THE ANT (HYMENOPTERA: FORMICIDAE) COMMUNITIES OF THE CENTRAL INTERIOR OF BRITISH COLUMBIA: ADAPTATIONS TO A TEMPERATURE-CONSTRAINED ENVIRONMENT.

by

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Abstract

Ants (Hymenoptera: Formicidae) in British Columbia are ubiquitous and abundant in most biogeoclimatic zones of the province, have a demonstrated role in ecological processes and are an important food source for many vertebrates such as birds and bears. The objective of my dissertation was to undertake the first broad examination of an ant community in BC, assess responses of the community to seral forest development and determine what habitat elements are associated with ant presence or absence. Ants are a challenging fauna to study, however, as their social structure and foraging strategies complicate sampling. I characterize the sampling issues associated with ants and develop a protocol to optimize field collection. Guided by this protocol, I examined the ant community of the sub-boreal forests of west-central BC. I show that the structure of the ant community is strongly influenced by seral age which I suggest is indicative of temperature sensitivity in this fauna. The ant community increased in abundance and diversity, following the Individualistic Hypothesis of succession, until at least 13-15 yr post-harvest. The community then began to decline as canopy cover increased. Non-harvested stands, with mean summer litter temperatures of <10 °C, were found to be largely devoid of ants. Most ant species were also shown to utilize woody debris for nesting, which is shown to have a significantly higher mean temperature as compared to soil, and may be a thermal refugia for ants. Ants selected specific decay classes and usually larger pieces of woody debris for nesting, as shown by logistic regression. It was also evident that ants were more likely to be found within 50-m^2 sampling units when members of the same species were also found there, likely indicative of secondary site colonization via budding from polygynous colonies. Artificial shading of wood used for nesting resulted in a reduction in utilization by ants supporting the hypothesis that insolative heating of woody debris is critical for ants. Overall the ant fauna was shaped by factors related to temperature and the dependence upon woody debris is indicative of the thermal advantages of this resource.

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Chapter 1. Introduction

Global ant biomass is roughly equivalent to that of humanity (Hölldobler and Wilson 2009) and may constitute a greater biomass than any other non-domesticated terrestrial animal taxon. Currently, over 12,000 species are recognized (Bolton et al. 2006) although it is estimated that up to 10,000 additional species have not been described (Wilson 1987). Ants are generally considered thermophilic (Hölldobler and Wilson 1990) making them particularly species-diverse and abundant in the tropics, semi-tropics and temperate zones. Although less species-diverse, they are also abundant at higher latitudes up to, and occasionally beyond the tree-line (Gregg 1972 Francoeur 1983). Ants are also abundant in both natural and anthropogenic landscapes, often being one of the most commonly seen epigaeic insects in urban environments.

All known ants demonstrate a particular and complex form of social behaviour called eusociality. Eusocial animals are characterized by overlapping generations, shared care of their young, and the control of reproduction by only one or a few members of the colony, creating a functionally sterile worker class (Wilson 1971). Social behaviour appears to confer a number of advantages over non-social competitors as suggested by their dominance in many communities. For example, eusocial insects were found to comprise 75% of the total insect biomass in a study of biodiversity in a tropical rain forest (Fittkau and Klinge 1973). Further, no major taxon (i.e., at least at the level of Family) of eusocial insects has been documented as extinct, nor are any known which are rare (Wilson 1987).

The social behaviour of ants has often become highly specialized to exploit specific ecological niches. Examples include the highly coordinated group hunting by the Old World driver ants (*Dorylus* spp.) and New World army ants (*Eciton* spp.) (Kronauer et al. 2007), the cultivation of fungi for food by the leaf-cutter ants (*Atta* and *Acromyrmex* spp.) (Seal and Tschinkel 2007), and the tending of honeydew excreting insects (mostly Hemiptera) in a manner analogous to dairy farming (Oliver et al. 2008). Social behaviour, however, can also be exploited either by other ants or other insects. For example, the genus *Polyergus* has evolved a form of obligatory slave-taking which makes these ants dependent upon raiding the natal nests of other ant species (usually *Formica* spp.). Foreign pupae are taken to their own nest, where they develop into workers that will act as functional slaves for the slave-taking species (Fischer-Blass et al. 2006; Bono et al. 2007). Other species of ants have taken the reliance on other species one step further by simply moving into the nests of other ant species and acting as social parasites (e.g., *Formicoxenus* spp. in *Myrmica* spp. nests) (Errand et al. 1997).

The complex behavioural adaptations that have arisen in ant species, remarkable because of the apparent limited repertoire of any individual ant, are created by the manner in which ants communicate among themselves. Fundamental to their social organizational strategy is the use of pheromones to both set priorities and provide directional information (Hölldobler and Wilson 1990). The emergent organizational efficiency, flexible under changing conditions, has formed the basis of a modelling technique called Ant Colony Optimization (ACO) (Dorigo and Gambardella 1997). This offers a new approach to develop optimal solutions to complex problems using a heuristic decision-making process founded on the pheromone based organizational strategy of ants. Although this modelling technique has found utility in a variety of applications ranging from designing automated manufacturing plants (Tiwari et al. 2006) to the design of mechanical trusses (Kaveh et al. 2008), there may be some irony in that it has also found its way back into the forest, as ACO is now being used to determine the optimal way to route logging trucks (Contreras et al. 2008).

Much of the research on ants has occurred in ecosystems not typical to BC (e.g., tropical, sub-tropical, temperate eastern North American). In these studies, ants have been shown to to play a role in seed dispersal (Gorn et al. 2000; Heithaus 1981), grain consumption (Brown et al. 1979), decomposition (Haines 1978), defoliation (Cherrett 1968) and soil nutrient turnover (Wagner et al. 1997; Nkem 2000; Risch et al. 2005). Although some of these functions may also occur in higher latitude coniferous forests, for example, soil nutrient turnover (Frouz et al. 2003), two specific ecological roles have been well established in ecosystems more typical of this province. These are the roles played by ants as predators of invertebrates and, in turn, as prey themselves for many vertebrates.

A study of ant predation, in a temperate meadow, determined that ants may remove up to 40% of the invertebrate prey biomass (Petal 1980). A direct count of the number of invertebrates being collected by three nests of *Formica lugubris* Zetterstedt, a European species artificially established in Quebec to examine their utility in the biocontrol of forests pests, found that, in a 10-min period, the three nests were each bringing in an average of 230 invertebrate prey items (McNeil et al. 1978). Additional work has more closely linked ants to specific invertebrate forest pests. *Camponotus herculeanus* L. and *Formica fusca* L. ants were observed attacking larvae of the forest tent caterpillar (*Malacosoma disstria* Hübner; Lepidoptera: Lasiocampidae) (Green and Sullivan 1950). Ants significantly reduced the number of western spruce budworm larvae (*Choristoneura occidentalis* Freeman; Lepidoptera: Tortricidae), on trees in which ants were allowed to forage as compared to trees in which ants were excluded (Campbell et al. 1983). Further, experimentally excluding ants from small Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western larch (*Larix occidentalis* Nutt)., trees resulted in a four times greater increase in injury from western spruce budworm (Carlson et al. 1984). Ants were also documented preying on eggs of the Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough); Lepidoptera: Lymantriidae), although study methodology was unable to quantify the predation rates specific to ants because of similar actions by birds (Torgersen and Mason 1987). The physical proximity of *Formica aquilonia* Yarrow ant colonies, was associated with reduced foliage loss in birch (*Betula pubescens* Ehrh)., during outbreaks of the autumnal moth (*Epirrita* (=*Oporinia*) *autumnata* (Borkhausen); Lepidoptera: Geometridae) (Laine and Niemelä 1980). They reported that trees within a few metres of the nests had defoliation rates of slightly greater than 30% while trees 30-40 m from the ant nest had defoliation rates of 60-70%. Ant exclusion from young sycamore (*Acer pseudoplatanus* L.), not only increased defoliation (1-1.6% with ants as compared to 6-10% without ants) but ant-excluded trees had significantly lower weights and shoot heights (Whittaker and Warrington 1985). Thus, the documented role of ants in controlling pest populations should be considered by forest managers in the context of maintaining healthy forests, especially during times of climatic change when forests are stressed and susceptible to insect damage.

Although ants are significant predators, they are also frequently prey to both invertebrates and vertebrates. Despite the nutritional content of ants being similar to that of other invertebrates (Redford and Dorea 1984), the social nature of ants creates a situation where large numbers of individuals are locally clustered. As a consequence, vertebrate myrmecophagy is common. In a literature review of the diet of 216 species of mammals, 53 species were reported as consuming ants (Redford 1987). In particular, predators often focus on either ant queens or the larvae/pupae which have a higher fat content (Redford and Dorea 1984).

Many species of birds are either generally dependent upon ants for food or require ants during the rearing of young. An examination of the stomachs of 108 species of birds in Utah found that 25 species contained ants (Knowlton et al. 1946). Ants are the primary food source for the pileated woodpecker (*Dryocopus pileatus* L.) (Beckwith and Bull 1985; Torgersen and Bull 1995) and, along with beetles, one of two food sources exclusively consumed by the northern flicker (*Colaptes auratus* L.) (Elchuk and Wiebe 2002). The Williamson's sapsucker (*Sphyrapicus thyroideus* (Cassin)), a species which in Canada is known only to occur in British Columbia, and was placed on Schedule 1 of the Species at Risk Act in 2006, is particularly dependent upon ants to successfully rear their young. The Williamson's sapsucker has been described as being more dependent upon ants during the breeding season than any other North American woodpecker (Beal 1911).

Bears also make extensive use of ants in their diet. A study of black bear (*Ursus americanus* Pallas), scat in Montana between 1959 and 1960 found that ants were the most common animal remains identified, appearing overall in 45.3% of all scats (Tisch 1961). Similar results were reported in black bear scats in Alaska, where 31% contained ants (Hatler 1972), and in Wyoming where about half of black bear scats held ants between May and June (Irwin and Hammond 1985). Although ants were frequently found in the scats reported above, the volume of scat comprised by ants was quite variable. Volumes were reported as low as 2% (Irwin and Hammond 1985), between 6 and 25% (Hatler 1972) or up to 49.7% of scat (Raine and Kansas 1990). Fewer studies have been performed on *Ursus arctos* L., but grizzlies (*U. arctos horribilis* Ord), were frequently observed turning over rocks in search of ants (Russell et al. 1979) and Eurasian brown bears (*U. arctos arctos* L.), were reported to have disturbed approximately half of all ant thatched mounds in a Scandinavian study (Elgmork and Unander 1999). Using stable isotope data, it was determined that meat (mammals) and ants comprised 20-40% of the diet of a population of plateau grizzly bears (*U. arctos horribilis*), in central British Columbia, just north of Prince George, although methodology did not allow a quantification of the percentage specific to ants (Ciarniello et al. 2007). Ant availability, however, is often considerable. In central Sweden, it was estimated that approximately 30.5-38.5 tonnes of ants were available for each brown bear (*U. arctos arctos*) (Swenson et al. 1999).

Given the ecological roles of ants, the paucity of ant ecological research specific to BC may result in biologists missing important connections. The purpose of this dissertation was to provide the first broad ecological study of forest ant communities in the central-interior of BC, and to assess the critical environmental elements that impact their presence or absence. There are some obvious limitations with such a study given the size of the central-interior and the range in moisture regimes from east to west that arise from the Coastal and Rocky Mountain ranges. A comprehensive examination of ant communities in the many biogeoclimatic zones is almost impossible. In a forestry context, however, two inter-related themes do arise when considering the ant fauna of BC. These are the extensive use of wood as a nesting resource, as first documented by Lindgren and MacIsaac (2002), and the role of temperature as a limiting factor to the distribution and abundance of the thermophilic ants. These inter-related themes are central in this dissertation. Before those subjects can be considered, however, an examination of the efficacy, limitations and biases of sampling methodologies must be considered in the context of the natural history of a socially organized insect.

As ants are normally rearing young throughout the colony life-cycle, colonies are usually permanently or semi-permanently anchored in the landscape perennially, a characteristic more typical for plants than many terrestrial animals (Andersen 1995). Although anchored on the nest, foraging ants disperse through the local environment in search of resources. As many species within the sub-family Formicinae specialize in honeydew collection, mostly from sap-sucking herbivorous insects (e.g., aphids or scale insects in the Order Hemiptera) (Hölldobler and Wilson 2009), these ants may form discrete trails between the colony and the honeydew source (McIver and Yandell 1998). As a consequence, the distribution of foraging ants in the environment is often not random at the scale of the foraging colony, but densely and specifically routed, leading to problems in interpreting the significance of counts of individual ants at any given sampling point (e.g., a pitfall trap, or small area soil/litter sample). Thus, the purpose of the second chapter of my dissertation was to investigate the most commonly used methods for sampling ants, evaluate their efficacy and then examine the utility and limitations of the collected information.

As noted earlier, ants are a thermophilic taxon, an attribute reflected in a strong latitudinal gradient in species diversity (Kusnezov 1957). For example, it was reported that there are approximately 2,233 species of ants in sub-Saharan Africa while all of Europe reports just 429 species (Hölldobler and Wilson 1990). Currently, 82 species of ants have been confirmed in BC (Higgins and Lindgren 2009) with more species found in southern than in the northern BC. A study of the impacts of cattle grazing on ant communities near Oliver and Osoyoos (49°N), identified 31 species of ants in 13 genera (Heron 2001) while 19 species of ants from 7 genera were identified in the Prince George area (54°N) (Lindgren and MacIsaac 2002). Although four sub-families of ants are recognized within BC, two, the sub-families Myrmicinae and Formicinae, represent the majority of ant species with 79 of the 82 species falling into either of these two taxa.

Globally, the sub-family Myrmicinae is a dominant group exploiting forest litter (Hölldobler and Wilson 2009). This is loosely true in BC as well, where these small-bodied, generally small-colony species, make extensive use of fine and coarse woody debris, as well as soil, especially soil under rocks, for nesting. Members of the cool climate specialist sub-family Formicinae are normally larger species (both in physical size of workers and size of colonies), making greater use of soil (often under rocks or with thatching) and coarse woody debris for nesting. It is suggested that this sub-family, one of the last to diversify in the early to middle Eocene (approximately 45 Ma), may have been unable to exploit filled niches in warmer climates because of the earlier diversification of other ant sub-families (i.e., the Ponerinae and Myrmicinae) (Hölldobler and Wilson 2009).

A geographical examination of ant community structure (i.e., from south to north) would be one method to approach the question of temperature sensitivity, but additional uncontrolled variables (e.g., moisture, vegetation, variable anthropogenic modifications) made this impractical. Thus, I examined the changes occurring within one ant community within forests of varying seral age where the developing canopy reduces the thermal energy reaching the ground. By limiting the study to a single biogeoclimatic zone (sub-boreal spruce, moist cold, variant 2) (Meidinger and Pojar 1991), the number of uncontrolled variables is reduced allowing for a better understanding of a single community. In Chapter 3, I examined the ant communities within this biogeoclimatic zone in post-harvest (2-3, 8-10, 13-15 and 23-25 y) as well as non-harvested stands.

In tropical areas, ants may be arboreal, nesting directly within trees (e.g., *Oecophylla* spp., weaver ants of Africa and Australia) but most are associated with the soil. In fact, the evolution of the metapleural gland, an antimicrobial gland ants use to keep soil-based nests free of fungi and bacteria, is considered a key macroevolutionary characteristic, driving the divergence of ants from ancestral wasps (Hölldobler and Wilson 1990). In BC, however, soil nesting is often modified or abandoned entirely, probably because of the cool soils common to all but the most southern regions of the province.

Ants nesting in cool soil can improve their thermal environment by nesting directly under rocks (Van Pelt 1963) or by using thatching to build mounds (Coenen-Staβ et al. 1980; Rosengren et al. 1987). Rocks, when exposed to the sun can rapidly gain heat as a consequence of their low specific heat, and hold some of that thermal energy during the night as a consequence of their mass (Cloudsley-Thompson 1956). Colonies of *Formica neorufibarbis* Emery, above the tree-line (3700-4000 masl) in Colorado, used rocks with a mean surface area of 145 ± 12 cm^2 (SE), which were significantly larger than the average rocks present in the area, 80 ± 17 cm^2 (SE), suggesting that the selection was not random (Billeck 2001). Ants that exploit this resource, however, may be limited in population growth by the number of suitable rocks and limited in colony growth by the area under the rocks (Thomas 2002). Given this, the utilization of rocks may be best suited to ant species with small colonies. In addition, the need for the rocks to be directly exposed to the sun (insolation) limits the habitats in which this expectation is met to areas of low vegetative growth (e.g., alpine) or well grazed grasslands.

Ants forming larger colonies often use thatching, that is, accumulation of dead plant material, to improve the thermal environment of their nests. Thatching enables the rapid shedding of precipitation which can act as a heat sink and creates a medium which can be quickly altered to maintain stable internal conditions (Coenen-Staβ et al. 1980; Rosengren et al. 1987). Openings can be increased to dissipate heat or decreased to retain heat within the nest as conditions dictate. The face of the nest can also be shaped to maximize insolation. Thatching can be such an effective medium for holding heat that temperatures inside the nest can reach 27 °C even when the surface of the nest is covered by several centimetres of snow (Rosengren et al. 1987).

With increasing latitude, soil may become less desirable for nesting, even with features such as rock or thatching, especially if the soil is moist. The high specific heat of water (Wenzl 1963), combined with cool temperatures, can lead to moist soil acting as a heat sink. This forces ants into the environment above the soil surface, which offers few nesting options. The leaf/needle litter layer and woody debris, however, are two potential niches. The thin litter layer in boreal and sub-boreal forests may offer marginal habitat to very small colonies that can tolerate the wide range in temperatures that would be expected in this environment. This may well be a possible nesting habitat for the minute *Leptothorax* spp. ants (sub-family Myrmicinae), but there is little evidence to suggest other species can exploit this niche. The other possible resource is woody debris.

A review of the literature indicates that ant utilization of coarse woody debris (CWD) as a nesting resource is positively associated with increasing latitude or cooling climate. Further, as the strength of this relationship is most evident in higher latitudes, higher elevations or cooler climates, where little work has been done with ants, this process has not been widely recognized. For example, although less than 10% of species use CWD as nesting habitat in Nevada (average latitude 38°N) (Wheeler GC and Wheeler J 1986), over 35% used CWD in North Dakota (average latitude 48°N) (Wheeler GC and Wheeler J 1963) and just under 60% of species collected near Prince George, BC, were CWD-associated (latitude 53°N) (Lindgren and MacIsaac 2002). As noted above, the latitude effect is also mirrored by cooling climate from geographic location or elevation. Colorado, at the same approximate latitude as Nevada, has a much greater percentage of dead wood-associated ants. Thirty three percent of the ant fauna in Colorado are associated with woody debris (Gregg 1963), as compared to under 10% in Nevada (Wheeler GC and Wheeler J 1986). Finally, work in Virginia (average latitude 37°30'N) above 1,050 masl, found that 41% of the ant fauna either preferred woody debris for nesting or frequently made use of this resource (Van Pelt 1963). Although this effect may also be influenced by variations in woody debris availability, the relative abundance of forested versus non-forested landscape, or competition from termites, the possibility of heat driving this relationship deserves consideration. Chapter 4 specifically modelled this relationship by examining the physical characteristics of wood that were associated with the presence or absence of the most locally common species of ants.

Although ant communities do appear to be sensitive to cooling conditions, it is possible that factors other than temperature may play a role. If temperature is the primary force affecting change, it should be possible to specifically test for a response from ants to an artificially altered environment. In cool environments, insolation is likely a critical source of heat upon which ants are dependent. Even ants adapted to cool environments have been shown to need to maintain their larvae at temperatures no lower than 15 °C (Elmes and

Wardlaw 1983). Given this, the direct blocking of insolation by shading should reduce a critical source of heat needed for colony development. In Chapter 5, I tested this hypothesis by building shading fences around two wood nesting species of ants to isolate this variable and assess the response of ants to a direct reduction in insolation and thus heat.

The primary intent of my dissertation was to follow one ant community within BC as it responds to declining temperature and assess what environmental variables were most critical in explaining ant presence or absence. I hope that the ecological characterization of this ant community, will provide some insight into the broader ant communities within the province and act as a foundation for the development of further hypotheses. In addition, I believe that this work will serve as a basic reference for biologists working with other organisms that may interact with ants. Chapter 6, the synthesis, integrates the findings of each investigation into the few themes that most significantly affect the forest ants of west-central BC.

Chapter 2. The efficacies and data limitations associated with sampling methodologies used for assessing ant communities[1]

Abstract

Despite the ubiquity of ants (Hymenoptera: Formicidae) in many habitats, sampling ants for ecological studies is problematic. Problems include biased estimates due to spatially focused foraging, an unknown relationship to absolute community structure information when using a common relative abundance sampling technique (pitfall traps), and a lack of habitat-specific rationales for differing sampling techniques. First, we considered a pitfall trap design, the Nordlander trap, in the specific context of sampling for ants. Four trap configurations (two Nordlander based, and two traditionally (Laurent) based), both with and without a raised cover, were tested in two different forest habitats. The Nordlander design without raised cover was equally efficacious to the Laurent design with cover, in sampling for total species richness, and showed no evidence of size-bias relative to the other designs tested. No vertebrates were captured in any of the pitfall trap designs used in this study. Second, the reliability of using individual capture rates in pitfall traps was tested experimentally. Traps were placed in a grid surrounding large thatching nests of the ant, *Formica obscuripes*, and the distribution of trapped foragers evaluated. The distribution was unique to each nest and highly patchy. Pitfall traps placed 10 m apart differed in capture rates by up to 120 individuals, including traps equidistant from the nest, suggesting that the use of individual ant counts in pitfall traps does not provide representative information. We concluded that only presence/absence information should be used. Third, abundance estimates of ant community structure were made in a simple grassland ecosystem by both pitfall trapping

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[1] First person plural is used throughout this chapter to reflect the contributions of others to both research design and field work.

(relative) and intensive area-based hand-sampling (absolute) for ant colonies, to compare the resulting community structure data. The most common ant collected in pitfall traps (relative abundance) was *Tapinoma sessile*, while the most common ant species identified by intensive hand-sampling (absolute abundance) for colonies was *Lasius crypticus* Wilson (Formicidae: Formicinae). Thus, ant community data obtained through relative sampling does not reflect the actual distribution of ant colonies, and should not be used as a proxy for absolute sampling estimates for this purpose. Finally, the efficacy of pitfall trapping and mini-Winkler extractors for litter sampling in estimating total species richness was compared in identical forest habitats. Estimates of total ant species richness by the incidence-based estimator (Chao2) were higher for pitfall sampling (10.55 ± 0.15 SE species), than for mini-Winkler litter sampling (9.0 ± 0.001 SE). Thus, pitfall trapping may be preferable to mini-Winkler litter sampling in estimating total ant species richness in the cool moist forests of west-central British Columbia.

Introduction

Sampling methodology is one of the first issues that require consideration in any ecological study. Unless the organism of interest is easily identified and the area of study is small, determination of species population parameters will require some form of estimation derived from partial sampling of the area of interest (Southwood and Henderson 2000). The choice of sampling methodology should take into consideration the goals of the study, the efficiency of field installation (King and Porter 2005), as well as the efficacy and biases of each sampling technique in the context of both the natural history of the organism under study (Bestelmeyer et al. 2000) and the habitat in which the sampling technique is being used

(Koivula et al. 2003). In addition, each technique should be evaluated for undesirable environmental impacts.

Pitfall trapping is a commonly used sampling methodology in ecological studies of ants (Hymenoptera: Formicidae). It is used for examining total species richness or community structure and is recommended by the Ants of the Leaf Litter (ALL) Protocol (Agosti et al. 2000). Pitfall traps usually consist of a round cup partially filled with a preservative solution, and placed into the ground with the lip flush to the surface (Laurent 1917; Woodcock 2005). In addition, they usually include a separate raised cover to reduce the risk of trap flooding during rainfall and slow the evaporation of cup solutions. This design is popular because simple cups are cheap to purchase, sample 24 h a day, and are easy to set in place. The traditional raised covers can be cumbersome to carry into the field and position, however. Further, there is little standardization in pitfall trap design, and discussion relating to tailoring the design to a particular fauna is lacking. Vertebrate bycatch is commonly a problem with the traditional Laurent design leading to both ethical issues and the spoilage of trap contents by vertebrate remains (Pearce et al. 2005).

The interpretation of pitfall trap catches is also an issue that requires consideration, especially given the natural history of ants. Ants are social insects that often form permanent to semi-permanent nest sites and forage within the surrounding habitat (Hölldobler and Wilson 1990). Some species form discrete, narrow trails leading directly to resource patches. These trails can be densely packed with travelling workers while adjacent habitat is depauperate in ants (Sanders 1972; McIver et al. 1997). To date, this problem has not been widely recognized in the context of pitfall traps, but it is of critical importance if consideration is given to relative abundance values based on the number of individual ants captured by pitfall traps as is frequently done (Savolainen and Vepsäläinen 1989; Bestelmeyer et al. 2000; Dunn et al. 2007).

