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Experimental evidence for mediation of competition by habitat succession

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Abstract. Habitat succession is thought to influence the importance of competition in assemblages. Competitive interactions are considered of critical importance in structuring ant assemblages, but field experiments show varied effects. I tested how succession in managed boreal forests affects the outcome of competition from dominant red wood ants, *Formica aquilonia*, through a removal experiment in replicated stands of three different ages (0–4, 30–40, and 80–100 years old). *F. aquilonia* abundance was reduced by 87%, and procedural controls showed no nontarget effects. The succession gradient revealed the full range of possible responses from ant species: decreases in 1–4-year-old stands, increases in 30–40-year-old stands, and no effects in 80–100-year-old stands, where diversity was lowest. Habitat succession thus regulates competitive interactions in this system. I propose a model for this system, where competitive effects depend on time since disturbance. In this case, soon after disturbance the dominant species facilitates increases in the abundance of other species. At intermediate times, competition reduces the abundance of some species. Finally, in long-undisturbed habitats, competitors may fail to evolve, particularly in high-stress environments. Interactions between competition and habitat succession may explain why structuring effects of ecologically dominant species appear inconsistent.

Key words: *ant assemblage; boreal forest; competition; dominant species; facilitation; field experiment; habitat succession; interaction; intermediate disturbance hypothesis; red wood ants; removal experiment; time since disturbance.*

INTRODUCTION

Habitat succession is hypothesized to determine the importance of competition in community structuring (e.g., intermediate disturbance hypothesis; Grime 1973, Connell 1978). Despite the status of competition as the “hallmark” of ant ecology (Hölldobler and Wilson 1990), recent manipulative studies suggest that the role of competition in structuring ant assemblages may be more limited than previously thought (Gibb and Hochuli 2004, King and Tschinkel 2006, 2008, Gibb and Johansson 2011). A possible explanation for the limited effect of competition in manipulative field experiments is that the outcome of competitive interactions is highly conditional. Factors shown to affect competition at small scales include temperature, humidity, habitat structure, parasitism, resource size, resource heterogeneity, and resource composition (reviewed in Parr and Gibb 2010).

The effect of habitat disturbance is of particular interest because both natural and anthropogenic distur-

bances can change habitat structure, thus altering assemblages through a combination of changes in habitat suitability and competitive interactions. For example, different species of red wood ant, *Formica rufa* group, are thought to structure assemblages at different stages of habitat succession (Punttila et al. 1996) and competitively dominant native species may use the simple habitat of access roads to colonize national parks (Gibb and Hochuli 2003) or may be favored by fire (Parr and Andersen 2008). Invasive species, which are often behaviorally dominant, may be associated not only with species-poor native ant assemblages, but also with habitat disturbances (Bolger et al. 2000, Menke et al. 2007, King and Tschinkel 2008), suggesting that negative outcomes for native ant assemblages may result from synergies between disturbance and competition.

Although there have been a number of experimental removals and additions of competitively dominant ants (summarized in Gibb and Johansson 2011), no studies have examined how habitat regulates competitive interactions in uninvaded assemblages. Here, I test whether the local effects of a competitively dominant ant are mediated by habitat succession. In the context of

