Field tests of interspecific competition in ant assemblages: revisiting the dominant red wood ants

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Summary

1. There has been considerable debate on the importance of competition in ecological communities, but its importance in structuring ant assemblages has often been uncritically accepted. Here, we briefly review field experiments examining competition in ant assemblages and use a removal experiment to test the effect of the classical territorial dominant ant, *Formica aquilonia*. Ants of this species group are thought to structure communities through a dominance hierarchy.

2. First, we used pitfall traps to compare the abundance of other ants in replicated sites with low and high densities of *F. aquilonia*. We found differences in community composition, in particular, *Camponotus herculeanus* was more common in low-density sites, in accordance with predictions. Differences in ant assemblages were not owing to differences in measured habitat variables.

3. We removed *F. aquilonia* from a set of high-density sites, using physical and chemical methods, and repeated these procedures at procedural control sites. One year after removal, abundances of *F. aquilonia* at removal sites were similar to those at low-density sites. However, the composition of other species did not change in response to *F. aquilonia* removal. Replication rates were identical in the mensurative and experimental components of this study, so this is unlikely to be owing to the analysis being insufficiently powerful.

4. We suggest three possibilities for the lack of difference. First, the study may have been too short term or small scale to detect differences. However, previous studies have shown effects on smaller spatial- and temporal-scales. Second, priority effects may be important in the successful colonisation by *F. aquilonia*. Thirdly, boreal ant assemblages may be too depauperate for redundancy in ecological roles and for competition to play an important structuring role.

5. We thus recommend that long-term large-scale experiments be considered essential if we are to distinguish between competing hypotheses in community ecology.

Key-words: community structure, dominance hierarchy, field experiment, *Formica aquilonia*, interspecific competition

Introduction

There has been considerable debate on the importance of competition in ecological communities (Connell 1983; Schoener 1983), but its importance in structuring ant assemblages has often been uncritically accepted. Studies world-wide report patterns of ants interacting in competitive hierarchies, where dominant ants suppress subordinate ants and more passive species benefit from this suppression (Savolainen & Vepsäläinen 1988; Savolainen, Vepsäläinen & Wuorenrinne 1989; Andersen 1990; Morrison 1996; Basu 1997). Ants are often observed fighting over food resources, and negative associations between species are common (Parr & Gibb 2010 and references therein). The need for experimental testing of the importance of competition has long been recognised in ecology (Connell 1983; Schoener 1983; Underwood 1986), but much of the evidence suggesting an important role for interspecific competition in communities is nonexperimental and attributes variations in morphologies, behaviours, habitat use and distributions to resource partitioning as a result of competition (Connor & Simberloff 1986). This applies particularly to the literature on competition in ant assemblages. This 'natural experiment' approach does not provide direct evidence that the process responsible for the pattern was competition (Underwood 1986).

Experimental manipulations of ant assemblages are difficult to perform, particularly in the field, so few such studies

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have been conducted (see Table 1 for a comprehensive list). In most cases, the species removed have been selected owing to their behavioural and numerical dominance (e.g. Majer 1976; Rosengren 1986; Andersen & Patel 1994; Gibb & Hochuli 2004), because they are invasive (King & Tschinkel 2006, 2008; Lebrun *et al.* 2007) or because they are known to interact strongly with other species (Pontin 1969; Kugler 1984; Sanders & Gordon 2003). Most experimental studies show some evidence of competition altering populations of one or more species. However, many of the pioneering studies do not provide convincing conclusions because they are poorly designed or insufficiently replicated. Notably, only Pontin (1969) attempts to control for the change in nest density that results from removals. Given that the target species are commonly selected owing to prior observations of competitive interactions, the incidence of significant effects is quite low and the evidence for hierarchical structuring limited.

Studies based on recruitment to large protein baits typically show strong responses to experimental removals e.g. Andersen & Patel (1994), Sanders & Gordon (2003), Lebrun *et al.* (2007). This is probably a result of local exclusion of species from concentrated resources that can be monopolised by dominant species. Previous authors have argued that this makes their value in measuring outcomes at the population level questionable because resource partitioning is widespread and spatial and temporal variation may promote coexistence (Hölldobler & Lumsden 1980; Ribas & Schoereder 2002; Gibb 2005; Parr & Gibb 2010). Despite the wealth of data on behavioural interactions at baits, the importance of competitive interactions between species in regulating ant populations is thus unclear. It is also worth noting that only three of the fourteen previous field experiments used procedural controls (Table 1). For removal experiments, in particular, which commonly involve the use of poisons, it is very difficult to determine how treatments might impact upon the populations of other species without such controls.

