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Hidden Potential of the Subdominant Ant *Formica lemani* Bondroit (Hymenoptera: Formicidae): The Formation of Large Nest Complexes and Restructuring Behavioural Stereotypes

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Abstract: The potential of subdominant ants of the *Formica fusca* group and their role in forests are still underestimated. Since ant behaviour is dependent on colony size, studying the functional organisation of nest complexes (NC) is most promising for a more accurate assessment of species capabilities. The study focused on the main ecological and ethological issues of the life activity of *Formica lemani* Bondroit within large NC (>150 nests) and beyond. After preliminary mapping of the *F. lemani* NC (main nests, trails, foraging trees), off-nest activity, aggressiveness, and trophobiotic relationships with aphids in and outside the NC territory were studied. Within the NC, the dynamic density, the intensity of movement on trails, and aggressiveness of *F. lemani* were significantly higher than beyond; the range of symbiont aphids was twice as small, with aphids on birches playing a key role in carbohydrate nutrition of *F. lemani*. The latter ensures accelerated restoration of trophobiotic interactions in spring and stability of the food supply until autumn. Combined with the lack of pressure from *F. rufa* group ants, this allowed *F. lemani* to maintain high population densities, and significantly increased its competitiveness, and role in plant protection against phytophages.

Keywords: aspen–birch forest; *Formica fusca* group; ant assemblages; hierarchical status; dynamic density; aggressiveness; trophobiosis; ant–aphid interactions

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1. Introduction

Ants of the *Formica rufa* group with complex social and territorial behaviour, forming large colonies and supercolonies, play one of the leading roles in terrestrial ecosystems, including forests, and are the major structuring force of ant assemblages [1–9]. Due to the complex organisation of the protected foraging area, specialisation of worker ants [10,11], and task partitioning among foragers collecting honeydew [12,13], obligate dominants of the *Formica rufa* group actively protect their resources from competitors, including natural enemies [14,15]. This allows the ants to utilise available resources more efficiently, maintain a stable resource base, and, at the same time, protect plants from leaf-eating insects.

Representatives of the *Formica fusca* group and the *Formica rufibarbis* group, previously referred to the subgenus *Serviformica* (hereinafter—the Serviformica group), have the status of subdominants in multispecies ant assemblages. In these species, foraging territories are usually unprotected, there is no specialisation among foragers, and solitary foraging is observed [8,16]. At the same time, the results of some studies indicate the presence of hidden potential in ants of this group. It was found experimentally that behaviour of subdominant ants of the genus *Formica*, in particular their social and territorial organisation, depend, to a large extent, on colony size and dynamic density of workers [10,11,16–19]. For example, when colony size of the *Formica cunicularia* Latreille and *F. picea* Nylander exceeds one thousand workers, the complexity of both the social structure of the ant colony and the territorial organisation of these ant species increases: colonies of both species begin to build mound nests and, at least partly, to protect their foraging territories [16,20]. Furthermore, besides the simple models of the organisation of honeydew collection, the use of more

complex models with protection of aphid colonies, was noted [13]. In the presence of natural and/or artificial objects that are able to accumulate heat (stone, stump, metal sheet, etc.), the construction of mound nests was also observed in *F. fusca* Linnaeus [10].

However, it should be noted that the dynamic density and colony size of subdominant ants from the Serviformica group are usually controlled and strictly regulated by obligate dominants of the *Formica* genus both within their foraging areas and during the occupation of new territories [7,11,21–23]. Nevertheless, the formation of stable nest complexes was noted in some species of the group—*F. cunicularia, F. cinerea* Mayr, *F. imitans* Ruzsky [10,18,19,24,25]. All this suggests that the hidden capabilities of the subdominant ants from the Serviformica group may be much broader than previously thought, and that the extent of their potential capabilities is still being underestimated.

One of the promising representatives of the group, in terms of studying hidden potential, is the northern black ant, *Formica lemani* Bondroit. It is a transpalaearctic boreomontane species that plays a subdominant role in forest ant assemblages [8,26]. In the forest–steppe and steppe zones, nests of *F. lemani* are confined to forest elements (aspen–birch stands, forest plantations, etc.). Like other species of the group, *F. lemani* primarily builds sectional nests in soil and often settles in dead wood. However, under certain conditions, such as scarcity of suitable habitats, it may form mound nests. The size of monogynous colonies of *F. lemani* does not exceed 1000 individuals, while polygynous colonies may reach from four to six thousand individuals. The foraging territory of *F. lemani* is usually not protected [8], and neither are its carbohydrate food sources, including aphid colonies (Novgorodova, unpublished data). This species usually uses tunnels to communicate between sections in the nest and to forage for food [8]. Formation of nest complexes in *F. lemani* has not been noted until recently. However, in 2020, a large nest complex of *F. lemani* was discovered for the first time in one of the aspen–birch stands in the south of Western Siberia (Novosibirsk Region, Russia) [27]. The nest complex immediately attracted attention due to the powerful ant trails on the trees, which were completely atypical for this species, and clearly visible even from afar. Studying the structural and functional organisation of such single-species nest complexes of subdominants of the genus *Formica* is highly important for assessing the potential functional capabilities of the species, as well as for predicting the effects of forced structural rearrangements of multispecies ant assemblages.

The main aim of the study was to explore the main ecological and ethological issues of the life activity in *F. lemani* from large settlements, utilising the example of the nest complex identified in the Novosibirsk Region (Russia) in 2020. The objectives of this research were: (i) to estimate the size and identify the main infrastructural elements of the territory of the large *F. lemani* complex nest; (ii) to identify behavioural patterns of the *F. lemani* foragers, including off-nest activity, aggressiveness, and organisation of honeydew collection, in and outside the nest complex; and (iii) to identify the features of trophobiotic relationships between *F. lemani* foragers from the large settlement and aphids.

2. Materials and Methods

The study was conducted in August–September 2020 and 2022 in the south of the Novosibirsk Region (Karasuk District, vicinity of Sheinfeld Village; Russia) in the territory of the *F. lemani* nest complex (NC) in an aspen–birch stand, as well as outside the nest complex—in the same or neighbouring aspen–birch stand.

