

Red wood ants in North America

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Red wood ants of the *Formica rufa* group are present in many conifer and mixed-conifer forests of northern Europe and Asia. These six species are part of the *Formica s. str.* subgenus, and build large above-ground organic mounds. In contrast, the taxonomic usage of the *F. rufa* group in North America seems to have a much broader meaning than in Europe and Asia. Twenty-four species and subspecies are placed in the North American *F. rufa* group, but only a few build large mounds. Our survey of the literature indicates that very little is known on the abundance and distribution of North American red wood ants, under what forest conditions they are found, and what role they may have in forest ecosystems. Environmental conditions (temperature, moisture), disturbances (fire, human), predation, and competition with other ant species are all possible factors that may explain why red wood ants predominate in many Eurasian but not in North American forests. Detailed studies on the distribution and ecology of red wood ants in North America are needed, especially the interaction and possible competition from carpenter ants (*Camponotus* spp.) in limiting their distribution. Finally, studies on the taxonomic relationships of the North American *F. rufa* group to the Eurasian *Formica s. str.* subgenus are needed to help understand the origin and development of red wood ants in North America.

Introduction

Red wood ants (*Formica s. str.*) are ubiquitous in many conifer and mixed-conifer forests of northern Europe and Asia, and have been the focus of extensive research on their social structure (e.g. Crozier & Pamilo 1996, Pamilo *et al.* 1997), geographical distribution and density (e.g. Kissling 1985), population dynamics and behavior (Klimetzek 1981), effect on invertebrate biodiversity (Hawes *et al.* 2002, Laakso & Setälä 1997, 1998, 2000), and impacts on tree

growth through their interactions with defoliators and aphids (Laakso & Setälä 2000). Extensive taxonomic and genetic research on the subgenus *Formica s. str.* has resulted in six species being placed in the *F. rufa* group, which build large, distinctive, dome-shaped mounds. *F. truncorum* Fabricius, which is also in the *Formica s. str.* subgenus, builds mounds that are smaller and more irregular-shaped than *F. rufa* species, and is not included in the *F. rufa* group.

In contrast, the taxonomy of the North American red wood ants is fragmented and outdated.

The last major revision dates back to Creighton (1950), and is in need of a modern update (A. Francoeur pers. comm.). Twenty-four species and subspecies are placed in the *F. rufa* group, which inhabit a wide range of forest, open woodland and grassland ecosystems in the United States and Canada (Hedlund 2002). However, only five of these species are reported to build large mounds characteristic of the Eurasian *F. rufa* group ants (Table 1). The other 19 species and sub-species are more similar to the Eurasian red wood ant *F. truncorum*, and cover their nests with varying amounts of organic debris, termed “thatch” in the North American literature.

Patterns of red wood ant distribution in North America

Relatively little is known on the genetics and ecological relationships among red wood ants and other *Formica* spp. in North American ecosystems (Hölldobler & Wilson 1990). The most

widespread species is *Formica obscuripes* Forel, which builds large mounds in prairie and dry forest ecosystems of the western United States and Canada (Fig. 1). Only three other species within the North American *F. rufa* group (*F. dakotensis* Emery, *F. integra* Nylander and *F. obscuriventris obscuriventris* Mayr) are found in 10 or more States (Fig. 2). Published distributions of most species in the United States show very disjunct patterns (Hedlund 2002). This is exemplified by *F. planipilis*, which is reported to be present in four widely scattered states (Fig. 2). Overall, it is unclear how complete these distribution records are, and the occurrence of an ant species in a certain state does not mean that it is widely distributed. For example, McIver et al. (1997) studied a *F. obscuripes* supercolony in an Oregon Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)/grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) stand, but failed to find *F. obscuripes* or any other red wood ant species on 160 km of transects through other mixed-conifer forests in Oregon.

Table 1. Overview of *F. rufa* group species in the United States and Canada (taken from Hedlund 2002).