Here, we present the results of an experiment testing the effect of removal of a species from one of the classical groups of dominant ants, the territorial red wood ants of the *Formica rufa* group. Savolainen & Vepsäläinen (1988) described a competitive hierarchy amongst the boreal ants, driven by this group, which has been highly influential in studies of competition in ant assemblages world-wide. It promoted an expectation that entire assemblages, rather than a few closely related species, will be affected by competition from dominant ants. In the case of boreal ants, assemblages are depauperate, resulting in a simple community structure. Savolainen & Vepsäläinen (1988) proposed that *Formica rufa* group ants, 'territorials', competitively exclude a group of nonterritorial species, known as 'encounterers', which behave aggressively towards individuals of alien colonies. A further group, the 'submissives', was expected to coexist with 'territorials', but in lower numbers, and to be negatively affected by 'encounterers'. Mensurative experiments suggest an important role for competition in structuring this hierarchy (e.g. Savolainen & Vepsalainen 1989; Savolainen,

Vepsäläinen & Wuorenrinne 1989; Savolainen 1991), but no study has empirically tested whether the perceived pattern is a result of competition or some other factor. Although Rosengren (1986) addresses the Fennoscandian fauna in a manipulative experiment on islands, results are difficult to interpret, owing to low replication and inherent differences between control and introduction sites.

In this study, we experimentally remove colonies of *Formica aquilonia* (Yarrow) in mainland boreal forests, using a replicated design and mensurative and experimental components of equivalent power. We ask: Does competition from *F. aquilonia* structure the ant assemblage? If *F. aquilonia* is important in structuring boreal ant assemblages, we hypothesise that the abundance of 'encounterers', specifically *Camponotus herculeanus*, will be greater at sites with low than high densities of *F. aquilonia*. Following Savolainen & Vepsäläinen (1988), a reduction in the density of *F. aquilonia* is predicted to lead to an increase in the abundance of *C. herculeanus* and 'submissive' species of the genus *Myrmica*.

Materials and methods

STUDY SITES

This study was conducted in the boreal forests of northern Sweden between the latitudes of 63·6°N and 64·5°N and longitudes of 19·7°E and 20·7°E (Fig. 1). All forests were dominated by Norway spruce, *Picea abies* (L.) (70–100%), although birches, *Betula pubescens* (Ehrh.) and *Betula pendula* (Roth), and Scots pine, *Pinus silvestris* (L.) were also common. The understory consisted mainly of dwarf shrubs (*Vaccinium spp.*), and soils were moist and of the sandy moraine type. We selected sites with an average tree age of 80–100 years. Such sites may never have been clear cut, but large trees had been selectively removed.

Sites that supported colonies of the northern red wood ant, *Formica aquilonia* (Yarrow), were the focus of this study. *Formica aquilonia* belongs to the *F. rufa* group, which consists of territorially dominant ant species that have been reported to structure ant communities (Savolainen, Vepsäläinen & Wuorenrinne 1989). It is the most common *F. rufa* group species in the central boreal region of Fennoscandia (Collingwood 1979) and forms polygynous and polydomous colonies throughout its range (Pamilo, Chautems & Cherix 1992).

Ten sites with low densities of *F. aquilonia* and ten sites with high densities were selected in May–June 2006 (Fig. 1). In low-density sites, there were no nests of *F. aquilonia* within approximately 100 m of a central point and very low worker activity was observed. High-density sites were centred around an active nest of *F. aquilonia*, which were part of a continuous colony with many nests. Inter-nest distances were approximately 50 m. Sites with low and high densities of *F. aquilonia* were geographically interspersed to avoid spatial autocorrelation. Low-density sites were selected in pairs that were located greater than 200 m apart, to obtain sites that were as comparable as possible for the procedural control treatment. The procedural control was performed at low, rather than high-density sites because we were interested in testing the effect of the procedure in an environment with a low density of *F. aquilonia*. This was because the removal was expected to result in low densities of *F. aquilonia*. It was thus logical to test the effect of the procedure at low-density sites.