The species identity of the *F. lemani* individuals from the studied NC was additionally confirmed by the results of the molecular genetic analysis (sample F24-1): by COI—genebank number OM722036 (https://www.ncbi.nlm.nih.gov/nuccore/OM722036.1 accessed on 25 May 2023), ITS1—OM728505 (https://www.ncbi.nlm.nih.gov/nuccore/OM728505.1 accessed on 25 May 2023), D2 28S—OM722055 (https://www.ncbi.nlm.nih.gov/nuccore/OM722055.1 accessed on 25 May 2023) [28].

2.1. The Main Characteristics of the F. lemani Nest Complex

To approximate the size and structure of the *F. lemani* nest complex, determine its boundaries and occupied territory, as well as identify the main infrastructural elements of the NC area, a schematic mapping of the *F. lemani* NC was carried out, indicating the main nests and trails, as well as foraging trees (hereafter—mapping). The mapping was carried out in two stages. At the first stage, in late September 2020 (at the time of discovery), the main part of the *F. lemani* NC was mapped. During that period, mainly the largest nests were mapped. Their location was identified by the tree foraging ant trails, strong enough to persist until the end of the season. The mapping was continued in the first half of August 2022 with confirming the location of the large nests, collecting extra information on the other nests, and mapping the system of foraging trails.

In the explored territory, the nests of the *Formica rufa* group were also mapped. The main characteristics of each anthill were noted. The diameter and height of each anthill mound were measured both without and including the soil base—embankment (d/D and h/H, respectively). For dead (degraded) ant nests, the diameter of the crater was measured.

2.2. Off-Nest Activity and Aggressiveness of the F. lemani Foragers

To identify the behavioural characteristics of the *F. lemani* foragers, we took into account the off-nest activity of the species studied (dynamic density of foragers and intensity of movement of foragers on foraging trees), as well as assessed the aggressiveness of foragers on tree trunks and in aphid colonies. The studies were carried out both on and off the area occupied by the *F. lemani* nest complex in the same stand. The investigations outside the NC were carried out at a distance of more than 20 m from the border of NC, which was clearly visible by green foliage and trails of *F. lemani* on birch trunks.

2.2.1. Dynamic Density

Dynamic ant density was assessed in August 2022 using standard methodology [8]. Ants were counted in three replicates in a 10 dm^2 (31.6 × 31.6 cm^2) plot bounded by a wire frame on legs. The number of ants that visited the site within 5 min was recorded, after which the average dynamic density (individuals/dm^2·min) was calculated. A total of 23 sites were surveyed: 13—in the territory of the NC; 10—beyond. In the territory of the *F. lemani* NC, the study plots were located at least 2 m from the nearest foraging trail of *F. lemani*.

2.2.2. Intensity of Movement of Foragers on Trees

The intensity of foraging movement on the trunks of main forage trees was assessed on birch (*Betula pendula* Roth) in early August 2022. A count of foragers crossing a conventional line in both directions at a height of about 1.3 m was carried out for 5 min (in triplicate) with subsequent averaging and recalculation for 1 min (individuals/min). When traffic of foragers was of high intensity, we used video recording and counted foragers in the laboratory. Testing was carried out on 29 selected trees located within and off the territory of the *F. lemani* nest complex (19 and 10 trees, respectively). The trunk diameter of the birches selected for testing ranged from 9 to 28 cm (at the site of forager counting), and the ratio of the trees of different size categories within and off the *F. lemani* NC was similar. The proportions of selected birches of three size categories in the territory of the NC and beyond were 9–15 cm—31.6% and 30.0%, respectively; 16–20 cm—42.1% and 40.0%; 21–28 cm—26.3% and 30.0%.

2.2.3. Ant Aggressiveness

We compared the aggressiveness of *F. lemani* foragers in the territory of the NC with the aggressiveness data of foragers tested outside it. Aggressiveness was assessed on birch trunks (diameter from 16 to 20 cm) and in aphid colonies of *Chaitophorus populeti* (Panzer) on aspen by evaluating the responses of ants to a simple artificial irritant (a dissecting needle) using the universal scale developed earlier and based on reactions

of ant foragers to various stimuli [13,29]. Aggressiveness of foragers was assessed on a 9-point scale: (0) avoidance—dropping down or running away; (1) tolerance—neutral reaction (ants do not react); (2) antennation—investigation of the irritant using antennae; (3) alert pose—standing still with mandibles slightly open and antennae slightly extended towards the irritant; (4) aggressive pose—the stance adopted by ants before an attack (stilt-legged posture; mandibles widely open, antennae directed towards the irritant or slightly upwards; usually with gaster extended forwards in order to spray acid); (5) threatening lunges—usually repeated rapid lunges towards the irritant with open mandibles, but without contacting it; (6) hit-and-run attack—sudden attack on the irritant ($\leq$1 s); (7) biting—short bites (less than 5 s); (8) death grip—a prolonged biting (ant seizes the irritant and does not loosen its grip for more than 5 s). If rapid change in ant reactions from one to another (increasing aggression to the irritant) was observed during testing, only the more aggressive reaction was used in the analysis. For each individual, testing was carried out at least 3 times. A total of 190 *F. lemani* foragers were tested, of which 145 foragers were tested within the NC studied (80 foragers on trunks, 65 honeydew collectors in 15 aphid colonies) and 45 foragers were tested beyond (30 individuals on trunks and 15 honeydew collectors in 15 aphid colonies).

2.3. Trophobiotic Relationships of F. lemani with Aphids

To identify trophobiotic relationships between aphids and representatives of *F. lemani* colonies from the nest complex, the above-ground parts of plants up to a height of about 2–3 m were inspected in the area occupied by the NC. The root part was investigated only in the presence of soil disruptions (result of ant activities) at the base of the plant. Similar studies were carried out outside the territory of the NC in the same and neighbouring aspen–birch stand, where only small single nests of *F. lemani* were recorded. Insects were fixed in 70% ethanol. A total of 362 samples were collected. Analysis of the material and further identification of aphids was carried out using Stemi 2000-C and Zeiss Axiostar Plus microscopes (Carl Zeiss MicroImaging GmbH, Göttingen, Germany). The aphids were studied on microscope slides prepared using Faure–Berlese fluid. When identifying aphids, an online identification and information guide was used, which includes current information on aphids [30]. The material is deposited at the Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences (Novosibirsk, Russia).