Species	Nest
<i>F. aterrima</i> Cresson	Not known
<i>F. claviceps</i> Cole	Under stones, banked with detritus
<i>F. ciliata</i> Mayr	Thatching sometimes utilized
<i>F. coloradensis</i> Creighton*	Large and dome-shaped with extensive use of thatch
<i>F. comata</i> Wheeler	Under stones, banked with thatch
<i>F. criniventris</i> Wheeler	Under stones, banked with thatch
<i>F. dakotensis</i> Emery*	Earthen mounds, under stones, in grass clumps banked with considerable detritus
<i>F. ferocula</i> Wheeler	Small crater nests
<i>F. fossiceps</i> Buren*	Under stones or fallen logs banked with thatch or low earthen mounds covered with thatch
<i>F. integra</i> Nylander*	In stumps, logs or under stones, debris commonly covers the nest
<i>F. integroides</i> Wheeler	Under logs and stumps banked with debris
<i>F. laeviceps</i> Creighton	Under stones and logs banked with little debris
<i>F. mucescens</i> Wheeler	Nests under stones, moderate use of thatching
<i>F. obscuripes</i> Forel**	Large mounds made of thatch
<i>F. obscuriventris clivia</i> Creighton*	Under logs and stones, moderate use of thatching
<i>F. obscuriv. obscuriventris</i> Mayr*	Under logs, moderate use of thatching
<i>F. oreas comptula</i> Wheeler	Under stones or logs, banked with detritus
<i>F. oreas</i> Wheeler*	Under rocks or logs covered with detritus, sizable mounds
<i>F. planipilis</i> Creighton*	Extensive use of thatching, moundlike
<i>F. prociliata</i> Kennedy & Dennis	Under stones or low mounds
<i>F. propinqua</i> Creighton*	Started under logs or stumps, considerable use of thatching
<i>F. ravida</i> Creighton*	Started under logs or stones, moderate use of thatching
<i>F. reflexa</i> Buren*	Not known
<i>F. subnitens</i> Creighton*	Under stones banked with debris or in dome-shaped mounds of thatch or detritus

* large thatched mound, + occurs in Canada

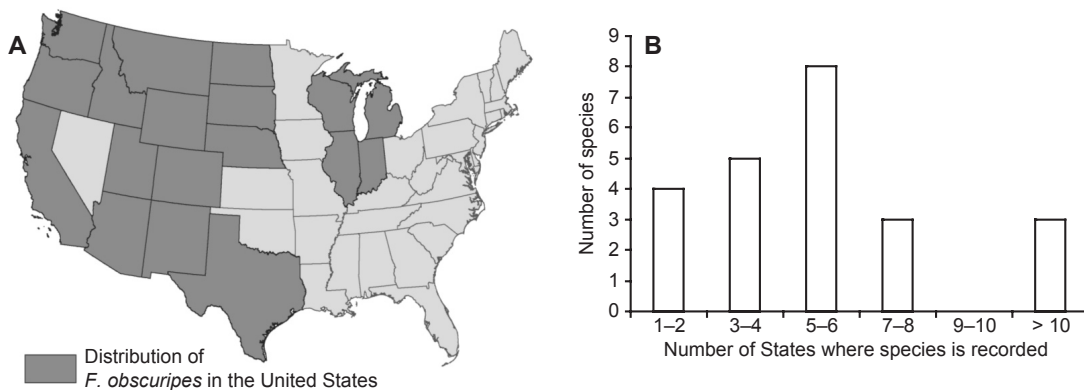


Fig. 1. — **A:** Distribution of *Formica obscuripes* in the United States. — **B:** Distribution of *F. rufa* group species in the United States. (Taken from Hedlund (2002); subspecies were combined to one species.)

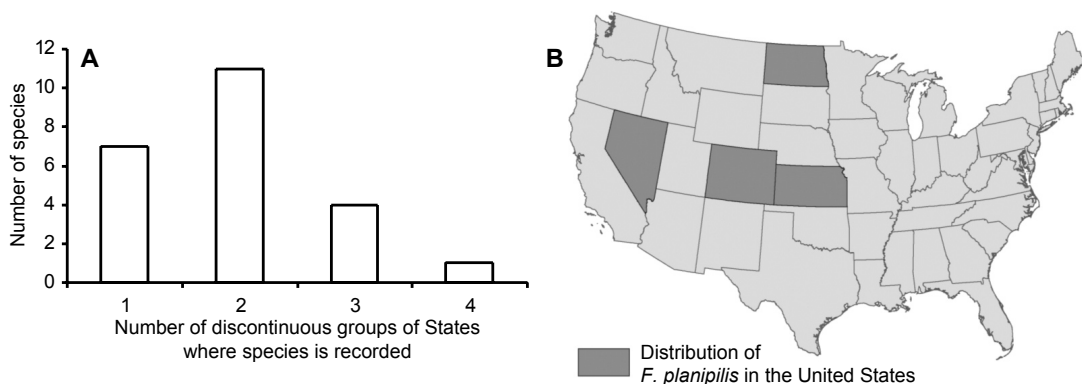


Fig. 2. — **A:** Fragmented distribution patterns of *F. rufa* group species. — **B:** Spatial distribution of *F. planipilis*. (Taken from Hedlund (2002); subspecies were combined into one species.)