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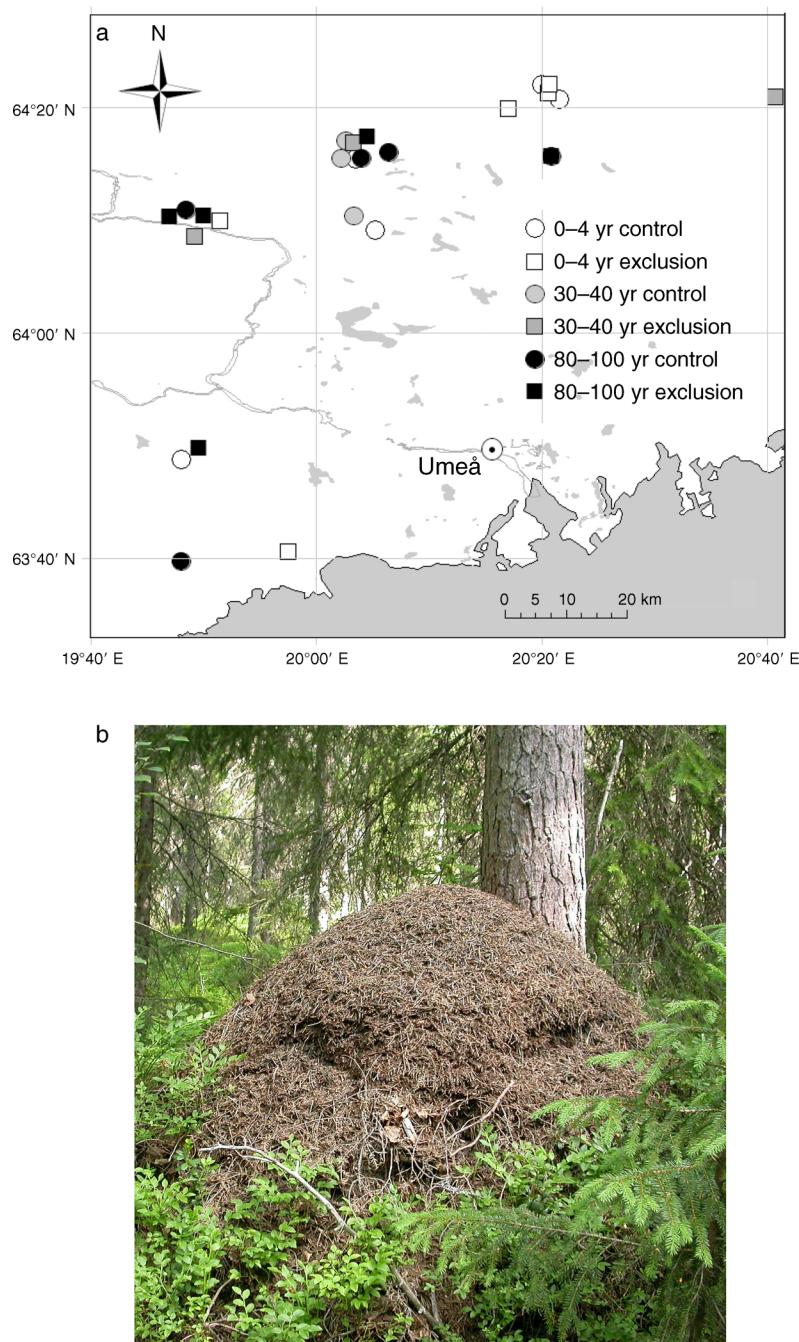


FIG. 1. (a) Distribution of study sites in boreal forests near Umeå in northern Sweden and (b) nest of the red wood ant *Formica aquilonia* in 80–100-year-old spruce forest.

the intermediate disturbance hypothesis (Grime 1973, Connell 1978), I expect that, for our target species, the red wood ant *Formica aquilonia*, the structuring effects of competition should increase with time since disturbance. I address this aim in a managed forest context, where stands of different ages present different environments to ants, both structurally and climatically. In particular, I ask: Does the effect of experimental

removal of a dominant species on assemblages depend on time since disturbance?

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 *B. 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. I selected replicate sites belonging to three different age categories: 0–4 years after clear-cutting, 30–40 years after clear-cutting; and sites with an average tree age of 80–100 years. These older sites may never have been clear-cut, but large trees had been selectively removed in past logging operations.

A competitive hierarchy is thought to be important in determining the structure of boreal ant assemblages. The hierarchy is said to consist of “territorial” ants, e.g., *Formica rufa* group species; “encounter” species, e.g., *Camponotus herculeanus*, which defend resources; and “submissive” species, e.g., *Myrmica* spp. which defend only their nests (Savolainen and Vepsäläinen 1988, Savolainen et al. 1989). Due to their highly interactive nature, encounter species are thought to be strongly suppressed by territorial ants, while submissive species are suppressed more weakly. As a territorially dominant ant, *F. aquilonia* (see Plate 1) was predicted to have strong negative effects on encounter species and weak negative effects on submissive species. Predictions for the competitive hierarchy do not mention regulation by habitat, but I suggest that effects might be expected to be strongest in more mature forests where colonies of *Formica aquilonia* (Yarrow) are largest and most prevalent (Gibb and Johansson 2010).