2.4. Data Analysis

A comparative analysis of the parameters of off-nest activity (dynamic density and intensity of foraging movement on trunks of birch trees), as well as the aggressiveness of *F. lemani* foragers in the territory of the NC and beyond, was carried out using the Mann–Whitney test. To compare the degree of aggressiveness of aggressive and tolerant foragers of *F. lemani* in the territory of the NC and beyond, the Mann–Whitney U Test with Bonferroni correction ($p < 0.017$) was used. To assess the relationship between intensity of foraging movement and trunk diameter, the Pearson correlation coefficient was calculated.

3. Results

3.1. The Main Characteristics of the F. lemani Nest Complex

In 2022, the surveyed *F. lemani* NC covered an area of about 4800 m^2 and included more than 150 large nests (Figure 1). Most nests were located at the bases of birch trees and inside logs or large branches of old fallen trees. The ants used old overgrown (and already hollow inside) large branches of birch trees as tunnels. In addition, a pronounced network of surface trails was observed in the territory of the *F. lemani* nest complex. Exchange trails (for the exchange of individuals and brood) were noted between nests located at the bases of trees at a distance of 4 to 6 m from each other. The main trails led to forage trees—birches and aspens. Visible even from a distance, trails on trunks consisted not only of honeydew collectors, but also of hunters who descended down the trunk with prey.

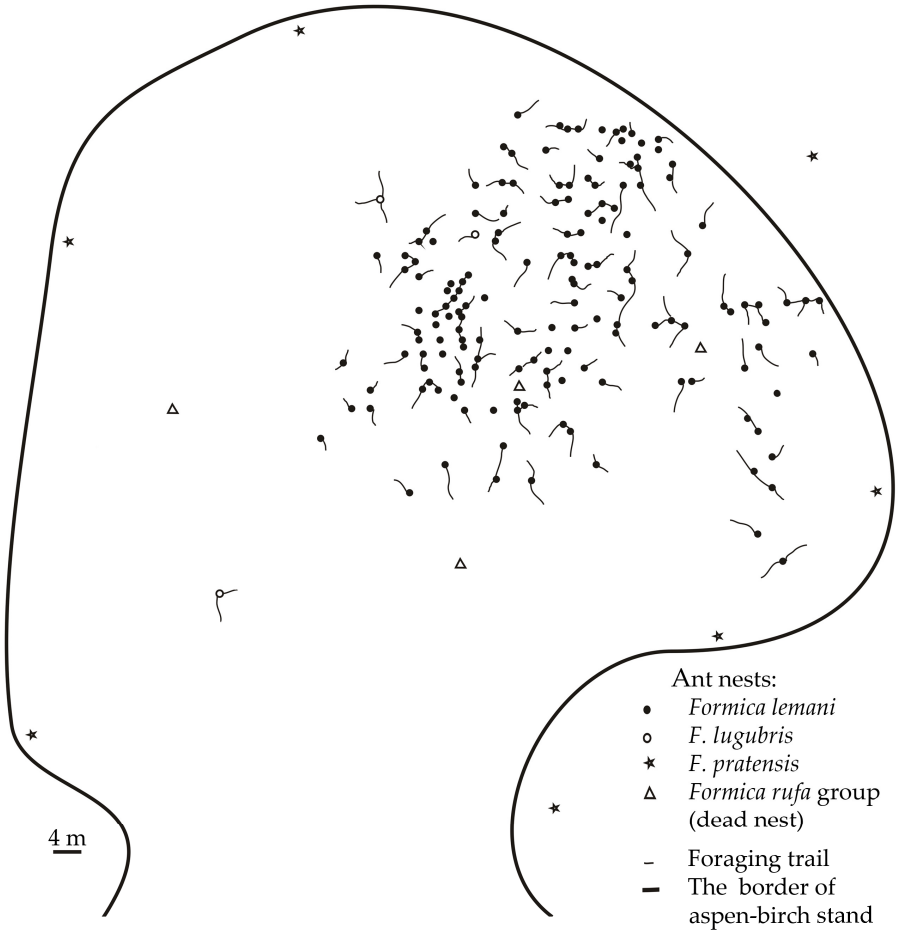

Figure 1. Schematic map of the nest complex of *Formica lemani* in the Karasuk District of the Novosibirsk Region in the vicinity of Sheinfeld Village (Russia).

Only three nests of *Formica rufa* group ants (*Formica lugubris* Zetterstedt) were recorded in the area of the studied nest complex. One *F. lugubris* nest (d/D = 55/90 cm, h/H = 20/40 cm; d/D = 60/105 cm, h/H = 30/45 cm) was located at a distance of about 30–40 m from the boundary of the *F. lemani* NC, 1 nest (d/D = 60/100 cm, h/H = 25/45 cm)—about 10–15 m from the NC. Another small nest with a flat dome (d/D = 45/50 cm; h/H = 5/25 cm) was found on the periphery of the nest complex (Figure 1). Nests of obligate dominants of the *Formica rufa* group with mound diameters (d) greater than 60 cm were absent in the area of the surveyed *F. lemani* NC.

Four craters from long-degraded nests of red wood ants (D = 110–120 cm) were recorded in this part of the aspen–birch stand, two of which were located directly in the territory of the *F. lemani* NC, and two were found outside.

Colonies of *Formica pratensis* Retzius were registered along the boundary of the aspen–birch stand only (Figure 1). The buffer zone between the foraging areas of *F. pratensis* colonies and the territory of *F. lemani* nest complex was about 15–20 m.

