Sharing versus monopolizing: distribution of aphid sources among nests within a *Formica exsecta* Nylander (Hymenoptera: formicidae) supercolony

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ABSTRACT

Food-for-protection mutualistic interactions are quite common between ants and other insects. Such myrmecophilous relationships are primarily characteristic of homopterans, e.g., aphids. Ants usually profit from these relationships by enriching their diet with the carbohydrate-rich byproducts of these insects, whereas aphids benefit mainly from protection against predators and competitors. In many ant species, the abundance of food sources, e.g., aphids, among other factors, allows the formation and persistence of large polydomous systems, the so-called supercolonies. Such systems imply a lack of aggression among workers from different nests, a high exchange rate of foragers, and an overlap of feeding grounds. The sharing ratio of aphid sources within a supercolony at sites with different ant-nest abundance provides an insight into the degree of integration of ant nests in such a system. We studied two areas with different ant-nest abundance in a large *Formica exsecta* supercolony in Romania over two consecutive years. The high density site (HD) contained larger and more numerous aphid colonies overall than the low abundance site (LD). In addition, ant nests tended more aphid colonies at the HD site but also shared these colonies, whereas at the LD site, aphid colonies were generally monopolized. Consequently, the overlap among feeding areas of ant nests was very frequent at the HD site, but almost completely lacking at the LD site. We conclude that while the HD site indeed reflects the integrative features of such a system, the LD site may constitute a loosely integrated part of the supercolony.

KEYWORDS: *Formica exsecta*, ants, aphids, foraging, mutualism, polydomy, supercolony

INTRODUCTION

Mutualism is increasingly recognized as a common and important ecological interaction. In ants, interactions with other insects that involve food in exchange for protection are quite common, particularly with aphids, whiteflies, scale insects, and mealybugs

(Hölldobler and Wilson, 1990; Blüthgen et al., 2000; Stadler and Dixon, 2005; Styrsky and Eubanks, 2007). Ants usually profit by feeding on the carbohydrate-rich byproducts of these insects, the so-called honeydew, while also preying on non-myrmecophilous species, and to some extent, even on mutualistic ones if food availability diminishes (Vepsäläinen and Savolainen, 1994; Stadler and Dixon, 1999, 2005; Novgorodova, 2005). Honeydew-producing insects are believed to benefit mainly from the protection against predators and competitors, but other advantages may also arise from ant attendance (see Stadler and Dixon, 2005; Styrsky and Eubanks, 2007 for comprehensive reviews). In extreme cases, the protective nature of this interaction can involve ants carrying the mutualistic partners into their nests (Lehouck et al., 2004) and even keeping them there (Depa and Wojciechowski, 2008).

Ant–aphid mutualism has evolved several times in aphids, even within the same genus (e.g., *Chaitophorus*) (Shingleton and Stern, 2003). The degree of ant-dependence differs among free-living ant-tended aphid species (Molnár et al., 2000), and the strength of such mutualistic relationships can exhibit annual variations within the same aphid species (Del-Claro and Oliveira, 2000). The strength of the mutualistic relationship also differs among aphid-tending ant species (Novgorodova, 2005).

The evolution of the mutualistic relationship between ants and aphids involves morphological changes in the aphids: some ant-tended aphid species have longer mouth parts, which allow them to exploit phloem fluid from twigs. Had they not been protected by ants, this feature would have normally made them vulnerable, as longer mouth parts are harder to retract when attacked by predators (Shingleton et al., 2005; Stadler and Dixon, 2005). Such adaptations may also allow these species to avoid interspecific competition by feeding at sites that are unavailable to untended species (Shingleton et al., 2005). The presence of ants has a generally positive effect on the abundance of ant-dependent aphids, most importantly through a direct reduction in the number of parasitoids or predators as well as the abundance of other herbivores (Karhu, 1998; Stadler and Dixon, 1999; Del-Claro and Oliveira, 2000; Punttila et al., 2004; Crutsinger and Sanders, 2005; Stadler and Dixon, 2005; Grover et al., 2008). More intricate mechanisms can also be involved. According to Stadler and Dixon (1999), *Lasius niger* influences positively the developmental rate of the myrmecophilous birch aphid, *Symydobius oblongus*, allowing the aphid to invest more in gonads and embryos. Fine-tuned behavioral responses are also common in honeydew producers: they may alter their feeding behavior and the composition of the honeydew in the presence of ant attendance (e.g., Banks and Nixon, 1958; Del-Claro and Oliveira, 1993; Styrsky and Eubanks, 2007). Finally, ant attendance can have community-wide effects by generally increasing the number of aphid species in a given area (Molnár et al., 2000). The magnitude of the effect, however, depends on the ant species involved (Novgorodova, 2005).

Ants benefit from aphid food sources mostly by obtaining a high quality and stable food source. The presence of such sources is very important for the sustainability and growth of ant colonies (see Holway et al., 2002; Espadaler et al., 2007; Styrsky and Eubanks, 2007; Czechowski and Vepsäläinen, 2009). The profitability of these sources is reflected in the fact that ants do not switch to alternative sources even when these are

very attractive (Del-Claro and Oliveira, 1993). Generally, the spatial distribution pattern of food sources can exert serious constraints on ant colony structure (e.g., Cerdá et al., 2002) or territory size (e.g., Vepsäläinen and Savolainen, 1994; Czechowski and Vepsäläinen, 2009). For example, food-source richness can affect ant-mound density; occurrence and density of wood ant mounds can be high on medium/rich sites and low on poor sites (Kilpeläinen et al., 2005). Finally, the spatial and temporal stability of permanently rewarding food sources, such as aphids, can lead to the formation and persistence of polydomous systems in ants through the budding of daughter nests (Pisarski, 1982a; Chapuisat and Keller, 1999; Debout et al., 2007).

Polydomy is a rather general trait in ants (see Debout et al., 2007, for a comprehensive review) that develops in two main scenarios: (1) gaining short-term ecological benefits in new, disturbed, or empty habitats, along with ensuring successful nest founding—mostly characteristic of invasive, introduced polygynous species (see Holway et al., 2002, for a review); and (2) selection for cooperative nest networks due to their strong constraints on dispersal and progressive habitat saturation, exploitation of stable habitats, and better monopolization of food sources—mostly characteristic of native species (see e.g., Chapuisat and Keller, 1999). Such polydomous systems, so-called supercolonies, can involve food-source sharing and exchange of individuals and brood among nests (Chudzicka, 1982; Pisarski, 1982a–f; Debout et al., 2007; Kümmerli and Keller, 2007), and the level of aggression between non-nestmates in these systems is usually very low or completely absent (Holzer et al., 2006; Martin et al., 2009). Such systems exert significant pressure on local arthropod, and particularly ant, communities, and thus represent advantages in the context of interspecific or intraspecific competition (Pisarski, 1982b,g; Holway et al., 2002; Espadaler et al., 2007).