Sites supporting high densities of the northern red wood ant, *F. aquilonia*, were selected in May–June 2006. *F. aquilonia* is the most common *F. rufa* group species in the central-boreal regions of Fennoscandia (Collingwood 1979) and forms polygynous and polydomous colonies throughout its range (Pamilo et al. 1992). I selected 10 sites in the age categories 0–4 and 80–100 yr and six sites in the 30–40 yr category, where *F. aquilonia* were less common. Sites were centered on an active nest of *F. aquilonia* in order to standardize sampling across sites and keep *F. aquilonia* abundance as constant as possible among stand ages. Nests were part of polydomous colonies and inter-nest distances were ~50 m. Nest densities are highest in 80–100 yr forests (Gibb and Johansson 2010). Sites of different ages were selected such that they were geographically interspersed to avoid spatial autocorrelation (Fig. 1a).

Treatments

F. aquilonia abundances were reduced in half of the sites ($n = 5$ for 0–4- and 80–100-year-old sites and $n = 3$ for 30–40-year-old sites), by applying treatments to all nests within 60 m of the central point of the site. The initial removal attempt involved digging up entire nests in removal sites in autumn/winter 2006–2007, when they were inactive. Nests were excavated down to the groundwater 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 recolonization from neighboring nests in early spring, when the sites were inaccessible due to snowmelt. The second removal attempt was conducted in July 2007 and was considerably more successful. A pyrethroid ester insecticide, deltamethrin 7.5 g/L, was diluted (40 mL per 10 L water) and 10 L was applied to each *F. aquilonia* nest within 60 m of the central point of a site in July 2007. Insecticide was applied to the dug-out remains of nests and to any new satellite nests that had established after the initial nest treatment. Procedural controls involving excavation of a similar volume of soil and application of the same quantity of insecticide to excavations were conducted in a set of five older forest sites and showed no significant effects of the removal treatments on nontarget ants (Gibb and Johansson 2011).

In previous experimental removals or additions of ants, responses have been observed within a matter of months to a year (Ryti and Case 1988, Gibb and Johansson 2011), suggesting that ants are able to respond rapidly to changes in their environment. Ants may respond to increased favorability in a number of ways, including an increase in worker numbers (Gibb and Hochuli 2004), the formation of new nests, often through nest budding or relocation to more favorable environments (Rosengren 1986, Gibb and Hochuli 2003), or increased alate production (Pontin 1969). This suggests that the two year time frame for this experiment is adequate to detect responses from ant assemblages.

Insect sampling

Epigaeic insects were sampled using pitfall traps in one “before” session and three “after” sessions. The single before session involved trapping between 8 June and 25 August 2006. The after sessions were performed in 2008 and were conducted in three equal periods from 8 June to 25 August. Data from the after sampling sessions were pooled such that one trapping period of approximately three months (79 days) was used for each year. Pitfall traps were preferred because they provide an index of ant activity, which I have assumed to be indicative of their importance in the ecosystem. Pitfall traps were protected from rain using a metal roof, and before and after abundance counts were similar, suggesting there was no loss of samples in the continuous three-month trapping period, compared with the three consecutive one-month periods.

Ten traps were placed in two sets of five around 5-m and 20-m points on a transect heading north from the central *F. aquilonia* nest. I thus present data from before and after periods of 20 540 trap-days each (79 days \times 10 traps per site \times 26 sites). At each point, the five traps were placed in a square formation including one central trap. Traps at the corner of each square were located 5 m from the central trap. Pitfall traps were ~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 focused on assemblage composition and the abundance of common and grouped uncommon “other” species in the 10 pitfall traps at each site. “Other ants” included species for which I collected fewer than 100 workers, i.e., *Leptothorax acervorum*, *Myrmica scabrinodis*, *Formica lugubris*, *Raptoformica sanguineus*, *Myrmica lobicornis*, and *Harpagoxenus sublaevis*.