Table 1. List of field removal or introduction experiments examining the effect of competition in ant assemblages

Details							Effects						
Study	Habitat and Locality	Species	Plots (m²)	Methods	% Succ	Design	ST	Time (wks)	Resp	Spp.	SR	Ab	Cm
Pontin (1969)[a]	Grazed field, UK	*Lasius flavus*	NR	Digging – removals and introductions	NR	C-6, X-2, I-3	B/D	104	A	1/1	–	–	–
		Myrmica spp.				C-5, X-5, I-5	B/D	104	A	1/1	–	–	–
Majer (1976)[a]	Cocoa farms, Ghana	*Oecophylla longinoda*	1600	Pruning,	87–98	C-2, X-2	B/D	64	K/A	–	–	–	–
		Macromischoides aculaetus		Insecticide	89–100	C-2, X-1	B/D	64	K/A	–	–	Yes	–
		Crematogaster depressa			NA	X-2	B/D	64	K/A	–	–	No	–
		Crematogaster clariventris			NA	X-1	B/D	64	K/A	–	–	–	–
		Crematogaster striatula			0	C-2, X-1	B/D	64	K/A	–	–	No	–
Cole (1983)	Mangroves Florida, USA	*Crematogaster ashmedi*	0·3–877	Introductions	NA	C-1, X-4	B/D	27	N	3/3	–	–	–
		Xenomyrmex floridanus			NA	C-2, X-4	B/D	27	N	3/3	–	No	–
Kugler (1984)	Forest Colombia	*Pogonomyrmex mayri*	4	Fencing, Digging	NR	X-1	B/D/A	0·5	O	–	–	–	–
		Ectatomma ruidum				X-1	B/D/A	0·5	O	–	–	–	–
Fox, Fox & Archer (1985)	Regenerating heathland SE Australia	*Iridomyrmex sp. A*	400	Petrol	NR	C-1, X-1	B/D	43	P	1/1	–	–	–
Rosengren (1986)	Barren/Scots pine Islands, Finland	*Formica truncorum*	400–20000	Introductions	NA	C-1, I-2	B/D	104	N	2/3	–	–	–
Haering & Fox (1987)	Regenerating heathland SE Australia	*Iridomyrmex sp. A*	108	Petrol	NR	C-4, X-4, x-1	B/D	43	T	1/1	–	–	–
		Iridomyrmex sp. C			NR	C-4, x-2	B/D	43	T	1/1	–	–	–
Ryti & Case (1988)[b]	Desert, California, USA	*Veromessor pergandei*	~2000	Insecticide	NR	C-4, X-4	B/D	117	O/F	0/2	–	–	–
		Pogonomyrmex californicus				C-4, X-4	B/D	117	O/F	0/2	–	–	–
		Myrmecocystus flaviceps				C-4, X-4	B/D	117	O/F	0/2	–	–	–
Andersen & Patel (1994)	Tropical savanna N Australia	*Iridomyrmex sanguineus*	36	Fence	~50–99	C-2, X-3, PC-2	B/D/A	7	B	2/5	Yes	Yes	–
		Iridomyrmex sanguineus		Fence		C-2, X-3, PC-2	B/D/A	7	P	0/1	Yes	No	–
Sanders & Gordon (2003)	Desert, Arizona USA	*Myrmecocystus spp.*	1963	Fence	NR	C-18, X-18	D	0·5	B	1/1	–	–	–
Gibb (2003)	Rock outcrops SE Australia	*Iridomyrmex purpureus*	1250	Caging *in-situ*	99·5	C-4, X-4, PC-4, ND-4	D	52	P	1/1	No	No	No
Gibb & Hochuli (2004)							B/D	52	O	1/4	No	Yes	–
Gibb (2005)							B/D	52	B	1/2	No	Yes	–
Valone & Kaspari (2005)	Desert Arizona, USA	Granivorous ants	2500	Insecticide	59	C-14, X-6	B/D	780	N	1/2	No	Yes	–
King & Tschinkel (2006)	Pasture Florida, USA	*Solenopsis invicta*	1600	Boiling water	60	C-5, X-5	B/D	104	P	–	No	No	–

Table 1. (Continued)

Study	Habitat and Locality	Species	Plots (m²)	Methods	% Succ	Design	ST	Time (wks)	Resp	Spp.	SR	Ab	Cm
Lebrun *et al.* (2007)	Open savanna Argentina	*Linepithena humile*	100	Boiling water	NR	C-9, X-6, PC-5-9	B/D	2·5	B	1/1	–	Yes	–
		Solenopsis invicta				C-9, X-7, PC-5-9	B/D	2·5	B	1/1	–	No	–
King & Tschinkel (2008)	Pine flatwoods, Florida, USA	*Solenopsis invicta*	1600	Introductions	NA	C-5, I-5, PC-5 (x3 disturbance levels)	B/D	~117	P	2/2	Yes	Yes	–
Gibb & Johansson (in press), H. Gibb (unpublished)	Boreal forests, Sweden – ~90 years	*Formica aquilonia*	1250	Insecticide & digging	79	C-5, x-5, PC-5, ND-5	B/D	75	P	0/2	No	No	No
	30-40 years					C-3, x-3				1/4	No	No	No
	0-4 years (Clear-cut)					C-5, x-5				2/4	No	Yes	Yes