It is also worthwhile to consider the relationship between estimates of relative abundance and absolute abundance. Pitfall trapping is a sampling methodology intended for relative abundance data, which is considered a population measurement that cannot be defined in terms of unit area or volume (Southwood and Henderson 2000). This is contrasted with sampling methodologies intended to estimate the absolute abundance of populations per unit area or volume. It is frequently assumed, or forgotten, that trapping bias may skew species abundances as compared to their actual densities within a given habitat (Lang 2000; Schlick-Steiner et al. 2006).

Although pitfall trapping is commonly used to sample ants, other methods are also frequently employed. The mini-Winkler litter extraction technique has been increasingly utilized and is also recommended by the ALL Protocol (Agosti et al. 2000). Mini-Winkler litter extractors are used to sample litter-associated ants from small fixed area plots, usually 1 m^2 or less (Olson 1991, Agosti et al. 2000). The literature varies with respect to reports of the comparative efficacies of pitfall trapping and mini-Winkler litter extractions in estimating total species richness. In addition, the use of baits to attract ants for the purpose of assessing community dominance over resources, is also commonly utilized. This technique was not studied here as initial experimentation was not successful in attracting ants in a reasonable period of time.

The first objective of this study, therefore, was to examine the efficacies and biases of pitfall trap designs, with respect to total species richness and ant size. A modified design called the Nordlander pitfall trap (Nordlander 1987, Lemieux and Lindgren 1999), which may offer some advantages in field use, was compared to the traditional Laurent pitfall trap with and without raised covers. Here the desire was to ensure it was equally efficacious in sampling for ant diversity as the Laurent design. The second objective of this study was to examine the precision of captures of individual ants in pitfall traps, by examining the distribution of ants in the immediate vicinity of large thatching nests of the western thatching ant, *Formica obscuripes* Forel (Formicidae: Formicinae). It was the third objective of this study to determine if the apparent ant community structure derived from a relative abundance estimation technique (i.e., pitfall trapping) is distinct from an absolute abundance technique (i.e., manual unit area sampling for ant colonies). Finally, the fourth purpose of this chapter was to examine the efficacies of pitfall trapping as compared to mini-Winkler litter sampling in estimating total species richness in the sub-boreal forests of British Columbia.

Methods

Pitfall trap efficacy

We compared Nordlander and traditional Laurent pitfall traps, both with and without raised covers, with respect to sampling bias in ant size and total species richness (Figure 2.1). Nordlander pitfall traps consisted of 237-ml plastic cups with snap-on lids (VWR Scientific Products, Catalogue number 44333-002). Cups had an inner diameter of 7.5 cm and a circumference of 23.6 cm. Approximately twenty-five 6-mm holes were inserted around the upper circumference just below the rim using a standard one-hole hand paper-punch. Following Bestelmeyer et al. (2000), the pitfall traps used in my studies are of medium size and use propylene glycol rather than ethylene glycol as a preservative. Propylene glycol has a relatively low mammal toxicity, with an LD_{50} of 20 g/kg (oral rat) (MBI 2008a), while ethylene glycol has an LD_{50} of 4.7 g/kg (oral rat) and is a demonstrated teratogen (MBI 2008b).

Holes were dug using a narrow garden trowel, and the cups placed into the ground such that the bottom of the holes were level with the surface of the soil/duff. A small amount of soil or moss was added to the top of the lid to reduce visibility to birds and mammals that might disturb the trap. Laurent pitfall traps consisted of the identical cups without the additional 6-mm holes or snap-on lids. These cups were positioned in the ground with the upper rim flush to the soil/duff surface (Figure 2.1). Raised covers consisted of a 20-cm square metal sheet with the corners bent down to hold the trap cover approximately 4.5 cm above the ground (Figure 2.1). A small amount of soil or moss was also added to the tops of the covers to reduce visibility to birds and mammals. Thus, four trap configurations were tested: Nordlander pitfall with no metal cover (NNC); Nordlander with metal cover (NWC); Laurent pitfall with no metal cover (LNC); Laurent with metal cover (LWC). Each trap was filled with approximately 80 ml of a solution of propylene glycol and water (25/75 by volume).

Trap designs were tested at two locations. The first was at the University of British Columbia research forest at Knife Creek (52°33'N, 121°53.4'W, approximately 860 masl) located approximately 30 km south of Williams Lake, British Columbia. The study plot was in a non-harvested reserve site within the interior Douglas-fir biogeoclimatic zone and dry-cold subzone, variant 3 (Meidinger and Pojar 1991). This stand was dominated by mature Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). The second test location was in a 15-yr post-harvest stand (54°28.8'N, 126°18'W, approximately 1,150 masl) near Topley, approximately 50 km east of Houston, BC. This test plot was located in the sub-boreal spruce

Figure 2.1 Pitfall trap designs tested at Knife Creek and Topley, BC. Each trap was filled with approximately 80 ml of preservative solution comprised of 25% propylene glycol and 75% water. Photos show: a) Nordlander design with no cover (NNC); b) Nordlander design with cover (NWC) (Note: cover moved for purposes of illustration); c) Laurent design with no cover (LNC); d) Laurent design with cover (LWC). Pen provided for scale.

biogeoclimatic zone and moist-cool subzone, variant 2 (Meidinger and Pojar 1991) and was dominated by lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm).

We laid out traps in randomized complete-block design at both sites. At the Knife Creek site, five replicates of each trap design were laid out with a distance of 10 m between traps and 25 m between replicate blocks. Traps were set on 6 June 2003 and removed two weeks later (n = 20). At the Topley site, an identical layout was used, although with 10 replicates and sampling was conducted over a 4 wk period between 25 June and 23 July 2004 (n = 40).

We identified ants collected from the pitfall traps in the laboratory (see "Ant Identifications and Nomenclature" below for details). Following identification, each ant was measured for alitrunk length (in lateral view) and maximum head width (in dorsal view) to the nearest 0.1 mm using a calibrated 10X ocular scale on a dissecting microscope (model Nikon SMZ-2B). Alitrunk lengths and head widths derived from all individuals, of any given species in any one pitfall trap, were averaged, to reduce the risk that a few traps might skew the data due to oversampling a large number of worker ants on a foraging trail.

We tested the data for homogeneity of variance using the Levene's test in STATA (Proc robvar) (STATA 9.2 ©1985-2007). Following this step, traps were compared for size bias in captures and differences in species richness by fixed-effects multiway ANOVA. Model variables included the trap type (Nordlander or Laurent), cover (with or without), interaction between trap type and cover, and replicate. Each site was tested independently. Catches in traps at the Topley site were collected twice, but were added together (pooled) for each individual trap for the analysis.

Relative abundance and the spatial distribution of **Formica obscuripes** *ants*

We examined the distribution of western thatching ant workers (*F. obscuripes*) in the immediate vicinity of their nest by sampling with Nordlander pitfall traps (NNC configuration, Figure 2.1). Five *F. obscuripes* nests, matched for approximate size and activity, were located on Becher's Prairie (51°58.2'N, 122°29.4'W, approximately 930 masl). Becher's Prairie is a cattle-grazed grassland within the interior Douglas-fir biogeoclimatic zone and very dry-mild subzone (Meidinger and Pojar 1991) approximately 50 km west of Williams Lake, BC. We surveyed the area around each nest to ensure that no other nests of the same species were within 100 m. Selected nests were separated by distances ranging from 162-788 m (average 448 m). Nordlander pitfall traps were placed each 10 m within a Cartesian coordinate 40×40-m grid centred on the nest such that there were 24 traps in total (no trap was placed directly on the nest in the center of the grid). These were set on 9-10 August 2002, and remained open for 14 days. Ants captured by the pitfall traps were identified in the laboratory (see "Ant Identifications and Nomenclature" below for details).

The total abundance of individual *F. obscuripes* captured was plotted spatially around the nest to qualitatively assess the pattern of distribution. The patterns arising from individual captures were visually assessed to determine if they were precise between nests. The range in captures for pitfalls equidistant to the nest was tabulated and examined for consistency.

Relative and absolute abundance estimates of ant community structure

We compared the relative abundance estimates of ant community structure derived from Nordlander pitfall trap (NNC design, see above) sampling to absolute abundance estimates derived from hand sampling for ant colonies in a structurally simple grassland ecosystem. Sampling was performed at Becher's Prairie (see above for details). We laid out five Cartesian coordinate 12×12-m plots along a transect within homogeneous grassland devoid of trees, with 50 m separating each plot. Pitfall traps were spaced 2 m apart within the 12×12-m grids, with no trap closer than 2 m to the edge of the grid, for a total of 25 traps. Pitfall traps were set on 7-8 August 2002, and remained for two weeks.

Following pitfall trap removal, we intensively hand-sampled the 12x12-m grid for ants by lifting rocks and loosening vegetation. When ants were located, the number was recorded as one of three classes (Few: 1 - 5; Several > 5; or Colony), and their position within the grid were recorded. Only ant species for which a colony identification was possible (i.e., ant species which have colonies that may have multiple entrances spread across some area were excluded because of the difficulty in identifying a single colony) and only identifications of colonies (i.e., where ant numbers were recorded as a 'colony' as opposed to 'few' or 'several') were included in the data analysis. For example, *Formica subpolita* Mayr, was frequently encountered during hand sampling but as this species may have deep nests with several access points within the grid, making identification of the number of colonies uncertain, they were not included in the data analysis. This was the only species recorded in this study that needed to be excluded. Counts were restricted to colonies because counts of individual ants can be highly variable depending upon weather (personal observation). Further, as the colony is conceptually the unit of organization, following the superorganism concept (Hölldobler and Wilson 1990), for this taxon, it is a more appropriate metric for assessing ant density.

We assessed the relative proportions of each ant species both by simple presence or absence in pitfall traps and by the total number of individual ants of a given species in all traps in each plot. In the former, if 11 out of 25 pitfall traps contained a given species, that species was initially recorded as 0.44, which was then adjusted as a percentage of the total ant fauna for that plot. In the latter, the total number of individuals of a given species in all pitfall traps in each plot were tallied and then expressed as a percentage of the total ant fauna for that plot. Absolute abundances were assessed by total counts of colonies per unit area that were then adjusted to a percentage of the total ant fauna per plot.

Data for each species were tested for homogeneity of variance using the Levene's test in STATA (Proc robvar) (STATA 9.2 ©1985-2007) then compared across the three sampling/tallying techniques by one-way ANOVA. Tests for differences between the three pairwise sampling/tallying techniques were performed using a *post-hoc* Bonferroni test (STATA 9.2 ©1985-2007) when the *F*-value was significant.

Sampling for total species richness

We sampled in three, 15-yr post-harvest sites within the sub-boreal spruce biogeoclimatic zone and moist-cold subzone, variant 2 (Meidinger and Pojar 1991) within 60 km of Houston, BC (54°24'N, 126°40.2'W) between June and August of 2004 (Appendix 1). The distances between three sampling sites varied from 25 to 78 km. The site age and time of year were chosen to coincide with maximal ant colony presence and activity based on previous research in the area. We positioned within each site, a 1-ha sampling plot, in which contact with natural or anthropogenic boundaries (e.g., forest edges, streams, roads etc.) was minimized. The 1-ha plot was laid out in a Cartesian coordinate 25x25-m grid to facilitate the location of randomly chosen sampling sites.

We set Nordlander pitfall traps (NNC configuration, see above) along four transects, each comprised of five traps, each separated by 20 m, for a total of 20 pitfall traps. Transect initiation points and azimuths were randomly determined, but were not allowed to overlap. Traps were operated for two non-consecutive two wk periods between late June and early July and then late July and early August of 2004 (Appendix 2.1).

Mini-Winkler litter extraction bags (Marizete Pereira dos Santos, Bahia-Brasil, CEP 45 660 000, Brazil) consisted of an inner nylon mesh bag capable of holding approximately 2 L of sample with 4-mm openings. This mesh bag was suspended on a metal frame entirely within a larger cotton enclosure, closed at the top, which funneled into a lower collection cup filled with approximately 80 ml of a 25% propylene glycol solution.

We collected litter samples from 0.5-m^2 sampling areas at randomly chosen locations within the 1-ha plots. Ten samples were taken twice from each 1-ha plot between late June and August of 2004 with at least two wks between subsequent sampling (Appendix 2.1). We laid out a 0.5-m^2 frame at the randomly chosen sampling location, and surface material was scraped into the centre of the frame. Any twigs or clumps of earth were broken-up by hand and then filtered through a 1-cm^2 wire mesh within a sifting bag. Only material that passed through the sifting screen was used for the sample, which was then placed into a plastic bag and transported to the Houston Forest Products mill, Houston, BC. The sample was then added to the mini-Winkler bags and hung for approximately 48 h in a shed where they were protected from rain and wind.

We assessed the efficacy of each sampling technique in estimating species richness by generating the Mao Tau expected species accumulation curves (Colwell 2006) for the samples, by a fitted logarithmic model (Soberón and Llorente 1993) and by the non-parametric incidence based estimator Chao2 (Walthur and Martin 2001; Colwell 2006). As sample size varied with technique (pitfall trapping, n = 120; mini-Winkler soil extractions, n

= 60) due to other project objectives, each estimation for the pitfall traps was derived from 60 randomly drawn samples from the total dataset to match the mini-Winkler sample size. We derived the expected species accumulation curve (i.e., the expected total species richness for any given sub-sampling effort within the full sampling protocol) using the rarified Mao Tau combinatorial algorithm (Mao et al. 2005) in EstimateS (Colwell 2006). This was then fitted to a non-asymptotic logarithmic function (see below) using SigmaPlot Version 9.0 (Systat Software Inc., San Jose, California, U.S.A.) to allow for extrapolation of the expected species accumulation dataset. Following Soberón and Llorente (1993), the logarithmic function $S(x) = 1/z \, ln(1 + zax)$ was used to fit data, where x is the number of samples (pitfall traps or mini-Winkler litter extractions), $S(x)$ is the number of species accumulated at a given x (Note: Soberon and Llorente (1993) described this equation as a function of sampling effort, specifically in units of time, here we use sample number as the unit of effort), and z and a are curve fitting parameters that control the rate of species accumulation (z is inversely proportional to accumulation while a is directly proportional to species accumulation). This model was then used to predict the number of samples required to add new species to the species list. In addition, the total species richness, as opposed to the observed species richness, was estimated by the incidence based estimator, Chao2, using EstimateS (Colwell 2006).

Ant identifications and nomenclature

We followed ant species nomenclature as revised by Bolton et al. (2006) except where more recent revisions have been made. We identified ants to species using the keys of Wheeler and Wheeler (1963), Francoeur (1973), Wheeler and Wheeler (1986), Naumann et al. (1999), and Hansen and Klotz (2005). Ants of the genus *Myrmica* were identified using an unpublished key provided by A. Francoeur[1].

Results

Pitfall trap efficacy

Fifteen species of ants from seven genera were identified across all trap types at Knife Creek (Table 2.1). The greatest number of species collected was in the genus *Formica* with seven species in total. *Formica aserva* Forel (Formicidae: Formicinae) was the most commonly trapped species. On average, 3.5 species were recovered per trap (Table 2.2) and a total of 170 ants were collected in all traps over the single 2-wk sampling period. Eleven species of ants in four genera were identified in all trap types at the Topley site (Table 2.3). Again, the genus *Formica* was the most common, with six species, but *Myrmica alaskensis* Wheeler (Formicidae: Myrmicinae) was the most commonly collected ant species. A mean of 2.5 species were collected per trap (Table 2.2) across trap types, and a total of 516 ants were collected over the 4-wk sampling period.

There were no significant differences among treatments (Nordlander with cover (NWC);Nordlander with no cover (NNC); Laurent with cover (LWC); Laurent with no cover (LNC)) at the Knife Creek site for captures of species per trap ($F = 2.09$; df = 7,16; $P = 0.14$). At the Topley site, both model factors (i.e., trap type (Nordlander or Laurent), and cover (with or without)), showed statistically significant differences in species richness, but there was also a significant interaction between trap type and cover ($F = 5.27$; df = 1,38; $P = 0.003$). This interaction was due to a reduction in catch by the Nordlander trap from a mean

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Table 2.1. Ant species captured by each of four pitfall trap designs at Knife Creek, British Columbia. The four pitfall designs were laid out randomly within five replicate blocks (n = 20) between 6 to 20 June 2003. Presence is indicated by ★.

Species	Nordlander		Laurent	
	with no cover (NNC)	with cover (NWC)	with no cover (LNC)	with cover (LWC)
Aphaenogaster occidentalis	★		★	★
Camponotus modoc		★	★	
Camponotus unk 1	★	★	★	★
Formica argentea	★	★		
Formica aserva	★	★	★	★
Formica fusca		★	★	★
Formica neorufibarbis	★	★	★	
Formica oreas	★			
Formica podzolica	★	★	★	★
Formica unk 1				★
Lasius pallitarsis	★	★		
Leptothorax muscorum	★		★	★
Myrmica alaskensis		★	★	
Myrmica fracticornis	★	★	★	★
Tapinoma sessile	★			
Total species richness	11	10	10	8

Table 2.2: Mean number of ant species collected (±SE) in each of four trap combinations in two test locations, Knife Creek and Topley, British Columbia. Knife Creek traps were laid out on 6 June, 2003 and collected on 20 June. Topley traps were laid out on 25 June 2004 and sampled on 9 and 23 July. Number of sample traps = n. Variance in the number of sample traps arises from animal disturbance or unrelocated traps.

			Knife Creek		Topley	
Trap design	Cover	Trap code	n	Mean number of species per trap (±SE)	n	Mean number of species per trap (±SE)
Laurent	Yes	LWC	4	2.7 (0.85)	10	2.8 (0.28)
Laurent	No	LNC	5	3.8 (0.2)	9	2.8 (0.35)
Nordlander	Yes	NWC	3	3.2 (0.85)	10	1.6 (0.21)
Nordlander	No	NNC	4	4.0 (0.08)	10	2.8 (0.33)
All traps			16	3.5 (0.36)	39	2.5 (0.17)

Table 2.3. Ant species captured by each of four pitfall trap designs near Topley, British Columbia. The four pitfall designs were laid out randomly within ten replicate blocks which were sampled twice. Traps were put in place on 25 June and sampled on 9 and 23 July 2004. Presence indicated by ★.

Species number	Nordlander		Laurent	
	with no cover (NNC)	with cover (NWC)	With no cover (LNC)	with cover (LWC)
Camponotus herculeanus	★	★	★	★
Formica accreta	★	★	★	★
Formica argentea	★		★	★
Formica aserva	★	★	★	★
Formica fusca	★		★	
Formica hewitti			★	★
Formica neorufibarbis	★	★	★	★
Leptothorax muscorum		★	★	★
Myrmica alaskensis	★	★	★	★
Myrmica fracticornis	★	★		★
Myrmica incompleta	★		★	★
Total Species Richness	9	7	10	10

of 2.8 species to 1.6 species when combined with a cover. The cover had no effect on the Laurent trap captures. (Table 2.2).

Head width and alitrunk length correlated strongly ($r > 0.9$ in both locations) so only one was used to assess trap type size bias. As head width has been shown to be a poor indicator of overall ant mass (Kaspari and Weiser 1999), alitrunk length was used in the analysis. Multiway ANOVA indicated no significant differences at the Knife Creek site for alitrunk length between trap types ($F = 0.84$; df = 1,16; $P = 0.382$), cover ($F = 0.01$; df = 1,16; $P = 0.915$), or for trap type and cover interaction ($F = 0.05$; df = 1,16; $P = 0.826$). This was also true for the Topley site ((trap types: $F = 0.75$; df = 1,16; $P = 0.395$), (cover: $F = 0.08$; df = 1,16; $P = 0.784$), (trap type and cover interaction: $F = 1.45$; df = 1,16; $P = 0.239$)).

Relative abundance and the spatial distribution of **Formica obscuripes** *ants*

The distribution of *Formica obscuripes* individuals in the immediate vicinity of their nests was unique to each nest and highly patchy (Figure 2.2). Areas of most concentrated captures differed for each nest. Most of the nests included large areas within the 40x40-m grid in which no *F. obscuripes* ants were captured despite a relatively close proximity of the traps to the nest. In particular, Nest 2 (Figure 2.2) collected only a single *F. obscuripes* ant in all grid pitfall traps despite the nest being normally active. Pitfall traps 10 m apart varied greatly in the number of individuals captured. In one case, one trap collected 120 ants while an adjacent trap, 10 m away, collected only 13 (Figure 2.2, Nest 3). In another instance, one trap collected 39 ants while the adjacent pitfall 10m away collected none (Figure 2.2, Nest 1). The maximum range in captures across the 24 pitfall traps at each nest overall was: Nest 1, 39; Nest 2, 1; Nest 3, 120; Nest 4, 24; Nest 5, 89.

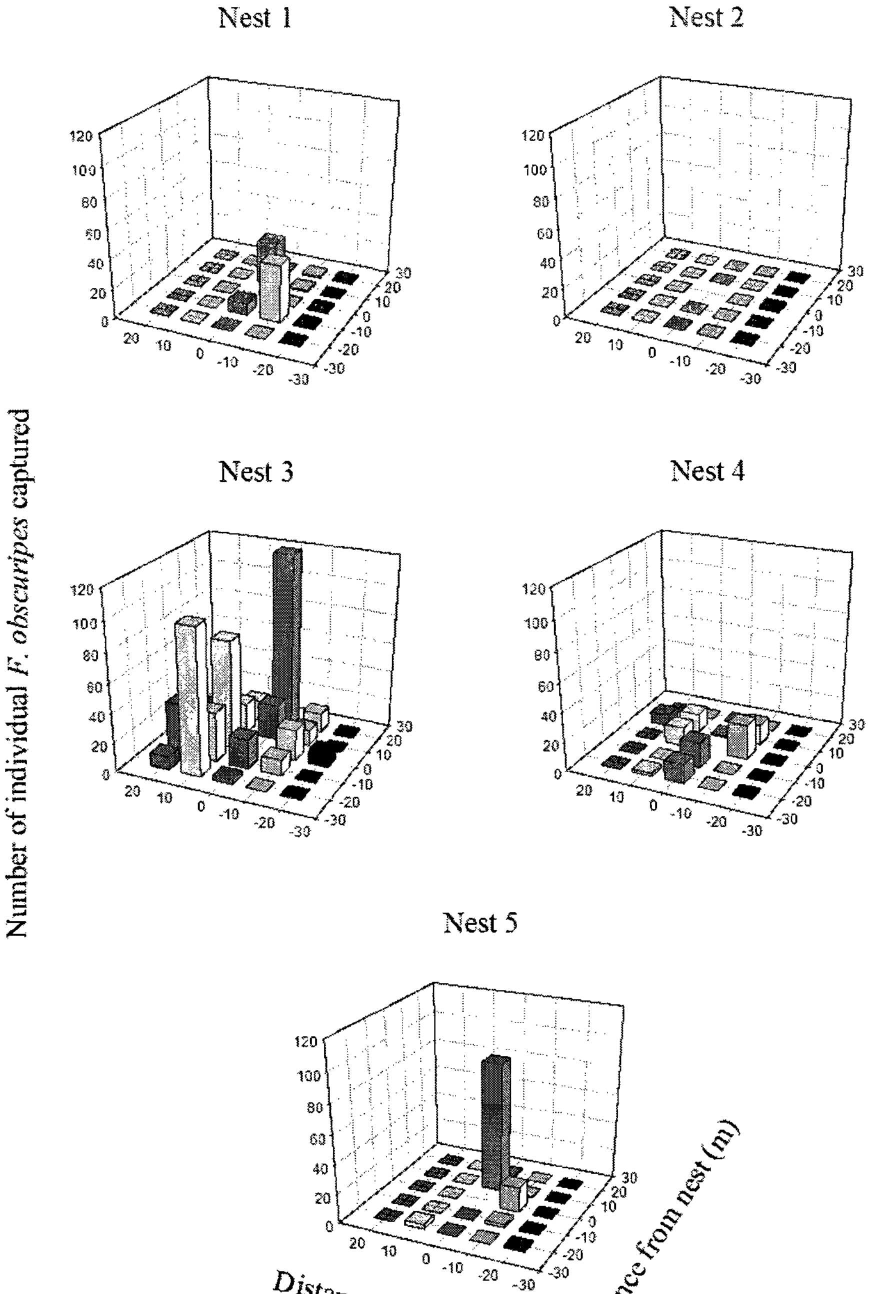

Figure 2.2. Three-dimensional column plots of the distribution of captured individual *Formica obscuripes* ants in Nordlander pitfall traps around 5 established nests at Becher's Prairie, a grassland ecosystem, in 2003. Nordlander pitfall traps were laid out each 10 m within a Cartesian 40x40-m grid for 14 days. Nest at position 0,0. Differing shade tones are used for visual contrast and do not represent any differences in the manipulated variable.