Although polydomous systems constitute an interesting study subject from many points of view (see Debout et al., 2007; Kümmerli and Keller, 2007), relatively few studies have addressed the problemtics of ant–aphid relationships within such systems (e.g., Werner et al., 1979; Pisarski, 1982c; Bliss et al., 2006; Bönsel, 2007). It is reasonable to assume that biases in ant-nest distribution and size within supercolonies can be caused by heterogeneity in the distribution and availability of permanent food sources, e.g., aphid colonies. For example, Werner et al. (1979) showed that *F. exsecta* nests tend to be aggregated around trees within a polydomous system, not just because of the better climatic conditions, but also because of the richer aphid sources, and that such nests are generally bigger. Bönsel (2007) hypothesized that the high nest-turnover rate in *F. pressilabris* could be caused by the high turnover rate in aphid colonies. Feeding areas of different nests within a polydomous system can also overlap to a great extent (Pisarski, 1982c), with common exploitation of food sources and sharing of feeding grounds leading to a high exchange rate of individuals among different nests (Chudzicka, 1982; Kümmerli and Keller, 2007). Ultimately, the constant exchange of individuals could be an important factor in integrating single nests into a supercolonial system. Consequently, the degree of aphid-source sharing among ant nests can be viewed as a good gauge of supercolonial integration.

Here, we analyze the distribution of aphid sources among nests within a supercolony

of the narrow-headed ant *Formica exsecta* Nylander, a relatively common Palaearctic mound-building wood ant species. A supercolony can consist of areas with different ant-nest densities, and it is plausible that such differences are caused by biases in the quantity and quality of aphid colonies, and are possibly also reflected in differences in the exploitation pattern of these colonies.

MATERIALS AND METHODS

The studied species

Formica (*Coptoformica*) *exsecta* Nylander, 1846, the narrow-headed ant, is a relatively common mound-building, pan-Palaearctic ant species, inhabiting areas of mixed and deciduous forests, mostly at forest edges, in forest clearings or in mountain pastures, from England to eastern Siberia and from southern Europe to Sweden (Seifert, 2000; Czechowski et al., 2002; Goropashnaya et al., 2007; Kümmerli and Keller, 2007; Schultz and Seifert, 2007). It is an aggressive, territorial ant, feeding on a wide range of food sources, from insects and other invertebrates to honeydew, which can satisfy a major portion of its energy needs (Werner et al., 1979; Pisarski, 1982c,d). A typical *F. exsecta* nest mound consists of a soil core covered by fine-cut dry plant material, with a diameter ranging from 10 cm in incipient nests to more than 1 m in mature nests, and reaching a depth of 1–1.5 m (Pisarski, 1982b; Seifert, 2000; Czechowski et al., 2002; Bliss et al., 2006). Nuptial flights occur from the end of July to the beginning of August (Pisarski, 1982b).

Both monogynous and polygynous colonies are frequent in *F. exsecta*; the latter can develop into large polycalic, polydomous systems (Werner et al., 1979; Chudzicka, 1982; Pisarski, 1982c–g; Skibińska, 1982; Czechowski, 1990; Seifert, 2000; Goropash-naya et al., 2007; Kümmerli and Keller, 2007; Martin et al., 2009). One nest can con-tain from several hundred to several hundred thousand individuals, and in polygynous nests, the number of queens can reach several dozen (Pisarski, 1982b; Sorvari, 2009). Large polycalic colonies are known from the Alps, central Europe, and European Rus-sia; these can comprise several hundred nests (Werner et al., 1979; Pisarski, 1987c,d; Seifert, 2000; Czechowski et al., 2002; Kümmerli and Keller, 2007; Martin et al., 2009). In such systems, nestmates sometimes show extremely low relatedness (Goropashnaya et al., 2007; Kümmerli and Keller, 2007). Large aphid colonies and a high stability of the aphid source are usually needed for the development of such polydomous systems (Pisarski, 1982d,e). *Formica exsecta* supercolonies can effectively displace other ant species, as well as other arthropods, from their territory (Pisarski, 1982c,d,g). Territories of monodomous colonies are generally smaller than those of the *F. rufa* group species, covering a few square meters to 20, or even 60 m^2 (Pisarski, 1982c; Czechowski, 1990; Sorvari, 2009). Although large polydomous systems can cover several hectares, the territory of an individual colony within such a system is usually equal to the area used by a monocalic one (Pisarski, 1982c). While ants from monogynous and monodomous colonies show high levels of aggression against conspecific aliens (Czechowski, 1990),

aggressive interactions are completely lacking in polycalic colonies, and the level of aggressive interactions is significantly reduced in complex polydomous systems comprised of polycalic colonies (Werner et al., 1979; Pisarski, 1982f; Skibińska, 1982; Martin et al., 2009). Consequently, nests within such a system usually do not establish intra-territorial boundaries (Werner et al., 1979; Pisarski, 1982f; Skibińska, 1982), there is permanent overlap of feeding grounds among neighboring nests, and food sources are permanently shared (Pisarski, 1982a,d).

Study area

Our investigations were carried out in the southern part of the Giurgeului depression, in the eastern Carpathians, near the village of Voslobeni (Harghita County, Romania, 46º36′N, 25º36′E, 780 m asl, Fig. 1.), in July of 2008 and 2009. The depression is one of the coldest regions in Romania; frosts are still common in May, and can already occur in September. In 2008, mean annual temperature was 6.3 ºC (t_{max} = 31.3 ºC, t_{min} = −25.2 ºC), and mean annual rainfall was 652.7 mm (Anonymous, 2009). The vegetation in the area and its surroundings was studied in detail by Margóczi et al. (2000), and the structure of its arthropod communities was analyzed by Gallé et al. (2000).

   There are at least five large polydomous systems of *F. exsecta* in the southern part of the depression, in addition to several monocalic or small polycalic colonies. The smallest polydomous system comprised 12 nests, while the largest, selected for the purpose of our study, comprised more than 1000 nests, stretching over more than 17 ha (Fig. 1). The *F. exsecta* population in the area features polygynous nests with low intranest relat-
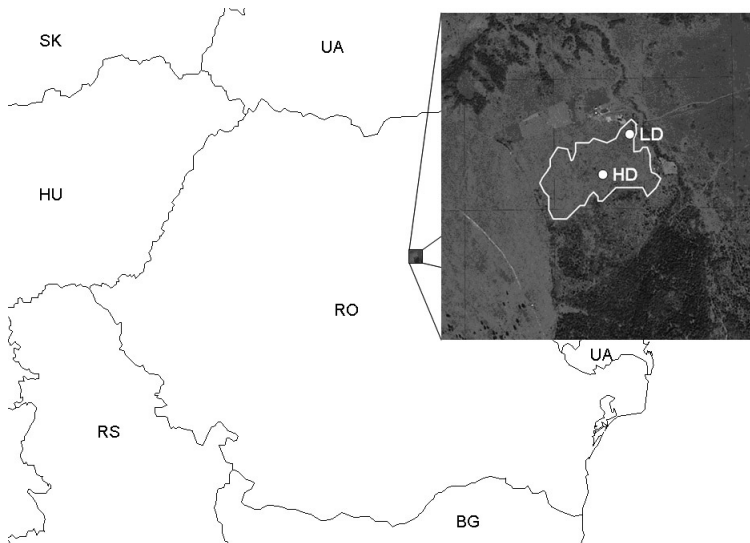

Fig. 1. Location of the study sites with outline of the studied *Formica exsecta* supercolony in Romania.