Habitat composition

Habitat surveys were conducted in August 2008, to quantify differences between stands of different ages and to determine whether differences in the abundances of *F. aquilonia* or any other ants between removal and control sites might be associated with differences in habitat structure. Quadrats were used to determine the dominant moss and herb species and the percent cover of the herbs, moss, leaf litter, needles, bare ground, and dead wood >5 cm in diameter. A total of nine quadrats of 1 m² were sampled within 20 m of the central *F. aquilonia* nest at each site.

DATA ANALYSIS

A generalized linear model (GLM) with a negative binomial response and log-link was used to test for differences in species abundance among different aged forests in 2006 on R (R Development Core Team 2010). A full model ANOVA tested the effects of the predictors stand age (0–4, 30–40, and 80–100 yr), treatment (control and partial removal of *F. aquilonia*), and their interaction on the habitat variables. A negative binomial GLM was used to model the effect of stand age, treatment, their interaction, and the covariate “abundance of the species in 2006” on the abundance of that species in 2008. The covariate was included to account for any effect of before abundance on after abundance. Abundance was highly correlated with occurrence in pitfall traps for all common species. Some species occurred only once or twice in 80–100-year-old forests, in which case stands of this age were excluded from the analysis of those species. For *C. herculeanus*, a zero-inflated Poisson GLM was used to test the effects of the treatment as zeroes were common in the data, but data were not overdispersed. Data for forests of different ages were pooled for *C. herculeanus* as there was no significant interaction between treatment and forest age. These analyses were repeated for occurrence data.

Permutational multivariate analysis of variance (PERMANOVA; Anderson 2003) was used to determine if assemblages of ants were affected by forest age, treatment, or the interaction between these factors. *F. aquilonia* was removed from the data set before this analysis was conducted so that the focus was on assemblages of other ants. PERMANOVA is capable of a direct additive partitioning of the variance for complex models and thus allows investigation of models which include interactions (Anderson 2001, 2003). Post

hoc tests of forest age, treatment, or their interaction were also performed using PERMANOVA. I used the Bray-Curtis dissimilarity measure and 5000 permutations of the data. Data were fourth-root transformed before analysis so that less abundant species had a greater influence on the outcome of the analysis than they would otherwise have had.

RESULTS

Over the 41 080 trap-days of the study, I collected 148 567 worker ants, 98.5% of which were *F. aquilonia*. The remaining 2166 individuals collected included, in order of decreasing abundance, *Myrmica ruginodis*, *M. sulcinodis*, *Formica lemani*, *Camponotus herculeanus*, *Leptothorax acervorum*, *Myrmica scabrinodis*, *Formica lugubris*, *Raptoformica sanguineus*, *Myrmica lobicornis*, and *Harpagoxenus sublaevis*. I also collected 166 mostly dealate reproductive individuals, 54% of which were *M. ruginodis*.

Habitat variables recorded in quadrats differed significantly between stands of different ages. In particular, moss cover increased with forest age, while bare ground decreased. Leaf litter cover was greater in 30–40 year stands than 0–4-year-old stands, while dead wood showed the opposite pattern. There were no significant effects of treatment on habitat (Appendix A).

Most ants showed strong habitat preferences (Fig. 2), with *C. herculeanus*, *M. ruginodis*, and other ants preferring 30–40-year-old forests over other forest ages. Of the common ants, *F. lemani* and *M. sulcinodis* were almost absent from 80–100-year-old forests and did not show a strong preference for 0–4-year-old or 30–40-year-old forests. *F. aquilonia* workers were most abundant in 80–100 year stands, but not significantly so.

Experimental treatments were successful in reducing *F. aquilonia* populations by 87% on average, with trends toward higher proportional success in 30–40-year-old forests (Fig. 2b, Table 1). Although the relative reduction in *F. aquilonia* in all forest ages was similar, the absolute success of the removal was lower in 80–100-year-old forests (Fig. 2b).