Relative and absolute abundance estimates of ant community structure

Six species of ants, *Tapinoma sessile* (Say) (Formicidae: Dolichodinerae); *Lasius crypticus* Wilson, *Formica obscuripes* Forel, *Formica subpolita* Mayr (Formicidae: Formicinae), *Leptothorax muscorum* (Nylander), and *Myrmica crassirugis* Francoeur (Formicidae: Myrmicinae) were identified from the five 12x12 m plots laid out in this study. All 6 species were identified from both pitfall trap sampling and hand-sampling. Of these, *F. subpolita*, which appears to excavate nests into the soil with multiple access locations, was excluded from the final analysis because of the difficulty in confirming the number of individual colonies.

The abundance determination of species within the ant community varied with both the sampling and analytical technique used to count ants and species (Figure 2.3). The most common ant collected in Nordlander pitfall traps (relative abundance), either assessed as simple presence/absence per trap per plot or in total individuals in all traps per plot, was *Tapinoma sessile*. The most common ant species identified by hand-sampling (absolute abundance) was *Lasius crypticus*. The least common species, by all methodologies, was *Leptothorax muscorum*. No colonies of *F. obscuripes* were identified during hand sampling of the plots, but this species did turn up in traps in two of the plots that were approximately 130 and 100 m from the nearest identified *F. obscuripes* nest, respectively.

Comparison of hand sampling (absolute abundance) to presence/absence per trap and total individuals in all traps (relative abundance) per plot by one-way ANOVA indicated a species-specific relationship. There were no significant differences between absolute or relative abundances for *F. obscuripes* ($F = 0.89$; df = 2, 12; $P = 0.49$), *L. muscorum* ($F = 1.21$; df = 2, 12; $P = 0.33$) or *T. sessile* ($F = 1.47$; df = 2, 12; $P = 0.27$). Hand sampling

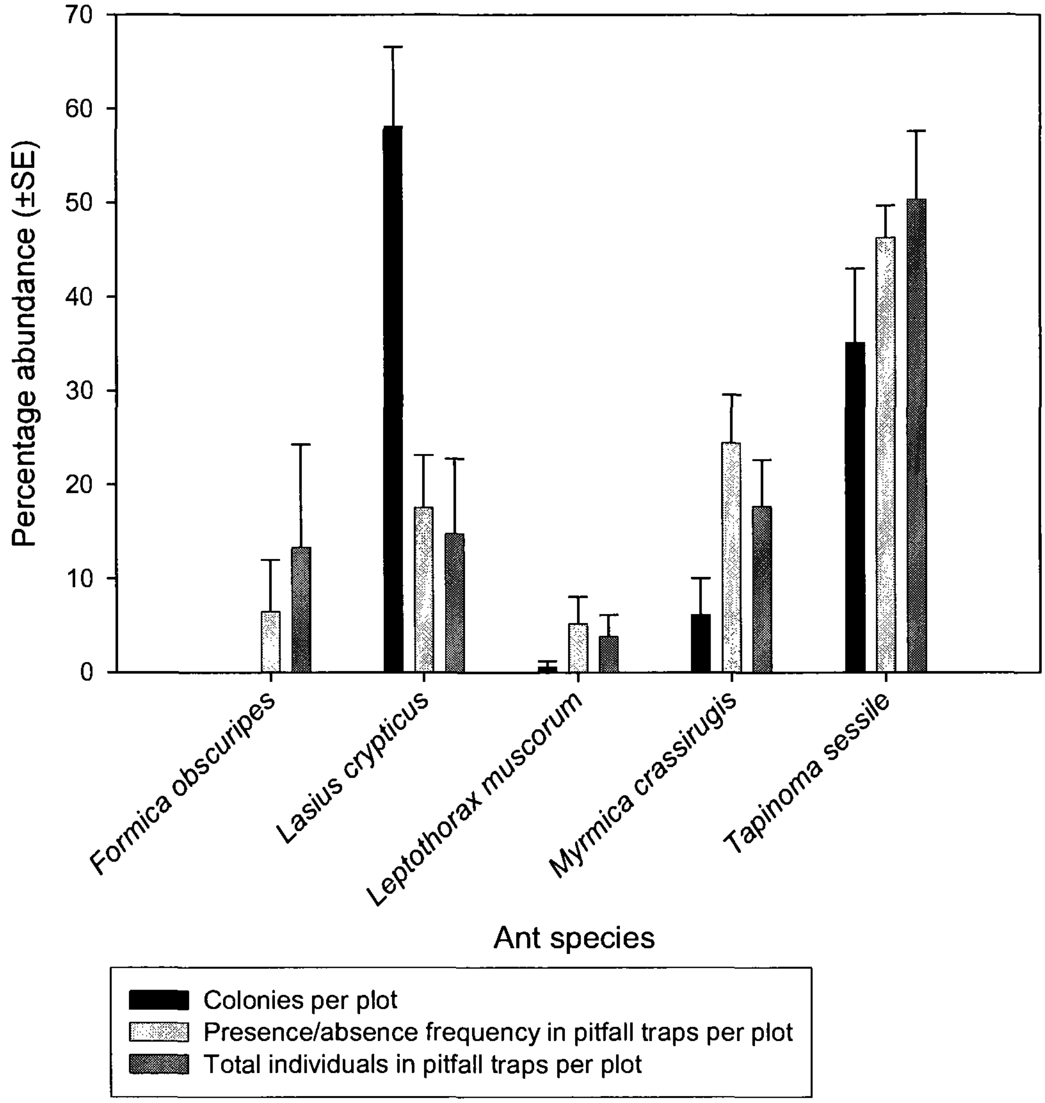

Figure 2.3. Apparent community structure, expressed as percentage abundance, of 5 species of ants at Becher's prairie, a grassland ecosystem, derived from relative and absolute abundance sampling of five 12x12 m plots in 2003. Relative abundance estimates (presence/absence frequency and total individuals per plot) were made using Nordlander pitfall traps which were laid out in a Cartesian grid each 2 m within each plot. Pitfall traps operated over a period of 2 wks. Absolute abundance estimates (colonies per plot) determined by hand sampling of the plots.

(absolute abundance), for *L. crypticus*, resulted in an abundance of just under 60% of the total assessed fauna, while pitfall trapping, by either simple presence/absence tallies or total individuals, indicated a relative abundance of under 20%. For this species, ANOVA across the three sampling/tallying techniques did indicate a significant difference ($F = 10.61$; df = 2, 12; $P = 0.002$). Absolute and relative abundances were significantly different in all three pairwise comparisons. Both comparing hand-sampling for *L. crypticus* to tallies of presence/absence from pitfall traps ($P = 0.007$) as well as comparing hand-sampling to tallying the total number of individuals of this species collected by pitfall traps in each plot ($P = 0.003$) indicated significant differences. Analysis of *Myrmica crassirugis* across the 3 sampling/tallying types also indicated a significant difference between groups ($F = 3.98$; df = 2,12; $P = 0.05$). Hand-sampling (absolute abundance) and tallies of presence/absence in pitfall traps (relative abundance) ($P = 0.05$) were shown to be significantly different by *post-hoc* Bonferroni analysis. Here the absolute community composition for *M. crassirugis* was approximately 6.2% as compared to an estimate of 24.5% derived from tallying presence/absence from pitfall traps. No significant difference was noted between hand-sampling and total individuals in all traps per plot ($P = 0.34$).

Sampling for total ant species richness

Nordlander pitfall trap sampling yielded the greatest number of species as estimated within the collected samples (Mao Tau), as well as total estimated species (Chao2) when compared to mini-Winkler soil-litter sampling (Figure 2.4). An estimate of 10.3 species (95% CI: 9.8, 10.8) from 60 Nordlander pitfall samples, as compared to 9.5 species (95% CI: 8.5, 10.1) for equivalent sampling with mini-Winklers (Table 2.4), indicating a small but significant difference, was derived from the logarithmic function modelled to the expected

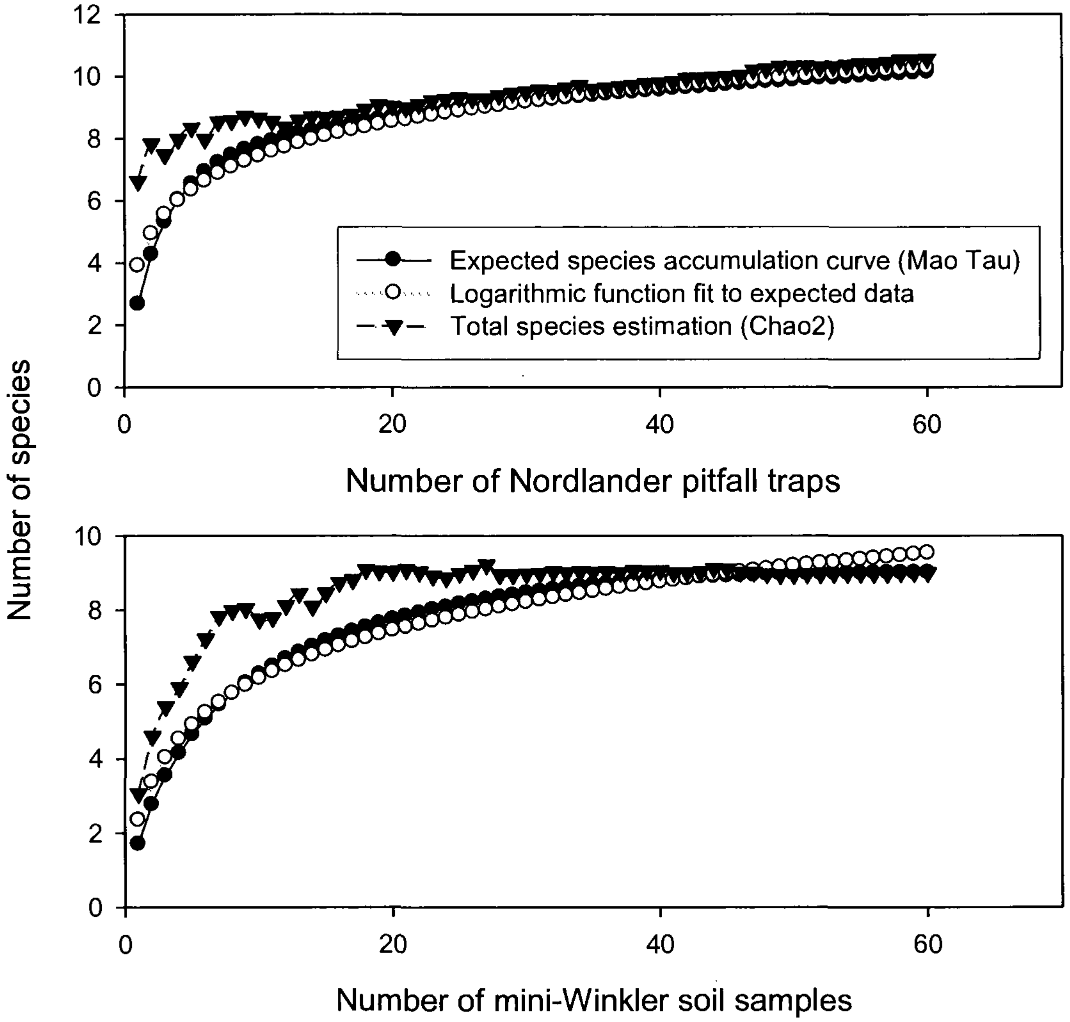

Figure 2.4. Expected species accumulation curve (Mao Tau), fitted logarithmic function ($S(x) = \frac{1}{z} ln(1 + zax)$) to the expected species accumulation curve, and incidence based estimator (Chao2) approximation of total ant species richness derived from 60 Nordlander pitfall traps and 60 mini-Winkler litter samples collected in 2004. Sampling was performed in three, 15-yr post-harvest pine forest plots (sub-boreal spruce biogeoclimatic zone, moist cold sub-zone, variant 2 (Meidinger and Pojar 1991)). Mao Tau curve and Chao2 data calculated using Estimate S (Colwell 2006) while the logarithmic function follows Soberón and Llorente (1993).

Table 2.4. Logarithmic parameters ($S(x) = 1/z * ln(1 + zax)$), statistical fit, and extrapolation of an observed mean species accumulation curve (Mao Tau, Estimate S) derived from Nordlander pitfall trap samples and mini-Winkler litter extraction samples (n = 60). Samples collected within 60 km of Houston, BC, between June and August 2004.

	Parameter	Estimate	SE	*t* statistic	*P* value
Nordlander pitfall trap[1]	z	0.6284	0.0153	41.057	<0.0001
	a	16.8924	1.9076	8.8554	<0.0001
Mini-Winkler litter extractor[2]	z	0.5227	0.0143	36.6645	<0.0001
	a	4.5953	0.4105	11.1934	<0.0001

[1] $R^2 = 0.9712$; Adjusted $R^2 = 0.9707$; Std Error Estimate = 0.2477; Estimated number of species at 60 samples = 10.27; Estimated number of additional samples, beyond 60, necessary to add one additional species = 53

[2] $R^2 = 0.9727$; Adjusted $R^2 = 0.9722$; Std Error Estimate = 0.2814; Estimated number of species at 60 samples = 9.52; Estimated number of additional samples, beyond 60, necessary to add one additional species = 42

species accumulation curve. Following the logarithmic function, it is estimated that an additional 53 Nordlander pitfall samples would be necessary to add one more species while mini-Winkler soil-litter sampling would require 42 more samples. Total species richness derived from 60 Nordlander pitfall samples was estimated at 10.55 ± 0.15 (SE) species as compared to 9.0 ± 0.001 (SE) species for mini-Winkler soil-litter sampling, by the Chao2 estimator.

Discussion

Pitfall trap efficacy

Pitfall traps were first described in the literature by Laurent (1917). They are especially popular with entomologists working with epigaeic invertebrates because they are inexpensive, easy to install, and sample 24 hrs a day (Agosti et al. 2000; Schlick-Steiner et al. 2006). A great number of design variations have been reported on in the literature, assessing, for example, the effects of variations in trap diameter (Abenspergtraun and Steven 1995; Work et al. 2002; Borgelt and New 2005), collecting fluid (Greenslade and Greenslade 1971; Lemieux and Lindgren 1999; Koivula et al. 2003), lids (Phillips and Cobb 2005), and surrounding habitat structure (Koivula et al. 2003; Phillips and Cobb 2005). In addition, modifications to improve how pitfall samples are collected (Vogt and Harsh 2003) and to eliminate the problems of rainfall flooding (Porter 2005) have been examined. Several general reviews attempt to summarize the complex literature on this simple technique (Greenslade 1973; Adis 1979; Spence and Niemelä 1994; Woodcock 2005), much of which is in turn reviewed in the specific context of ants for the ALL Protocol (Bestelmeyer et al. 2000).

Largely ignored in the literature, however, is the problem of vertebrate bycatch. Traditional open pitfall traps, here called Laurent traps following Laurent (1917), can easily trap small vertebrates. The Nordlander pitfall trap (Nordlander 1987; Lemieux and Lindgren 1999; Pearce et al. 2005) may provide a solution to this problem. As designed for this study, the only access is through the 6-mm holes, which should be large enough for all ants but too small to allow for vertebrate bycatch.

No vertebrates were captured in any of the trap designs utilized at either of the two sites used in this study, so the relative performance of the two trap designs could not be directly assessed. Other studies have shown considerable benefits of the Nordlander design in this regard, however. Although vertebrate bycatch using the Nordlander design has been reported (Lemieux and Lindgren 1999; Pearce et al. 2005), two points are relevant. First, the entrance holes in both of these studies were 13 mm in diameter because of interest in capturing large carabid beetles, as contrasted with 6-mm in this experiment, intended for the capture of ants. Second, both papers reported a reduction in vertebrate captures as compared to the Laurent design (Note: the Laurent trap was called a Barber trap by Lemieux and Lindgren (1999)). Lemieux and Lindgren (1999) report that only a single vertebrate was captured in the Nordlander design, as compared to 13 in the Laurent design. Pearce et al. (2005) reported that only 5% of total vertebrate captures occurred in the Nordlander design when compared to Laurent and funnel style pitfall traps. Thus, the literature establishes an advantage to the Nordlander in this regard, and it is likely, although not established here that the smaller openings used in our study would be even more efficacious. The lack of vertebrate bycatch recorded for the Laurent pitfall traps of our study confound any certain conclusions here, however. It is likely that the smaller cup sizes used in our study as compared other work (Lemieux and Lindgren 1999; Pearce et al. 2005) contributed to the reduction in vertebrate bycatch. Additional and extensive use of the Nordlander design in the other experiments detailed in this dissertation were also free of vertebrate bycatch. As vertebrate bycatch is a concern for institutional ethics committees in Canada operating under the guidelines established by the Canadian Council on Animal Care (CCAC 2005), the Nordlander pitfall trap is advantageous. Further, given the spoiling of trap contents by dead vertebrates, their elimination reduces sample loss.

We found that the Nordlander design was no more difficult to install in the field than conventional pitfall traps, although Pearce et al. (2005) reported difficulty with this design. The Laurent design normally includes a physically separate cover fashioned from various materials (e.g., wood, metal, plastic etc.) to protect the trap from flooding during rainfall and reduce evaporation of the trapping fluid. As this cover is an additional component that may affect trap captures because of potential behavioural biases (positive and negative) for some insects to move under a cover, this feature was also studied in combination with the Nordlander trap.

An interaction between pitfall trap design (Nordlander or Laurent) and the presence or absence of a cover, did show a significant effect on the number of species sampled at the Topley site. Both trap design and cover combined such that the Nordlander trap with cover sampled the least species as compared to all others (Table 2.2). In practice, however, the Nordlander is used without a cover. This latter design combination was equally efficacious (Table 2.2) as the Laurent with cover thus reducing concerns about trap efficacy.

The results at the Knife Creek site indicated no significant differences between factors. This may be a result of the fewer replicates installed (5 vs 10) and shorter sample period (2 vs 4 wk) at the Knife Creek site as compared to the Topley site, respectively. This, however, also failed to indicate a problem associated with the sampling efficacy of the Nordlander without cover. Further, despite the significant effect found at the Topley site for species richness, no effect was noted for ant size (alitrunk length), suggesting that trap designs did not differ with respect to their size bias. This was an initial, and fortunately unfounded, concern given the possibility that a large ant might perceive a 6-mm hole as constricting and therefore avoid an interaction.

The Nordlander trap has several other advantages. First, there is no need to carry large covers into the field. Second, the small holes act to reduce the amount of debris blown into the trap, reducing the need to clean samples prior to specimen processing and decreasing the risk of captured invertebrates escaping the trap by crawling up debris (e.g., twigs). Third, with a small amount of moss or soil placed on the lid, the traps are inconspicuous, reducing interference by curious vertebrates. Fourth, if the traps are pulled out of the ground by a curious vertebrate, the solution is not directly accessible for ingestion through the open top characteristic of the Laurent design and will spill out through the holes reducing the risk of poisoning. Finally, these traps are no more expensive than any other pitfall cup design and the holes can be added quickly in the lab or field with a standard 6-mm hole paper-punch. Overall, we therefore recommend the Nordlander pitfall trap design (NNC) for ecological studies that involve sampling of epigaeic ants.

Relative abundance and the spatial distribution of **Formica obscuripes** *ants*

The data derived from the trapping of epigaeic invertebrates is normally considered suitable for determination of relative abundance information (Southwood and Henderson 2000). These data may be calculated from tallies of total individuals or from simple presence-absence (incidence) observations. It is common in the myrmecological literature for tallies of total individuals captured to be used to derive relative abundance data (Savolainen and Vepsäläinen 1989; Bestelmeyer et al. 2000; Parr and Chown 2001; Wang et al. 2001b; Schowalter et al. 2003; Borgelt and New 2005; Dunn et al. 2007). The natural history of ant species and the manner in which they are distributed in the environment, however, should make myrmecologists wary of this approach.

Ants are social insects that usually create permanent to semi-permanent nests from which they forage. Foraging often results in the identification of resource rich patches (e.g., honeydew producing aphids) to which the colony recruits a great number of workers, often along well established trunk trails reinforced by pheromones (Sanders 1972; Hölldobler and Wilson 1990; McIver and Yandell 1998). This is especially the case for ant species that have large foraging territories (e.g., thatching ants (McIver and Yandell 1998) or carpenter ants (Sanders 1972)), in which the distances required to reach resource-rich patches necessitate efficient travel. It would be expected that pitfall traps placed in close proximity or directly upon such a trail may accumulate a great number of individual ants, while an identical trap just a short distance away may sample few. Further, the capture of large numbers of individuals may not be indicative of suitable resources in the immediate vicinity (few metres or tens of metres) of the pitfall trap as these individuals may simply be travelling through to a distant resource. As noted previously in this study (Results: *Relative and absolute abundance estimates of ant community structure)* thatching ants, *Formica obscuripes*, were captured 100 and 130 m from the nearest identified nest.

The patchy distribution of *F. obscuripes* around the five nests studied here suggest that the movement of workers is unique to each nest (Figure 2.2) as would be expected for an ant focusing on the specific resources available within its foraging territory. In a Finnish study, (Savolainen and Vepsäläinen 1989), two pitfall traps placed 5 m apart captured 30 and 1813 individuals of the boreal ant, *Formica polyctena* Foerster, at a distance of 10 m from their nest, and 9 and 564 individuals at a distance of 60 m. This is consistent with the distribution in our study of *F. obscuripes*, which is ecologically similar to *F. polyctena* (Figure 2.2). In one instance, one pitfall trap collected 13 ants, as compared to 120 individuals in another pitfall trap just 10 m distant (Figure 2.2, Nest 3). Traps surrounding one active colony (Figure 2.2, Nest 2) yielded only a single individual throughout the entire 40x40 m grid sampled by 24 pitfall traps. The likely explanation is that this colony had well established trunk trails leading out of the study grid and that the pitfall traps had not intercepted any of these.

Some authors have attempted to resolve the problem of highly variable captures of individuals by mathematically transforming the abundance capture data. Attempts to reduce the problem of oversampling individuals in single pitfall traps have been made by using a square root transformation of the total individuals captured (Vanderwoude et al. 1997; Hamburg et al. 2004). Another approach was to use a natural logarithm transformation for the same purpose (Bestelmeyer 2000). Other solutions reported in the literature include taking the number of individuals of a given species in a pitfall trap and dividing them by the total number of individuals of all species in the same trap to determine a proportional occurrence per pitfall trap or by adjusting the raw abundance of individuals by multiplying them by the frequency of occurrence (Lindsey and Skinner 2001; Wang et al. 2001a). Although such transformations would reduce the extent of the problem, no biological rationale is provided to validate the specific transformations used.

Other authors, however, prefer to use frequency of occurrence data exclusively (Romero and Jaffe 1989; Osborn et al. 1999; Andersen et al. 2002; Martelli et al. 2004), where each species is tallied only as present or absent in each pitfall trap. This is a more cautious approach to interpreting pitfall trap data that gives consideration to the natural history of ants. It is supported by the distribution of *F. obscuripes* reported here. As such, it is adopted as the standard approach to quantifying ant communities in this dissertation where relative abundance data is used.

Relative and absolute abundance estimates of ant community structure

Absolute abundances are defined as population counts that arise from sampling a landscape or specific habitat per unit area or volume while relative abundances refer to sampling data that cannot be translated into taxon density estimates (Southwood and Henderson 2000). Ideally, ecological samples will allow for estimates of absolute abundance that, in turn, can be used to assess population densities and parameters such as biomass or life history tables (Schlick-Steiner et al. 2006). Unfortunately, this normally requires unit area or habitat area searches that often provide little data for large effort (Southwood and Henderson 2000). In the case of small invertebrates such as ants, only small areas can be effectively sampled in such a quantitative manner because of difficulties in locating nests, especially small cryptic nests (Anderson 1997) unless the nesting characteristics allow for focused searching (e.g., species that nest in woody debris). As a consequence, sampling techniques are designed to concentrate on the taxon of interest such that relative abundances are derived that allow for comparisons of communities in space or time (Southwood and Henderson 2000). The issue that needs to be identified, however, is the relationship between the apparent community structure derived from relative abundance sampling and the less biased, at least in the context of ant colonies, estimates of absolute community structure.

As pitfall traps are passive, they are activity-abundance biased, generating relative abundance data skewed in this direction (Lang 2000). Hand sampling per unit area, however, provides abundance estimates that can be used to assess the absolute community composition. In the case of ants, counts of ant colonies represent the most appropriate metric for assessing presence or absence given the theoretical consideration of the ant colony as a superorganism (Hölldobler and Wilson 2009) and the observation that the apparent abundance of foraging ants varies greatly with weather, time of day and season. In this study, we chose a grassland ecosystem to compare the apparent community structure arising from these two sampling methodologies as this structurally simple ecosystem allows for accurate hand sampling of small areas.