aWhen data were provided in the paper and the analyses appeared inappropriate (most commonly pseudoreplicated), we reanalysed the data using ANOVA or a Kruskal–Wallis test on JMP 7 (SAS Institute 2007). bRyti & Case (1988) combine inter- and intra-specific effects for analyses of alates and territory size, so these are not reported here. % Succ. = % removal success (calculated as 100–100*(mean abundance in removal plots/mean abundance in control plots): NR = Not recorded, NA = Not applicable; Design: C = Control, X = Removal, x = Partial Removal, I = Introduction, PC = Procedural Control, ND = Control site with none or low numbers of the excluded species, replication rates are also provided e.g. C-2 indicates two control replicates; ST = Sampling times: B = Before, D = During, A = After release of the target species; Resp. = Responses measured: A = Alate counts, B = baits, F = food harvested, K = insecticidal knockdown, N = Looking for nests, O = observation transects, P = Pitfall traps; Spp. = Individual species; Effects; Spp. = territory size; SR = Species richness; Ab = Total abundance; Cm = Community composition (tested using ANOSIM). When considering 'Effects', readers should also consider the sample sizes noted under 'Design' when assessing the validity of the reported findings.
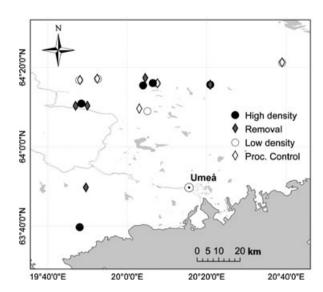

Fig. 1. Map of the study area in northern Sweden, showing water bodies in grey and the location of the study sites. Paired low-density and procedural control sites were usually less than 500 m apart and therefore appear to overlap on the map.

TREATMENTS

F. aquilonia abundances were reduced in half of the high-density sites (*n* = 5), by applying treatments to all nests within 60 m of the central point of the site. Comparable disturbances were applied in the procedural control sites. The initial removal attempt involved digging up entire nests in removal sites in autumn/winter 2006–2007, when they were inactive. In procedural control sites, we dug an equivalent number of holes of similar size. Nests were excavated down to the ground water level or until there were no visible galleries i.e., 0·5–1·5 m. This method had limited success, possibly as a result of rapid recolonisation from neighbouring nests in early spring, when the sites were inaccessible owing to snow melt. The second removal attempt was conducted in July 2007 and was considerably more successful. A poison, deltamethrin 7·5 g l^{-1}, was diluted (40 mL per 10 L water) and applied directly to all nests of *F. aquilonia* within 60 m of the central point of a site. Poison was applied to the dugout remains of nests and to any new satellite nests that had established after the initial nest treatment. This treatment was repeated at procedural control sites. The abundance of *F. aquilonia* decreased significantly after treatment (Fig. 2a). After treatment, we thus had five paired sites with low densities of *F. aquilonia*, henceforth referred to as 'Low density' and 'Procedural control' sites, five sites with high densities of *F. aquilonia* 'High density' and five sites where densities had been significantly reduced 'Removal' (Fig. 1).

INSECT SAMPLING

Epigaeic insects were sampled using pitfall traps in one 'Before' session and three 'After' sessions. The single before session involved trapping between 8th June and 25th August, 2006. The after sessions were performed in 2008 and were conducted from approximately 8th June to 3rd July, 3rd July to 2nd August and 2nd August to 25th August. These three sessions were pooled for analysis such that they covered an identical time frame to the 'Before' samples. Pitfall traps were preferred because they provide an index
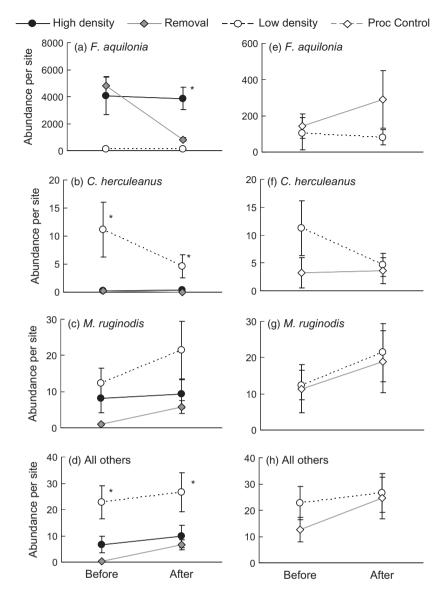
Fig. 2. Interaction plots showing mean ± SE abundance before (June–August 2006) and after (June–August 2008) the removal and procedural control treatments were performed. Plots (a) to (d) compare low ant density, high ant density and removal sites. Plots (e) to (h) show low ant density and procedural control sites. * significantly different at $P < 0.05$ (see Table 2 for details of the analyses).