Table 1
Number and density of ant nests and aphid colonies at the LD and HD sites in 2008 and 2009

Sites	2008		2009 (original area)		2009 (expanded area)	
	HD	LD	HD	LD	HD	LD
No. of ant nests	39	14	40	14	42	20
Ant nest density (no. of nests/10 m²)	0.57	0.12	0.58	0.12	0.52	0.09
No. of aphid colonies	214	50	369	68	450	99
Aphid colony density (no. of colonies/m²)	0.31	0.04	0.53	0.06	0.56	0.05

edness ($r = 0.22 \pm 0.06$) (Goropashnaya et al., 2007). The recent study by Martin et al. (2009) on the largest supercolony in this area showed that the level of aggression was reduced between ants originating from different nests, even if quite distant. The largest supercolony, the subject of the present study, is located in a fen meadow with *Molinia caerulea*, *Deschampsia caespitosa*, *Festuca pratensis*, *Briza media*, *Nardus stricta*, *Succisa pratensis*, *Filipendula ulmaria*, *Stachys officinalis*, and *Cirsium palustre* as the most abundant or characteristic plant species. The area is overgrown with scattered small trees and saplings of *Betula pubescens*, *Picea abies*, *Frangula alnus*, and *Salix* spp. The meadow is fairly intensely grazed by cows for most of the year. We chose two areas within the supercolony that clearly differ in the density of nests: a high density (HD) site with 39 and 42 nests in 2008 and 2009, respectively, and a low density (LD) site with 14 and 20 nests in 2008 and 2009, respectively (Fig. 1, Table 1). The HD site is situated in the central part of the supercolony. Initially, we studied an area of 684 m² in 2008, but the following year we expanded the study area to 807 m². The density of ant nests was 0.57 and 0.52 nests/10 m², respectively. The LD site is located at the border of the supercolony, covering 1117 m² in 2008, and which expanded the following year to 2113 m². The density of the ant nests was 0.12 and 0.09 nests/10 m², respectively. The changes in ant-nest densities from 2008 to 2009 may be attributed to the expansion of the study areas, as nest abundance in the initial areas is almost identical for both years (Table 1). The difference between ant-nest densities of the two sites was ca. five-fold in favor of the HD site for both years.

Sampling methods

All plants with aphids and all *F. exsecta* nests were recorded at both study sites; ant nests and aphid-infested plants visited by *F. exsecta* were later mapped. In the following, every plant with aphids is referred to as a separate aphid colony. Within each plant, the stem length occupied by an aphid aggregation was measured in mm. The number of aphids within each aggregation was counted in 2009, but not in 2008. We assessed whether the length of the occupied stem could be used as a fair quantitative characteristic of an aphid group. For this purpose, 122 aphid aggregations were collected randomly from birch twigs near the study sites in both years (27 and 95 groups, respectively). The

stem lengths occupied by the aggregations were measured previously, when the aphids were preserved in ethyl alcohol and specimens were counted under a microscope in the laboratory. As the vast majority of the aphids were sucking on birch twigs (see below), we assumed that collecting only from birch would not significantly bias the analysis. The majority of aphids belonged to the genera *Symydobius* (92.62% of samples) and *Monaphis* (5.74% of samples), of which *Symydobius* spp. are obligatory myrmecophilous species (e.g., Stadler and Dixon, 1999). For each aphid colony, the identity of tending *F. exsecta* nests was determined on the basis of ant routes established between the visited aphid colony and the ant nests.

Data analysis

Observations referring to a single aphid specimen/plant (n = 9 and 7 at the HD and LD sites, respectively) were excluded from the analysis. The occurrence of a single aphid on a plant was considered incidental and not as evidence for the existence of a stable aphid colony. Single aphids that were clearly separated from additional groups of aphids occurring on the same plant were included only in the analysis of the number of aphids/ plants, but excluded from any analysis of the length of plant stem occupied by aphids (n = 8 and 3 at the HD and LD sites, respectively).

Analysis of the aphid samples collected outside the study sites revealed that the length of the occupied plant stem by an aphid group is indeed a direct function of the number of aphids within a group (Fig. 2). Because in 2008 only the length of the oc-
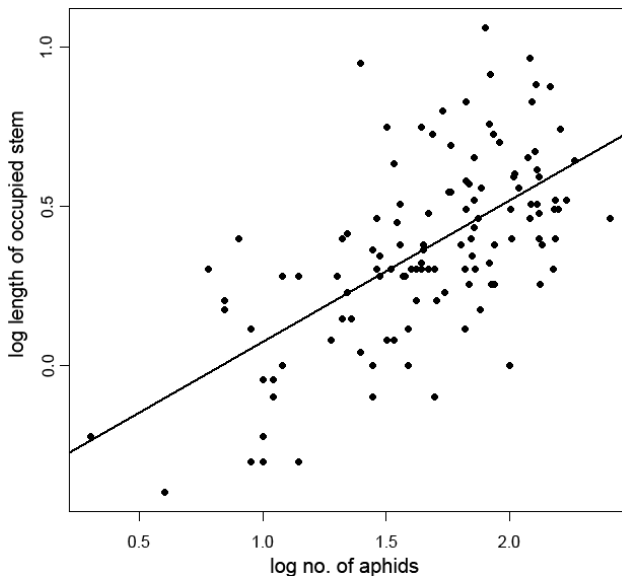

Fig. 2. Relationship between number of aphids in an aphid aggregation and the length of the occupied plant stem (linear regression $r^2 = 0.38$, F = 75.94, $p < 0.0001$, b = 0.44, t = 8.71, $p < 0.0001$, n = 122).

cupied stem was measured, we used both characteristics of the aphid groups (length of occupied plant stem and number of aphids) throughout the analyses.

The size of each *F. exsecta* nest was measured in 2009 in order to calculate the above-ground volume of the mound. We used the formula for the volume of an elliptic paraboloid (Bliss et al., 2006): $V = 1/2 * \pi * r_1 * r_2 * h$, where r_1 is the largest radius at bottom, r_2 is the radius perpendicular to r_1, and h is the height above ground. The spatial distribution of ant nests was analyzed using the nearest-neighbor method developed by Clark and Evans (Clark and Evans, 1954, in Southwood and Henderson, 2000).

The normality and homogeneity of variances of datasets were tested in the case of parametric tests. If the datasets were not normally distributed, log-transformations were applied. Non-parametric methods were used only if the normality requirements were not fulfilled. All statistical analyses were carried out using the R 2.9.1 and SPSS 14.0 statistical packages.