Most notable was the observation that of the 6 species encountered, *Lasius crypticus* was the most common ant colony in the context of absolute abundance, but was much less common when considered in the context of relative abundance (i.e., pitfall traps) (Figure 2.3). This is likely because this species is reported to normally tend root aphids or mealybugs for honeydew (Wheeler and Wheeler 1963; Wheeler and Wheeler 1986) and is likely less epigaeic than other species. *Tapinoma sessile* (see Appendix III for comments on natural history) was the most relatively abundant species as determined from pitfall trapping, but less in absolute abundance (Figure 2.3), although not significantly. This species is an active epigaeic forager that recruits quickly to food resources, a characteristic that makes them a common and efficient house pest (Wheeler and Wheeler 1963). As pitfall traps are biased toward this behaviour, the high capture rates are to be expected. In addition, the absolute abundance of *Myrmica crassirugis* also differed significantly from relative abundance as determined through tallying pitfall captures by presence-absence (Figure 2.3). Finally, it is notable that the absolute abundance of *Formica obscuripes* was zero despite these ants being recovered in pitfall traps. In our study area, *F. obscuripes* nests were spatially scattered at distances frequently greater than 100 m and were unlikely to be included in the small plots used for this study. This observation, however, illustrates a basic limitation of absolute abundance sampling in that intensive hand sampling is necessarily limited spatially and will miss large ant colonies that forage over large areas. *Formica obscuripes* was captured in pitfall traps in two of the plots which were 130 and 100 m from the nearest nest. In addition, one plot was just 40 m from the nearest *F. obscuripes* nest, yet no workers of this species were captured in any of the 25 pitfall traps. As noted earlier, this is indicative of the highly individualistic and patchy distribution of these ants.

Our data show great variability with respect to the concordance of relative and absolute abundance estimates by different species of ants. It follows that myrmecologists need to understand that, depending on the ant species studied, relative abundance estimates do not necessarily reflect absolute abundances and that ant communities may be structured very differently from what may be derived from pitfall trapping. Consequently, unit area sampling for ant colonies should be the preferred sampling methodology where objectives and conditions permit.

Sampling for total species richness

The need to rapidly assess the total species richness of a given taxon in a defined area is central to many ecological and conservation based studies. Although a wide variety of techniques exist, three are particularly common in the myrmecological literature. These are pitfall trapping, litter extraction (of which the mini-Winkler extractor is very common), and baiting (Bestelmeyer et al. 2000). The use of baits was found to be untenable in the low density ant communities typical in the cool-moist sub-boreal forests of west-central BC. Several attempts with this technique during the course of our study failed to attract any ants to randomly placed baits over a period of 30 min. Pitfall traps and mini-Winkler litter extractions are, however, potentially viable sampling methodologies for estimating total species richness in these forests.

Nordlander pitfall trapping was shown to be more efficacious in both actual (i.e., Mao Tau) and estimated total species richness (i.e., Chao2) although the differences were not large (1-2 species for Mao Tau and Chao2, respectively). Logarithmic modelling of the Mao Tau species accumulation curve indicated, however, that it would require only 42 additional litter samples to add one more species to the species list while it would take 53 additional Nordlander pitfall trap samples. This is likely because the logarithmic model for the mini-Winkler extractions does not appear to be as close to an asymptote as is the case for the Nordlander pitfall samples (Figure 2.4). Thus, both methodologies seem fairly similar in efficacy with respect to total species richness with a slight advantage to the Nordlander pitfall trap overall. Species collected by mini-Winkler extraction were entirely a sub-set of those collected by Nordlander pitfalls traps. It should be noted, however, that while 60 pitfall traps were randomly used in the analysis to be consistent with the 60 mini-Winkler litter samples collected, a total of 120 Nordlander pitfall traps were operated overall because of additional project objectives. The 120 Nordlander pitfall traps collected a total of 11 species as compared to 9 species in the 60 mini-Winklers.

To date, there have been no equivalent examinations of the efficacy of these sampling techniques in boreal or sub-boreal forests although the results of my study are generally consistent with the pattern reported for upland ecosystems in Florida (King and Porter 2005). The literature is not consistent in this regard, however. A study in a South African savanna reported greater species captures by pitfall traps (20 species captured per 15 pitfall trap samples with 62-mm diameter traps) as compared to mini-Winkler litter extractions (9 species captured per 15 samples with 0.5-m^2 soil samples) (Parr and Chown 2001). In contrast, others have found mini-Winkler litter extractions much more efficient at collecting species than pitfall trap sampling (Olson 1991; Fisher 1999; Martelli et al. 2004). In the tropical rainforests of eastern Madagascar one study recovered five times the number of species using mini-Winklers as compared to small pitfall traps (18-mm diameter) (Fisher 1999). In the tropical forests of Costa Rica, using similar methodologies, another study did not discover as great a disparity between methods, but did report that mini-Winklers sampled 87% of the total ant species captured as compared to 54% through pitfall traps (Olson 1991). This logically suggests that mini-Winkler soil extractions are particularly useful where a well developed litter ant fauna exists (e.g., tropical forests). In contrast, in temperate hardwood and pine forests in Tennessee it was found that litter sifting yielded 1.2-2.5 times the number of species as pitfall traps (Martelli et al. 2004). The poor performance of pitfall traps in this study may have arisen from the relatively short period (48 h) of trapping. Unfortunately, there is no standardization with respect to pitfall trap operation times which makes comparisons of alternative techniques difficult. Pitfall trap captures equal to or higher than mini-Winkler sampling have been reported, when traps were operated over 72 h (Parr and Chown 2001; King and Porter 2005). In our study, pitfall traps were operated for 2 wk following Lemieux and Lindgren (1999), who used the same trap design (albeit larger) and operated in similar habitats. This seems appropriate for a relatively low density fauna typical in cool forests.

Overall, mini-Winkler sampling appears to be more efficacious with respect to sampling species richness in tropical ecosystems where a large litter community of fairly small ant species is well established. In other ecosystems, comparisons between litter extraction and pitfall trapping may be distorted by the length of time pitfall traps are operating. Increasing the length of time pitfall traps are placed in the ground will naturally increase species captures without adding additional work for the field crew, making this technique generally more efficacious in any ecosystem lacking a well developed ant litter community.

The time required to install pitfall traps in the field was not measured in this study. Thus, a quantitative comparison with litter extraction using mini-Winkler extractors could not be made. The number of steps involved in locating randomly placed sampling plots, collecting, sifting, and then filling extraction bags and hanging samples for mini-Winklers was clearly longer than positioning a transect and installing pitfall traps. One study did assess the time associated with the collecting and sorting of mini-Winkler samples and pitfall trap samples and reported that mini-Winkler samples took approximately 1 h of field work per sample as compared to approximately 45 min of field work per sample for pitfalls (King and Porter 2005). Another study, while not providing specific time measurements, indicated that mini-Winklers took more than twice as long in the field as compared to an equivalent number of pitfall traps (Parr and Chown 2001). This would be consistent with my experience in this study. One further consideration relating to mini-Winkler litter extractions is the requirement for dry litter conditions. Ants, especially small species, will be trapped in the sample bags if the litter is wet, limiting extractions. Thus, planned field work can be disrupted by weather. It should be noted, however, that mini-Winkler extractions require only one visit to the field site, while pitfall trapping require at least two, one to install and one to collect. For sites with difficult access, this may be an important consideration.

As all sampling methodologies will show some bias in the species sampled, it may be advisable to use more than one technique in any ecological study. Ant species collected by mini-Winkler extraction were reported to be an average of 2.5 mm long as compared to 3.5 mm for pitfall trapping (Olson 1991). While this finding seems reasonable, as large bodied ants, that are typically fast moving, should be more likely to fall into pitfall traps and might in turn escape mini-Winkler sampling during the initial sifting stage, this result has not been replicated. Another study reported seeing a similar trend but noted a lack of statistical significance for this observation (Parr and Chown 2001). Ants species sizes were not measured in our study.

Of the total species richness of 11, pitfall trap samples (n = 120) contained two unique species while no unique species were found by mini-Winkler sampling (n = 60). The disparity in sample sizes should be noted, however. In addition, the relatively low species diversity typical in the cool-moist forests of west-central BC necessarily reduces the pool of species that could be unique to a given methodology. In an upland Florida ecosystem with a total species richness of 94, working with equal sample sizes, 13 unique species were recovered from mini-Winkler samples as opposed to eight in pitfall trap samples (King and Porter 2005). In a South African savanna with a total species richness of 34, no unique species were reported from mini-Winkler samples (0.5 m^2 which were equivalent to my study) while 5 unique species were recovered from 62-mm diameter pitfall trap samples (Parr and Chown 2001). In hardwood and pine forests in Tennessee with a total species richness of 23, eight unique species were reported in mini-Winkler samples as compared to two in pitfall traps (Martelli et al. 2004). Pitfall captures were found to be entirely redundant to mini-Winkler litter samples in Madagascar where total species richness was 381 (Fisher 1999). Finally, work in Costa Rica where total species richness was 135, recovered 62 unique species from mini-Winkler samples as compared to 18 from pitfall traps (Olson 1991). As pitfall traps are biased toward fast moving epigaeic invertebrates, it is not surprising that litter sampling is usually capturing more unique species, especially in tropical/sub-tropical habitats with a well developed litter fauna. In the cool forests where our study was conducted, all species of ants are more or less epigaeic.

Most studies have shown both mini-Winkler litter sampling and pitfall trapping to produce unique species, suggesting that it is ideal to use both techniques when developing species diversity lists. Where a well established litter ant community is known to exist (e.g., tropical rain forests), mini-Winkler sampling is clearly superior to pitfall trapping. However, where this is not the case, pitfall sampling is often equal or superior to mini-Winkler sampling, especially if pitfall traps are allowed to remain in the ground for an extended period. In sub-boreal forests, the relatively species-impoverished ant fauna and poorly developed litter fauna suggest that pitfall trapping may be adequate for developing a total species richness estimate.

Summary

The Nordlander pitfall trap is well suited to sampling ants, demonstrating an equal efficacy in estimating species richness with no size related bias when compared to the traditional Laurent pitfall trap. Given the association of this design with excluding vertebrate bycatch this pitfall trap configuration has been exclusively used for work in this dissertation. As ant distributions around nests have been shown to lack precision, captures of individuals (i.e., abundance information), is unreliable at the scale of individual pitfall traps. As a consequence, only incidence-based information should be derived from pitfall traps and this was the principle employed for all work presented here. Even with the constraint of deriving only incidence-based information from pitfall traps, it still must be recognized that this provides only relative abundance information, across traps, and that this may not reflect absolute abundances. As absolute abundance information has greater utility, where possible it should be collected. In the primary habitat (sub-boreal forest) examined in this dissertation, most ants are woody debris associated. This allows for efficient collection of absolute abundance information and thus, this formed the primary sampling technique used throughout this dissertation. Where pitfall traps are particularly valuable is in the estimation of total species richness. The work here demonstrated that they were slightly superior to mini-Winkler litter sampling for the same purpose. Given, however, that the literature suggests that habitat, especially litter development, can affect the relative efficacy of these two sampling techniques, any attempt to estimate total species richness in previously unstudied habitat, should employ both techniques. Overall, in this dissertation, only Nordlander pitfall traps and mini-Winkler litter extractors were utilized for the purpose of estimating total species richness, while unit area searches of woody debris were used to derive absolute abundance estimates of ant populations in the sub-boreal forests of west-central British Columbia.

Chapter 3. The ant (Hymenoptera: Formicidae) communities of sub-boreal forests of west-central British Columbia[1]

Abstract

The objective of this study was to examine the ant community structure in the sub-boreal forests of British Columbia and determine how this community structure differs in post-harvest forest stands of differing seral age. Ant communities were characterized in lodgepole pine-leading forests by hand-sampling of coarse woody debris (CWD), pitfall traps and mini-Winkler samples of forest floor litter over five seral ages. Seventeen species of ants were identified across all seral ages. Overall changes observed in the ant community were shown to relate to the "Individualistic Hypothesis" of successional theory, and are further shaped by species life history characteristics and environmental tolerances. The most common ant species found in this study were similar to the ant fauna identified in North American habitats known to be climatically marginal for ants. When compared to Fennoscandian ant communities, a common pattern of increasing ant abundance after disturbance followed by declining abundance with later seral age was noted. Two differences were apparent, however, with respect to the Fennoscandian ants. These were the greater use of CWD as a nesting substrate and the absence of soil-based thatching ants in sub-boreal forests of west-central British Columbia. The relative lack of CWD may be a factor explaining the paucity of CWD nesting ants in Fennoscandian forests while the higher soil moisture in the sub-boreal forests of BC may be an important factor in explaining the absence of soil-nesting ants.

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[1] First person plural is used throughout this chapter to reflect the contributions of others to both research design and field work.

Introduction

Ants are known to be a thermophilic fauna (Hölldobler and Wilson 1990), which is evident by a decline in species diversity with increasing latitude (Kusnezov 1957). Although a recent taxonomic catalogue provides a global total of 11,477 extant species of ants (Bolton et al. 2006), only some 82 species were reported for British Columbia (Higgins and Lindgren 2009). Despite this relative paucity in species diversity, ants are very common throughout most of BC, especially in the south (Naumann et al. 1999), and are rare only in cool and closed forest canopies (Higgins and Lindgren 2006).

Although a few entomologists have collected ant species within BC in an attempt to develop a species list (Buckell 1927, 1932; Blacker 1992; Blades and Maier 1996), or establish habitat associations (Lindgren and MacIsaac 2002) almost no work has been done to characterize a localized ant community. The sole exception was a study to examine the impact of cattle grazing on ant communities in the extreme southern Okanagan region of BC (Heron 2001), which would not be expected to resemble, in structure or ecologically, an ant community in the sub-boreal forests of BC. Further, no studies have followed ant communities through seral change in BC.

Examinations of ant communities with seral changes have also been rare in Canada. The only example of such research in Canada examined ant succession in the lichen-spruce forests of Quebec (Lafleur et al. 2006). In Fennoscandia, there has been more interest in successional changes in ant communities because of the belief that dominant thatching ants may play a keystone role in ecosystem processes in these forests (Punttila 1996; Savolainen et al. 1989; Seppä et al. 1995, Kilpeläinen et al. 2005). The ant fauna of Fennoscandian forests, however, is quite different from that of the sub-boreal forests of BC. Thatching ants are not as dominant in BC as they are in Fennoscandia, and ants are seldom mentioned in ecological surveys of Fennoscandian coarse woody debris (Jonsson and Kruys 2001). Dead wood, however, is a common nesting resource in the sub-boreal forests of BC (Lindgren and MacIsaac 2002; Higgins and Lindgren 2006).

Thatching and the use of dead wood as nesting materials are both adaptations to improve the thermal conditions of nests in cool climates (Rosengren et al. 1987; Higgins and Lindgren 2006), suggesting that temperatures are affecting ant autecology. The decline in ground temperatures resulting from decreased insolation with advancing seral age (see Chapters 4 and 5) is also likely to affect the ant community. It was the primary purpose of our study to examine ant communities in forests of varying seral age, and consider those communities in the context of the ecological hypotheses forwarded to explain successional change. In addition, we compare these ant community assemblages to other habitats known to be climatically marginal for ants, including the boreal forests of Fennoscandia and North America. Finally, we provide some hypotheses for the observed differences, focusing on the importance of coarse woody debris and temperature.

Methods

We used records from Houston Forest Products (HFP, now West Fraser Mills Ltd., Houston, British Columbia), to identify non-harvested and post-harvested sites (seral ages: 2-3, 8-10, 13-15, 23-25 yr) in lodgepole pine-leading (*Pinus contorta* Dougl. var. *latifolia* Engelm) stands within the sub-boreal spruce biogeoclimatic zone and moist-cold subzone, variant 2 (SBSmc2) (Meidinger and Pojar 1991). All post-harvest sites had been replanted by HFP with lodgepole pine because of the commercial potential of this species in the area. We identified a minimum of three replicate sites from each seral age within a 100-km radius of Houston, BC (54°24'N, 126°40'W). For non-harvested sites and 8-10 yr post-harvest sites, four replicate sites were established. Replicate sites varied in distance from 5-100 km from each other. We then positioned a 1-ha sampling plot within each site so that contact with natural or artificial boundaries (e.g., streams, roads, slopes) was minimized. The plots were reference-flagged as a Cartesian x,y grid with 25-m spacing. Sampling locations were determined using random x,y numbers and then paced off from the nearest flagged reference point.

Our study was conducted between 2003 and 2005 (Appendix II) with all sampling for ants occurring between late June and mid-August. Non-harvested plots and 8-10 yr post-harvest plots were sampled in 2003, 13-15 and 23-25 yy post-harvest plots in 2004, and 2-3 years post-harvest plots in 2005. Sampling included hand-sampling of strip plots for coarse woody debris (CWD), pitfall trapping and mini-Winkler sampling of forest floor litter. Coarse woody debris was comprised of both downed woody debris (DWD) and stumps. Downed woody debris was defined as pieces of downed wood of any length with a large end diameter ≥10 cm. The threshold for inclusion of a stump was a cut end diameter of 10 cm. Downed woody debris and stumps were sampled within two 4×100-m strip transects within each 1-ha sampling plot. Each strip consisted of two 4×50-m sub-strips positioned at right angles to each other and sharing a 10-m offset centre to avoid overlaps between strips. The centre point was randomly positioned within the 1-ha plot, but the 4×50-m strips were allowed to extend beyond the boundaries of the plot.

Within each sampling strip, we opened CWD by hand and/or hatchet to locate and sample ant colonies. Ants were placed in 1.5-ml plastic snap-cap vials (Fisher Scientific, Fisherbrand, Cat No. 05-408-129) containing 95% ethanol for later identification in the laboratory. If possible, we collected at least 5 individuals from each colony. Data within each strip were recorded by 4×12.5-m subsections (50 m^2), which were used as sampling units for the purpose of analysis. We assessed all pieces of DWD within the strip, regardless of ant presence or absence, for large-end diameter, large-end diameter at strip boundary, small-end diameter at strip boundary, length in strip, total length, percentage bark, and the decay class of the sapwood and heartwood (Maser et al. 1979). Equivalent measurements were also made on stumps when the centre point of the stump was located within the sampling strip.

We monitored site temperatures using iButton® 1 Wire Thermocron® DS1921G dataloggers (Maxim Technologies, Dallas, TX). During the summer of 2005, one iButton temperature datalogger was randomly positioned within each 1-ha plot approximately 1 cm underneath the surface forest duff layer. We chose this depth to best measure the temperature which epigaeic foraging ants would be experiencing, while blocking direct insolation that might result in high radiative temperature readings. Temperatures were recorded on the dataloggers every 30 min between 8 July and 18 August. We then derived daily temperature and amplitude means by modelling site data to a sine curve using SAS (Proc NLIN) (SAS 9.1 ©2002-2008).

Pitfall traps consisted of 237 mL plastic cups with a lid diameter of 8 cm. The pitfall design was modified from Nordlander (1987), as described in Chapter 2.

We performed forest floor litter sampling for ants using the mini-Winkler litter sample bag extraction technique (Agosti et al. 2000). We collected two sets of 10 randomly placed surface litter samples (0.5 m^2) with at least one month between sets. Surface litter was scraped loose by hand and trowel then sifted through a screen with an approximately 2.5-cm mesh. Large debris was broken up by hand, as extensively as possible, and also sifted. We then placed each sample in a mini-Winkler extraction bag, and the bags were hung in a utility shed for approximately 48 h at ambient temperatures to protect them from the weather and from being physically disturbed (Agosti et al. 2000).

We compared study sites for relative species distributions by non-metric multidimensional scaling (NMDS) using PC-ORD, (Version 5, McCune and Mefford 1999). Non-metric multidimensional scaling separations, using the Sorensen (Bray-Curtis) distance measure, were performed three times independently to assess for local minima. Total species richness estimates, based on CWD sampling only and derived from pooled seral age replicate sites, were calculated with the incident based estimator, Chao2, using EstimateS, Version 8 (Colwell 2006) while the Shannon and Simpson Indices were calculated manually following Magurran (1988).

Ants were identified to species as described in Chapter 2: Ant Identifications and Nomenclature.

Results

Distinct heterogeneity between seral ages, with the exception of 8-10 and 13-15 yr post-harvest sites where some overlap was noted, was observed from non-metric multidimensional scaling (NMDS) of relative species distributions between study sites, derived from the hand sampling of CWD in strip plots (Figure 3.1). The heterogeneity among replicates within each seral age class, as determined subjectively from the plotted variability between sites in the two-dimensional space of the NMDS analysis, decreased between the earliest (i.e., 2-3 yr post-harvest) and mid-seral age of this study (13-15 yr post-harvest) and then increased in the two later seral ages (Table 3.1). A steady increase in species diversity through the first 4

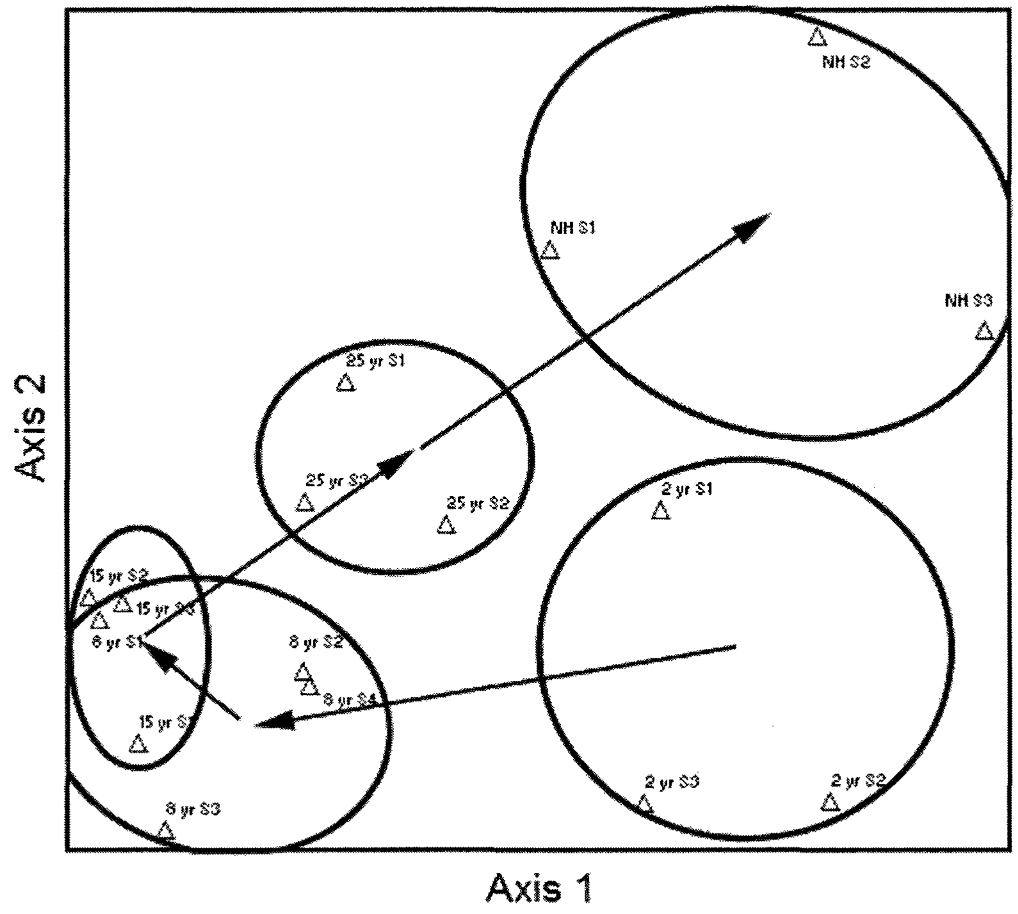

Figure 3.1. Non-metric multidimensional scaling (Bray-Curtis distance measure) of relative species diversity within seventeen 1-ha sampling plots, as determined by strip-plot sampling of coarse woody debris. Four plots were non-harvested (NH) although one is missing here as the complete absence of ants necessitated its exclusion, three were 2-3 yr post-harvest (2 yr), four 8-10 yr post-harvest (8 yr), three 13-15 yr post-harvest (15 yr), and three were 25 yr post-harvest (25 yr). Site replicates indicated by S1-S4 as appropriate. Sampling occurred from 2003-2005.

Table 3.1. Species diversity indices (Shannon index (H') and Simpson index (1/D)), and total species estimation (Chao2), for ant communities as determined by hand sampling of strip plots for coarse woody debris, in five seral ages of post-harvest and non-harvested plots in sub-boreal forests of west-central British Columbia from 2003-2005.