While information on red wood ants in the United States is limited, even less is known about their distribution and occurrence in Canada. Based on a literature survey, Lindgren and MacIsaac (2002) documented two species, *F. obscuripes* and *F. obscuriventris*, in northern British Columbia, while Francoeur (1997) found only *F. dakotensis* in the Yukon Territory. Hedlund (2002) mentioned that 10 of the 24 North American *F. rufa* group species and subspecies occur in Canadian provinces (Table 1), but no detailed distribution information was given. In 1950, the North American red wood ant, *F. integroides*, was introduced into New Brunswick as a potential biological control agent against the western spruce budworm (*Choristoneura occidentalis* Freeman), but without success (Youngs & Campbell 1984). Between 1971 and 1973, other red wood ants (*F. lugubris* from Italy and *F. obscuripes* from

Manitoba) were brought into Quebec (Finnegan 1975, 1977), which indicated that no local red wood ant species were present in these Canadian forests. As of 1977, *F. obscuripes* was considered established at one of the two release sites where it was protected from another *Formica* species (*F. sanguinea* Latreille) and the carpenter ant *Camponotus pennsylvanicus* (DeGeer). Mounds of *F. lugubris* were still active in the mid-1980s (J. McNeil pers. comm.), but it is not known whether these ants are present today.

Why are red wood ants more prevalent in Eurasia than in North America?

Germany, Switzerland, and Finland have been important centers for red wood ant research for

the past 60 years. Much of this literature has been summarized in two books by Gösswald (1989a, 1989b). In contrast, our survey of the literature indicates that these ants are rare or absent in many North American ecosystems. Numerous studies have shown that mounds can be thermoregulated by red wood ants, thus enabling early breaking of nest dormancy in the spring (e.g. Rosengren *et al.* 1987, Gösswald 1989a, Laakso & Setälä 1997). This lengthens the breeding and foraging season as compared with that of non-mound building species (Hölldobler & Wilson 1990). The wide geographical distribution of the Eurasian *F. rufa* group, and the dominant role they play in northern Eurasian forest ecosystems, supports the theory that building a large above-ground mound gives these ants a competitive advantage over other invertebrates in cold climates. However, this seems not to hold true for North American red wood ant species, since they are rarely found in North American forests.

The six Eurasian *F. rufa*-group species apparently evolved during the Pleistocene (Goropashnaya *et al.* 2004), and the construction of large, elaborate above-ground nests by these ants was likely a response to the cold conditions during this period. Therefore, one possible explanation for the lack of large mound-building ants in North America is that a similar Pleistocene evolution in ant nest-type did not occur in the North American Pleistocene. However, since there are mound-building red wood ant species in North America (Table 1), they are either related to the Eurasian *F. rufa*-group ants, or this trait has evolved separately in North America. Genetic analyses of red wood ant species in the Eurasian *Formica s. str.* subgenus by Goropashnaya *et al.* (2004) indicated that these ants were restricted to a single refugial area at different times during the late Pleistocene, followed by rapid expansions when the ice retreated. A Bering Sea land bridge from Siberia to Alaska was present several times during this period (Hopkins 1967), thus it would have been possible for Asian red wood ants to cross into North America from Siberia. However, some common Siberian mammals (e.g. musk deer, woolly rhinoceros, and squirrels) did not cross into Alaska during this time, and it is theorized that their emigration was halted because the land bridge was not forested (Flerow

1967). If this lack of a forest gateway would have restricted the movement of red wood ants into North America is not known. Unfortunately, no genetic comparisons of red wood ants in Eurasia and North America have been conducted to date (A. Goropashnaya pers. comm.).

Whether the red wood ants on both continents developed independently, or if they are all descendants of a common ancestor, the question remains why Eurasian species dominate their forest communities, while the North American species do not. Several possible abiotic and biotic factors may explain the different abundance and distribution of red wood ants in Eurasian and North American ecosystems: (i) environmental conditions, (ii) disturbance, (iii) predation, and (iv) competition for resources (Fig. 3).

Environmental conditions

Both temperature (summer and winter) and precipitation (total amount, seasonality and frequency) may influence the survival and functioning of ant mounds. Although above-ground mounds have the benefit of heating up more rapidly on a daily and/or seasonal basis, they may be more vulnerable to temperature extremes, as they lack insulation as compared with nests built in mineral soil. These mounds also have a greater surface area to volume ratio, which could be disadvantageous when temperatures are at an extreme (Hölldobler & Wilson 1990). Rainfall patterns may also be a factor in mound formation. The habit of North American *F. rufa* group species placing thatch over nests in dry soils may reduce the need for reliable rainfall (Weber 1935), but it is not known to what extent.