RESULTS

Distribution of aphid colonies and ant nests

A total of 214 and 50 aphid colonies were recorded at the HD and LD sites, respectively, in 2008 (Figs. 3,4; Table 1), and 450 and 99 aphid colonies were counted in 2009 (Figs. 3,4; Table 1). Almost all aphid colonies were tended by *F. exsecta* at the HD site, with the exception of two colonies in 2008 and one colony in 2009 that were tended by *Lasius niger*. At the LD site, 38 (76%) and 91 (86.6%) aphid colonies were tended by *F. exsecta* in 2008 and 2009, respectively, whereas the remaining colonies were exploited by *L. niger* (nine and six colonies), *Formica sanguinea* (three and one colonies) and *F. pratensis* (one colony in 2009). Although the increase in number of aphid colonies may be attributed to the expansion of the initial study areas in 2009, intrinsic changes within the aphid population cannot be excluded, at least in the case of the HD site, where the density clearly increased in the initial study area from one year to the next (Table 1). In both years, the HD site, although smaller, contained more aphid colonies than the LD site. The majority of aphid colonies tended by *F. exsecta* were sucking on stems of *Betula pubescens* saplings (93% and 94%) at the HD site in 2008 and 2009, respectively, whereas only a few aphid colonies were found on *Genista tinctoria* (three colonies in 2009), *Salix*spp. (two colonies in 2008 and 22 in 2009), and *Populus tremula* saplings (two colonies in 2009). The same was true for the LD site, where 92% and 96.7% of the *F. exsecta*-tended aphid colonies were found on twigs of birch saplings and the rest on *Salix* spp.

Annual variations were also detected in the case of *F. exsecta* nests, although to a much lesser extent (Figs. 3,4; Table 1). In 2008, 39 and 14 ant nests were recorded at the HD and LD sites, respectively. In the following year, four and one new, incipient, nests appeared at both sites. In addition, two and six nests were incorporated from the peripheral areas of the previous year's study sites. Only three nests at the HD site and one nest at the LD site disappeared from one year to the next. In 2009, ant mounds were generally larger at the HD site: mean HD = 24.96 dm³ (±20.3), mean LD = 11.32 dm³
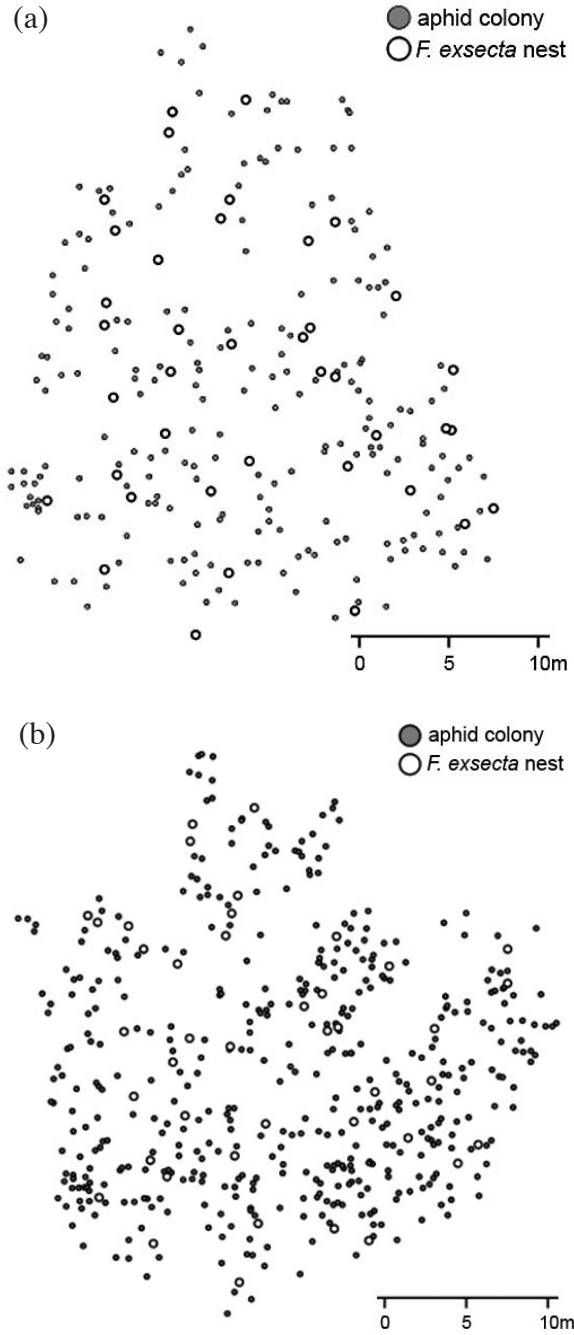
Fig. 3. Ant nests and aphid colonies at the HD site in (a) 2008 and in (b) 2009.

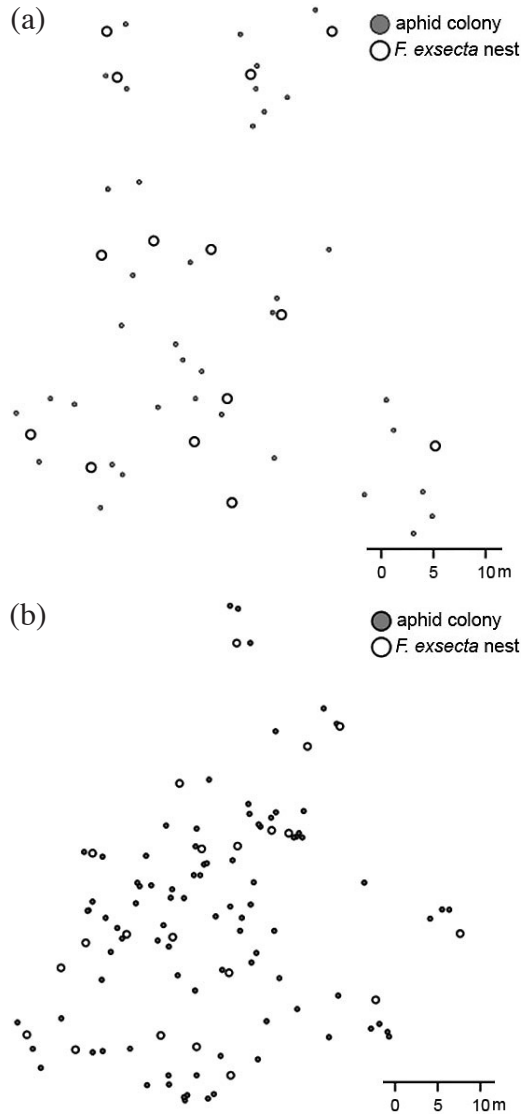Fig. 4. Ant nests and aphid colonies at the LD site in (a) 2008 and in (b) 2009.

(±7), Welch-test $t = 3.89$, $n_{HD} = 42$, $n_{LD} = 20$, $p < 0.001$. The largest nest was 76.87 dm^3, while the smallest was only 0.28 dm^3. The nearest-neighbor analysis revealed that ant nests were randomly distributed at the HD site in both years: $R = 1.11$, $t = 1.31$, $p > 0.05$ in 2008, $R = 1.07$, $t = 0.82$, $p > 0.05$ in 2009. At the LD site, in contrast, their pattern seemed to be more regular in both years: $R = 1.46$, $t = 3.33$, $p < 0.05$ in 2008, $R = 1.33$, $t = 2.85$, $p < 0.05$ in 2009.