3.2. Off-Nest Activity and Aggressiveness of the F. lemani Foragers

3.2.1. Dynamic Density

The dynamic density of *F. lemani* in the territory of the NC was almost 3.9 times higher than beyond (Figure 2). The dynamic density of *F. lugubris* in the vicinity of the small, weakened nest of this species within the studied NC was 7.5 times as low as the *F. lemani* (0.06 and 0.45, respectively). Single individuals of *Camponotus herculeanus* (L.) and *Leptothorax acervorum* (Fabricius) were recorded only on the periphery of the studied NC.

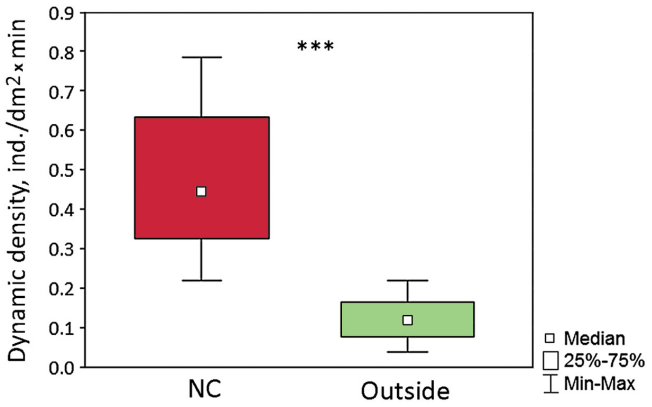

Figure 2. Dynamic density of *Formica lemani* within the territory of the nest complex (NC) and beyond (Outside). Mann–Whitney U Test: ***—$p < 0.0001$.

3.2.2. Intensity of Movement of Foragers on Trees

A significant positive correlation between the intensity of movement of foragers and the diameter of trunks of selected birch trees at the survey site was found only for the territory of the *F. lemani* nest complex (r = 0.577, $p = 0.01$). However, outside the NC, the correlation was insignificant (r = 0.223, $p = 0.537$), so further comparison was made for total data, without taking into account the influence of the trunk diameter. The intensity of movement of *F. lemani* foragers on the birch trunks within the territory of the NC was significantly higher than beyond in the same stand, and reached 123.6 individuals/min (Figure 3). Outside the studied NC, the movement intensity of *F. lemani* on birch trunks did not exceed 5.2 individuals/min (Figure 3).

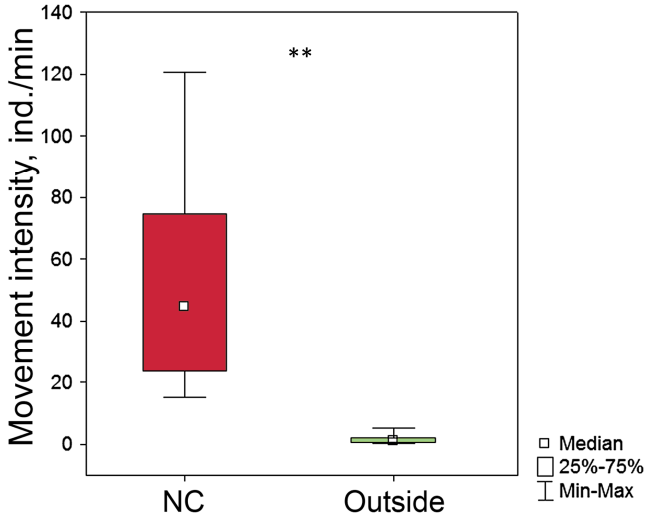

Figure 3. Movement intensity of *Formica lemani* foragers on trunks of birch trees within the territory of the nest complex (NC) and beyond (Outside). Mann–Whitney U Test: **—$p < 0.001$.

3.2.3. Aggressiveness

The aggressiveness of *F. lemani* foragers in the territory of the studied nest complex was generally significantly higher than outside it both on birch trunks (Mann–Whitney criterion, U = 351.5, $p < 0.001$) and in aphid colonies (U = 168.0, $p < 0.001$) (Figure 4).

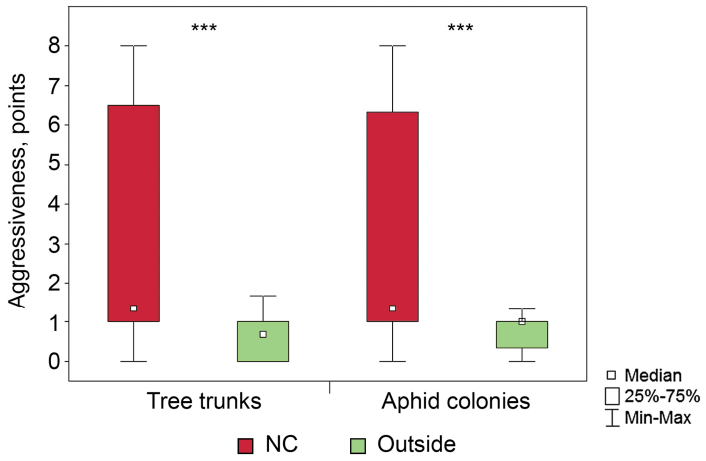

Figure 4. Aggressiveness of *Formica lemani* foragers on the trunks of birch trees and in the aphid colonies of *Chaitophorus populeti* on aspen trees within the territory of the large nest complex (NC) and beyond (Outside). Mann–Whitney U Test: ***—$p < 0.001$.

Outside the NC, both on the trunks of forage trees and in aphid colonies, *F. lemani* foragers showed only non-aggressive reactions (0 to 2 points) in response to stimulus presentation: average aggressiveness indices of most individuals fell within the range (0; 1] points (Figure 5).