Climatic differences between Europe and North America may be a factor in the distribution patterns of red wood ants. While Europe is located farther north than the U.S. and southern Canada, it is influenced in part by the Gulf Stream and would have a more moderate climate than the continental regimes that predominate in North America. However, red wood ants are common throughout northern Russia, which would have comparable temperature and moisture extremes as in North America. While climatic conditions in northern Russia and North America appear

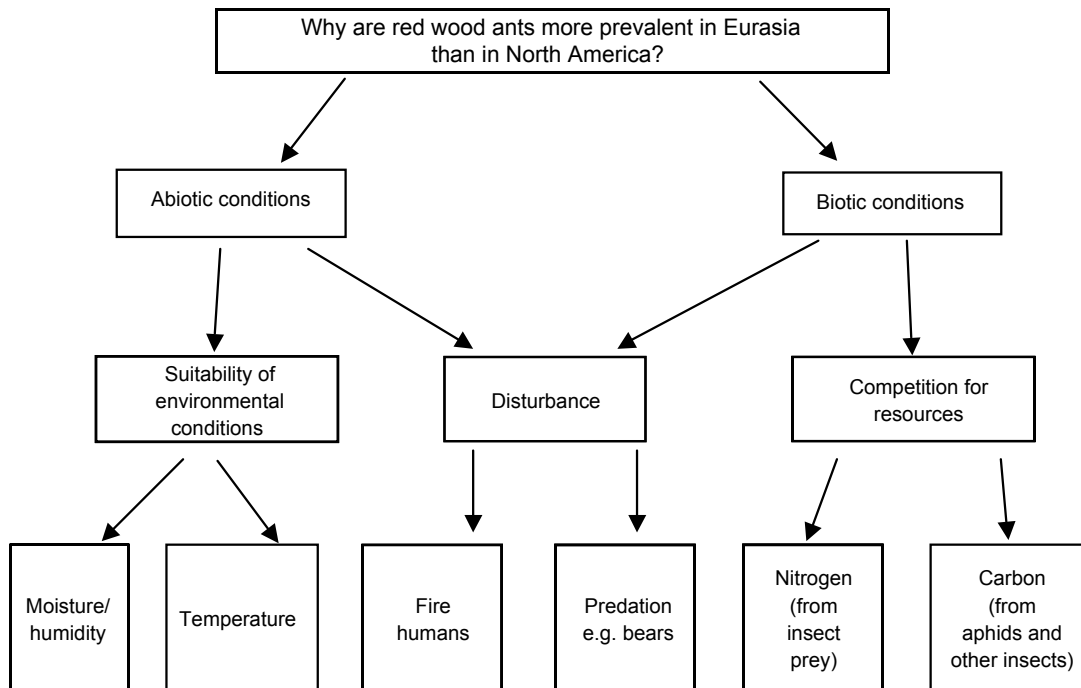


Fig. 3. Factors that could influence populations of red wood ants in Eurasia and North America.

similar, the composition and structure of their forests do differ both in flora and fauna. Therefore, interactions among climate and biotic factors (e.g. forest cover type) and abiotic factors (e.g. topography) resulting in differences in ant species distributions cannot be ruled out.

Disturbances

Mound disturbance and destruction could have major impacts on the survival of red wood ants. Ant mounds are readily destroyed by wildfire (Bradley 1972), which has been much more common in North America than in Europe during the past 500 years (Pyne *et al.* 1996). Marcot *et al.* (1997) reported that *F. obscuripes* mounds in southern Idaho decreased to less than 20 percent of their original number after a fire. They concluded that fire occurring every few years would likely drive these colonies to extinction. The lack or low occurrence of wildfires in Europe would allow red wood ants to thrive and increase their presence in forested ecosystems. Wildfires are still common in Russia, but we could not find

any information on the relationship of red wood ants to forest fire history in this region.

In addition to wildfire, human disturbance could have contributed to the abundance of red wood ants in Europe. Many European forests were intensively managed and fragmented during the 19th and 20th centuries, and were subject to severe air pollution. Ant mounds also experienced extensive destruction after World War II (Kneitz 1965, Gösswald 1989b, Travan 1998). Consequently, conservation programs were enacted in many European countries to protect nests from destruction and to promote their reestablishment. *Formica aquilonia*, *F. lugubris*, *F. polycтена*, *F. pratensis*, and *F. rufa* are still listed on the IUCN Red List of threatened species (IUCN 2003). It is likely that current protection efforts have changed the distribution and population size of red wood ants in many European countries, and their populations may be artificially high in parts of Europe as a result of protection efforts (L. Sundström & D. Chérix pers. comm.). However, we could not find any information on how humans may have impacted red wood ant distribution and frequency in North America and Russia.