The abundance of several common species examined showed significant interactions between stand age and treatment (Table 1, Fig. 2c–l). Similar patterns were observed for occurrence data, where the interaction for other species was significant (Appendix B). This suggests that partial removal of *F. aquilonia* had different effects in forests of different ages. Consistent with predictions, removal sites supported higher abundances than control sites for 30–40-year-old forests for *M. ruginodis*. Analyses for *C. herculeanus*, where forest age was pooled, showed that abundance was significantly greater in partial removal than control sites ($Z = 1.99$, $P = 0.047$), but effects appeared strongest in 30–40-year-old forests (Fig. 2d). The opposite pattern was observed for 0–4-year-old forests. Here, occurrences of *Myrmica* spp. and other ants increased in control sites, but not removal sites. Effects in 80–100-year-old forests were

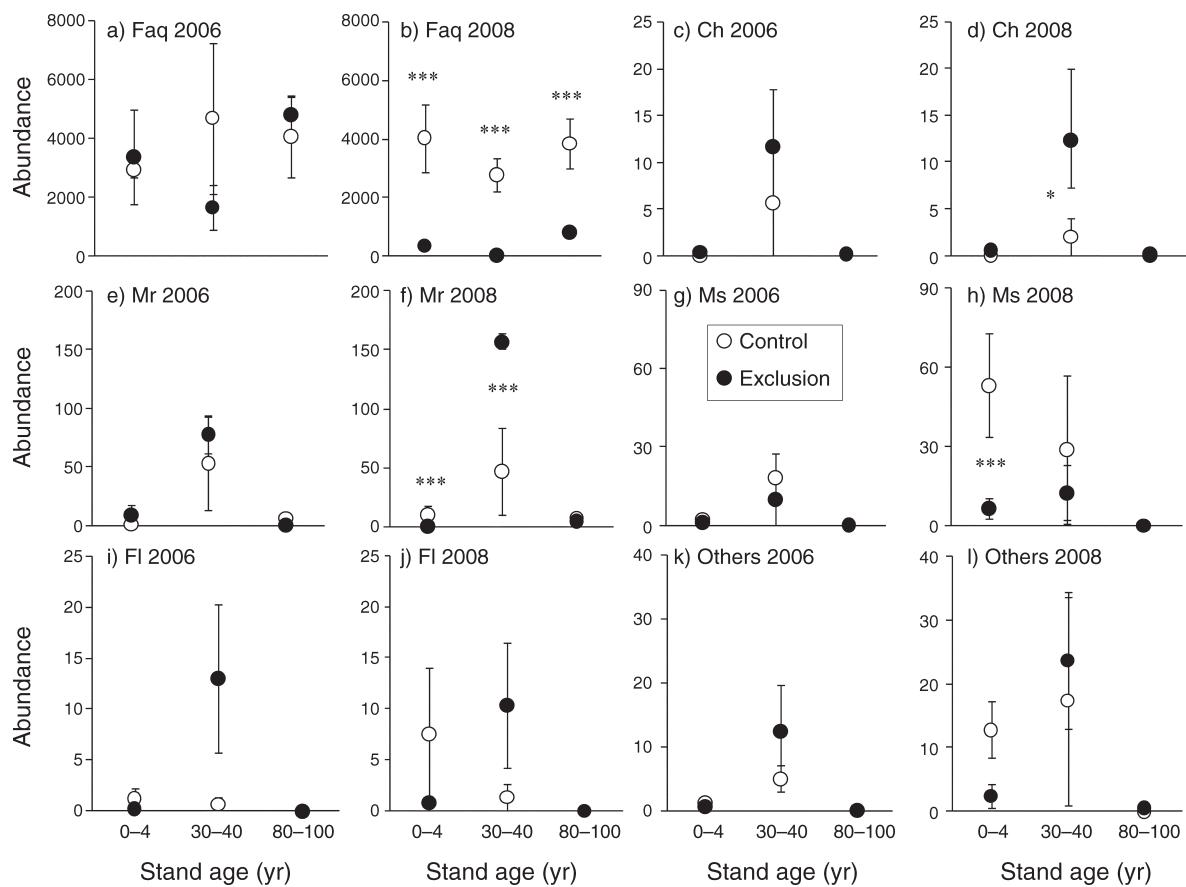


FIG. 2. Abundance (mean \pm SE) of common species in pitfall traps before (2006) and after (2008) removal of *F. aquilonia* was conducted. Some error bars are too small to be seen. Abbreviations are: Faq, *Formica aquilonia*; Ch, *Camponotus herculeanus*; Mr, *Myrmica ruginodis*; Ms, *Myrmica sulcinodis*; Fl, *Formica lemani*; others, other ant species. Analyses of abundances in 2006 revealed significant habitat preferences for Ch ($\chi^2_{2,22} = 16.03, P = 0.0003$), Mr ($\chi^2_{2,22} = 15.30, P = 0.0005$), Ms ($\chi^2_{2,22} = 41.75, P < 0.0001$), Fl ($\chi^2_{2,22} = 20.51, P < 0.0001$), and others ($\chi^2_{2,22} = 35.32, P < 0.0001$). Faq did not show significant habitat preferences ($\chi^2_{2,22} = 1.26, P = 0.533$), but sites were selected because they supported healthy colonies of this species, and traps were deliberately placed close to nests of this species. Significance in contrasts (Table 1) is indicated by asterisks.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