Site seral age	Number of plots	Total number of samples	Shannon Index (H')	Simpson Index (1/D)	Total species estimation Chao2 (95% CI)
2-3 yr post-harvest	3	48	1.14	2.83	4 (4.0,4.3)
8-10 yr post-harvest	4	64	1.39	2.83	9 (9, 9)
13-15 yr post-harvest	3	48	1.45	3.35	12.9 (10.3,34.7)
23-25 yr post-harvest	3	48	1.55	4.17	10.9 (8.3, 32.4)
Non-harvested	4	64	0.54	1.41	3 (3.0, 3.3)

seral ages (i.e., from 2-3 yr to 23-25 yr post-harvest) was shown by Shannon`s Index (H′), despite the estimation of total species richness peaking in the third seral age (13-15 yr post-harvest), as determined by Chao2 (Table 3.1). In non-harvested sites where few ants were located, species diversity (H′) drops to its lowest overall value (Figure 3.1). This pattern is mirrored by Simpson's dominance index (1/D). Total species richness grew through the earlier seral ages (i.e., 2-3 yr to 13-15 yr post-harvest) but then declined in older stands (23-25 yr post-harvest and non-harvested stands) as indicated by Chao2 (Table 3.1), although the differences between 13-15 yr post-harvest and 23-25 yr post-harvest stands are not considered significant, as indicated by the confidence intervals (Table 3.1).

The highest daily mean soil temperatures were recorded in the earliest seral age (2-3 yr post-harvest) with temperatures just over 14 °C between June and August of 2005 (Table 3.2). Mean temperatures declined steadily with seral age and were below 10 °C in non-harvested plots. Although daily mean soil temperatures dropped approximately 5 °C over the 5 seral ages, daily mean temperature amplitudes dropped by approximately 13 °C, indicating increasingly stable, but lower temperatures with increasing seral age. Datalogger failures occurred in one of the three 2-3 yr post-harvest plots, as well as in one of the four non-harvested plots.

Overall 17 species of ants were collected by all techniques used in this study (i.e., hand sampling of CWD in strip plots, Nordlander pitfall trapping, and mini-Winkler soil/litter sampling) (Table 3.3). Of these, 14 were found during CWD sampling, 12 by Nordlander pitfall trapping, and 10 by mini-Winkler soil/litter sampling. In all cases, except one, the species missed by each technique were uncommon. The one exception was *Myrmica fracticornis* Forel, which was commonly captured by Nordlander pitfall trapping

Table 3.2. Mean daily soil temperatures and temperature amplitudes taken over 40 days between July 8 and August 18, 2005 in five seral ages within the moist-cool sub-boreal (SBSmc2) forests of west-central British Columbia. Temperatures recorded by iButton® dataloggers each 30 minutes.

Seral Age	Mean Temperature (°C ± SE)	Mean Temperature Amplitude (°C ± SE)
2-3 yr post harvest (n = 2)	14.3 ± 1.5	17.7 ± 8.5
8-10 yr post harvest (n = 3)	12.5 ± 0.1	10.9 ± 1.3
13-15 yr post harvest (n = 3)	11.8 ± 0.3	9.3 ± 0.5
23-25 yr post harvest (n = 3)	11.0 ± 0.2	6.5 ± 0.8
Non-harvested (n = 2)	9.4 ± 0.2	4.7 ± 0.1

Table 3.3. Ant species (Hymenoptera: Formicidae) collected in the sub-boreal spruce, moist cold (SBSmc2) biogeoclimatic zone and subzone in British Columbia, Canada. Species list represent collections made from 2003-2005 in post harvest sites at ages 2-3, 8-10, 13-15, and 23-25 yr as well as non-harvested sites. Taxonomy follows Bolton et al. (2006) except where more recent revisions were available.

- Family
  - Sub-family
    - Species group
      - Species

- FORMICIDAE
  - Myrmicinae
    - *Leptothorax muscorum* (Nylander)
    - *Myrmica alaskensis* Wheeler
    - *Myrmica incompleta* Provancher
    - *Myrmica detritinodis* Forel
  - Formicinae
    - *Camponotus herculeanus* (Linnaeus)
    - *Camponotus noveboracensis* (Fitch)
    - *Lasius pallitarsis* (Provancher)
    - *Lasius alienus* (Foerster)
    - *Polyergus breviceps* Emery
    - *Formica fusca* group
      - *Formica accreta* Francoeur
      - *Formica argentea* Wheeler
      - *Formica fusca* Linnaeus
      - *Formica hewitti* Wheeler
      - *Formica neorufibarbis* Emery
    - *Formica rufa* group
      - *Formica dakotensis* Emery
      - *Formica obscuriventris* Mayr
    - *Formica sanguinea* group
      - *Formica aserva* Emery

(Table 3.4) and mini-Winkler litter extractions (Table 3.5), but not found within CWD. *Myrmica fracticornis* was captured in all stands except those that were non-harvested. In 13-15 year post-harvest stands, for example, this species was captured in 30% of pitfall traps (n = 120) and 23% of mini-Winkler soil/litter extractions (n = 60). One species, *Formica dakotensis* Emery, captured by a pitfall trap, is a new record for BC although its presence is not surprising as it is known to occur in northwestern Alberta (Sharplin 1966, Wu and Wong 1987) and in the Yukon (Francoeur 1997).

In all ant colonies identified during CWD sampling, five species comprised 90-95% of ants identified. These were *Leptothorax muscorum* (Nylander), *Myrmica alaskensis* Wheeler, *Camponotus herculeanus* (L.), *Formica neorufibarbis* Emery and *F. aserva* Forel (see Appendix III for more complete natural history notes) in order of overall colony abundance. Total observed species abundance, as determined by all sampling methodologies, was highest in the three mid seral ages (i.e., 8-10, 13-15, and 23-25 years post-harvest sites), varying over this time frame by only a single species within each sampling methodology (Table 3.6).

Ant colony abundance varied with seral age (Figure 3.2). Established ant colonies in the 2-3 yr post-harvest plots consisted largely of small-bodied ant species with small-population (less than 200 workers) colonies (*L. muscorum* and *M. alaskensis*). Maximum ant colony abundance was documented in the 13-15 yr post-harvest plots where colony densities reached approximately 10 per 50 m^2. Ant colonies were rare in non-harvested plots, with approximately 0.3 colonies per 50 m^2. In one non-harvested plot, no ant colonies were located at all.

Table 3.4. The percentage of pitfall traps capturing individuals of six species of ants across five seral ages in the sub-boreal spruce biogeoclimatic, moist-cold subzone, variant 2 (SBSmc2) (Meidinger and Pojar 1991) forests of west-central BC. Pitfall trapping was conducted from 2003-2005.

Seral Age	Ant species					
	Camponotus Herculeanus	*Formica aserva*	*Myrmica alaskensis*	*Leptothorax muscorum*	*Formica neorufibarbis*	*Myrmica detritinodis*
2-3 yr post harvest (n = 2)	0.8	0	0.8	0	2.5	0.8
8-10 yr post harvest (n = 3)	5.0	31.9	15.0	10	21.3	10.0
13-15 yr post harvest (n = 3)	44.2	65.8	20.0	38.3	31.7	30.0
23-25 yr post harvest (n = 3)	47.5	18.3	29.2	10.8	4.2	19.2
Non-harvested (n = 2)	0	0.6	0.6	0.6	0.6	0

Table 3.5. The percentage of mini-Winkler litter samples capturing individuals of six species of ants across five seral ages in the sub-boreal spruce biogeoclimatic, moist-cold subzone, variant 2 (SBSmc2) (Meidinger and Pojar 1991) forests of west-central BC. Mini-Winkler sampling was conducted from 2003-2005.

Seral Age	Ant species					
	Camponotus Herculeanus	*Formica aserva*	*Myrmica alaskensis*	*Leptothorax muscorum*	*Formica neorufibarbis*	*Myrmica detritinodis*
2-3 yr post harvest (n = 2)	0	0	0	30	0	0
8-10 yr post harvest (n = 3)	0	16.2	28.7	66.2	11.2	12.5
13-15 yr post harvest (n = 3)	11.7	23.3	23.3	68.3	3.3	23.2
23-25 yr post harvest (n = 3)	1.7	1.7	26.7	63.3	6.7	15.0
Non-harvested (n = 2)	0	0	13.7	1.2	0	0

Table 3.6. The total number of species of ants captured by three sampling methods (mini-Winkler litter extractions, Nordlander pitfall traps, coarse woody debris (CWD) hand sampling) across five seral ages in the sub-boreal spruce biogeoclimatic, moist-cold subzone, variant 2 (SBSmc2) (Meidinger and Pojar 1991) forests of west-central BC. Collections were conducted from 2003-2005.

Seral age	Sampling methods		
	Hand sampling of CWD	Nordlander pitfall traps	Mini-Winkler litter extractions
2-3 yr post-harvest (n = 2)	4	5	2
8-10 yr post-harvest (n = 3)	8	11	8
13-15 yr post-harvest (n = 3)	9	11	9
23-25 yr post-harvest (n = 3)	8	10	8
Non-harvested (n = 2)	3	6	2
Total species (excluding species shared between seral ages)	14	12	10

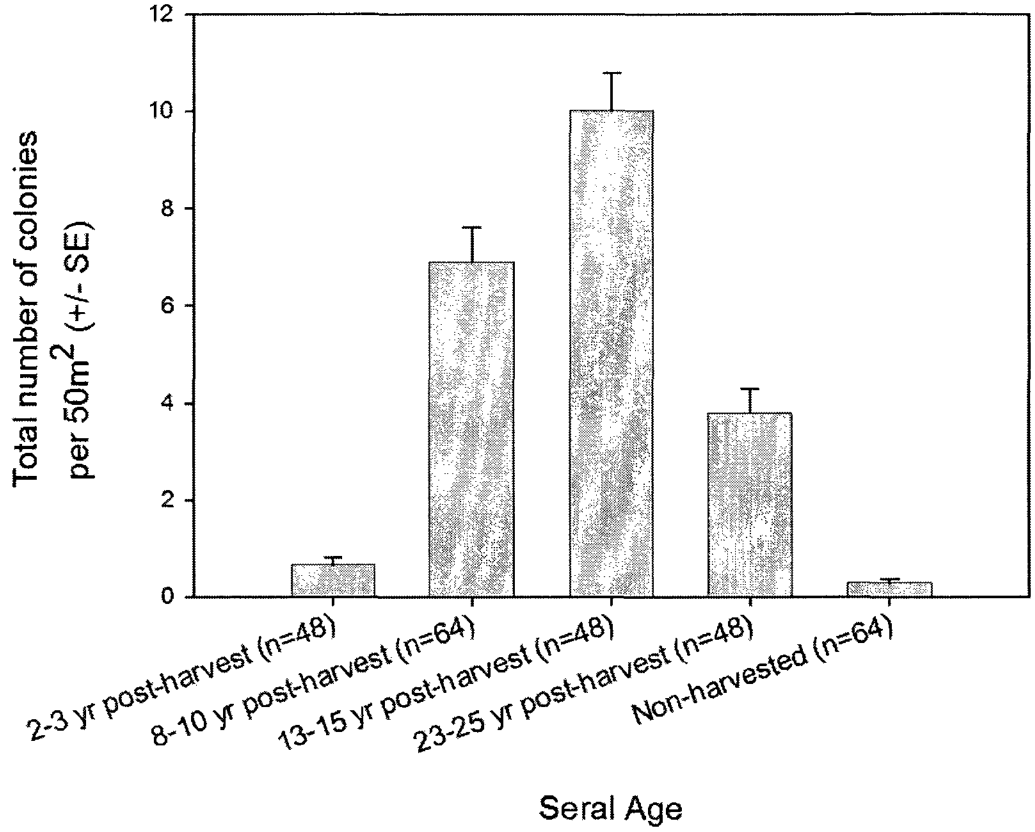

Figure 3.2. The number of colonies of all species of ants nesting in coarse woody debris per 50 m2 (±SE) in stands of five differing seral ages. All stands were located within the sub-boreal spruce biogeoclimatic zone, moist-cold sub-zone, variant 2 (SBSmc2) forests of west-central BC (Meidinger and Pojar 1991) and sampled from 2003-2005.

Both the overall size and composition (Figure 3.3) of the ant community in CWD varied with seral age. In the earliest seral age (2-3 yr post-harvest), *L. muscorum* was the most common species but the relative abundance of this species declined after the 13-15 yr post-harvest seral age. That decline is contrasted by an increase in the relative abundance of *M. alaskensis*, which was the most common species in non-harvested plots. These 2 species always accounted for greater than 60% of identified nests in CWD within each seral age. In the last seral age (non-harvested plots), *M. alaskensis* alone was responsible for over 90% of the total colonies identified (Figure 3.3).

Camponotus herculeanus was present in the 2-3 yr post-harvest sites although all colonies located were young, consisting of a queen and several workers. The number of colonies identified increased with seral age, peaking in the 13-15 yr post-harvest plots with approximately one colony per 50 m^2, and then declining. No mature colonies of *C. herculeanus* were located within the sampling strip-plots of non-harvested sites. Despite a low relative abundance of colonies, this species was common in pitfall traps in 13-15 and 23-25 yr post-harvest sites, being found in 44% (n = 120) and 47% (n = 120) of pitfall traps respectively (Table 3.4).

Colonies of *F. aserva* were first located in the second seral stage (8-10 yr post-harvest). This species became slightly more common in the third seral stage (13-15 yr post-harvest) reaching a density similar to *C. herculeanus* of almost 1 colony per 50 m^2. *Formica aserva* almost disappeared in the 23-25 yr old post-harvest stands, however, with only two colonies identified. Peak pitfall captures of this species were in 8-10 and 13-15 yr post-harvest sites where they were found in 32% (n = 160) and 66% (n = 120) of pitfall traps respectively (Table 3.4).

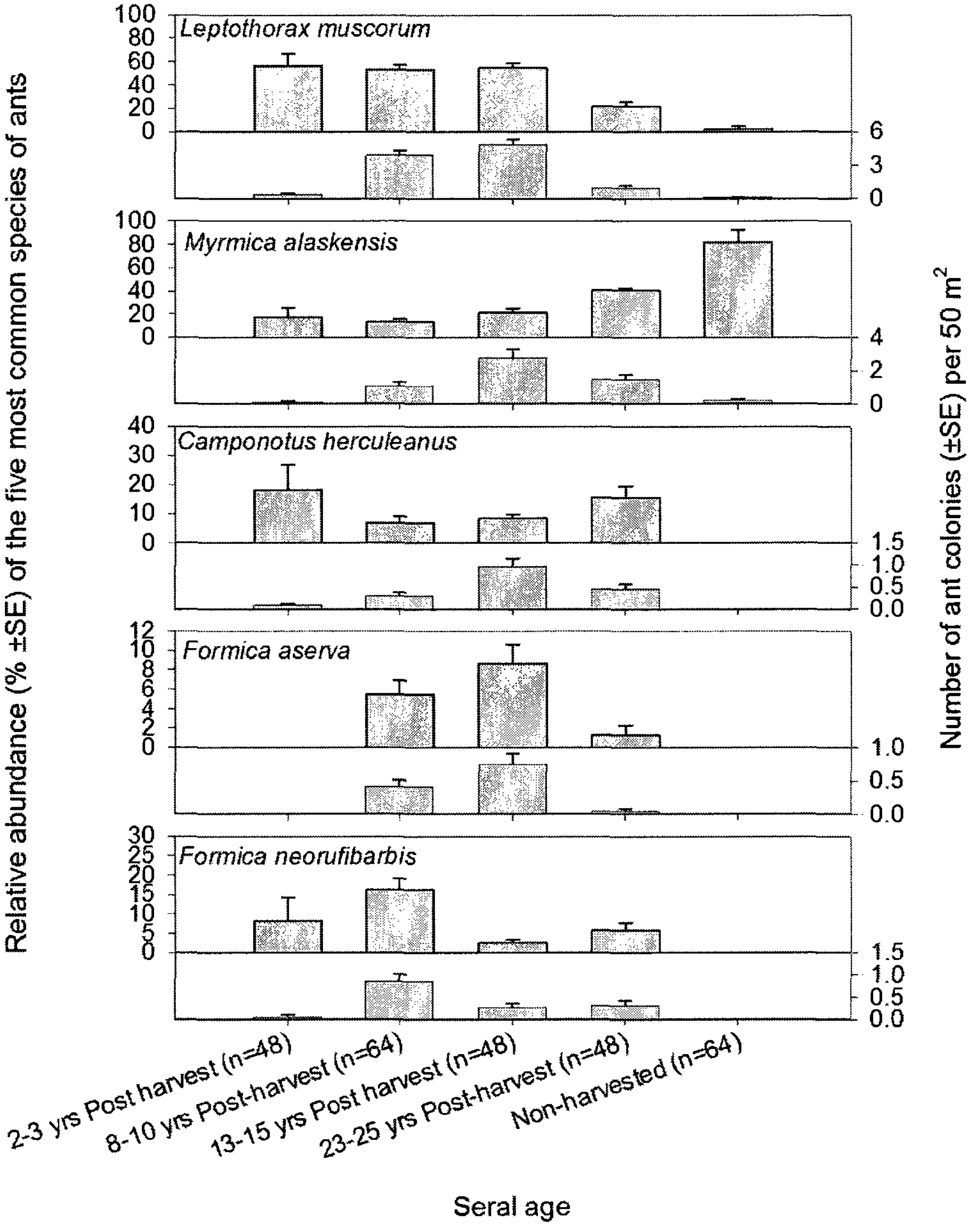

Figure 3.3. The relative percent abundance (± SE) of ant species colonies and number of colonies per 50m^2 (± SE) located within coarse woody debris in five seral ages in the sub-boreal moist-cool, variant 2 (SBSmc2)(Meidinger and Pojar 1991) forests of west-central BC.

Although most species peaked in colony abundance in the 13-15 yr post-harvest sites (Figure 3.3), *F. neorufibarbis* did not. This species was present in the 2-3 yr post-harvest plots (0.06 colonies/50m^2), became more common in the 8-10 yr post-harvest plots (0.86 colonies/50m^2), but then declined in abundance in the 13-15 yr post-harvest plots (0.27 colonies/50m^2), which was a time when the four other common species were increasing in abundance. Colony abundance remained at similar numbers in 23-25 yr post-harvest sites (0.31 colonies/50m^2) and then this species also disappeared in the non-harvested sites. Mini-Winkler captures also declined between 8-10 and 13-15 yr post-harvest sites with *F. neorufibarbis* present in 11% (n = 80) and 3% (n = 60) of samples, respectively (Table 3.5). Pitfall captures, however, did not decline between these seral ages. *Formica neorufibarbis* was found in 21% (n = 160) of pitfall traps in 8-10 yr post-harvest sites and 32% (n = 120) of pitfall traps in 13-15 yr post-harvest sites (Table 3.4).

Overall, only a few colonies (n = 18) and species (n = 3) were located within coarse woody debris in the non-harvested sites. Total colony density for all ant species was 0.28 colonies/50m^2 in these sites. Only approximately 2% (n = 160) of all pitfall traps captured ants (Table 3.4). Mini-Winkler litter extractions were more successful with 15% (n = 80) yielding ants, of which all were *M. alaskensis* with the exception of a single discovery of *L. muscorum* (Table 3.5).

Discussion

NMDS and biodiversity indices

The ant community assemblages were more homogeneous within seral age replicates despite the physical separation of some replicate sites by distances of approximately 115 km, as shown by non-metric multidimensional scaling (NMDS) (Figure 3.1). The only exceptions were the 8-10 yr post-harvest and 13-15 yr post-harvest sites, where some overlap was evident. This latter observation may be explained as a consequence of a similar species assemblage differing largely in abundance, with the 13-15 yr post-harvest sites having a greater number of colonies (Figure 3.2). The heterogeneity that did exist within replicate seral ages decreased as the earliest seral age developed up to the 13-15 yr post-harvest sites, and then began to increase following this age (Figure 3.1). This may reflect some variation in how ant communities initially establish within newly available areas, compounded by low numbers, followed by a coalescing of community structure as most common colonizers arrive and establish over time. In seral ages later than 13-15 yr post-harvest, as thermal conditions begin to become less favourable (see below), the community begins to disassemble, but again, with each site following a relatively unique path. In viewing the NMDS figure (Figure 3.1) it is possible to interpret Axis 1 as reflecting species diversity, with fewer species to the right. Axis 2 may reflect a shift in species dominance, with *Leptothorax muscorum* toward the bottom and *Myrmica alaskensis* toward the top.

Both Shannon's and Simpson's diversity indices, calculated from pooled seral age replicates, followed the same pattern with seral age despite the former being more sensitive to species diversity and the latter being more sensitive to evenness (Magurran 1988) (Table 3.1). Although both the estimated total species richness, Chao2 (Table 3.1), and the density of ant colonies (Figure 3.2) peaked in the 13-15 yr post-harvest sites, both Shannon's (H') and Simpson's (1/D) indices peaked in the 23-25 yr post-harvest sites. Despite the higher estimation of total species richness by Chao2, however, in 13-15 yr post-harvest sites as compared to the 23-25 yr post-harvest sites, the difference is not statistically significant (see 95% CIs, Table 3.1), and an examination of the dataset suggests much greater evenness in the

23-25 yr post-harvest sites. This is likely weighting both diversity indices toward a higher value in the 23-25 yr post-harvest sites.

Overall patterns of succession

The process of ecological succession has been the subject of active research for over 100 years. Initially, Gleason (1917) and Clements (1916) defined two competing views of this process, with Gleason's "Individualistic Hypothesis" becoming generally supported as environmental data became available (McCook 1994; Cook 1996). This hypothesis, now theory, suggests that succession is simply a process in which individual species respond (via presence or absence) to the prevailing abiotic site conditions. Since then, various modifications to the Individualistic Hypothesis have been proposed but the most influential have emphasized the varying roles of life history strategies (Drury and Nisbet 1973), species interactions (Connell and Slayter 1977) and evolved environmental tolerances (Pickett 1976). The overall pattern of ant community succession seen in this study is consistent with the Individualistic Hypothesis of Gleason (1917). Given the depauperate ant community present in the non-harvested sites of this study, the damage to soil and woody debris during harvesting (Higgins and Lindgren 2006), and the tendency of mated queens to select open areas for nest founding (Wilson and Hunt 1966, see Chapter 4), it is likely that ants found in early seral ages (i.e., 2-3 yr post-harvest) have arrived through queen dispersal from source areas in the surrounding landscape, which, in this study, was a mosaic of managed forest of varying seral age.

It has been argued that most species that come to define later seral stages arrive early (Drury and Nisbet 1973). Of the 5 most common species of ants identified in this study, 4 (*C. herculeanus*, *M. alaskensis*, *L. muscorum* and *F. neorufibarbis*) were located in the 2-3 yr post-harvest sites. Only *F. aserva* may have required some facilitation (Connell and Slayter 1977), to establish, as it is likely dependent upon ants of the species group *Formica fusca* (e.g., *F. neorufibarbis*) to exploit for nest founding (Francoeur 1983) (see below).

As additional ant species were mostly rare, it is possible that either their densities in the 2-3 yr post-harvest sites were too low for detection or their arrival required dispersal from more distant sites, delaying their appearance. Rates of arthropod colonization have been shown to decline with distance from a source, especially for ants (Simberloff and Wilson 1969). The current managed landscape with forests of differential seral ages, however, is likely more amenable to ant dispersal and colonization than the pre-anthropogenic landscape (DeLong and Tanner 1996), especially in the cool-moist forests of this study which had a mean fire return interval of 133 years (95% CI: 113-160 yr) (Steventon 2002). Closely packed and interconnected cutblocks would be expected to increase suitable habitat patches for the thermophilic ants (Hölldobler and Wilson 1990), while reducing relatively inhospitable matrix (non-harvested forest) in the landscape. It should be noted, however, that this landscape would not have been so fragmented when the 23-25 yr post-harvest plots examined in this study were initially harvested. As a consequence, it is possible that the lower ant densities noted for these sites may have been influenced by a lower rate of initial colonization. Having said that, these sites were still likely close to anthropogenically opened landscape near local lumber mills, towns and ranches.

This initial community, through succession, would then have been shaped by the individual life history strategies (e.g., colony life cycles, colony sizes) (Gleason 1917, Drury and Nisbet 1973) and the evolved environmental tolerances of each species (Pickett 1976). The attribute most likely to play a critical role in shaping the community structure by interacting with life history strategies and evolved tolerances is temperature although other factors such as available prey cannot be conclusively discounted. Daily mean site litter temperatures (to which foraging ants would be exposed), between June and August, were highest in the earliest seral age (2-3 yr post-harvest) at approximately 14 °C and then steadily declined by approximately 1 °C with each later seral age (Table 3.2). This pattern was even more evident for daily mean litter temperature amplitudes, declining by 13 °C over the 5 seral ages (Table 3.2). For a thermophilic taxon such as ants, it is likely that each species will have a minimum environmental temperature threshold which will cause them to fall out of the community. Whether that sensitivity is greatest to mean temperatures or to temperature amplitudes cannot be determined here. I would argue that temperatures (means or amplitudes) appear to be adequate until after the 13-15 yr post-harvest seral age.