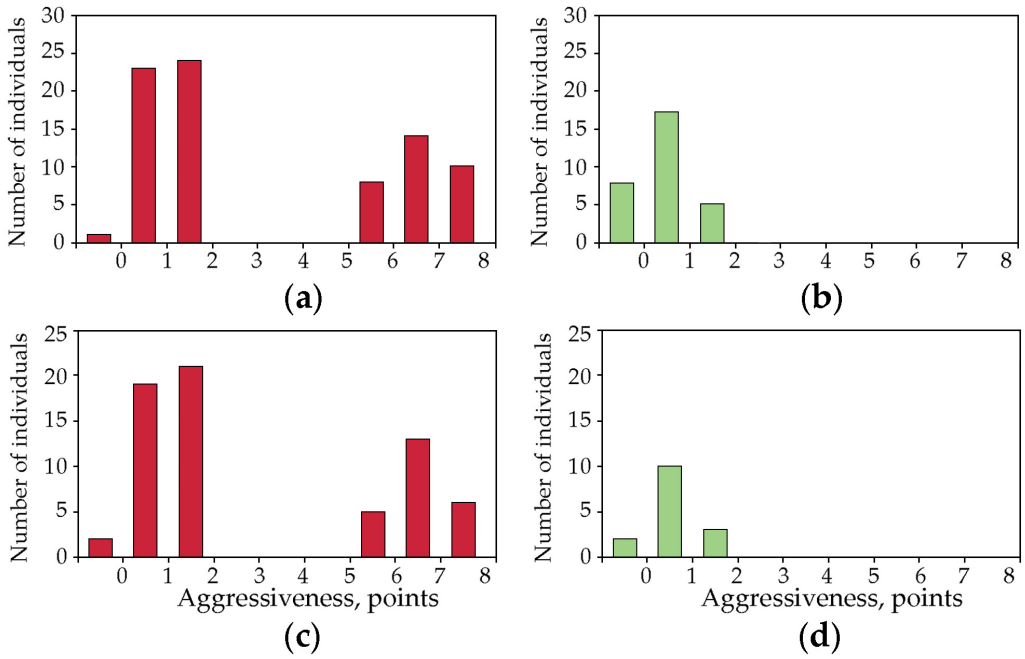

Figure 5. Differentiation of the *Formica lemani* foragers by the degree of aggressiveness in the territory of the large nest complex (red) compared to the foragers beyond the NC (green): (**a**,**b**)—the results of testing on the trunks of forage trees (*Betula* spp.); (**c**,**d**)—the results of testing in the aphid colonies. Aggressiveness scale: 0—avoidance; 1—tolerance; 2—antennation; 3—alert pose; 4—aggressive pose before an attack; 5—threatening lunges; 6—hit-and-run attack; 7—short bites (<5 s); 8—death grip (a prolonged biting for more than 5 s).

In the territory of the nest complex, two groups of foragers with different degrees of aggression—tolerant vs. aggressive—were clearly distinguished both on the trunks of forage trees and among the honeydew collectors tested in aphid colonies. The spectrum of responses of tolerant individuals was similar to that observed outside the NC (0–2 points, very rarely 3 points): the average aggressiveness of most individuals fell within the ranges

of (0; 1] and (1; 2] points (Figure 5). Aggressive foragers responded to stimulus presentation by predominantly demonstrating hit-and-run attacks, short bites, and death grip, while threatening lunges were recorded in isolated cases (6–8 points respectively, rarely 5 points): average aggression scores of most tested individuals fell within the range (6; 7] points (Figure 5).

The degree of aggressiveness of honeydew collectors of *F. lemani* beyond the nest complex and tolerant foragers within the territory of the NC (both on the selected trees and in aphid colonies) was similar and significantly lower than that of aggressive foragers in the NC territory (Figure 6).

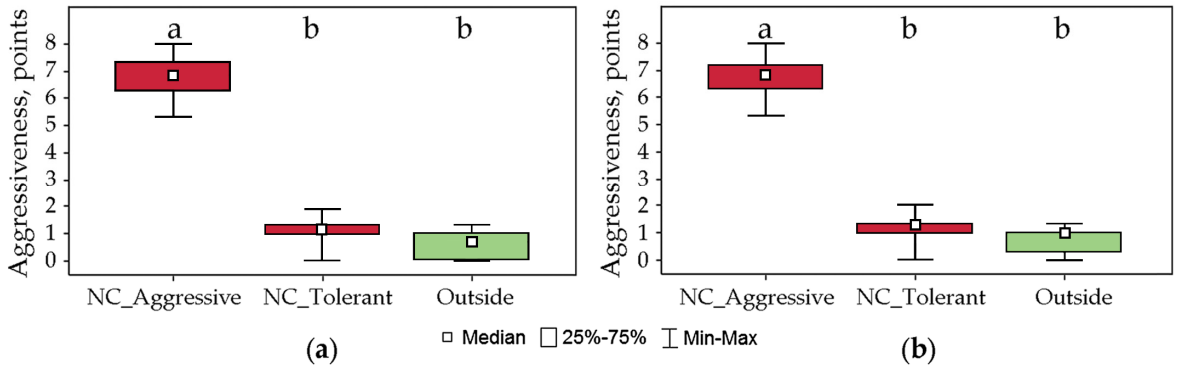

Figure 6. The degree of aggressiveness of aggressive and tolerant foragers of *Formica lemani* in the territory of the studied nest complex (NC) compared to the *F. lemani* foragers beyond the NC territory (Outside): (**a**) the results of testing on the trunks of foraging birch trees; (**b**) the results of testing in the aphid colonies (*Chaitophorus populeti*) on aspen trees. Different letters above the data (a,b) indicate significant differences (Mann–Whitney U Test with Bonferroni correction, $p < 0.0001$); identical letters (b) indicate non-significant differences ($p > 0.017$).

3.3. Trophobiotic Relationships between F. lemani and Aphids

The structure of trophobiotic relationships between *F. lemani* and aphids in the territory of the nest complex and beyond had some differences (Table 1). In the NC territory, *F. lemani* visited aphid colonies of only seven species from seven genera of four subfamilies: Aphidinae—three species, Calaphidinae—two, Thelaxinae and Chaitophorinae—one species each (Table 1). Dendrobiont species predominated and accounted for 57.1% of the total number of symbiont species. Their colonies were located on birches (*Symydobius oblongus* (von Heyden), *Glyphina betulae* (L.), *Callipterinella tuberculata* (von Heyden), and aspens (*Chaitophorus populeti* (Panzer)). On herbaceous plants, only single colonies of aphids *Metopeurum fuscoviride* Stroyan (on *Tanacetum vulgare* L.), *Aphis fabae* Scopoli (on *Sonchus arvensis* L.), and *Semiaphis horvathi* (Kaltenbach) (on *Silaum silaus* (L.) Schinz & Thell.) were noted.