nonsignificant (see also Gibb and Johansson 2011). Responses were consistent for *M. ruginodis* and other ants across forest ages, but not significant in all cases (Table 1; Appendix B).

Permutational ANOVA testing the effects of age and treatment on species composition revealed a close-to-significant interaction between age and treatment (pseudo- $F_{2,18} = 1.84, P = 0.057$), a nonsignificant effect

TABLE 1. Negative binomial generalized linear models testing the effects of stand age, partial removal of *Formica aquilonia*, the interaction between these factors, and the covariate 2006 abundance (of the response species) on the abundance of common ant species in 2008 in the boreal forests of northern Sweden.

Source	df	<i>F. aquilonia</i>		<i>Myrmica ruginodis</i>		Species richness		<i>M. sulcinodis</i>		<i>F. lemani</i>		All others		
		χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	
Treatment	1,24	43.09	<0.0001	8.31	0.0039	0.22	0.6373	1,14	9.41	0.0022	0.00	0.9567	0.14	0.7049
Age	2,22	11.78	0.0028	96.60	<0.0001	14.72	0.0006	1,13	0.04	0.8501	1.44	0.2300	4.95	0.0260
2006 abundance	1,21	5.40	0.0202	7.73	0.0054	0.18	0.6677	1,12	13.05	0.0003	18.15	<0.0001	0.05	0.8292
Age × treatment	2,19	20.70	<0.0001	22.58	<0.0001	1.23	0.5395	1,11	7.31	0.0068	0.46	0.4955	2.05	0.1523

Notes: *M. sulcinodis*, *F. lemani*, and “all other” ants were rare in 80–100-year-old stands, so this category was excluded from analyses of these species. Significant effects from the analysis are shown in bold. Significant results from contrasts are as follows: *F. aquilonia*, all ages, control > exclusion, $P < 0.001$; *M. ruginodis*, 0–4 year, control > exclusion, $P < 0.001$; 30–40 year, exclusion > control, $P < 0.001$; species richness, 80–100 year < 1–4 year, $P < 0.05$; 80–100 year < 30–40 year, $P < 0.01$; *M. sulcinodis*, 0–4 year, control > exclusion, $P < 0.01$; all others, 80–100 year < 30–40 year, $P < 0.05$.