of ant activity, which we have assumed to be indicative of their importance in the ecosystem. Nest counting was considered less useful in this habitat because of the poor detectability of the nests of most ant species and the high variability in the abundance of ants between different nests of the same species. Winkler traps were not used because they provide only a very temporally limited sample.

Ten traps were placed around 5 m and 20 m points on a transect heading north from the central *F. aquilonia* nest or an equivalent point in sites with low densities of *F. aquilonia*. At each of these points, five traps were placed in a square formation with one central trap. Traps at the corner of each square were located 5 m from the central trap. Pitfall traps were approximately 6 cm in diameter and contained 70% propylene glycol as a preservative. Worker ants were extracted from the pitfall traps in the laboratory, counted and identified to species using Collingwood (1979) and Douwes (1995). Analysis of ant abundances focused on individual species, assemblage

composition and the groups described in Savolainen & Vepsäläinen's (1988) competition hierarchy (territorials, encounterers and submissives).

HABITAT SURVEYS

Habitat surveys were conducted in August 2008 to determine whether differences in the abundances of *F. aquilonia* or any other ants between sites with high and low abundances of *F. aquilonia* might be associated with differences in habitat structure. Slope and aspect were measured at the centre of each site. Four band-transects of 20 m in length and 5 m in width were used to sample trees and coarse woody debris (CWD) within 20 m of the central nest or equivalent point. The basal diameter and species of all trees were recorded within this area. CWD greater than 1 m in length and 10 cm in diameter was also measured and classified as lying or standing, and decay stage was determined (as in Gibb *et al.* 2005). Within the transects,

smaller quadrats were used to determine the dominant moss and herb species and the percentage cover of the herbs, moss, leaf litter, needles, bare ground and dead wood. A total of nine quadrats of 1 m^2 were sampled per site.

DATA ANALYSIS

To determine whether our experimental treatment had affected the ant fauna, we first tested for differences between low ant density and procedural control sites for the most common species across years. We then tested for differences between high ant density, low ant density and removal sites. Repeated measures ANOVA on JMP (SAS Institute 2007) was used to test these differences for *F. aquilonia*, *Myrmica ruginodis* and all ants other than *F. aquilonia* (variances all nonheterogeneous after log$_e$ transformation). Data for *Camponotus herculeanus* were better fitted by a negative binomial response distribution, so the function glm.nb in the package MASS on R (R Foundation for Statistical Computing, 2005) was used to test before and after separately. Overall compositional differences between assemblages before and after the removal were tested using analysis of similarities (ANOSIM, Clarke 1993), with *F. aquilonia* excluded from the data set. We used a 4th-root transformation, a maximum of 4999 permutations of the data and the Bray-Curtis similarity measure, which ignores joint absences.

Principal components analysis on correlations was used to reduce the number of habitat predictors because many habitat variables were inter-correlated. This also eliminated the need for corrections for multiple comparisons and helped us to detect simultaneous responses to certain combinations of variables (Hildén 1965). ANOVA was used to test for differences in the first three principal components representing habitat composition. We tested for differences between high-density control and removal sites and low-density sites. Because procedural control and low-density sites were paired, only low-density sites were used in this analysis, but results were similar when procedural control sites included instead. ANOSIM was used to test for differences in the dominant ground-cover species (including herbs and mosses) between plots in low-density, removal and high-density sites.

Results

ANT ABUNDANCES

We collected ants belonging to 12 species during this study. Other than *F. aquilonia*, *Camponotus herculeanus* and *Myrmica ruginodis* were the only species that could be considered to be sufficiently common to warrant separate analysis (i.e. occurred at a minimum of 50% of sites). We also collected individuals of *Myrmica longinodis*, *Myrmica rubra*, *Myrmica scabrinodis*, *Myrmica sulcinodis*, *Formica exsecta*, *Formica lemani*, *Formica sanguinea*, *Harpagoxenus sublaevis* and *Leptothorax acervorum*. Effects on these less common species were considered through the assemblage analyses (ANOSIM). No 'territorial' species other than *F. aquilonia* were collected, and *C. herculeanus* was the only 'encounter' species. Several 'submissive' species, mainly *Myrmica* spp. and *L. acervorum,* were collected, so submissive species were considered separately.