The main source of carbohydrate food for *F. lemani* from the nest complex was honeydew of aphids on woody plants, mainly on birch trees. Powerful trails of *F. lemani* foragers were observed on the majority of birch trees (90%) located in the territory of the studied NC. Outside the boundary of the nest complex (in the areas of similar size both in the same and neighbouring aspen–birch stands), 1.7–1.9 times more aphid species (12 and 13, respectively) associated with *F. lemani* were identified (Table 1). The proportion of aphid species whose colonies were located on herbaceous plants in the same aspen–birch stand was 66.7% (out of 12 species), and in the neighbouring one—69.2% (out of 13 species). In total, 15 species of aphid symbionts of *F. lemani* were identified beyond the NC studied (Table 1). These species belonged to nine genera of four subfamilies.

Table 1. Trophobiotic relationships between *F. lemani* and aphids within the territory of the studied nest complex (NC) and beyond—in the same (Outside_1) and in the neighbouring (Outside_2) aspen–birch stands (+—single cases; ++—common; +++—numerous; – none).

No	Aphids (Subfamily, Genus, Species)	Plants	NC	Outside_1	Outside_2
	Thelaxinae				
1	*Glyphina betulae* (L.)	*Betula pendula* Roth, *Betula* sp.	+++	+	+
	Calaphidinae				
2	*Callipterinella tuberculata* (von Heyden)	*Betula pendula*, *Betula* sp.	+++	+	+
3	*Symydobius oblongus* (von Heyden)	*Betula pendula*, *Betula* sp.	+++	+	+
	Chaitophorinae				
4	*Chaitophorus populeti* (Panzer)	*Populus tremula* L.	++	+	+
5	*Sipha (Rungsia) elegans* Del Guercio	*Elytrigia repens* (L.) Desv. ex Nevski., Poaceae	–	+	+
6	*S. (Rungsia) maydis* Passerini	*Elytrigia repens*, *Festuca pratensis* Hudson	–	+	–
	Aphidinae				
7	*Aphis craccae* L.	*Vicia cracca* L.	–	–	+
8	*A. craccivora* Koch	*Vicia* sp.	–	+	–
9	*A. fabae* Scopoli	*Sonchus arvensis* L.	+	+	+
10	*A. franzi* Holman	*Seseli libanotis* (L.) C. Koch	–	+	+
11	*A. hieracii* Schrank	*Hieracium umbellatum* L.	–	–	+
12	*A. silaumi* Bozhko	*Silaum silaus* (L.)	–	+	+
13	*Rhopalosiphum oxyacanthae* (Schrank)	*Dactylis glomerata* L.	–	–	+
14	*Metopeurum fuscoviride* Stroyan	*Tanacetum vulgare* L.	++	+	+
15	*Semiaphis anthrisci* (Kaltenbach)	*Anthriscus silvestris* L.	–	+	+
16	*Semiaphis horvathi* Szelegiewicz	*Silaum silaus* (L.) Schinz & Thell.	+	–	–
	Total number of species:		7	12	13
	On woody plants		4	4	4
	On herbaceous plants		3	8	9

In aphid colonies beyond the studied nest complex, only solitary unspecialised foragers of *F. lemani* were observed, which did not show any aggressive reactions to the irritant (Figures 5 and 6). These foragers themselves collected and carried honeydew to a nest, leaving the aphid colonies unattended.

In the territory of the NC, *F. lemani* used more complex behavioural models with the clear division of honeydew collection and protection of symbionts between foragers with low and high levels of aggressiveness, respectively (Figures 5 and 6). Therefore, tolerant individuals performed the functions of collecting and transporting honeydew to their nests and were significantly less aggressive (Figures 5 and 6).

Among the honeydew collectors tested in aphid colonies, usually about 20%–30% of foragers (rarely 50% of individuals) demonstrated aggressive behaviour and performed the functions of guards. Aggressive ants almost did not collect honeydew, these individuals quickly responded to the appearance of foreign objects and protected their symbionts from various competitors, including aphidophages and other ant species.

4. Discussion

In the forest–steppe and steppe zones in the south of Western Siberia, as in other parts of the *Formica lemani* range, the northern black ant is confined to forest communities, where it usually plays the role of subdominant [8,26]. In the studied area, an atypical ant assemblage, rather unique for the forest–steppe landscapes of the south of Western Siberia, with the absolute dominance of *F. lemani*, has formed. At first glance, the area of the *F. lemani* nest complex does not appear to be too large (about 0.005 km^2), at least compared to the areas of red wood ant supercolonies that can exceed 2.5 km^2 [9,31]. However, the significant reorganisation of various ecological and ethological aspects of the life of this species is impressive.

According to our long-term research in the south of the Novosibirsk Region (2000–2022), in this territory, *F. lemani* usually lives in sectional nests in the soil, as well as inside old stumps, logs, and large branches of fallen trees, etc. This ant typically uses tunnels to communicate between sections of the nest and for foraging, which is consistent with the results of other studies [8].

In the territory of the studied nest complex, in addition to the tunnels that are quite common for the species, a pronounced network of foraging trails was discovered, which was similar to a functional structure of the trail system of red wood ants. The trail network in the NC territory included exchange trails between nests at the bases of birches, as well as foraging trails leading to trees (birch, aspen), where workers not only actively collected honeydew, but also hunted. Among the foragers descending down a trunk, a large number of honeydew collectors with swollen abdomens, as well as hunters with prey (caterpillars, various dipterans, aphids), were noted. Some of noted exchange trails can be classified as exchange–foraging trails, since they were used by *F. lemani* for both purposes—exchange of individuals and brood, and organisation of foraging (being part of the foraging network). According to our preliminary observations, the presence of exchanges between most of nests in the NC territory, with regular transitions of individuals, may indicate that the studied nest complex of *F. lemani* is a single supercolony, which apparently consists of several polycalic systems (an ant colony simultaneously inhabiting several nests with different functions). However, additional detailed studies are needed to obtain more precise information on this issue.