Differences in the quantity of aphid sources between the two sites

The plant stems occupied by aphids were significantly longer at both sites in 2008: (1) median$_1$ = 18, median$_2$ = 6.2, Mann-Whitney z = 8.08, p < 0.0001, n$_1$ = 212, n$_2$ = 441 at the HD site; (2) median$_1$ = 15, median$_2$ = 6.65, Mann-Whitney z = 5.15, p < 0.0001, n$_1$ = 39, n$_2$ = 88 at the LD site. In contrast, the total length of stems occupied by aphid aggregations per plant did not differ significantly between sites in either of the years (Fig. 5). Nevertheless, there were more aphid aggregations per plant at the HD site in
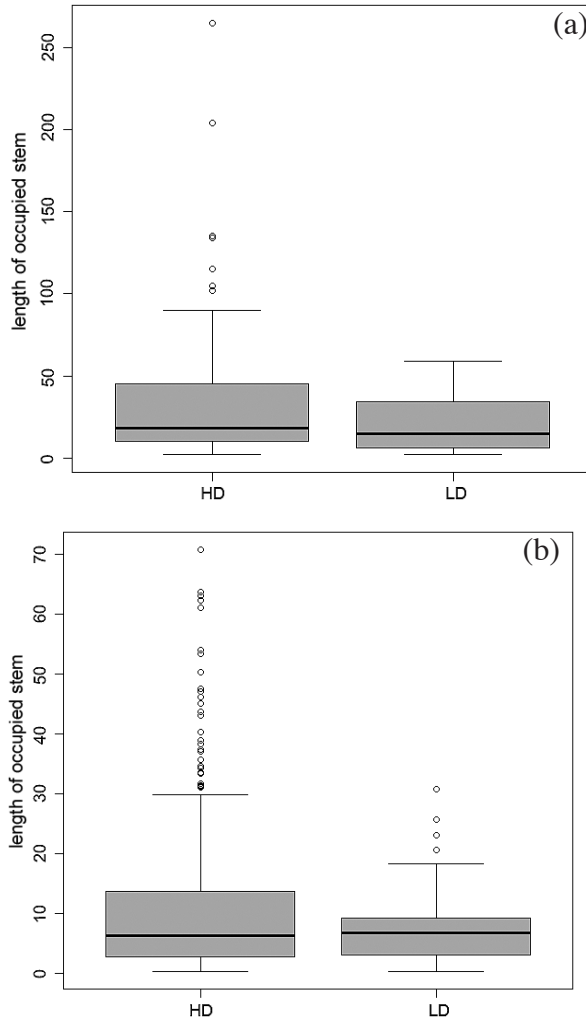

Fig. 5. Total length of the occupied plant stems by aphid colonies at the study sites (Mann-Whitney-test) (a) in 2008 (z = 3.12, p = 0.15) and (b) in 2009 (z = 4.07, p = 0.33) (median, quartiles, minimum–maximum values, and outliers).
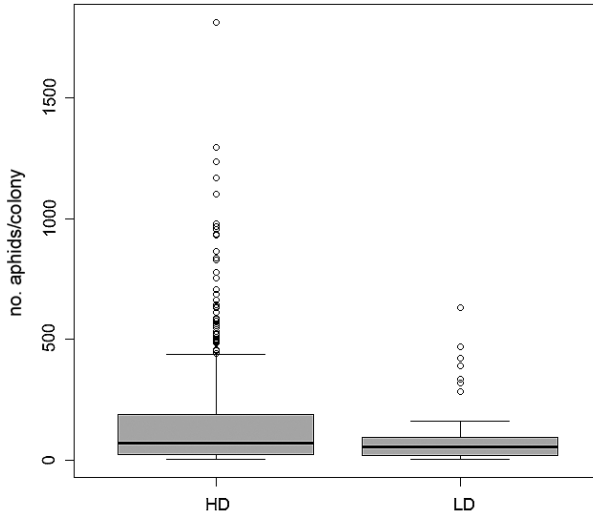
Fig. 6. Number of aphids per plant at the two sites in 2009 (Mann-Whitney z = 5.05, n_{HD} = 449, n_{LD} = 91, p = 0.004) (median, quartiles, minimum–maximum values, and outliers).

2009: median HD = 4, median LD = 3, Mann-Whitney z = 5.84, p = 0.006. Aphid colonies contained a significantly higher number of aphids at the HD site than at the LD site in 2009 (Fig. 6.). Consequently, while aphid colonies generally occupied the same stem length in both areas, aphid density was higher at the HD site. This seems to contradict the claim that the stem length occupied by aphids is a function of aphid density (see Data Analysis section). This contradiction can be resolved, however, if we consider the differences in the vegetation structure and microclimate between the two sites. Grazing pressure was higher at the LD site, which could result in a lack of smaller birch saplings and lower vegetation cover, thus ultimately affecting the distribution of aphids within aggregations. However, definite conclusions can only be drawn on the basis of specific studies, i.e., analysis of the sites' vegetation structure (Csata et al., in prep.).

Sharing or monopolization?

Analysis of the ant routes leading to aphid colonies allowed us to identify the ant nests that tended specific aphid colonies. Because the number of aphid colonies was clearly higher at the HD site, it could be assumed that one *F. exsecta* nest exploited more aphid colonies at the HD site than at the LD site. Indeed, data from both years revealed that a given ant nest usually tended more aphid colonies at the HD site (Fig. 7). In extreme cases, the number of aphid colonies exploited by a single ant nest was as high as 43 at the HD site in 2009, whereas rarely reaching more than 10 colonies at the LD site (Fig. 7). The same ant nests tended more aphid colonies in 2009 than in the previous year at both sites: (1) Wilcoxon sign-test z = –5.2, n = 36, *p* < 0.0001 at HD site; (2) pairwise *t*-test t = –3.77, n = 13, p = 0.002 at LD site. In addition to the high number of tended aphid
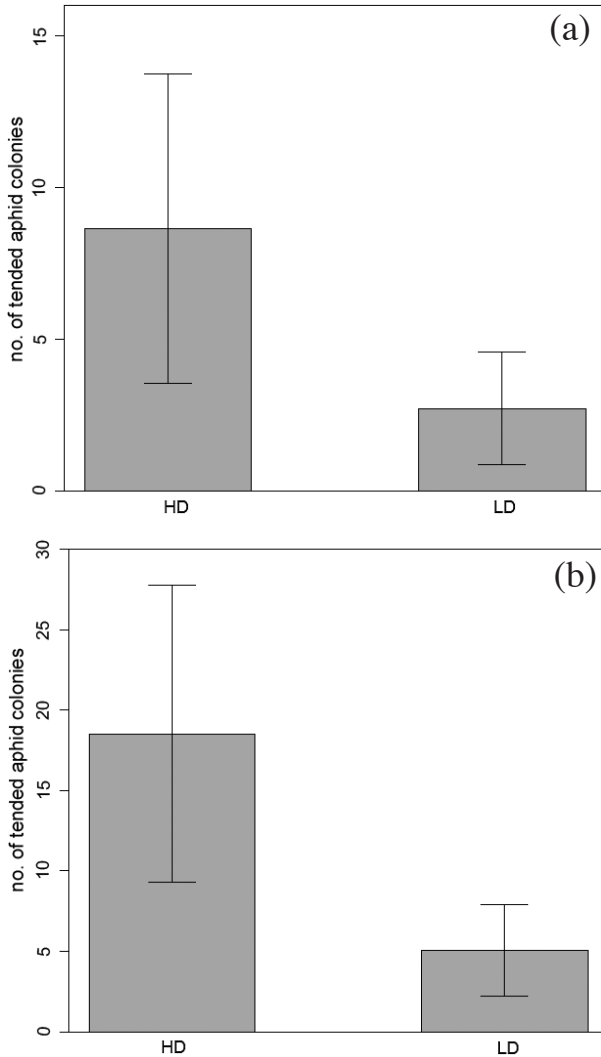
Fig. 7. Number of tended aphid colonies per ant nest at the two sites (Welch-test) (a) in 2008 (t = 6.2, $p < 0.0001$) and (b) in 2009 (t = 8.62, $p < 0.0001$) (mean ±SD).