Repeated measures analysis showed that ant abundances and assemblage composition did not differ between procedural control and low-density sites before or after treatments were performed (Tables 2 and 3, Figs 2e–h). This suggests that the treatment is unlikely to have had broad effects on the ant assemblages and was thus a valid way of removing the dominant species without unwanted side effects.

Interactions between time and treatment were significant only for *F. aquilonia* (Table 2, Fig. 2a). In 2006, we found clear differences in the abundance of *F. aquilonia* between high-density sites and low-density sites and no differences between 'removal' sites and high-density sites. The removal treatment reduced abundances of *F. aquilonia* significantly, such that abundances in removal sites in 2008 differed from high density, but not low-density sites. The removal was thus successful in reproducing abundances very similar to those

Table 2. Summary of univariate analyses of the effects of the experimental treatments on ant abundances: repeated measures ANOVAS were performed for *Formica aquilonia*, *Myrmica ruginodis* and all others, and generalised linear models with a negative binomial response distribution were used to test effects on *Camponotus herculeanus* separately before and after treatment application. Significant effects are shown in bold text

Source	d.f.	F	P	F	P	F	P	F	P		z	P
Procedural control vs. Low density												
Between		*F. aquilonia*		*M. ruginodis*		Submissives		All others		*C. herculeanus*		
Treatment	2,12	0·85	0·380	1·40	0·267	0·05	0·825	0·38	0·552			
Within										Before (2006)		
Time	1,12	4·32	0·068	0·16	0·695	3·35	0·105	0·73	0·416		1·28	0·201
Time × Treatment	2,12	0·01	0·911	0·01	0·932	0·01	0·930	0·06	0·807	After (2008)	0·29	0·774
Low density vs. High density vs. Removal												
Between		*F. aquilonia*		*M. ruginodis*		Submissives		All others		*C. herculeanus*		
Treatment	2,12	24·66	**< 0·0001**	3·56	0·061	0·01	0·939	7·97	**0·006**			
Within										Before (2006)		
Time	1,12	3·26	0·096	3·59	0·083	2·97	0·108	3·10	0·104	Low vs. High	−4·11	**< 0·0001**
Time × Treatment	2,12	11·88	**0·001**	0·60	0·563	0·49	0·495	0·93	0·422	High vs. Removal	1·55	0·122
Post-hoc contrasts		Time × Treatment						Treatment		After (2008)		
Low vs. High		0·94	0·351					6·77	**0·023**	Low vs. High	−3·48	**< 0·0001**
Removal vs. High		13·34	**0·003**					1·74	0·212	High vs. Removal	1·27	0·205
Removal vs. Low		21·37	**0·001**					15·39	**0·002**			

Table 3. Summary of analysis of similarities testing the effects of the experimental treatments on ant assemblages. *Formica aquilonia* was excluded from these analyses. Significant effects are shown in bold text

Comparison	Before (2006)		After (2008)	
	Global R	*P*-value	Global R	*P*-value
Procedural control vs. Low density	−0·088	0·659	−0·164	0·841
Low density vs. High density vs. Removal	0·334	**0·034**	0·164	**0·037**
Post-hoc tests				
Low vs. High	0·286	0·056	0·286	0·056
Removal vs. High	0·095	0·222	0·026	0·429
Removal vs. Low	0·398	**0·008**	0·764	**0·018**

found in low-density sites, but was not a complete removal of the species.

Despite the clear reduction in *F. aquilonia* abundance, other ant species did not show any response to the removal treatment. Abundances of *C. herculeanus* differed significantly between sites with low and high densities of *F. aquilonia*, in both 2006 and 2008. Partial removal of *F. aquilonia* did not result in changes in populations of *C. herculeanus* in removal sites, i.e. the interaction between time and treatment was not significant (Table 2, Fig. 2b). Similar patterns were observed for 'other ants' (Table 2, Fig. 2d). Abundances of *M. ruginodis* showed a nonsignificant tendency to be higher in sites with low densities of *F. aquilonia* and no interaction between time and treatment (Table 2, Fig. 2c). No effect of *F. aquilonia* abundance was observed for 'submissive' species either before or after the experimental removal (Table 2). Assemblage composition differed significantly amongst treatments (ANOSIM, Table 3). *Post-hoc* tests showed that assemblages in low-density sites differed from removal sites. Differences between low- and high-density sites were close to significant ($P = 0.056$). This was true in both 2006 and 2008, suggesting that the removal of *F. aquilonia* in early 2007 did not alter the assemblage of other ants.