Searching for food on trees is not something special for *F. lemani*. A striking difference from the usual lifestyle of the northern black ant in the territory of the studied nest complex is the very high off-nest activity (dynamic density, intensity of movement of foragers along the trails). This is manifested in the presence of trunk trails with high intensity of *F. lemani* movement, which were easy to see on birch trees with white bark even from a distance. According to our data, the intensity of *F. lemani* movement on the trunks of foraging trees in the territory of the nest complex was significantly (about 32 times) higher than outside, and the dynamic density of *F. lemani* within the NC territory was almost 4 times as high as beyond.

Outside the studied nest complex of *F. lemani*, small colonies of this species were not detected to have protected foraging areas. The collection of aphid honeydew was carried out by single unspecialised foragers, who independently collected and carried honeydew to their nests, continuously leaving colonies of symbiont aphids unattended. This is the simplest type of honeydew collection in ants [13] that usually corresponds to the lowest level of symbiont protection by ants against aphidophages [14].

In the territory of the NC, the behaviour of *F. lemani* differed significantly from that typical of small colonies of this species. The aggressiveness of foragers on the trunks of forage trees and in aphid colonies was 4–5 times as high. In addition, increased territorial organisation was observed. Due to the highly increased dynamic density and aggressiveness of foragers, the NC territory was almost completely controlled by *F. lemani*. Single individuals of other species (*Camponotus herculeanus* (L.), *Leptothorax acervorum* (Fabricius)) were noted only in the peripheral part of the *F. lemani* nest complex.

The only small degrading nest of *F. lugubris* with an almost flat mound, the height (h) of which was only 5 cm and the diameter (d) of about 50 cm, was also located on the periphery of the nest complex; the dynamic density of *F. lugubris* in the area of this anthill was 7.5 times lower than the dynamic density *of F. lemani*. The only trail of foragers from the *F. lugubris* nest led to the tree adjacent to this anthill. The weak construction, size, and shape of the anthill, combined with low off-nest activity, indicated the grave condition of the colony [8].

As for three other nests of *F. lugubris* found in the same stand but outside the NC, the mound diameter (d) of these anthills did not exceed 60 cm, corresponding to the minimal parameters of permanent residential nests of red wood ants aged 1–2 years [8]. The absence of large colonies of red wood ants in the study area allowed *F. lemani* to avoid interspecific social control typical of ant assemblages that include obligate dominants of *Formica rufa* group [7,21,22].

At the same time, despite the absence of red wood ants, fairly high efficiency in protecting woody plants from leaf-eating insects was noted in the territory of the studied *F. lemani* NC during the years of the field research. Hence, during outbreaks of gypsy moth (*Lymantria dispar* (L.)) in 2020 and 2022, the area occupied by the *F. lemani* nest complex was clearly distinguished from the background of neighbouring areas affected by the pest, mainly due to its preserved green foliage. A special assessment of the degree of damage to the leaves was not carried out; however, the border of the *F. lemani* NC was quite well noticeable (Figure 7).

In aphid colonies within the territory of the *F. lemani* NC, the use of more complex behavioural patterns was observed with the partial division of collecting honeydew and protecting symbionts by more aggressive foragers. Both in aphid colonies and on trunks of forage trees, a clear division of the two groups of tested ant individuals—aggressive and tolerant—was observed according to their responses to the irritant (stimulus). Observations of ant behaviour before testing showed that tolerant workers with a low degree of aggressiveness were engaged in collecting honeydew and transferring the collected honeydew to other individuals. Aggressive ants exhibited the full range of aggressive reactions to any external intervention (the approach of aphidophages, other insects and the researcher, the presentation of an artificial stimulus, etc.). On tree trunks, the lowest rates of aggressiveness were seen in foragers with swollen abdomens, which were engaged in transporting honeydew to their nests. This is consistent with the research data on the aggressiveness of *Formica rufa* group ants, which perform different functions—protecting aphids, and collecting and transporting aphid honeydew [13].

Our work makes clear the presence of specialisation in groups of foragers visiting individual aphid colonies, with the division of functions of collecting honeydew and protecting symbionts corresponding to at least a medium level of specialisation [13]. To more accurately determine the depth of specialisation of honeydew collectors, and to answer the question how exactly the collected honeydew is transported (whether there are specialists in delivering honeydew to the ant nests or not), additional research is required.

In the territory of the nest complex of *F. lemani*, the range of aphid symbionts of the northern black ant turned out to be twice as small as beyond, with aphids on birches playing a key role in carbohydrate nutrition of *F. lemani*. It was birch trees that served as key elements in the formation of the NC structure and its trail network. Large nests of *F. lemani* were located at the bases of birches with a trunk diameter of 20–25 cm (Figure 7), the main foraging trails also led to birch trees. Foragers of *F. lemani* usually reached rare colonies of aphids on herbaceous plants through tunnels, using old hollow large branches of birch trees in the forest litter.