colonies per ant nest, many *F. exsecta* nests shared the same aphid colony at the HD site, whereas nests at the LD site usually monopolized aphid colonies (Fig. 8).

In addition to *F. exsecta* nests generally tending more aphid colonies at the HD site, tended aphid colonies were also significantly larger, as demonstrated by the total length of plant stems occupied by aphids per exploiting ant nest: (1) mean HD = 251.24 cm (±152.69), mean LD = 59.07 cm (±43.03), Welch-test t = 6.94, $n_{HD} = 38$, $n_{LD} = 14$, $p < 0.0001$ in 2008; (2) mean HD = 202.56 cm (±115.02), mean LD = 33.72 cm (±25.56),
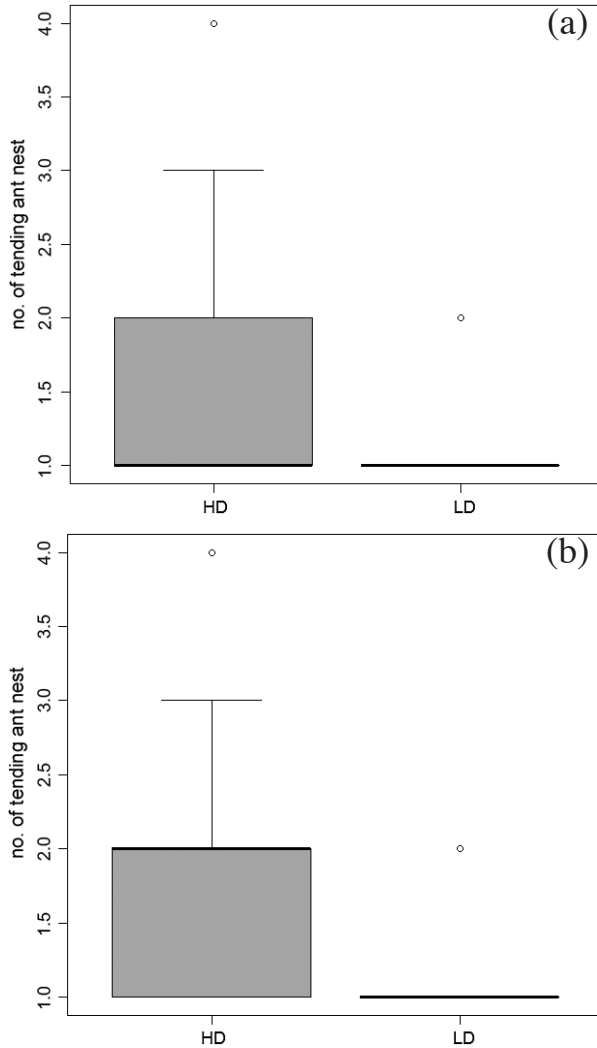
Fig. 8. Number of tending ant-nests per aphid colony at the two study site (Mann-Whitney-test) in (a) 2008 (z = 10.69, n_{HD} = 212, n_{LD} = 38, p < 0.0001) and in (b) 2009 (z = 15.29, n_{HD} = 449, n_{LD} = 91, p < 0.0001) (median, quartiles, minimum–maximum values, and outliers).

Welch-test t = 9.06, n_{HD} = 42, n_{LD} = 20, p < 0.0001 in 2009. Because aphid colonies were shared by more ant nests at the HD site, while usually monopolized at the LD site, it is reasonable to assume that the above difference is merely a side effect of sharing. The sum of "fair" shares of an ant nest from the "common goods" at the HD site may thus essentially be the same as the aphid "asset" of a non-sharing ant nest at the LD site. Thus, for each aphid colony, we calculated the hypothetical share of aphids for each ant
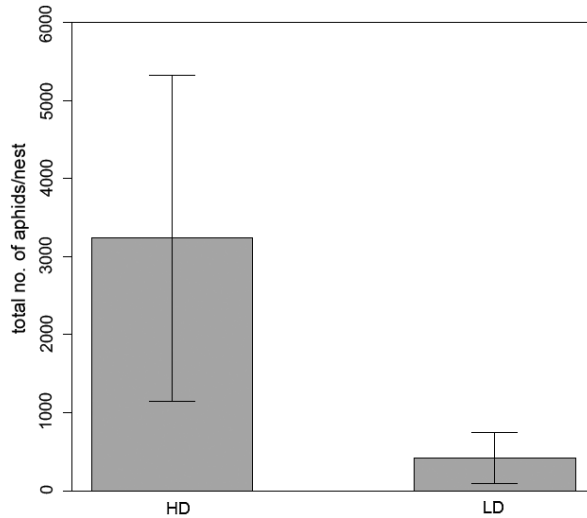
Fig. 9. Total number of aphids tended by an ant nest at the study sites in 2009 (Welch-test t = 8.5, n_{HD} = 42, n_{LD} = 20, $p < 0.0001$) (mean ±SD).

nest by dividing the stem lengths occupied by an aphid colony by the number of tending ant nests. The resulting shares per nest were summed for each ant nest separately. These per-nest values were then compared between the two sites. The analysis of the per-nest sums still yielded significant differences between the two sites in favor of ant nests at the HD site in both years: (1) mean sum of shares HD = 150.84 cm (±90.03), mean sum of shares LD = 59 cm (±44.36), Welch-test t = 4.92, n_{HD} = 39, n_{LD} = 14, $p < 0.0001$ in 2008; (2) mean sum of shares HD = 106.1 cm (±69.69), mean sum of shares LD = 30.66 cm (±25.26), Welch-test t = 6.2, n_{HD} = 42, n_{LD} = 20, $p < 0.0001$.