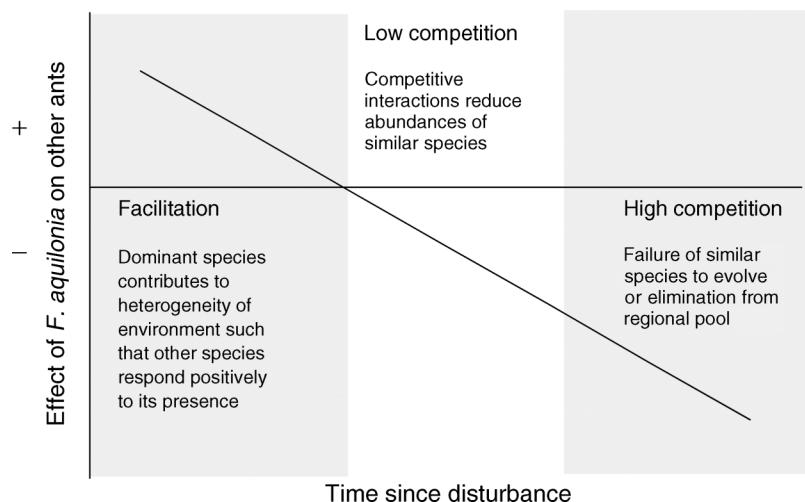


FIG. 3. Conceptual diagram of where, along the gradient of habitat succession, one might expect to find effects of competition from *F. aquilonia*. Facilitation may occur in highly disturbed early-successional habitats, but competitive effects of *F. aquilonia* may increase as time since disturbance increases. However, competition may only be detectable in contemporary experiments if it has not limited species richness in evolutionary time. In high-stress environments, such as the boreal forests in this study, niches may be broader (Schwilke and Ackerly 2005). If *F. aquilonia* occupies a broader niche, it may outcompete or prevent the evolution of similar species.

of treatment (pseudo- $F_{1,18} = 1.66$, $P = 0.184$) and a significant effect of age (pseudo- $F_{2,18} = 13.07$, $P = 0.001$). Post hoc tests on the interaction showed a significant difference in species composition between treatment and control sites for clearcuts (global $R = 0.381$, $P = 0.016$), but not other site types. Forests of different ages clearly all supported different assemblages of ants.

DISCUSSION

This study suggests that the effect of competitively dominant species on assemblages depends on time since disturbance, in agreement with theory (Grime 1973, Connell 1978). However, changes were not in direct agreement with predictions for *F. aquilonia*; I expected limited effects of competition soon after and large effects long after disturbance. In contrast, removal of *F. aquilonia* resulted in declines in the abundance of other species in 0–4 year stands, increases on 30–40 year stands, and minimal effects in 80–100 year stands. Here I consider the mechanisms driving these responses and suggest a model that explains when the influence of competition should be most easily observed.

In recently disturbed sites, i.e., 0–4-year-old stands, the presence of *F. aquilonia* appeared to facilitate the success of other species, particularly *Myrmica* spp. Physical attributes of these stands may differ enough from older forests to reverse the effects of interactions. For example, temperature, which depends on successional stage, may regulate competitive interactions (Cerdá et al. 1988, 1997, Santini et al. 2007). Habitat complexity may also reduce competitive interactions (Petren and Case 1998, Gray et al. 2000, Gibb and Parr 2010), so the greater cover of dead wood in 0–4-year-old

stands may limit competitive interactions with *F. aquilonia*. Biotic effects may also be important. The positive response of *Myrmica* spp. is unlikely to be due to relaxation of competition due to suppression of another ant species as no ant species responded positively to the removal of *F. aquilonia* from clearcuts. However, it is possible that *F. aquilonia* suppresses predators of other ants in 0–4-year-old stands or that dead *F. aquilonia* workers provide an important food source for *Myrmica* spp. and thus facilitate a population increase.

Sites of intermediate age, where removals were most successful, showed responses in agreement with predictions: two species benefited from the removal of *F. aquilonia*. This is suggestive of competition. In contrast, in the long-undisturbed sites, no significant effects of *F. aquilonia* removal were detected. Although absolute numbers of *F. aquilonia* at these sites were higher than at intermediate-aged sites, the relative reduction was similar to that in other stand ages (Fig. 2a, b). Species richness was lowest in these sites, which is probably the result of a failure of species to evolve for those conditions. Ants reach their greatest diversity in warm, dry habitats (Andersen 1995, Dunn et al. 2009) and mature boreal forests were the coolest, wettest, and least diverse of the habitats examined. Mature boreal forests are therefore likely to be less favorable for ants than forests in earlier successional stages, thus reducing opportunities for the coexistence of similar species. In agreement, nests of a number of *F. rufa* group species can be found in 0–4 and 30–40-year-old stands in the study area, but only *F. aquilonia* occurs in 80–100-year-old stands (Gibb and Johansson 2010).