Predation

Predators could also have a major impact on easily accessible above-ground ant nests. Bears have been shown to feed on ant mounds in both North America and Eurasia, and can also be a factor in maintaining ant populations in some ecosystems. Auger *et al.* (2004) consider ants a predictable and ubiquitous source of food for bears after finding the remains of ants from five genera (including *Formica*) in 33% of bear scat collected in Utah. Similar results were found in a study conducted in northern Minnesota (Noyes *et al.* 1997). Studies in Sweden and Slovenia have reported that bears excavate between 8% and 33% of all mounds within their feeding range, and that ants comprised up to 16% of their diet (Swenson *et al.* 1999, Grosse *et al.* 2003). Consequently, the elimination of bears in large parts of Europe may have increased red wood ant abundance and contributed to their current dominance in many European forests. Similar to wildfires, bears are still common in Russia. Unfortunately, we could not find any information on how they affect red wood ant populations in Russian forests. Other animals (e.g. the green woodpecker *Picus viridis* L.) have also been reported to feed on *F. rufa* group nests in Europe (Rolstad *et al.* 2000). However, it is not known how much they would affect the development and survival of red wood ant populations in forest ecosystems.

Competition for resources

Both carbon and nitrogen are important resources necessary for the survival of any insect. The primary carbon source for red wood ants in both North America and Eurasia is honeydew collected from aphids, while other nutrients are obtained from feeding on tended aphids and other invertebrates (e.g. Gösswald 1989a, Rosengren & Sundström 1991). In Europe, red wood ants are usually the dominant ant species within the ecosystem they inhabit, and have little competition for aphids or other prey items (e.g. Gösswald 1989a). Since information on red wood ants in North America is generally lacking, it is not known what role they play in ecosystems where they are present, or if they are inhibited or

restricted by other ant or insect taxa that compete for the same resources (Fig. 3).

One insect taxon that potentially competes with red wood ants in North America is carpenter ants, *Camponotus* spp. There are over 900 *Camponotus* spp. worldwide, with 50 species found in the United States and Canada. These ants are very common in North American forests, and excavate nest sites in tree stumps, woody residue, and living trees. Similar to red wood ants, carpenter ants also feed on honeydew from aphids (Hansen & Klotz 2005). Carpenter ants have been the subject of many studies in the United States and Canada (e.g. Sanders 1964, Youngs & Campbell 1984, Wang *et al.* 2001), but the impact of these ants on other ants and insects in forest ecosystems is unclear. Some studies suggest carpenter ants may be important predators of forest pests (e.g. Youngs & Campbell 1984), but other studies suggest their impact on other insects may be limited (Sanders & Pang 1992). When *F. obscuripes* from western Canada was introduced into a Quebec forest, the nests were repeatedly attacked by *C. pennsylvanicus* (DeGeer) during the early stages of establishment (Finnegan 1977).

In contrast, the number of *Camponotus* species present in Europe is much lower than in North America. Czechowski *et al.* (2002) reported that only five *Camponotus* species occur in the Palearctic, and they found all of them in Poland. Collingwood (1979) found three of the five species in Germany, one in Denmark, and two in Sweden, Norway and Finland. While low species number does not mean a low density of carpenter ant nests, the little information we found indicates that carpenter ants in Eurasian forests are present in much lower numbers than red wood ants, and are submissive to them when occurring in the same habitat (Savolainen *et al.* 1989, D. Agosti pers. comm.). We are not aware of any studies that directly addressed the competitive interactions between *Camponotus* spp. and red wood ants in either North America or Eurasia.

Conclusions

Interactions among climate, disturbance, predators, and competition with other ant species are

all possible factors to explain why red wood ants predominate in many Eurasian but not in North American forests. Our survey of the North American literature indicates that very little is known on the abundance and distribution of North American red wood ants, under what forest conditions they are found, and what role they may have in forest ecosystems. Detailed studies on the distribution and ecology of red wood ants in North America are needed, especially the interaction and possible competition from carpenter ants in limiting their distribution. Finally, studies on the taxonomic relationships of the North American *F. rufa* group to the Eurasian *Formica s. str.* subgenus are needed to help understand the origin and development of red wood ants in North America.

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