Additionally, aphid colonies tended by one ant nest also contained more aphids at the HD site, as revealed by the 2009 data (Fig. 9). In this case, the previously mentioned hypothetical shares were calculated by dividing the number of aphids within an aphid colony by the number of tending ant nests. The comparison of per-nest values also yielded significant differences between the two sites in favor of ant nests at the HD site: mean HD = 1658.29 aphids (±1227.67), mean LD = 374.63 aphids (±323.99), Welch-test t = 6.33, n_{HD} = 42, n_{LD} = 20, $p < 0.0001$. The size of an ant nest is also relevant to the number of aphid colonies tended; bigger ant nests usually visited more aphid colonies at both sites: (1) Pearson r = 0.49, n = 42, $p < 0.001$ at the HD site; (2) Pearson r = 0.51, n = 20, p = 0.02 at the LD site. Bigger ant nests also tended more aphids at both sites: (1) Pearson r = 0.38, n = 42, p = 0.01 at the HD site; (2) Pearson r = 0.52, n = 20, p = 0.01 at the LD site.

Minimum foraging areas of ant nests

The higher density of aphids combined with a higher density of *F. exsecta* nests at the HD site suggested that the distance between an aphid colony and its ant attendant nest(s)

should be smaller at the HD site than at the LD site. The statistical comparison confirmed that aphid colonies were generally closer to their tending ant nests at the HD site (Fig. 10). While aphid colonies were usually only a few meters away from a tending ant nest at the HD site, this distance often exceeded 4–6 m at the LD site. Overall, these data corroborate observations by Pisarski (1982c) and Sorvari (2009), according to which the penetration range of a specific nest's foragers rarely exceeds 5–8 meters.
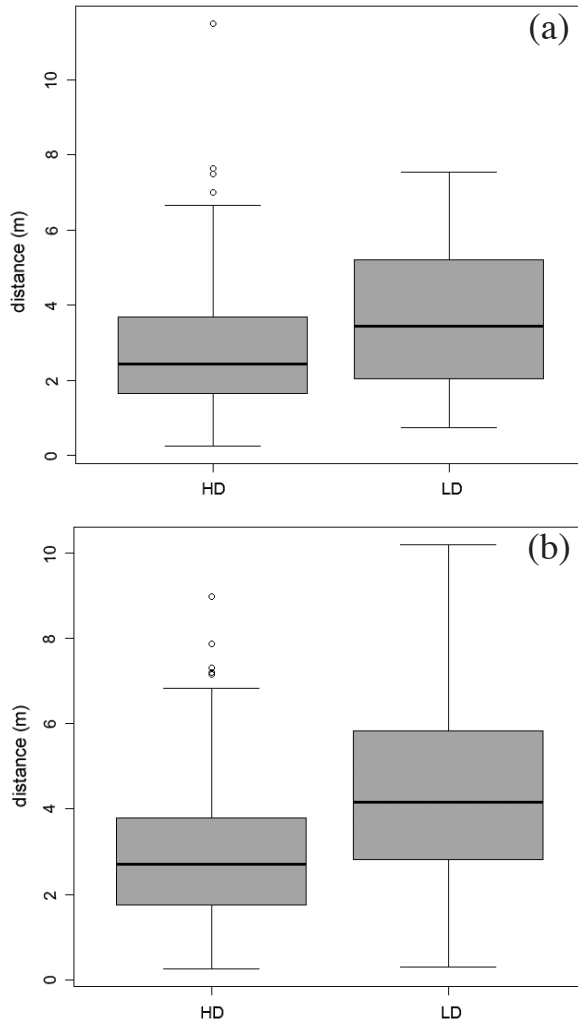
Fig. 10. Distance between ant nests and tended-aphid colonies (Mann-Whitney-test) (a) in 2008 (z = -2.76, n_{HD} = 337, n_{LD} = 38, p = 0.005) and (b) in 2009 (z = -6.17, n_{HD} = 790, n_{LD} = 101, $p <$ 0.0001) (median, quartiles, minimum–maximum values, and outliers).

The minimum foraging area of an *F. exsecta* nest could be estimated based on the observed range of visited aphid colonies. As expected, based on the observation that ant nests very rarely shared aphid colonies at the LD site, the minimum foraging ranges were well separated, with almost no overlap at the LD site (Fig. 11). The high degree
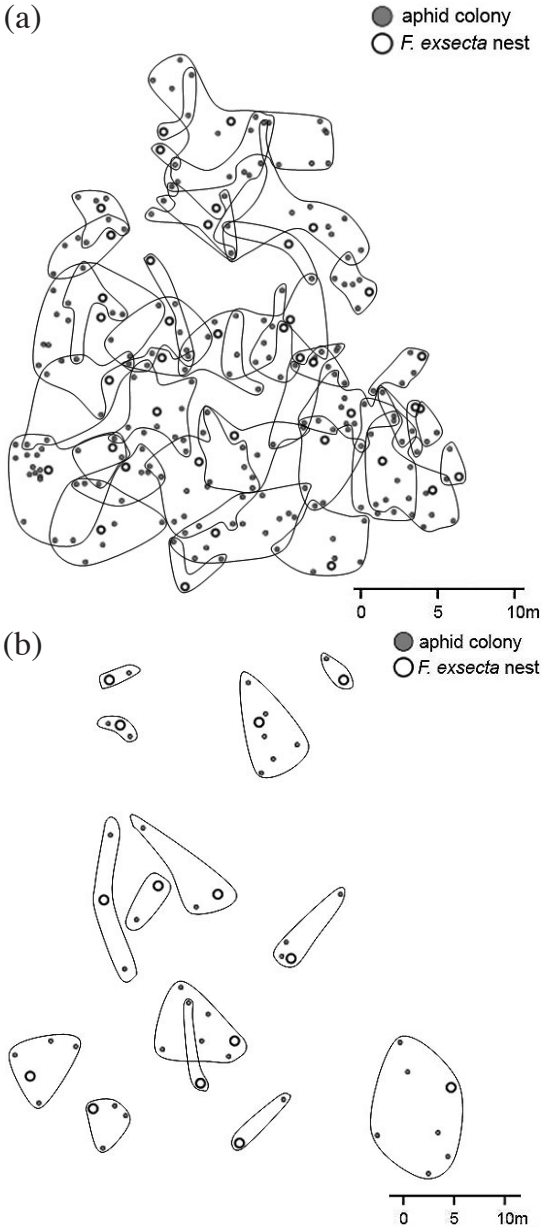

Fig. 11. Minimum foraging areas of ant nests based on the position of tended aphid colonies (a) at the HD and (b) at the LD sites in 2008.

of aphid-colony sharing at the HD site suggested an opposite trend, as was indeed confirmed by the map of minimum foraging areas (Fig. 11), showing multiple overlaps between these areas.