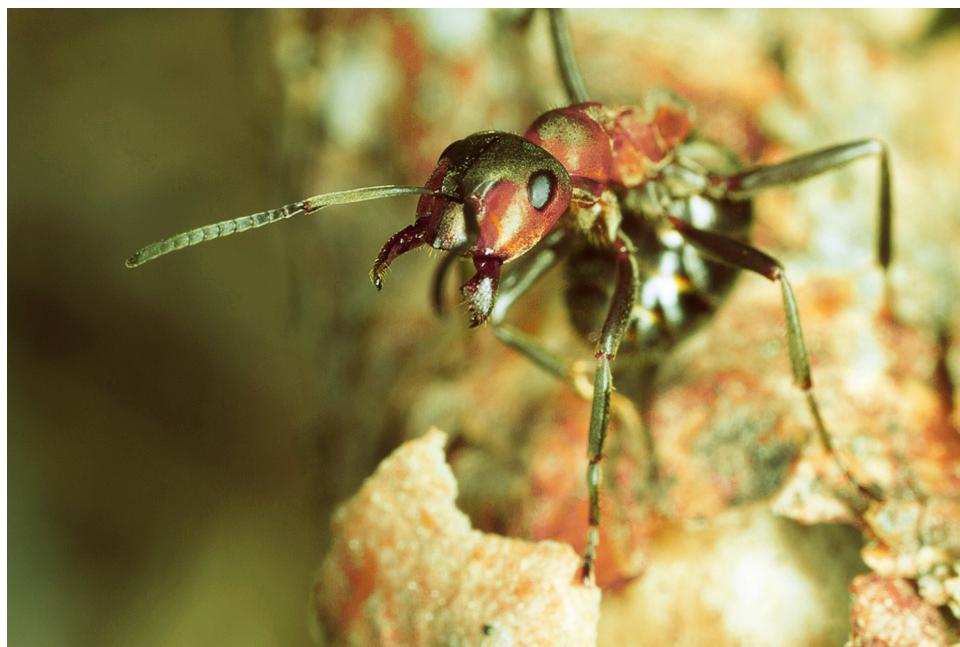


PLATE 1. *Formica aquilonia* behaves aggressively toward potential threats. Photo credit: Ray Wilson.

These responses suggest that competition may vary predictably with habitat succession: in this system, facilitation decreases and competitive exclusion increases with time since disturbance until there is a loss of competitors from the species pool or a failure of competitors to evolve (Fig. 3). This results in a positive association with the dominant species soon after disturbance, a strongly negative association at intermediate times after disturbance, and no detectable association long after disturbance. This contrasts with predictions from the intermediate disturbance hypothesis (Grime 1973, Connell 1978) and the dominance-impoverishment rule (Hölldobler and Wilson 1990, Parr et al. 2005), in that the dominant species may facilitate the coexistence of other species at early successional stages.

It is important to note that the relationship with succession is likely to depend on the dominant species selected for study. *F. aquilonia* is most abundant in the cool moist habitats considered stressful to ants (Andersen 1995), but many competitively dominant species thrive most in the open habitats occurring not long after disturbance. While no similar species may coexist in this low-diversity, stress-tolerant assemblage, niche differences may be much smaller in low-stress, high-diversity environments (Schwilke and Ackerly 2005). Similar species may therefore be more likely to coexist in low-stress environments, making competition easier to detect (e.g., Gibb and Hochuli 2004).

These findings have implications for our expectations of where we might observe contemporary competitive structuring in assemblages. They suggest that inconsistencies among previous studies examining the effects of

ecologically dominant native ants on native assemblages may be a result of differences in the competitive environment due to habitat succession or disturbance regime.

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APPENDIX A

ANOVA testing for differences in the percent cover of herbs, moss, bare ground, leaf litter, and coarse woody debris between stands of different ages and treatments (*Ecological Archives* E092-158-A1).

APPENDIX B

Negative binomial generalized linear models testing the effects of stand age, partial removal of *F. aquilonia*, the interaction between these factors, and the covariate 2006 occurrence (of the response species) on the occurrence of common ant species in 2008 (*Ecological Archives* E092-158-A2).