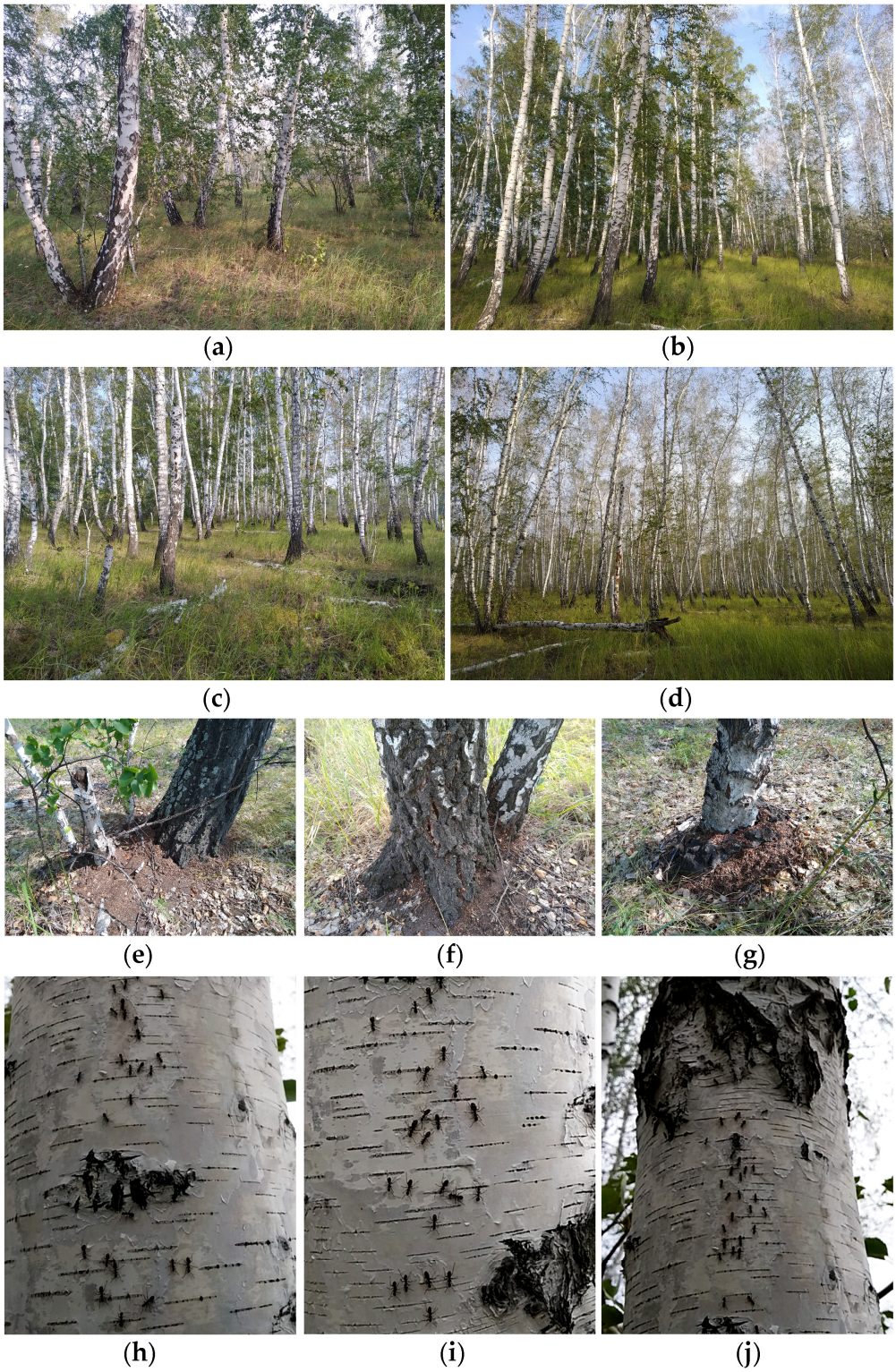

Figure 7. The territory of the studied nest complex (NC) of *Formica lemani* in the aspen–birch stand in the south of the Novosibirsk Region in the vicinity of Sheinfeld Village (Russia): (**a**) the central part of the *F. lemani* NC; (**b**)—the border of the studied NC; (**c**)—view of the nest complex (green foliage) from the adjacent territory; (**d**)—the adjacent territory (the photo is taken from the border of the *F. lemani* NC); (**e**–**g**)—large nests of *F. lemani* in the territory of the studied NC; (**h**–**j**)—foraging trails of *F. lemani* on birch trees in the NC territory.

In ants of the *F. rufa* group, the structural and functional organisation of polycalic systems and supercolonies has similar basic principles, including dendrobiont aphids as a main source of carbohydrates, and trees (host plants of myrmecophilous aphids) as a core element of trail system and territorial structure [1,10,11,32,33]. In addition to aphid honeydew, ants may use other sources of carbohydrates, including extrafloral nectaries [1,10,33,34]. Aspen leaves may also have small glands at the base of the leaf that secrete nectar attracting ants [35]. We also noted similar extrafloral nectaries in aspen (*Populus tremula* L.) in the south of Western Siberia. However, according to our observations, ants usually visit foliar nectaries of *Populus tremula* L. only in spring while aphids are absent or limited. During our investigation of the *F. lemani* NC in August–September (2020, 2022), such sort of ant–plant association was not noted both on and off the area occupied by the studied nest complex. To further understand the role of various resources, including foliar nectaries on aspen, in the life of the studied nest complex of *F. lemani*, detailed investigation of this issue throughout the season (starting in April–May) is required.

Beyond the studied nest complex, aphids on herbaceous plants prevailed among *F. lemani* symbiont aphids. Only single foragers of *F. lemani* were found on trees, which, when possible, collected honeydew in colonies of aphids visited by red wood ants. This stealing behaviour is quite common among subdominant ants of the genus *Formica* [13]. The obtained results are consistent with the data that in the presence of red wood ants, the strong ecological pressure from these dominants forces co-occurring species to adapt by changing their activity in space or time, and behaviour, including foraging strategy (e.g., choosing smaller food pieces or using less rewarding sources) [7,36–41]. At the same time, our data clearly demonstrate the great potential of subdominant ant species.

5. Conclusions

Overall, the formation of the nest complex with a high density of nests and numbers in *F. lemani* is apparently caused by the lack of pressure from the obligate dominants of *Formica rufa* group, which allowed *F. lemani* to use the honeydew of obligate myrmecophilous aphids on trees (birch, aspen) as the main resource in carbohydrate nutrition. Close interaction with aphids on wood plants gives ants a number of significant advantages: it promotes accelerated restoration of trophobiotic interactions with aphids in spring, and ensures relative stability of the food supply and the ability to regularly obtain sufficiently large volumes of carbohydrate food throughout the season. Combined with the lack of abundance control by red wood ants, this allowed *F. lemani* not only to increase, but maintain high population densities, as well as to demonstrate more complex behaviours. Altogether, this significantly increased the *F. lemani* competitiveness, as well as the role of this species in the plant protection against phytophages.

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