Camponotus herculeanus (see Appendix 1 for brief species natural history) was present as a pioneer species in the earliest seral stages showing strong dispersal ability. Solitary queens were frequently encountered in these sites although they were not included in the final tabulated data because their success in initiating a colony could not be verified. The noted initial decline in relative abundance after the first seral age (i.e., 2-3 yr post-harvest) would appear to be a consequence of colony establishment by other species with more rapid colony development life history strategies (Figure 3.3). The pattern of change in absolute abundance (i.e., the number of colonies per 50 m^2) is typical of most of the species of ants followed in this study, that is, a steady rise in absolute abundance, peaking in 13-15 yr post-harvest sites followed by a decline (Figure 3.3). This pattern is most likely shaped by temperature, which is presumably adequate over the first three seral ages but limiting in the last two (Table 3.2). The incidental discovery of a single mature colony outside of the sampling area at one site indicates that this species can persist in these cool forests, albeit at low densities.

The fact that *C. herculeanus* were the most frequently captured ants in pitfall traps in the 13-15 and 23-25 yr post-harvest sites (Table 3.4), in spite of a decline in the absolute abundance of colonies may suggest that while fewer colonies are persisting in 23-25 yr post-harvest sites, those that did were larger and foraging more widely. It is probable that favourable local micro-environmental conditions (e.g., arising from increased insolation because of a single tree blow-down, a wetland edge, or from an elevation change) may allow a carpenter ant colony to persist in older seral ages (i.e., 23-25 yr and older). As individual *C. herculeanus* queens can reach ages of 20 yr or more (Hölldobler and Wilson 1990), it is possible that colonies persisting in the 23-25 yr post-harvest stands initially established in early seral ages. The incidental observation of a mature *C. herculeanus* colony in older stands, as noted earlier, may be a consequence of micro-environmental thermal conditions meeting minimum colony needs, however, it might also suggest that queen replacement is occurring in some colonies. *Camponotus herculeanus* satellite colonies (queenless colonies that form around the periphery of a foraging area close to resources) will occasionally accept a queen and become a natal colony (Akre et al. 1994). This has not been documented in natal colonies directly but seems plausible, especially in colonies that have recently lost their queen, and would explain how a colony can exist in habitats where colony founding seems unlikely, even 20+ years earlier. Despite this possibility, clearly the presence of *C. herculeanus* in non-harvested forests is rare, at least in the biogeoclimatic subzone where we did our research.

The absence of *Formica aserva* (frequently reported in the literature by its junior synonym *F. subnuda* (Bolton et al. 2006)) in the earliest seral age may be an example of facilitation (Connell and Slayter 1977) modifying the Individualistic Hypothesis of succession. This species is a facultative slave taker (Francoeur 1983), usually initiating colonies as a parasite of a *F. fusca* species-group colony. *Formica aserva* queens typically initiate a colony by entering a *F. fusca* species-group colony, killing the queen, and assuming control over the workers (Punttila 1996), a type of dependent nest founding using parasitism (Stille 1996). In Finnish boreal forests, it was noted that fully one third of all species of ants used parasitic dependent nest founding (Punttila et al. 1991). Of the five most common ant species in my study, only *F. aserva* is known to initiate nests in this manner, however. *Formica aserva* is thus likely dependent upon the establishment of a suitable slave species prior to colony initiation. In my study, the most common potential slave within the *F. fusca* group was *F. neorufibarbis.* This species was present as a pioneer species in the earliest seral age and likely became a host to many *F. aserva* queens and subsequent colonies. *Formica neorufibarbis* slaves were twice identified within *F. aserva* nests during the course of this study, whereas none of the other *F. fusca* species-group present (*F. accreta* Francoeur, *F. argentea* Wheeler, *F. fusca* L, *F. hewitti* Wheeler) were ever encountered as slaves. It should be noted, however, that these latter species were not common and none were identified in the earliest seral age.

Another modification to the Individualistic Hypothesis, evolved environmental tolerances (Pickett 1976), may also be evident in affecting the presence of *F. aserva* in the ant community of these forests. *Formica aserva* may be more sensitive to cooler conditions than any of the other common ant species in this community. The decline in absolute abundance was dramatic between 13-15 yr post-harvest sites and 23-25 yr post-harvest sites (Figure 3.3). This was also reflected in pitfall traps (Table 3.4) and mini-Winkler (Table 3.5) captures although the decline was not as strong. This might suggest, as with *C. herculeanus,* that a few natal nests were present in suitable micro-sites where conditions were warmer, while workers were more tolerant of cooler conditions and able to forage in a cooler forest. It was reported that the raising of brood in the natal nest of a *Myrmica* spp. ant was the most sensitive stage in colony development, and that mean temperatures of 15 °C within the nest were the minimum tolerated (Elmes and Wardlaw 1983). Experimental manipulation of *F. aserva* nest temperatures by shading (see Chapter 5), support the hypothesis that the natal nest of this species is also highly temperature sensitive.

The interaction between *F. aserva* and *F. neorufibarbis* may also explain the unusual pattern of abundance (relative to other species) demonstrated by *F. neorufibarbis* to seral change. The absolute abundance of *F. neorufibarbis* colonies increased through the first 2 seral ages of this study (2-3 and 8-10 yr post-harvest) but were markedly reduced in third seral age (13-15 yr post-harvest) (Figure 3.3), a time when the abundance of the four other common ant species peaked. This depression in absolute abundance may arise from the nest founding behaviour of *F. aserva* described above, and subsequent slave raids by established *F. aserva* colonies (although these latter raids are considered infrequent for this species (Savolainen and Deslippe 2001)). Further, the absolute abundance of *F. neorufibarbis* colonies did not change between the 13-15 and 23-25 yr post-harvest sites, despite declining temperatures to which *F. aserva* appeared sensitive. This suggests that declining site temperature (Table 3.2) was not a likely reason for the decline in colony numbers between 8-10 and 13-15 yr post-harvest, and that other factors such as parasitic dependent nest founding by *F. aserva* may have been a factor. Thus, here the presence or absence of *F. neorufibarbis* may be an example of a species interaction (Connell and Slayter 1977) modifying the Individualistic Hypothesis of succession.

The most abundant species in this study were *Leptothorax muscorum* (often reported in North American literature by its junior synonym *L. canadensis* Provancher) (Bolton et al. 2006) and *Myrmica alaskensis*, both in the subfamily Myrmicinae. Both species, especially *L. muscorum* (Heinze 1993b), are physically small, do not form large colonies, and forage within approximately 2 m of their nest sites (Brian et al. 1965) (see Appendix I.3). Thus, there is extensive space available in harvested sites for nest establishment and foraging. Both were pioneer species although *L. muscorum* was the most common in the earliest seral ages (2-3 yr to 13-15 yr post-harvest) (Figure 3.3). The opposite was true for *M. alaskensis* which increased in relative abundance with seral age and was the only ant regularly found in non-harvested sites, despite a reduction in its absolute abundance in later seral ages (i.e., 23-25 yr post-harvest and non-harvested sites) as compared to earlier seral ages (Figure 3.3). The presence of *Myrmica* spp. ants in the oldest forests of both Fennoscandia (Punttila et al. 1991, 1994) and Russia was noted (Dulsskii and Putyatina 2004). In both of these cases, it was not the only ant species capable of living in this habitat, however. Similarly, it was noted that *Myrmica* spp. ants were the most common ants in the oldest lichen-spruce forests of Quebec (Lafleur et al. 2006), and *M. alaskensis* was identified near the treeline in northern Canada (Francoeur 1983). Thus, *Myrmica spp.* ants, and *M. alaskensis* specifically, appear to be particularly cold tolerant. Despite this, *M. alaskensis* was still rare in non-harvested forests where daily mean litter temperatures were below 10 °C (Table 3.2), and on one occasion its presence was clearly associated with a small gap in the non-harvested forest canopy.

Overall, daily mean litter summer temperatures at or above 11 °C appear necessary for most species of ants in the sub-boreal forests of west-central British Columbia.

The paucity of soil- and litter-nesting ants

Throughout this study, no ant colonies were discovered directly in the soil. While gross examination of the soil and litter did not reveal obvious ant colonies (e.g., thatched mounds, soil crater nests, or nests under rocks), one species that may have been missed in this habitat was *Myrmica fracticornis*. This species was never discovered within CWD, yet it was captured in pitfall traps (Table 3.4) and mini-Winkler litter samples (Table 3.5) relatively frequently. This suggests that this ant is not associated with CWD, at least not within the size parameters defined in this study (i.e., >10 cm large end diameter). One study, near Prince George, BC, did record this species in very rotten wood with a mean diameter of 4-8 cm, a size class not examined in my study (Lindgren and MacIsaac 2002). *Myrmica fracticornis* (often described in the literature by junior synonym, *M. detritinodis* Emery)was identified nesting in CWD (size was not defined) in the southern lichen-spruce forests of Quebec, but this was an infrequent nesting site as compared to non-CWD locations (e.g., under lichen, moss, fine litter, etc.) (Lafleur et al. 2006). In this latter study, a negative relationship between CWD percentage ground cover and the presence of *M. detritinodis* was noted.

The rare capture (twice in eighty samples in 8-10 yr post-harvest sites) of more than a dozen of *L. muscorum* workers, with a queen in some mini-Winkler litter extractions, does suggest that this small ant (body length <5 mm), with colonies consisting of a few dozen workers (Heinze 1993a), was possibly nesting in fine woody debris, litter, or soil. These cannot be confirmed as colonies, however, as queens were frequently captured (e.g., eight times in 80 samples in the 8-10 yr post-harvest sites) in the mini-Winkler litter extractions without workers. Consequently, the association between the queens and workers within the $0.5m^2$ samples may be a coincidence. This species was associated with woody debris in 80% of identifications in one study (Lindgren and MacIsaac 2002), while others found this species to be entirely woody debris associated (Béique and Francoeur 1968; Lafleur et al. 2006). Work in recently clearcut and non-harvested forests along the central coast of Oregon, was unable to locate any soil or litter nesting ants (Nielsen 1986). All ant species discoveries were in wood. In central BC, near Prince George, where conditions are warmer and drier than those typical of forests in this study, it was reported that 12 of 19 species were woody debris associated (Lindgren and MacIsaac 2002). Overall, it seems likely that the large majority of the ant species are associated with CWD in the sub-boreal forests of west-central BC.

Relationships to other communities

A total of 39 species of ants were identified when sampling broadly over the boreal forest ecosystems of Quebec (Francoeur 2001). Given this, the 17 species (Table 3.3) we found in a single biogeoclimatic zone and sub-zone (sub-boreal spruce, moist cold, variant 2) (Meidinger and Pojar 1991) would appear to be unexceptional. Our results are also similar to a study in the southern lichen-spruce forests of Quebec where 13 species were identified (Lafleur et al. 2006). Further, studies in Finnish taiga (Punttila et al. 1994), and in old-growth Russian forests (Dulsskii and Putyatina 2004), both identified 19 species of ants.

In particular, the most common ant species identified in our study appears to be similar to fauna found in North American habitats known to be climatically marginal for ants. The 5 most common species identified (*Leptothorax muscorum*, *Myrmica alaskensis*, *Camponotus herculeanus*, *Formica neorufibarbis* and *Formica aserva*) were all included within the 6 species found near the tree-line of Quebec (Francoeur 1983). Of 4 species of ants identified near Churchill, Manitoba, three (*L. muscorum*, *F. neorufibarbis*, and *C. herculeanus*) belonged to the 5 most common species of this study (Gregg 1972). The fourth species reported was *Myrmica brevinodis* Emery (a junior synonym of *M. incompleta* (Provancher) (Bolton et al. 2006) was also found in this study. Finally, in a study of ant pollination in the alpine tundra of Colorado, only two species, *F. neorufibarbis* and *L. muscorum*, were identified, both of which were common in our study (Petersen 1977).

Although most species reported in these studies of climatically marginal habitat (Francoeur 1983, Gregg 1972, Petersen 1977) were also found in our study, their species lists did not correspond to the most climatically challenging habitat of our work, non-harvested forest, where few ants were recorded (Figure 3.3). These cited studies all report finding *L. muscorum* and *F. neorufibarbis,* whereas in our study, only 1 colony of *L. muscorum* and no colonies of *F. neorufibarbis* were found in coarse woody debris (CWD) in non-harvested forests. These species did appear, albeit rarely, in pitfall traps (0.6% of pitfalls for both species) (Table 3.4) and mini-Winkler samples (1.25% of mini-Winkler samples for *L. muscorum* but no captures of *F. neorufibarbis*) (Table 3.5) in non-harvested forests, however, indicating that they do persist at very low densities. Soil temperatures may offer an explanation for these disparities. It is possible that the alpine tundra (Petersen 1977), and more open forests at or near the tree-line (Francoeur 1983, Gregg 1972) allowed for greater insolation and higher temperatures in the soil than existed within the closed canopy of non-harvested plots of this study (Table 3.2). Unfortunately, soil temperatures were not recorded in either of these studies. Working above 1000 masl in the Czech Republic, however, it was demonstrated that insolative heating of the soil was greater where living vegetative biomass was lower (Tesař et al. 2008).

Although Canadian studies equivalent to this project are lacking, there have been several studies examining changes in the ant fauna of Fennoscandia with seral age (Savolainen et al. 1989; Punttila et al. 1991; Punttila et al. 1994; Seppä et al. 1995; Punttila 1996; Punttila and Haila 1996). The pattern of increasing ant colony abundance followed by a decline as seen in our study (Figure 3.3) was also noted (Punttila et al. 1991). Fennoscandian forests, however, appear to differ from the forests in this study in at least two ways.

First, as noted above, it is immediately apparent upon examination of the ant fauna in our study that most species are nesting in wood. Coarse woody debris offers many advantages over soil-nesting in cool climates, especially in post-harvest sites where the water table is commonly elevated (Sun et al. 2001). Coarse woody debris has a low specific heat (1.23 kJ^{-1} kg^{-1} C^{-1} at 25 °C (Wenzl 1963)), which should allow it to gain heat quickly through insolation and then hold some of that heat through the night as a consequence of its mass. The material itself offers extensive nesting opportunities and allows a colony to move brood internally to maximize heat opportunities. It also elevates the colony above both the ground which, as noted above, is often wet (Ballard 2000; Sun et al. 2001), and low vegetation such as grass.

This relationship between ants and CWD is not evident in Fennoscandia where a special publication comprehensively reviewing the ecology of woody debris rarely mentioned ants (Jonsson and Kruys 2001). Post-harvest CWD volumes in Fennoscandia, however, have been reported as much lower than is typical for managed Canadian forests.

Volumes in Sweden were reported on average at only 6.1 m^3 ha^{-1} (Fridman and Walheim 2000) as compared to our study, in which 8-10 year post-harvest sites had an average volume of 119.9 m^3 ha^{-1}. Such volumes are fairly typical for stands in BC (Lofroth 1998). Thus low volumes of CWD in Fennoscandian forests may be one part of the explanation for the lack of use of wood by ants.

The second notable difference between the ant community in this study and those reported from Fennoscandian forests was the domination of mature forest sites by thatching ants of the *Formica rufa* species-group (Savolainen et al. 1989). These species are relatively large (typically >8 mm), abundant and capable of monopolizing resources through aggression (Savolainen et al. 1989). Although thatching ants of the *F. rufa* group (e.g., *F. obscuripes*, *F. planipilis*) are present in the drier and warmer forests in BC, they were not present in the forests examined in our study. Soil moisture may also be a factor here. The focal sites for our study were located within a moist biogeoclimatic subzone (Meidinger and Pojar 1991) as this was the most common biogeoclimatic subzone in this region. Further, clearcut harvesting has been documented to lead to a rise in soil moisture (Ballard 2000, Elliot et al. 1998). Moist soil, especially in a cool, late seral forest can act as a heat sink for colonies initiating in or near the soil, thus removing soil-dependent species from the community.

The paucity of thatching *F. rufa* group ants in some North American forests has been noted and several hypotheses have been suggested to explain this observation (Jurgensen et al. 2005). Among these are temperature, moisture, disturbance frequency, bear predation and competition from carpenter ants. Data on thatching nest densities in forests where they do occur in BC are lacking although anecdotal observations of their abundances suggest they may only reach densities that are typical for Fennoscandian forests under infrequent circumstances (McIver et al. 1997; Lindgren, unpublished data). They are certainly found in disturbed areas where bear predation is common and carpenter ants are present, although their interactions with the latter may merit closer examination. Tentatively, this suggests that moisture and temperature, especially in the soil, may be central in explaining their relative absence in British Columbian sub-boreal forests. Still, this is not entirely satisfactory and further investigation is warranted to answer this question. In particular, the interaction of moisture with temperature needs much more attention.

The primary *Formica* spp. wood-nesting ant filling the general niche of thatching ants in our study was *F. aserva*. This species disappeared relatively early during seral advancement, however, presumably as a consequence of poor tolerance to declining temperatures, as noted earlier (also see Chapter 5). This leaves *C. herculeanus* as the only large, territorial and aggressive ant in these sub-boreal forests. *Camponotus herculeanus* does not appear capable of thriving in non-harvested sites either (Figure 3.3), however, leaving this niche mostly vacant. Thus, non-harvested forests in this cool region are largely devoid of ants with only the occasional colony of *M. alaskensis* or *L. muscorum* exploiting scattered suitable microsites.

Summary

Ant communities appear to thrive in the early seral ages created in the managed forest landscapes of the sub-boreal forests of west-central British Columbia. The ant communities are well defined by seral age and appear to show a predictable pattern of development, likely constrained by temperature as stands regenerate and closing canopies restrict insolation to the forest floor. Each species of ant has unique life history strategies and environmental tolerances that shape the overall ant community at each seral age. While large bodied and aggressive ants such as *F. aserva* and *C. herculeanus* develop through early seral ages, as evidenced by pitfall trap captures, the most common colonies are small-bodied, small colony species such as *L. muscorum* and *M. alaskensis*. Only *M. alaskensis* appears marginally tolerant of the cold and moist conditions typical of non-harvested sites. This genus of ant has been documented as tolerant of similar cool forests in Quebec, Fennoscandia and Russia.

We were unable to conclusively document any soil or litter nesting species in this study, unlike equivalent forests in Fennoscandia. The reason for this is still uncertain but the near absence of woody debris as a nesting alternative in Fennoscandian forests, and the cool temperatures and high soil moisture of forests in west-central BC may be factors. The use of coarse woody debris by most species of ants in this study is a defining characteristic of this fauna and is probably most advantageous as a mechanism to avoid nesting in soil. Overall the ant communities of these forests must confront a temperature limited environment and life history strategies must adapt to maximizing heat gain and avoiding heat loss.

Chapter 4. Critical habitat elements, with an emphasis on coarse woody debris, associated with ant presence or absence in the moist cold sub-boreal forests of the interior of British Columbia[1]

Abstract

Given both the ubiquity and ecological roles described for ants in British Columbia, an understanding of the habitat elements critical to predicting their presence is desirable. We used logistic regression to model the presence or absence of ants in sub-boreal lodgepole pine forests of west-central British Columbia. Methodological emphasis was placed on the association between ants and coarse woody debris (CWD) because of a high degree of utilization of this resource for nesting. Five species of ants, *Camponotus herculeanus*, *Formica aserva*, *F. neorufibarbis*, *Leptothorax muscorum*, and *Myrmica alaskensis,* comprised approximately 90% of all captures in samples of CWD within five seral ages (2-3, 8-10, 13-15, 23-25 yr post-harvest, and non-harvested stands). Seral age, presence of other ant colonies of the same species, decay class of CWD, its surface area, and whether the wood was downed woody debris or a stump, were significant variables affecting ant presence or absence, as determined from logistic regression models. There was a 28% increase in the odds of locating an ant colony in woody debris for every 1 m^2 increase in surface area. All species had an increased likelihood of being found within a 50-m^2 sample if other colonies of the same species were present. In addition, where species showed a significant response, there was positive selection for older decay classes, and the utilization of stumps as compared to downed woody debris. These results are explained in the context of ant species autecology as it relates to living in cool climates.

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[1] First person plural is used throughout this chapter to reflect the contributions of others to both research design and field work.

Introduction

Predicting the presence or absence of species within their geographic range has been of interest to biologists for many years (Steinitz et al. 2005; Vojta 2005). In particular, presence-absence models are important to conservation biologists attempting to define critical habitat elements necessary for species protection (MacKenzie 2005; Littlewood and Young 2008) and increasingly, to identify habitats that may be open to the introduction of invasive species (Worner and Gervey 2006; Watts and Worner 2008). Such models are also of use to ecologists attempting to define the ecological niche of poorly understood species or species assemblages.

Despite the ubiquity of ants in Canadian forests, and their linkage to many ecosystem processes (Gorn et al. 2000; Nkem 2000; Risch et al. 2005), there has been no attempt to define necessary habitat requirements through presence-absence modelling. Ecological work on the boreal ant fauna in Fennoscandia has been more extensive, but has been largely focused on ecological factors shaping community structure. For example, changes in ant community structure with seral advancement, has been described (Punttila et al.1991; Punttila et al. 1994; Punttila and Haila 1996), as well as adaptations to enhance ant survival in cool coniferous forests (Seppä et al. 1995; Punttila 1996). The effects of intra-taxon competition on community structure has also been investigated (Savolainen et al. 1989; Punttila et al. 1996). Unfortunately, no direct consideration has been given to what elements in the habitat are required for the ant community itself.

The current inability to define the critical habitat elements required by ants in Canadian forests is concerning because of the many documented roles that ants are known to play in other ecosystems. In addition to pest control (Finnegan 1974; Torgersen and Mason 1987; Way and Khoo 1992), these include soil-nutrient turnover (Wagner et al. 1997), seed dispersal (Heithaus 1981; Gorn et al. 2000), grain consumption (Brown et al. 1979), and decomposition of organic material (Haines 1978). Ants have also been found to be an important food source for birds (Torgersen and Bull 1995) and large omnivorous vertebrates such as black (Noyce et al. 1997) and grizzly bears (Elgmork and Unander 1999; Swenson et al. 1999).

A dependence of ants upon coarse woody debris (CWD) was emphasized by one study that identified 12 of 19 species near Prince George, in central British Columbia, using woody debris as a nesting medium (Lindgren and MacIsaac 2002). This apparent high rate of use makes this habitat element a prime candidate for closer examination to better define this association. The purpose of this study is to identify the critical habitat elements, with emphasis upon coarse woody debris (CWD), here separated into stumps and downed woody debris (DWD), that affect ant presence-absence in moist-cold sub-boreal lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm) forests of the west-central interior of British Columbia.

Methods

We used records obtained from Houston Forest Products (West Fraser Mills Ltd., Houston, British Columbia), to identify non-harvested and post-harvested sites (seral ages: 2-3, 8-10, 13-15, 23-25 years) in lodgepole pine-leading stands within the sub-boreal spruce (SBS) biogeoclimatic zone and moist-cold (SBSmc) subzone (Meidinger and Pojar 1991). More specific site information and methodologies for sampling ants in woody debris, monitoring site temperatures, and identifying ant species are provided in the Methods section for Chapter 3.

We used logistic regression to relate site variables to ant presence or absence. After assessing for correlations, model variables were identified by backwards stepwise logistic regression using STATA (Proc logit) (STATA 9.2 ©1985-2007), as no earlier studies existed to allow for *a priori* selection of potential model variables. Initial categorical variables included: nesting location (downed woody debris or stumps); seral age class (Note: seral age class (1-5) was chosen over mean site temperature for modelling because of concern that the use of temperature would give the appearance of a continuous variable, when, in fact, the data would consist of only a single temperature parameter characterizing the seral age. Temperature data were not collected for each piece of woody debris), and decay class. Initial continuous variables included: large end diameter; length (height in stumps); piece surface area; surface area of all woody debris within 50-m^2 sample; percentage bark; number of colonies of the same species of ant within same piece of wood; number of colonies of same species of ant within 50-m^2 sample; number of colonies of other species of ant within the same piece of wood; number of colonies of other species of ant within the 50-m^2 sample. Where correlations exceeded 0.5 only one parameter was chosen for inclusion in the initial model. In addition, we dropped specific categorical classes if that class contained less than four data to avoid quasi-complete separation (Tables 4.1 and 4.2) (Menard 2002). Only parameters for which the *P*-value was <0.05, were maintained in the final model. A *post-hoc* analysis for co-linearity was performed on the final model parameters to ensure no values were <0.2. We assessed the accuracy of each final model by its Receiver Operating Characteristic (ROC) area under the curve (AUC) score following Swets (1988), given that the sampling methodology would be expected to have a high accuracy in measuring presence/absence.