DISCUSSION

The presence of aphid colonies together with other rich food sources may shape ant communities by allowing aphid-tending ants to become numerically (and, in the case of certain species, also behaviorally) dominant, reducing the abundance and success of other ant species. Under optimal conditions, colonies of certain aphid-tending ants can develop into large polydomous systems (Pisarski, 1982a; Debout et al., 2007). These factors, among others, could have led to the formation of the *F. exsecta* supercolony that was the subject of the present study. Although mostly stable, such polydomous systems show certain variations in time and space that can be attributed to some extent to the dynamics of the aphid sources. According to Bönsel (2007), high nest-turnover rate within polydomous systems of *F. pressilabris* may be caused by the unpredictability of aphid sources. The foraging range of colonies can also shrink or expand as a function of changes in aphid-source distribution, as documented in *F. polyctena* (Vepsäläinen and Savolainen, 1994; Czechowski and Vepsäläinen, 2009). In the present case, very few changes occurred in the number of *F. exsecta* nests during the study years. The relatively high stability found for the ant nests suggests suitable habitat conditions, with the persistence of available food sources possibly being one of the most important stabilizing factors. The general differences we found between the two sites are consistent with the conclusions of other studies (Werner et al., 1979; Pisarski, 1982e; Kilpeläinen et al., 2005), suggesting that ant-nest density depends on the availability of food sources. Nests were more abundant at sites with higher aphid density. Additionally, ant nests tended more aphid colonies at the high density site and generally sustained bigger mounds, which may correlate with higher worker numbers. The observations by Werner et al. (1979) have likewise established that *F. exsecta* nests are bigger at sites with more aphid colonies. The aphid-tending activity of ants can depend both on the size of the ant nest and the number of aphid aggregations per plant (Grover et al., 2008). Moreover, ants can regulate their foraging behavior according to aphid honeydew-production (Mailleux et al., 2003). Although we did not make any direct observations on the distribution of foragers among aphid colonies, the fact that the bigger ant nests exploited more and larger aphid colonies also suggests that nest size affects tending activity of ants.

   Differences in the density of aphid colonies may also account for differences in the spatial patterns of ant nests, as suggested by the nearest-neighbor analysis, although other underlying factors cannot be excluded. As polydomous systems may comprise separate polycalic colonies (Debout et al., 2007), even intraspecific competition could have caused the regular distribution of nests, as found at the LD site. Polydomous systems comprised of mutually aggressive polycalic colonies are known in *F. exsecta* (Werner et al., 1979). The existence of such rival units within the studied supercolony would support the hypothesis that competition may have shaped the nests' spatial pattern

at the LD site. Nevertheless, a recent study by Martin et al. (2009) of the same *F. exsecta* supercolony suggests otherwise. Since these authors did not study the two sites in detail, the existence of more or less separate colonies at the LD site cannot be excluded.

Ants are clearly influenced by the abundance of aphids in many ways, but this relationship works both ways. Aphid density may also be positively affected by the density of ants, while the distance from the tending nest may have a negative effect on aphids (Karhu, 1998). For example, *Lasius niger* regulates the abundance of the myrmecophilous birch aphid *Symydobius oblongus* directly by regrouping aphids into aggregates of ca. 50–70 individuals per birch sapling (Stadler and Dixon, 1999). In *F. exsecta*, we found higher aphid numbers per plant, but this does not exclude the existence of the same regulatory behavior in this species. It would be interesting to determine whether *F. exsecta* indeed redistributes aphids to "empty" plants, e.g., in late spring, thus being directly responsible for the observed spatial distribution of aphids within the supercolony.

In addition to the influence of ants, changes in weather can also mediate the dynamics of aphid density (Vepsäläinen and Savolainen, 1994), as can attributes of the host plant species. According to Punttila et al. (2004), numbers of aphids correlated positively with the height of birch trees on which they were found. We therefore need to determine whether the height of birch saplings differs between the two study sites and may indeed contribute to the differences found between the two sites (Csata et al., in prep.). Although the area is subject to cow grazing almost throughout the year (with the exception of winter), there is bias in grazing pressure that could support this hypothesis. The LD site is more intensely grazed due to its proximity to the cows' shelter, and higher grazing pressure probably results in altered vegetation structure. To some extent, grazing by cows could be beneficial for *F. exsecta* supercolonies, as it keeps trees and other vegetation below a certain height, although too-intense grazing can represent a major threat for this species (Werner et al., 1979). Trampling can reduce vegetation cover and prevent nests from budding by destroying incipient nests. Similarly, it can also affect aphid population growth and survival by reducing vegetation cover. A reduction in aphid population, in turn, could eventually reduce the growth rate or survival of ant nests.

The foraging range of *F exsecta* is relatively small compared to that of the *F. rufa* species group. While the foraging radius of *F. polyctena* extends well beyond 100 m from its mound (e.g., Vepsäläinen and Savolainen, 1994), that of *F. exsecta* is roughly 8 meters (Pisarski, 1982c; Sorvari, 2009; and the present study), although differences can occur between nests with different food-source availability. As noted by Pisarski (1982c), the richer an area, the smaller the territory size of *F. exsecta* is. Indeed, the average distance between an ant nest and the aphid colony it tended was lower at the HD site. Feeding areas of different nests within a polycalic system overlap to a great extent (Pisarski, 1982c), as we observed at the HD site of the supercolony. The sharing of food sources and feeding grounds implies frequent contact among individuals from different nests and also trophallaxis, which ultimately leads to constant information exchange between different nests (Pisarski, 1982a).

Exchange of foragers in *F. exsecta* polydomous systems is quite frequent (Werner et al., 1979; Chudzicka, 1982; Kümmerli and Keller, 2007) and its rate may show seasonal,

and even daily variations, while also depending on nest state and food richness at the sites (Chudzicka, 1982). Kümmerli and Keller (2007) found that the drifting ratio in an *F. exsecta* supercolony (the proportion of marked workers found in nests other than the ones they originated from) increased from $5.9\% \pm 4.1\%$ after two days to $85.1\% \pm 7.7$ after one month. Workers marked at a specific nest could later be found at eight other nests on average, with a maximum detected dispersal distance of 20.2 m (Kümmerli and Keller, 2007). The fairly constant exchange of individuals could be an important factor in integrating single nests into a polycalic system. The low level of aggression found among *F. exsecta* individuals in the studied supercolony (Martin et al., 2009), along with the high degree of overlap between feeding grounds, suggests a high level of worker exchange at the HD site. In contrast, the almost complete lack of overlap of feeding grounds at the LD site implies a lower level or even absence of worker exchange. However, our measurements of ant-nest density at the LD site are in accordance with previous observations on *F. exsecta* supercolonies (Werner et al., 1979; Kümmerli and Keller, 2007), suggesting that the LD site represents at least an "average" area of an *F. exsecta* supercolony with a relatively high worker exchange rate (see Kümmerli and Keller, 2007). Coupled with the magnitude of differences we found in the overlap of minimal feeding-ground areas, this finding implies that worker exchange rate is extremely high at the HD site. We therefore conclude that the HD site is a fully integrated supercolony system in every respect, whereas the LD site may constitute a loosely integrated part of the supercolony that may also contain separate poly- and/or monocalic colonies. Nevertheless, the results of Kümmerli and Keller (2007) suggest that considerable worker exchange among nests can occur even in this case. Regardless of the origin of the ant nests at the LD site, it is plausible that an increase in aphid colonies (e.g., due to reduction in grazing pressure) will lead to a stronger integration of these nests, whereas a decrease in these sources will result in a further "disintegration" of this part of the supercolony.

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