Nesthügel waren bei *F. aquilonia* eindeutig größer, aber die Unterschiede in der Fouragierdistanz gingen nicht auf die Unterschiede in der Nestgröße zurück, denn die Fouragierdistanz war bei *F. aquilonia* auch dann größer, wenn der Effekt der Koloniegröße statistisch kontrolliert wurde. Die kleineren Fouragierbereiche von *F. exsecta* könnten durch die Fähigkeit der Art, dichte Nestverbände zu bilden, ausgeglichen werden, aber in fennoskandischen borealen Wäldern lebt die Art in vorübergehend offenen Lebensräumen und verschwindet vor dem Kronenschluss wieder. Die Art könnte somit für den Schutz vor blattfressenden Forstinsekten eine geringere Bedeutung als *F. aquilonia* haben. *Formica aquilonia*

hingegen lebt, wie auch andere polydome Mitglieder der *Formica rufa* LINNAEUS, 1761 Gruppe, auch im Inneren alter Bestände und hat große Fouragierbereiche und weitverzweigte Nestverbände. Diese Art könnte somit ein größeres Potenzial haben, Bäume gegen blattfressende Forstinsekten während der Lebensdauer eines Waldes zu schützen.

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