HABITAT SURVEYS

Principal components analysis on the habitat variables showed that the first three axes explained 68% of the variation in the data (Appendix S1). PC1 was indicative of a high percentage cover of moss, low percentage of needles and leaves and a high volume of lying CWD. PC2 was indicative of a percentage of herb cover, low percentage of bare ground, small average basal diameter of trees and high dead wood volume. PC3 indicated a high cover of bare ground and deciduous leaves and high average and maximum basal diameters. None of these principal components differed significantly between treatments (Appendix S1), suggesting that habitat was similar. ANOSIM also showed no significant differences in dominant ground-cover vegetation species between

high- and low-density and removal sites (Global R $= -0.03$, $P = 0.589$).

Discussion

In agreement with previous studies (Savolainen & Vepsäläinen 1988; Savolainen, Vepsäläinen & Wuorenrinne 1989), we found significant differences in ant assemblages between sites with high and low abundances of *Formica aquilonia*. As predicted, the encounter species, *Camponotus herculeanus*, had lower abundances in the presence of the dominant species. While this suggests that *F. aquilonia* may be important in structuring ant assemblages, reduction in *F. aquilonia* populations to levels similar to those found in low-abundance sites did not result in corresponding changes in the other ant fauna after 1 year. Procedural controls showed that this was not owing to limitations of the methods. We were also unable to find any differences between the habitats of sites with low and high densities of *F. aquilonia*, suggesting that habitat does not drive these associations. We believe that there are two possible explanations for the failure of ant assemblages to respond to *F. aquilonia* removal. Firstly, it is possible that the experiment was not sufficiently large, both temporally and spatially, to observe responses in populations of other ants. Secondly, *F. aquilonia* may not structure ant assemblages and differences in abundances may be a result of other biotic or abiotic factors. We consider these hypotheses in detail in the following paragraphs.

It is unclear whether longer experiments are more likely to find significant effects, partly because many of the longer-term experiments on the competition ecology of ants have not included adequate replication or controls. The longest study yet performed for ants involved the removal of an entire trophic level and revealed effects in only a small proportion of years (Valone & Kaspari 2005). However, many studies reporting effects of competition find that they occur within hours to months after the removal or addition is performed (e.g. Fox, Fox & Archer 1985; Haering & Fox 1987; Sanders & Gordon 2003; Gibb & Hochuli 2004). King & Tschinkel's (2008) 3-year experimental introduction of *Solenopsis invicta* showed clear effects on the abundance of other ants within 1 year. While processes in boreal systems may operate more slowly than in temperate systems (Sierra *et al.* 2009), even Rosengren's (1986) 2-year introduction study showed that 70% of the reported change in ant populations occurred within the first year. There was no trend in our data suggesting that statistically undetectable changes had occurred (Fig. 2). However, we detected very few alates of *C. herculeanus* during the study, so we cannot exclude the possibility that a more representative outcome may take considerably longer than 1 year for some communities.

Although the spatial scale of this study is consistent with that of previous studies that have shown significant effects (e.g. Sanders & Gordon 2003; Gibb & Hochuli 2004; Gibb 2005), it is possible that a larger spatial scale for the exclusion would have been appropriate. Within a 50 m radius, the removal was effective, but if alate *C. herculeanus* wandered

much further than this distance before locating a suitable nest site, they would have encountered aggressive *F. aquilonia* workers in high densities. We are not aware of any studies that have investigated colony founding in this species outside of laboratory situations. However, it is clear that the effectiveness of relatively small-scale exclusions may depend on the scale at which colonising ants respond to their environment.

The second alternative to consider is that *F. aquilonia* may not be a structuring force in ant assemblages, possibly because low temperature stress is more limiting than competition (Andersen 1995). There is much literature discussing the important role of this species, the extent of partitioning of resources amongst boreal ants and the hierarchical structuring of ant species assemblages (Savolainen & Vepsäläinen 1988; Savolainen & Vepsalainen 1989; Savolainen, Vepsäläinen & Wuorenrinne 1989). Very little of this previous work is experimental at the scale required to determine the impact of territorial ants on assemblages. Although previous studies, such as Rosengren (1986), suggest a strong role for competition, inadequate replication and differences between control and introduction sites (Table 1) make the data very difficult to interpret. In this study, we have tested the effect of the presence of *F. aquilonia* on the abundance of other ants and found no significant effects or trends. This is despite clear differences between sites with low and high ant densities and an identical replication rate and therefore similar power in the mensurative and experimental components of the study. It is thus necessary to consider what might be causing the patterns observed in the mensurative study if it is not competition from *F. aquilonia*.