Table 4.1. Number of colonies of five species of ants identified as nesting within five decay classes of coarse woody debris (following Maser et al. 1979). Sampling occurred across five seral ages of sub-boreal forest in west-central British Columbia from 2003-2005. Note: thirty-five pieces of CWD were lacking decay class data.

Ant species		Decay Class				
		1	2	3	4	5
Camponotus	absent	31	1268	815	192	8
herculeanus	present	0	20	32	7	0
Formica	absent	31	1260	815	194	8
aserva	present	0	18	32	5	0
Formica	absent	31	1248	826	192	7
neorufibarbis	present	0	30	21	7	1
Leptothorax	absent	31	1018	687	183	7
muscorum	present	0	260	160	16	1
Myrmica	absent	31	1182	699	152	6
alaskensis	present	0	96	148	47	2

Table 4.2. Number of colonies of five species of ants identified as nesting within coarse woody debris across five seral ages of sub-boreal forest in west-central British Columbia from 2003-2005.

Ant species		Seral Age (yr)				
		2-3	8-10	13-15	23-25	Non-harvested
Camponotus herculeanus	absent	467	736	545	277	298
	present	6	20	24	13	0
Formica aserva	absent	473	730	540	301	298
	present	0	26	29	1	0
Formica neorufibarbis	absent	470	709	566	292	298
	present	3	47	3	10	0
Leptothorax muscorum	absent	456	537	387	277	297
	present	17	219	182	25	1
Myrmica alaskensis	absent	467	687	434	228	283
	present	6	69	135	74	15

Results

In total, 14 species of ants were identified from the CWD sampling in this study (see Chapter 3, Table 3.3). Of these, five species (*Camponotus herculeanus* (L.), *Formica aserva* Forel, *F. neorufibarbis* Emery, *Leptothorax muscorum* (Nylander), and *Myrmica alaskensis* Wheeler) (see Appendix III for basic information relating to the natural history of these species) represented greater than 90% of all identifications. As a consequence, these species will be the focus of the results and discussion reported here.

The highest mean daily soil temperatures were recorded in the earliest seral age (2-3 yr post-harvest) with temperatures just over 14 °C (See Chaper 3, Table 3.2). Litter temperatures declined steadily with seral age and were below 10 °C in non-harvested plots. Daily mean amplitudes also dropped with increasing seral age. Mean amplitudes in 2-3 yr post-harvest plots were just under 18 °C although the standard error (8.5 °C) is high for these plots as one plot datalogger failed, reducing the number of plots providing data to two. A datalogger failure also occurred in one non-harvested plot where mean daily amplitudes were recorded below 5 °C from the two remaining plots.

Assessment of the models developed for each of the five most common species as well as for all five species collectively, by their ROC AUC score, indicates that the models reliability can be considered as "confident" (ROC AUC score between 0.75 and 0.9 (Table 4.3) except for the *F. neorufibarbis* model which had a ROC score of 0.72 (Swets 1988).

Several patterns across species were evident from the logistic regression models (Table 4.3). The first was the strong response to seral age. Ant colonies (all species pooled) were more common in seral ages 8-10, 13-15 and 23-25 yr post-harvest, with the greatest abundance in 13-15 yr post-harvest plots ($\beta = 1.63$, $P < 0.001$) (Table 4.3). Colonies were least abundant in both 2-3 yr post-harvest plots ($\beta = -1.48$, $P < 0.001$) and non-harvested plots ($\beta = -1.93$, $P < 0.001$). Only a total of 16 colonies of ants representing two species were identified in non-harvested plots (Table 4.2). The extent to which each species increased or decreased in colony numbers varied with each seral change although most, *F. neorufibarbis* excepted, followed the pattern noted above (Table 4.3).

The second significant pattern was the relationship between the presence of other colonies of the same species within the 50 m^2 sample in which the colony was identified. The odds of finding a member of a particular species always increased if other members of that species were present within the sample. This varied from a weak response for *L. muscorum*, which showed a 19% (i.e., a odds ratio of 1.19) increase ($P < 0.001$) in the odds of finding this species for each colony already located, to over 300% for *F. aserva* ($P < 0.001$) (Table 4.3).

This pattern was reversed for two species (*C. herculeanus* and *F. aserva*) when considering the presence of other species within the 50 m^2 sampling unit. There was a weak 5% reduction in the odds of finding *C. herculeanus* for each colony of another species identified but a stronger 59% reduction for *F. aserva*. When the spatial scale was reduced to the same piece of wood, three species, *F. aserva*, *L. muscorum*, and *M. alaskensis*, showed a decrease in the odds of their presence with each identification of another species. For example, there were 34% lower odds ($P = 0.002$) of finding a colony of *M. alaskensis* in a piece of wood for each colony of another species also located in that wood (Table 4.3).

Three species (*C. herculeanus*, *L. muscorum*, *F. aserva*) responded positively to pieces of wood with a larger surface area. There was a 120% increase in the odds of finding *C. herculeanus* in pieces of wood with each increase in surface area of 1 m^2 ($P < 0.001$) and

Table 4.3. Parameter coefficients (β with SE in parentheses) obtained from backwards stepwise logistic regression for five species of ants and all ants collectively. Data derived from coarse woody debris sampling of 5 seral ages (2-3, 8-10, 13-15, 23-25 years post-harvest and non-harvested forest) of sub-boreal forest in west-central British Columbia from 2003-2005. Each model differs from the constant only model with $P < 0.001$. Odds ratios (provided in italics in square brackets below the parameter estimates) are not included for categorical variables where the odds ratio cannot be meaningfully interpreted. CAHER: *Camponotus herculeanus*; FOASE: *Formica aserva*; FONEO: *Formica neorufibarbis*; LECAN: *Leptothorax muscorum*; MYALA: *Myrmica alaskensis*.

Model Parameter	All Ants	CAHER	FOASE	FONEO	LECAN	MYALA
Nest Location						
Downed Woody Debris	-0.15 (0.05) $P = 0.006$		-0.83 (0.16) $P < 0.001$			-0.29 (0.08) $P < 0.001$
Stumps	0.15 (0.05) $P = 0.006$		0.83 (0.16) $P < 0.001$			0.29 (0.08) $P < 0.001$
CWD surface area of piece (m^2).	0.25 (0.12) [*1.28*] $P = 0.038$	0.79 (0.19) [*2.2*] $P < 0.001$	0.73 (0.28) [*2.08*] $P = 0.008$		0.63 (0.15) [*1.89*] $P < 0.001$	
CWD surface area within 50 m^2 sample (m^2)					-0.05 (0.02) [*0.95*] $P = 0.02$	-1.11 (0.04) [*0.89*] $P = 0.002$
Other ant colonies of the same species within 50 m^2 sub-section	a	0.87 (0.10) [*0.39*] $P < 0.001$	1.11 (0.14) [*3.03*] $P < 0.001$	0.84 (0.11) [*2.31*] $P < 0.001$	0.17 (0.02) [*1.19*] $P < 0.001$	0.44 (0.03) [*1.55*] $P < 0.001$

Table 4.3 Continued

Model Parameter	All Ants	CAHER	FOASE	FONEO	LECAN	MYALA
Other colonies of different species with 50 m^2 sub-section	a	-0.05 (0.03) [*0.95*] $P = 0.04$	-0.89 (0.25) [*0.41*] $P < 0.001$			
Other colonies of different species in same piece of CWD	a		-0.93 (0.24) [*0.41*] $P < 0.001$		-0.26 (0.11) [*0.77*] $P = 0.02$	-.41 (0.13) [*0.66*] $P = 0.002$
Percentage Bark (%)						0.01 (0.00) [*1.01*] $P = 0.4$
Coarse Woody Debris						
Decay Class 2	-0.38 (0.08) $P < 0.001$		-0.79 (0.22) $P < 0.001$			-0.51 (0.13) $P < 0.001$
Decay Class 3	0.20 (0.08) $P < 0.001$		0.10 (0.21) $P < 0.001$			0.15 (0.11) $P < 0.001$
Decay Class 4	0.18 (0.12) $P = 0.13$		0.69 (0.30) $P = 0.02$			0.36 (0.16) $P = 0.02$
Seral Age Class						
Seral Age 1 (2-3 yr post-harvest)	-1.48 (0.16) $P < 0.001$	-1.02 (0.35) $P = 0.003$	b	b	-1.41 (0.21) $P < 0.001$	-1.43 (0.35) $P = 0.01$
Seral Age 2 (8-10 yr post-harvest)	1.19 (0.10) $P < 0.001$	-0.26 (0.22) $P = 0.24$			0.33 (0.11) $P = 0.003$	0.04 (0.17) $P = 0.80$

Table 4.3 continued

Model Parameter	All Ants	CAHER	FOASE	FONEO	LECAN	MYALA
Seral Age Class continued						
Seral Age 3 (13-15 yr post-harvest)	1.63 (0.11) $P < 0.001$	0.56 (0.24) $P = 0.02$			0.88 (0.11) $P < 0.000$	0.06 (0.18) $P = 0.70$
Seral Age 4 (23-25 yr post-harvest)	0.63 (0.12) $P < 0.001$	0.72 (0.22) $P = 0.001$	b		0.20 (0.15) $P = 0.17$	1.04 (0.18) $P < 0.001$
Seral Age 5 (Non-harvested)	-1.97 (0.24) $P < 0.001$	b	b	b	b	0.27 (0.25) $P = 0.27$
Receiver Operating Characteristic	0.79	0.81	0.86	0.72	0.78	0.88
Pseudo-R^2	0.22	0.18	0.22	0.09	0.16	0.32

a: These parameters were not applicable in this model and were not included.

b: These specific data have too few of the species to make a solution reliable (Menard 2002).

a 108% increase for *F. aserva* ($P = 0.008$) (Table 4.3). Finally, two species (*F. aserva*, *M. alaskensis*) were both more likely to be found in stumps than in downed woody debris and found in wood of decay class 3 or 4 as compared to decay class 2, despite the abundance of wood in decay class 2 (Figure 4.1). Only one parameter that was included in the initial full models failed to show significance ($P \leq 0.05$) for any species. This was the number of colonies of the same species within the same piece of wood.

Discussion

The major objective of this study was to determine what environmental attributes, with an emphasis on woody debris, were significant in determining ant presence or absence. Accurate modelling of presence-absence has traditionally been considered difficult because of uncertainty in the veracity of absence data (Vojta 2005, Kéry and Schmidt 2008), especially when modelling highly mobile vertebrate distributions. The solution has traditionally been to resample habitat to develop probabilities of absence (Mackenzie 2005). In the case of social insects such as ants, however, the ability to locate and accurately identify largely stationary colonies (Hölldobler and Wilson 1990), especially when they are nesting in a readily identifiable substrate such as coarse woody debris, should reduce the risk associated with single sampling methodologies and make dichotomous modeling techniques such as logistic regression appropriate.

A strong feature emerging from the regressions (Table 4.3), which has been extensively discussed in Chapter 3, is the effect of seral age on three of the five common species in this study. *Formica neorufibarbis* and *F. aserva* will be discussed later as they are the exceptions here, possibly because of their interdependence. We consider seral age as a proxy for

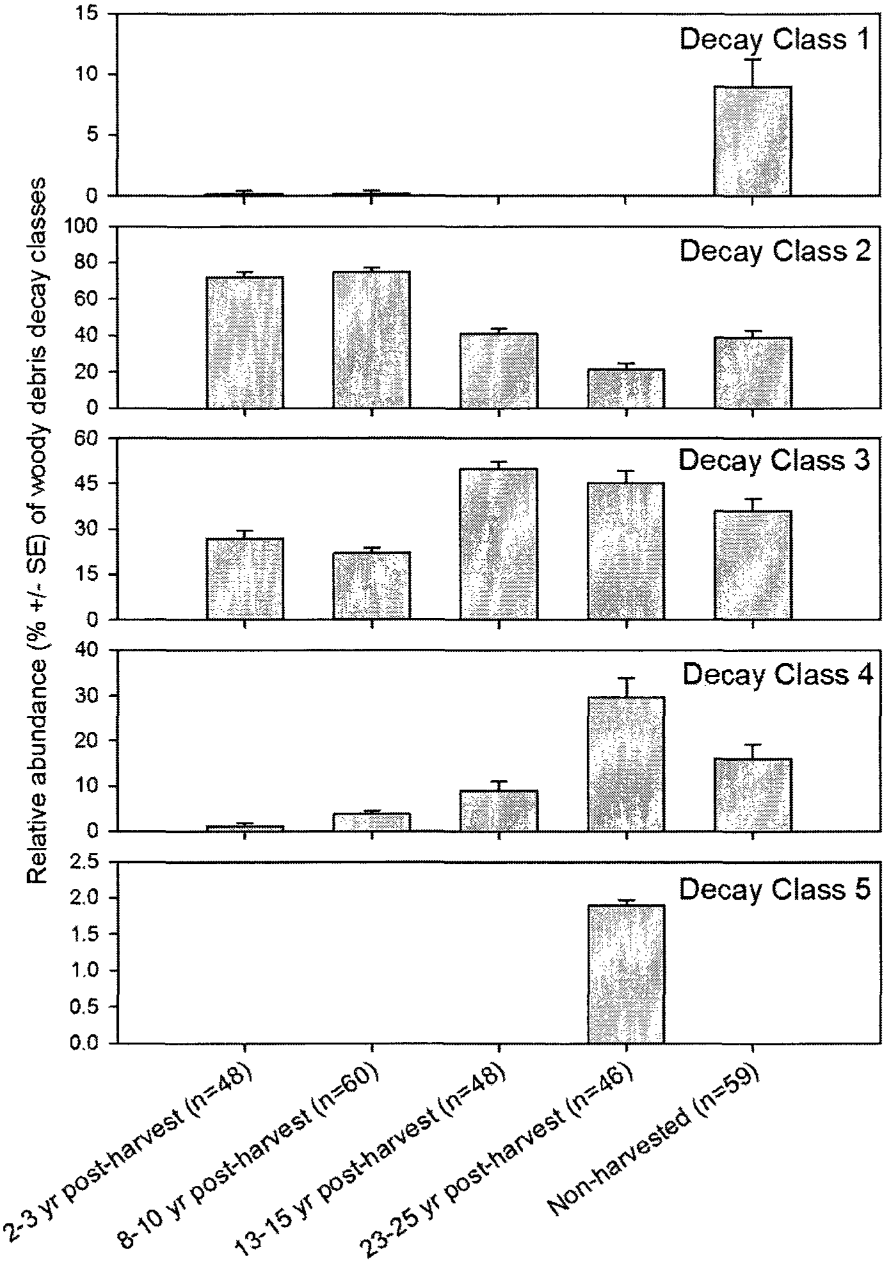

Figure 4.1. The mean relative distribution of decay classes (following Maser et al. 1979) in $50m^2$ samples for coarse woody debris and stumps from 5 seral ages in the moist cold sub-boreal (SBSmc2) forests of the west-central interior of British Columbia. Samples collected from 2003-2005.

temperature (see Chapter 5) through the decreased insolation associated with a developing forest canopy, and consider it one of the most important variables affecting the presence or absence of ants in these forests. Ant communities, overall, build through the first three seral ages (Table 4.2) where litter temperatures between June and August had means ranging from approximately 14 to 12 °C. As seral age progressed beyond this, the ant community began to decline. Non-harvested sites, where mean daily temperatures between June and August were below 10 °C, hosted virtually no ant colonies, suggesting that temperature appears to be the most powerful force shaping overall ant presence or absence. See Chapter 3 for a more complete discussion of this subject.

Models were limited on occasion by complete or quasi-complete separation of data, that is, the complete or near absence of ants in specific seral ages (Table 4.2), which confounds logistic analysis, requiring that some seral ages be dropped for some species (Menard 2002). For example, *F. aserva* was completely absent in 2-3 yr post-harvest sites, increasingly common until reaching 13-15 yr post-harvest sites and then reduced to only 1 record in 23-25 yr post-harvest sites (Table 4.2). Despite the rise and sudden decline with seral age, these comparisons had to be dropped from the models, making it appear seral age was not an important variable for this species. Subjectively, however, when considering all evidence, one can deduce that 2-3 yr post-harvest plots are devoid of this species due to insufficient time for colony founding, whereas approaching 23-35 yr, canopy closure has led to insufficient temperatures to sustain colonies of this highly thermophilic species. Hence, in cool sub-boreal forests, *F. aserva* is restricted to older severely disturbed areas, occurring only after canopy removal.

The second feature shared across all species was the increase in the odds of finding a given species of ant if a colony of that same species has already been located within its 50 m^2 sampling unit (i.e., there is clustering). One possible explanation for this is that four of the five common species of ants in this study are known to be polygynous (i.e., colonies contain multiple queens). Polygyny has been documented in *F. aserva* (Savolainen and Seppä 1996), *F. neorufibarbis* (Francoeur 1983; Billeck 2001, 2003), and is considered a general characteristic of *Myrmica* spp. (Elmes and Keller 1993), and *Leptothorax* spp. ants (Heinze 1993b, Heinze et al. 1996). Species displaying this characteristic often, but not exclusively, reproduce through colony budding. Budding is a type of dependent nest founding (Stille 1996), in which one or more newly mated queens, with workers, disperse by walking from their natal nest to a new nesting site (Heinz 1993b; Punttila et al. 1994).

Polygyny may arise when the dispersal of solitary queens is associated with a high mortality risk, as is reported for cool climates (Rosengren et al. 1993). Solitary ants of *Leptothorax* spp. were shown to have a lower survival rate through the winter than those clustered in groups of 50 (Heinze et al. 1996). An as yet undescribed species of *Leptothorax* in eastern Canada (*Leptothorax* sp. A), in which many virgin queens were wingless, making colony foundation through budding obligatory, has been described (Heinze 1993b). Polygyny and subsequent budding would reduce the risk of colony extinction and allow the species employing this strategy to begin to spread within isolated suitable patches. It is important to note, however, that while budding is a dispersal option for many species of polygynous ants, it is unlikely to be exclusive, and dispersal by flight is also utilized (Cherix et al. 1991).

Finding additional colonies of *C. herculeanus* was also improved when other colonies were located (Table 4.3) despite the fact that this species is monogynous (Heinze and Hölldobler 1994) except in rare circumstances (Akre et al. 1994). It is common, however, for this species to establish satellite colonies in which larvae and pupae may be raised, making it difficult to distinguish natal from satellite nests and giving the appearance of multiple colonies (Hansen and Klotz 2005). This form of polydomy may yield similar benefits to polygyny. It is also possible that as the forest matures, certain satellite nests may find themselves in thermally more suitable locations and the colony could shift the natal nest to that location. This has not been documented, although satellite nests of *C. herculeanus* have been shown to accept new queens and becoming natal in this manner (Akre et al. 1994).

Although polygyny has been documented for *F. aserva*, the degree of polygyny is weak. An analysis of genetic relatedness within nests of this species in Alberta, adjusted for rates of multiple mating typical of its species-group, suggested an average of 1.3 queens per colony (Savolainen and Seppä 1996). Field observations reported by the same authors were consistent with this finding. Clustering, while it may be promoted by weak polygyny, likely also relates to the parasitic dependent nest founding behaviour which is believed to be common within the *F. sanguinea* species-group to which *F. aserva* belongs (Hölldobler and Wilson 1990; Mori and Moli 1998). Newly mated queens of this species-group have been observed to initiate a colony by entering nests of ants within the *F. fusca* species-group, killing the resident queen, and taking over the existing foreign colony, especially incipient colonies. *Formica neorufibarbis* is a member of the *F. fusca* species-group and is the most likely host species for this form of parasitic dependent nest founding in this study area. As *F. neorufibarbis* is polygynous, its distribution through budding may then shape the initial distribution of *F. aserva*, explaining the clustering illustrated in the regression model (Table 4.3). Thus, it is most likely that the inclusion of the model parameter relating to the positive effect of the presence of the same species is an indicator of polygyny, polydomy, and/or parasitic dependent nest founding based on a polygynous host species.

Although polygynous and polydomous colony expansions may be a common mode of colony spread in boreal forests, queen flights into new habitat is also common (Cherix et al. 1991; Heinze 1993b; Punttila 1996) and the regression models may provide some information about habitat selection. Habitat selection during such flights has been little studied because of the difficulties in exactly anticipating the timing of mating flights and following queens as they disperse. In one rare study conducted in the eastern United States, it was determined that queens of the species *Lasius neoniger* Emery and *Solenopsis molesta* (Say) were usually capable of avoiding unsuitable habitat at the landscape element level (i.e., forest vs. meadow in this study) during their mating flights (Wilson and Hunt 1966). Of the thousands of mated *L. neoniger* queens observed in their study, only three were later found in the forest, leading to the hypothesis that a form of coarse- and fine-filter was used during the nuptial flight. It was suggested that queens landed randomly within a suitable landscape element (e.g., meadow), but once on the ground queens had to locate the best nesting site within a few meters or increase the risk of predation if they travelled any greater distance.

At the coarse scale of landscape elements, solitary queens were never located in non-harvested stands but were frequently recorded in early seral ages (e.g., no *Camponotus* queens were located in strip sampling in non-harvested sites but 18 were located in the 2-3 yr post-harvest sites). Rare colonies of *L. muscorum* and *M. alaskensis* were located in non-harvested stands, but only where there were either small openings in the canopy or more open forest structure, indicating that some queens must disperse within this landscape element and possibly select such openings at an intermediate scale. At the intermediate 50 m^2 scale in post-harvest sites, odds ratios derived from wood surface area (Table 4.3) did not show strong selection, indicating that it either may not be an important factor or is simply the wrong scale for selection.

It was notable that one parameter only weakly expressed overall was an effect of the presence of different species within the 50 m^2 sampling unit (Table 4.3). *Camponotus herculeanus* showed slight reduction (5% odds ratio) in the probability of cohabiting with other species at the 50 m^2 sampling scale and only *F. aserva* indicated a strong negative response (59% odd ratio). It would be expected that there would be reduced odds of locating most ant species within the same 50 m^2 sampling unit of other species, if competitive exclusion was structuring the community as has been documented in other ant communities (Savolainen and Vepsäläinen 1988; Cerdá et al.1997; Alinvi et al. 2008). This finding, in our study, would suggest that allospecific competition is not a significant factor, at least not at this scale. We would suggest that this might arise from the transient environmental conditions typical in these forests. Ants have only a few years before environmental conditions deteriorate (i.e., after 13-15 years post harvest) and may not be able to saturate the environment to an extent adequate to begin to show competition. It should be noted, however, that exclusion was evident for three species (*F. aserva*, *M. alaskensis*, and *L. muscorum*) at the level of the wood itself. In all three cases there was a reduced odds of finding each species if other species were present. Thus, some competition is evident at the nesting scale. It is likely that most colonies establish in uncolonized wood and then repel allospecific arrivals.

The physical characteristics of wood used for nesting (i.e., size, decay class, and use of downed wood debris or stumps) were not strongly selected for across all species. Further, wood use by *F. aserva* may be an artifact of an initial choice by its host species, *F. neorufibarbis*, complicating interpretation (see below). In general, however, where a significant selection of a given physical characteristic is evident in more than one species, the direction of selection is consistent across other species also showing selection. For example, some species select for wood of greater surface area but none prefer smaller pieces, and some species prefer the older decay classes (i.e., decay classes 3 or 4) but none prefer younger (i.e., decay classes 1 or 2). In both specific cases there appears to be a clear advantage to these choices. Larger pieces of wood would be ideal for larger species of ants with large colonies and older decay classes should be easier to excavate for nesting. Some autecological factors may explain why some species of ants did not show a significant selection for these characteristics. In the case of decay class, *C. herculeanus*, is a strong excavator and may not be dependent upon softer wood for nesting. In addition, the lack of preference demonstrated by *L. muscorum* might be explained by the minute size of these ants, where workers are thin and typically only 2.5-3.5 mm in total length. These ants are likely able to exploit tiny cavities beneath the bark or cracks unavailable to other species. *Leptothorax* spp. are known to be pioneer species in boreal forests (Punttila et al. 1994) and may be adapted to exploiting the early decay classes available following natural disturbances. Finally, some species selected stumps as compared to downed woody debris. The rationale for this choice is unclear, although I will suggest one possible advantage to this nesting medium in Chapter 5.

The regression model for *F. neorufibarbis* was notable in that, only the presence of other ant colonies of the same species within 50 m^2 was found to be a significant model parameter. This species was also exceptional in lacking a unimodal distribution across seral ages (Table 4.2). It is possible that the paucity of significant associations is arising from a relationship with *F. aserva*, that is altering its distribution such that parameter associations are conflicting pre- and post-relationship. As noted earlier, *F. aserva* is believed to initiate colonies through parasitic nest founding, using *F. neorufibarbis* in these forests as its most common host. Parasitic nest founding may explain the lack of a unimodal abundance curve as the peak in the *F. aserva* population in 13-15 yr post-harvest stands depresses the *F. neorufibarbis* population. Parasitism might also result in a change of the type of wood used by *F. neorufibarbis*, by removing this species from their initial choice and restricting them to wood not used by *F. aserva*. The significance of parasitic nest founding could be tested by modelling *F. neorufibarbis* wood choice in the earliest seral age, prior to the appearance of *F. aserva*. Unfortunately, there were few *F. neorufibarbis* colonies in the 2-3 yr post-harvest plots (Table 4.2), making it impossible to model wood choice prior to the hypothesized contact with *F. aserva*. In support of this hypothesis, however, it was noted in Finland that a similar relationship did result in the host species being removed from presumed optimal habitat and restricted to sub-optimal habitat (Puntilla 1996).