Habitat was an obvious first point of call (e.g. Majer, Delabie & McKenzie 1997; Vepsäläinen *et al.* 2000; Gibb 2005; Sanders *et al.* 2007; Blaum *et al.* 2009), but we were unable to find any differences in the structure or composition of habitats that might affect ant composition. Stand age and density have previously been shown to be most important in determining the presence of red wood ants (Travan 1998; Domisch, Finer & Jurgensen 2005; Gibb & Johansson 2010), but these did not differ between high- and low-density sites. We found no differences in the species composition of the groundcover, suggesting that moisture and nutrient levels were similar between sites with low and high densities of *F. aquilonia*. It is possible that we failed to measure the most important habitat components, but our habitat surveys were thorough (see Methods) and covered important nesting habitats such as dead wood, so should have detected any important differences in habitat structure and ground-cover species composition.

Another possible explanation for the failure of species to respond to the removal of *F. aquilonia* is that community composition is decided by the dispersal and establishment stages of organisms (Ryti & Case 1988; Eriksson & Eriksson 1998; Hubbell 2001; Price & Morin 2004; Andersen 2008). Priority effects were implicated in a previous (island-based) study of the assembly of Fennoscandian ant communities (Vepsäläinen & Pisarski 1982). Our study suggests that nega-tive associations between *F. aquilonia* and other ants exist, but that populations of other ants may not be strongly affected by *F. aquilonia*. Although an established colony of *F. aquilonia* appears rather formidable, the alates that make up the foundation stage of colonies are very vulnerable (Hölldobler & Wilson 1990). Rather than *F. aquilonia* limiting other ants, recruitment of *F. aquilonia* might be limited by predation on alates (cf. Wiernasz & Cole 1995; Billick, Cole & Wiernasz 2004). In fact, nests of *Formica* spp. are generally secondarily polygynous, i.e. the daughters of the resident queens are recruited back (Chapuisat & Keller 1999), so it is likely that successful founding by alate queens is rare. The negative association between *F. aquilonia* and *C. herculeanus* observed in the mensurative part of this study would thus be equally well explained by limitation owing to predation on *F. aquilonia* alate queens by *C. herculeanus*. The dominance hierarchy model proposed by Savolainen & Vepsäläinen (1988) assumes that competition is asymmetric and driven by *F. rufa* group ants. However, it is not impossible that the asymmetry operates in the opposite direction in earlier life stages. Such alternative explanations should be considered (and later tested) when appropriately replicated and controlled experiments fail to show the predicted result.

Although red wood ants are numerous and aggressive and have been shown to affect the size of prey items collected by *Formica fusca* (Savolainen 1991), they may have a relatively low level of overlap in their ecological roles with other ants in this relatively depauperate assemblage. Previous studies (Laakso 1999; Lenoir 2003; Lenoir, Bengtsson & Persson 2003) have found little effect of *F. rufa* group ants on the soil fauna, suggesting that that is not an important component of their diet. Instead, red wood ants are significant consumers of honeydew and arboreal insects (Oekland 1930; Wellenstein 1952; Zoebelein 1956, Horstmann 1974; Skinner 1980; Domisch *et al.* 2009; Gibb & Johansson 2010), a role that does not appear to be significantly replaced by other species in their absence. Removal of the ecologically dominant ant *Iridomyrmex purpureus* resulted in changes in abundance only of a set of congeneric species that were able to occupy honeydew resources formerly guarded by *I. purpureus* (Gibb 2003; Gibb & Hochuli 2004). In low-diversity boreal forests, there may be no redundancy in this role. Although previous studies do not suggest a strong latitudinal gradient in the outcomes of experimental exclusions of ants (see Table 1), it is likely that global trends exist in the levels of competition and therefore functional redundancy in assemblages. These trends deserve further investigation. While we could not find a short-term effect of *F. aquilonia* removal on other ants, it is likely that significant effects occurred in the canopy, where they are important predators and consumers of honeydew (Lenoir 2003).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Loadings of habitat variables on each of the principal components.

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