Summary

Coarse woody debris is clearly a vital resource for the ant community in the sub-boreal forests of west-central British Columbia. Although ants appear to be able to utilize a broad range of woody debris sizes and decay classes, it is clear that large pieces are preferred by many species, especially those forming larger colonies (e.g., *C. herculeanus* and *F. aserva*). Thus the retention of larger pieces of woody debris should be a management objective as ants are ecologically important from a number of perspectives (e.g., as food for bears (Noyce et al. 1997; Elgmork and Unander 1999; Swenson et al. 1999) and birds (Torgersen and Bull 1995). Although the CWD volumes encountered in our study appear adequate for use by the ant fauna, concerns may arise from any significant reduction in post-harvest CWD volumes. Sweden, with much lower post-harvest volumes as compared to British Columbia has already identified over 500 woody debris dependent invertebrates that are at risk of extirpation (Jonsell et al. 1998). Desire to reduce post-harvest CWD volumes, to increase wood fibre availability to emerging bio-energy corporations, should be considered with extreme caution if we want to protect the organisms dependent upon this resource and the ecological processes to which they are fundamental.

Chapter 5. The effect of shading on persistence of ant nests in dead-wood in a sub-boreal forest[1]

Abstract

Ants are known to be a thermophilic fauna with relatively fewer species at higher latitudes. They are ubiquitous in the sub-boreal forests of west-central British Columbia in the early seral ages of forest succession, but individual species begin to disappear at varying seral ages as the canopy closes and insolation declines. In an experiment, we tested for the persistence of 2 wood-nesting ant species in response to reduced insolation through shading in an environment documented to support their normal habitation. Twenty nests of each ant species, *Leptothorax muscorum* in downed woody debris (DWD) and *Formica aserva* in stumps, were randomly divided into control and treatment pairs. The treatment nests were shaded using vertical sheets of landscape fabric placed on three sides for a period of approximately 2 months. Shaded DWD had a mean temperature approximately 2 °C lower than control DWD while shaded stumps were approximately 1.5 °C cooler than controls. At the end of the experiment, we opened all wood and examined them for colonies of each species. A statistically significant reduction in both *L. muscorum* and *F. aserva* colonies was discovered in shaded wood, as compared to controls, in a pattern consistent with the manner in which each species has been observed to respond to advancing seral age. Temperature monitoring during the experiment allowed for comparison of the thermal attributes of shaded and control DWD, stumps, and non-shaded soil. Mean soil temperatures were lower than either stumps or DWD, possibly explaining the near absence of soil-nesting ant species in

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[1] First person plural is used throughout this chapter to reflect the contributions of others to both research design and field work.

these forests. Stumps, in both treatments, were found to have a higher mean temperature and lower temperature amplitude than DWD despite similar volumes.

Introduction

Ants (Hymenoptera: Formicidae) are considered to be a thermophilic fauna (Hölldobler and Wilson 1990). This is evident globally as a decline in species-diversity with increasing latitude (Kusnezov 1957) and elevation (Sanders et al. 2007). Such a decline is also evident within British Columbia. In the grasslands of southern British Columbia (49 °N), Heron (2001) identified 31 species of ants from 13 genera. In the west-central interior of BC (54 °N), 17 species from 6 genera have been identified (See Chapter 3). Of these 17 species, most are present primarily in early seral sites, where insolation reaches the ground, and hence ground temperatures are sufficiently high. The ant fauna in non-harvested forests, where little insolation reaches the ground, is almost non-existent in this region (Higgins and Lindgren 2006).

In a study examining a variety of hypotheses regarding the inverse relationship between elevation and ant species diversity, it was concluded that only temperature-related hypotheses were relevant (Sanders et al. 2007). Ants found at higher latitudes have physiological adaptations to low temperatures that are distinct from those of southern ant communities. They respond more quickly to small increases in temperature, under cool conditions, as compared to ants from lower latitudes (Elmes and Wardlaw 1983; Nielsen et al. 1999). This adaptation is hypothesized to exploit what little heat may be available in a cool climate. This same adaptation was also reported within a single species collected from different latitudes (Elmes et al. 1999). The rate of larval development (Kipyatkov et al.

2004; Kipyatkov and Lopatina 2002), as well as body and colony size, are also influenced by temperature (Kaspari 2005).

In addition to physiological and anatomical adaptations, behavioural adaptations are also evident in temperate climates. Variations in life-history strategies, such as an increasing frequency of dependent nest founding (Heinze 1993a; Seppä et al. 1995) have been noted for boreal ants. This strategy, highly variable in its specific form, involves the establishment of new nests with a pre-existing supply of workers and is thought to be an adaptation to the high rate of mortality associated with independent nest founding by solitary queens (haplometrosis) (Punttila and Haila 1996). In particular, solitary queens have been shown to have a high rate of mortality over the first winter in boreal forests (Heinze et al. 1996). As a consequence, ants in temperate climates appear to be under strong forces of natural selection to adapt to a more challenging environment.

The choice of nesting substrate in temperate climates is another element in which maximizing potential heat gain should be a priority. Northern temperate soils can be cool, and potentially a heat sink, especially if they are moist. Nesting under small rocks or the building of thatching nests are two options for optimizing the thermal environment of the nest. Rocks have a low specific heat (0.75 kJ kg^{-1} °C for average minerals) and high thermal conductance (Hillel 2004) and can therefore gain heat quickly from insolation, unless they are shaded by vegetation. Although soil has approximately the same specific heat (0.8 kJ kg^{1} °C for dry soil) (Brady and Weil 2002) as rock, the low heat conductance of soils arising from their porous structure (Brady and Weil 2002) make rock a much better substrate for heat gain. Suitable rocks for nesting may not always be available, however.

Thatching, another option in cool soils, is a more elaborate and dynamic nesting medium that ants can modify to regulate heat. The low thermal conductance (i.e., high insulation properties) that would be expected of loose thatch, would allow metabolic heat generated by the ants to remain within the nest. It was reported that thatching ants can open or close passageways into their nests to control ventilation and thereby regulate internal temperatures (Rosengren et al. 1987). The primary problem for ants initiating a nest either under rock or building a thatched mound is that the nest must be started in soil. As environmental temperatures decline with increasing latitude or elevation, especially in areas with moist soil, ant communities appear to increasingly utilize dead wood as a nesting resource (Higgins and Lindgren 2006). Dead wood offers a number of desirable qualities for nesting. It is often elevated above the surrounding herbaceous vegetation as a consequence of its diameter, by spanning depressions in the forest floor, or by leaning against elevated rocks or across other pieces of coarse woody debris (CWD), increasing its insolation. It also has a low specific heat that enables it to gain heat quickly through the day (Wenzl 1963), and does not have the high moisture content typical of northern forest soils (Ballard 2000) that can act as a heat sink, especially post-harvest (Elliot et al. 1998; Mäkitalo and Hyvönen 2004). Ants nesting in galleries constructed within wood will also be able to move brood to specific locations in which temperatures are ideal. The heat gain of wood, like rock, is dependent upon external sources, however. Wood can gain or lose heat through conduction with the soil, conduction and convection with the air, or through insolation (i.e., radiative heating). Insolation through exposure to the sun should be very important in cool early seral forests.

In this chapter, we experimentally explore the relationship between temperature and nest site selection, by two species of ants, *Leptothorax muscorum* (Nylander) and *Formica aserva* Forel (formerly *F. subnuda* Emery). *Leptothorax muscorum* and *F. aserva* are common members of the sub-boreal and boreal ant communities in Canada (Francoeur 1983, 1997; Gregg 1972). *Leptothorax muscorum* (see Appendix III for more complete natural history) is a pioneer species in boreal forests (Punttila et al. 1994), and is common in CWD (Higgins and Lindgren 2006). These small ants, with workers not exceeding 5.0 mm (typically 2.5-3.5 mm), form colonies consisting of a few dozen workers, often with multiple queens (Heinze 1993a). As *Leptothorax* spp. colonies have been documented at densities of up to $4/m^2$ (Heinze 1994), suggesting a small foraging area, the discovery of foragers on woody debris is likely indicative that their natal nest is within that piece of wood. This allows for the probable identification of nesting sites in wood without destructive sampling.

Formica aserva (see Appendix III for more complete natural history) in contrast is a larger ant with average worker size of approximately 6-8 mm (Naumann et al.1999) that forms colonies known to contain between 3,000-4,000 workers (Savolainen and Deslippe 1996). This ant also frequently nests in CWD, especially stumps (Wu and Wong 1987, see Chapter 4) and is known to be a facultative slave-maker (Savolainen and Deslippe 2001). Firm tapping on wood hosting this species will result in aggressive swarming allowing nest site identification.

As both species, *L. muscorum* and *F. aserva*, demonstrated a decline in abundance with increasing forest seral age (Chapter 3), we hypothesized that both species had a low tolerance to poor thermal conditions. In this chapter, we first tested the hypothesis that ant choice of woody debris over soil, as a nesting resource, was thermally driven. We predicted that woody debris (both downed woody debris and stumps) would be warmer than soil. We then tested the hypothesis that insolation is an additional critical heat source for woody debris nesting ants, by reducing nest temperatures, through shading, and assessing the persistence of each species under such conditions. Finally, we report on some *post-hoc* findings regarding the relationship between downed woody debris and stump temperatures.

Methods

Shading of **Leptothorax muscorum** *colonies in downed woody debris*

We conducted this study between June and August of 2005 in a 15 yr-old post-harvest stand (53°58.2'N, 127°6.6'W) located in the sub-boreal spruce biogeoclimatic zone and moist-cold subzone (Meidinger and Pojar 1991), approximately 55 km south of Houston, British Columbia. Stand age and the time of year were selected to optimize ant colony abundance and activity respectively, based on previous research in this area. The stand was previously pine-leading and had been replanted by the harvesting licensee with lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.).

We located 10 replicate pairs of pieces of downed woody debris (DWD), (i.e., CWD mostly in contact with the soil and exclusive of stumps), containing nests of *L. muscorum* for the examination of shading on colony persistence. One member of each pair was randomly selected as the control. As destructive sampling would have been necessary to confirm the presence of *L. muscorum* colonies in the wood, the presence of active workers on the surface of the wood was used as a proxy. Pieces of DWD lying closest to a 90° azimuth were selected because this position was parallel to the maximal sweep of the sun. Actual piece azimuths ranged from 68-108°. All pieces selected exceeded 2.5 m in length with a minimum large end diameter of 10 cm. We then cut these pieces to 2.5 m by a hand saw, without altering the azimuth, to minimize piece disturbance. Pairs were located so that they were within 20 m of each other, and were matched as closely as possible for large end diameter. All pieces were of decay class 2, following Maser et al. (1979). Large and small end diameters were recorded, and the volume (V) and total surface area (lateral surface area with ends) (SA) were calculated as a geometric frustum (i.e., a truncated geometric cone):

$$V = \frac{1}{3}\pi h(r_1^2 + r_2^2 + r_1 r_2);$$

$$SA = \pi(r_1 + r_2)(\sqrt{(r_1 - r_2)^2 + h^2}) + (\pi r_1^2) + (\pi r_2^2);$$

where h is the length, r_1 is the large end diameter and r_2 the small end diameter. This allowed for the determination of any significant differences in physical characteristics between shaded and control pieces and for comparison to monitored temperature profiles.

The necessary height and length of the shading fence was determined from astronomical data obtained from the University of Oregon, Solar Radiation Monitoring Laboratory, Sun Path Chart Program (http://solardat.uoregon.edu/SunChartProgram.html). Data for the summer solstice (June 21) was used to determine the minimal azimuth of sunrise (45°), maximal azimuth of sunset (315°) as well as maximal solar elevation gain at local zenith (60°). These data were then used to determine the minimum height of the fencing fabric taking into account piece size and offset from a piece azimuth of 90°.

We constructed the shading fences using landscape fabric (Easy Gardener 1.29 × 15.2-m (4 × 50-foot) grey Heavy Duty Commercial Landscape Fabric, Model 25080MJC, for the bottom panel, and Easy Gardener 0.91 × 15.24 m (3 × 50 foot) black Heavy Duty Commercial Landscape Fabric, Model 22342MJC for the top panel) as the fencing material because of its high resistance to tearing. Polyvinyl chloride (PVC) conduit (3.2 cm (1.25 inch) diameter), cut to approximately 60 cm in length with one angled end to ease entry into the ground, were pounded into the ground around the selected woody debris and used to support and anchor 3.7 m long (12 foot), 2.6 cm (1.0 inch) diameter, steel EMT (electrical metal tubing) posts to hold the landscape fabric. PVC sleeves were also pounded into the ground around controls, but steel posts and landscape fabric were omitted. A fence length of 3 m was used along the southern edge of each piece of woody debris with two sides to the east and west also 3m long. The fence was open to the north. Landscape fabric was added to the southern boundary to a minimum height of 2 m and held in place by plastic zip ties. This height was maintained for the southern 1.5 m of each side panel and then height was allowed to drop to 1.2 m for the remainder of the side panel. This configuration blocked any direct sunlight from reaching the woody debris. An approximate gap of 10 cm was provided at the bottom of the fence to allow for movement of air.

Following a trial installation of 2 fences on 6 June, we discovered on 10 June that both had been destroyed by bear activity. These were repaired and left in place. As there was no further disturbance to the trial fences, all fences were put in place on 21 June. No additional damage occurred.

We monitored the temperature of each piece of woody debris using iButton® 1 Wire Thermocron® DS1921G dataloggers (Maxim Technologies, Dallas, TX). One datalogger was placed within each piece of wood near the horizontal and vertical centre on the north facing side. To insert the dataloggers, first a cap approximately 3 cm^2 in area and 1 cm deep was removed, intact from the wood by chisel. Once the cap was removed, a hole 1.8 mm wide was drilled toward the approximate centre of the wood piece. The datalogger was then inserted into the hole and a piece of softwood dowel 1.8 mm in diameter was cut to a length appropriate for each hole. The edges around the dowel were then closed by silicon sealant which also served to seal the cap back in place. String glued to the datalogger ran out of the hole and edge of the cap to facilitate recovery. The dataloggers were programmed to record temperatures each thirty minutes between 06 July and 21 August of 2005. In order to monitor site soil temperatures, ten dataloggers were paired with *L. muscorum* and *F. aserva* treatments, in unshaded areas, at a depth of 10 cm following the protocol of Stathers and Spittlehouse (1990). Five of the ten dataloggers were randomly assigned to *L. muscorum* treatments and five to *F. aserva* treatments. They were programmed to record temperatures over the same time period as those placed in downed woody debris. One of the soil dataloggers failed over the course of the experiment.

The experiment was terminated on 21 August of 2005, 61 days after the placement of the fences. Each piece of woody debris was destructively sampled by hatchet to count the number of *L. muscorum* colonies. A colony was defined as a cluster of more than 15 ants with no visible tunnels connecting to adjacent colonies.

Shading of* Formica aserva *colonies in stumps

The methods and dates for testing the effect of shading on *F. aserva* colonies followed that of *L. muscorum* with a few modifications. First, although *F. aserva* uses both stumps and DWD as nesting material it is more common in stumps in this study area (see Chapter 4) and thus only stumps were examined. Second, stump volume was assessed by considering the stump as a geometric cylinder (i.e., from cut diameter and height) rather than a frustum, as used for DWD, because of the difficulties created by roots in accurately measuring basal diameters at ground level. Third, fence height and lengths were adjusted as appropriate for the size of the stumps. As the diameter of the stumps were much smaller than the 2.5-m DWD lengths used for *L. muscorum*, the southern edge of the fence shading the stumps were never more than 1.5 m in length as compared to 3 m for pieces of DWD hosting *L. muscorum*. Fourth, given that stump diameters were often too large to reach the centre with available drill bits, dataloggers were placed within each stump 10 cm from the north lateral surface at the vertical midpoint. Fifth, at the end of the experiment, colonies were tallied as present when more than 100 workers with larvae and/or pupae were discovered. Most stumps were opened for examination by chainsaw as opposed to hatchet.

Analysis of ant colony response to shading was performed with one-tailed paired t-tests, given the hypothesis that shading would reduce ant colony abundance, using STATA (Proc ttest) (STATA 9.2 ©1985-2007). To ensure that the randomly assigned treatment groups did not differ significantly in wood volume or surface area, two-tailed paired t-tests were performed.

Analysis of wood and soil temperature data

We recovered all dataloggers (soil, downed woody debris, stumps) when the downed woody debris and stumps were opened to count ant colonies. Temperature measurements from each datalogger were obtained and the mean of each time synchronized record (n = 2044 for each datalogger) was taken across dataloggers for each treatment. The resulting mean data were fitted to a sine curve using SigmaPlot (Proc Waveform, Sine, 4 Parameter) (SigmaPlot 11 ©2008). Mean amplitude and temperature parameters derived from the sine curves were used with the standard error and relevant *t* statistic ($t_{(0.05,2044)}$) to determine 95% confidence intervals, which were then used to assess parameters for significant differences.

A comparison of stump and downed woody debris temperatures

Following tabulation of study data is was observed that mean stump temperatures appeared to be higher than those for DWD. Following this observation, stumps and DWD were compared for volume and surface area, and then mean temperatures were assessed for significant differences using 95% confidence intervals.

Results

Soil, stump and downed woody debris temperatures

Both means and amplitudes varied significantly between soil, control stumps and control DWD (Figure 5.1). The mean temperature of control stumps (13.5 °C ± 0.04 (SE)) were higher than control DWD (12.7 °C ± 0.06 (SE)) and soil (11.1 °C ± 0.02 (SE)). All three groups (soil, control stumps and control downed woody debris) significantly differed from each other as indicated by their 95% confidence intervals (Table 5.1). Temperature amplitude (one half full amplitude) means also varied significantly between control stumps (3.0 °C ± 0. 06 (SE)), control downed woody (5.9 °C ± 0.08 (SE)), and soil (1.0 °C ± 0.02 (SE)). It should be noted that while control stumps had the highest mean temperature, control DWD had higher temperature amplitudes (Figure 5.1). As with temperature means, 95% confidence intervals indicated a significant difference between all treatments.

Shading of **Leptothorax muscorum** *colonies in downed woody debris*

No significant differences were found between the volumes (t = 1.01, df = 9, P = 0.34) or total surface area (t = 0.98, df = 9, P= 0.74) of pieces of wood assigned to the control or shaded treatments (Table 5.2). Counts of colonies of *Leptothorax muscorum* in control and shaded pieces of woody debris at the end of the 61 days of shading, however, did differ significantly (t = 2.09, df = 9, P = 0.03) (Table 5.3). Shaded pieces of woody debris hosted a mean of 1.9 colonies of *L. muscorum* as compared to control pieces hosting 2.6 colonies. Sine modelled temperature profiles (Figure 5.2) show statistically significant declines in both amplitude and mean temperature (Table 5.1) in shaded pieces of DWD when compared to

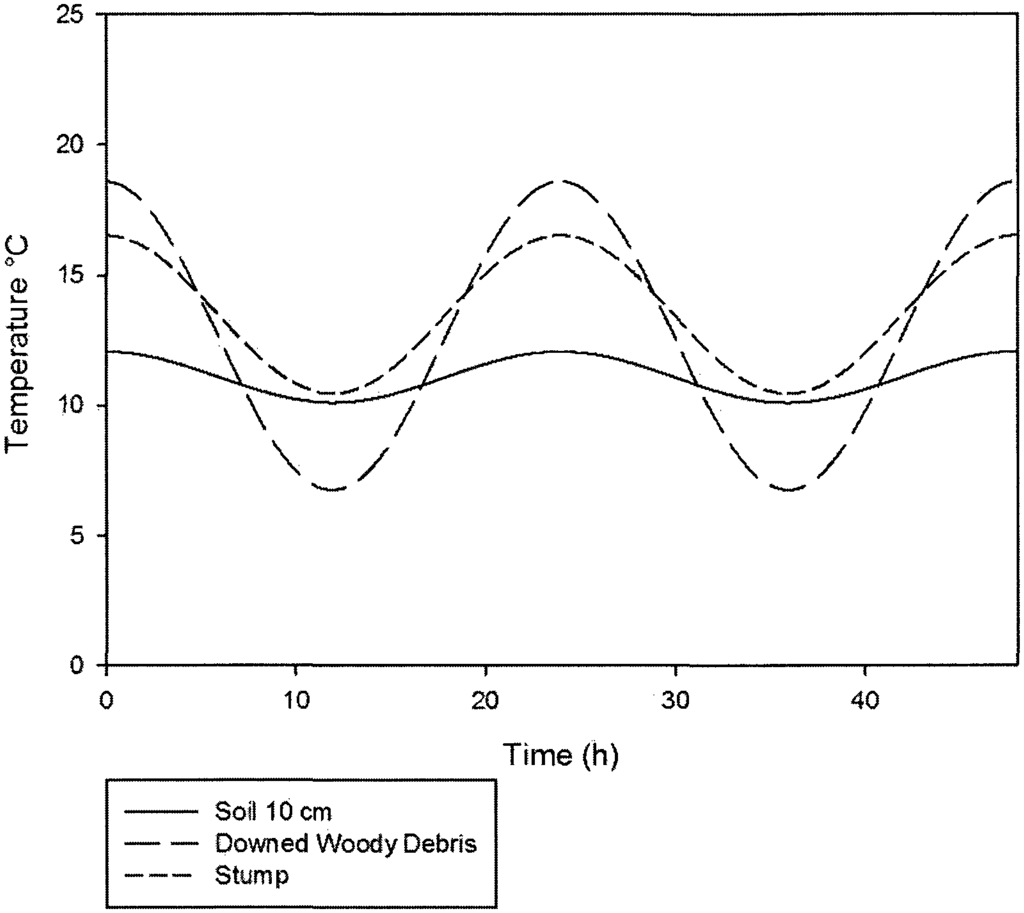

Figure 5.1. Soil (n = 9), control stump (n = 10), and control downed woody debris (n = 10) sine modelled temperature profiles collected over 42 days. Soil temperatures measured at a depth of 10 cm. Stump temperatures measured approximately 10 cm deep below the bark. Downed woody debris temperatures monitored approximately in the centre of the piece. Forty eight hours of modelled data shown here to allow curves to be compared. See Table 5.1 for sine curve fit estimates.

Table 5.1: Sine curve coefficients and model fit estimates of woody debris (stumps and downed woody debris) and soil temperatures monitored over 42 days. Temperature measurements in replicates were time synchronized and models were fit to the mean of each time synchronized replicate. Data were fit to the model $Y = A + B \sin(\frac{2\pi x}{C} + D)$ where A is the mean temperature, B is one half the total amplitude, C is the period (constant at 24 hrs) and D is a horizontal fit parameter. All model and coefficient estimates were $P < 0.001$.

Treatment	A (°C ±SE)	95% Confidence Intervals	B (°C: ±SE)	95% Confidence Intervals	F statistic (df)	R^2
Stump: control	13.5 (0.04)	13.6,13.4	3.0 (0.06)	3.2,2.9	851.7 (3,2044)	0.56
Stump: shaded	12.1 (0.04)	12.2,12.0	2.6 (0.06)	2.8,2.5	628.1 (3,2044)	0.48
DWD: control	12.7 (0.06)	12.8,12.6	5.9 (0.08)	6.1,5.8	1704.1 (3,2044)	0.71
DWD: shaded	10.8 (0.05)	10.9,10.8	4.1 (0.07)	4.3,4.0	1102.2 (3,2044)	0.62
Soil	11.1 (0.02)	11.1,11.1	1.0 (0.02)	1.0,0.9	519.9 (3,2044)	0.43

Table 5.2. Comparison of downed woody debris volumes (m^3) and total surface area (m^2) assigned to the control and shaded treatments. Volumes and surface areas were calculated as a frustum. Treatments compared by 2 tailed *t*-test.

	Treatment		*t*	df	Probability
	Control	Shaded			
Mean volume (m^3 ± SE)	0.054 ± 0.009	0.058 ± 0.009	1.01	9	$P = 0.34$
Mean total surface area (m^2 ± SE)	1.31 ± 0.11	1.36 ± 0.11	0.98	9	$P = 0.74$

Table 5.3. The number of *Leptothorax muscorum* colonies in each paired control and shaded piece of woody debris after 61 days. A colony was counted when a cluster of more than 15 ants were found without tunnels connecting to any adjacent colonies. Treatments compared by 1 tailed *t*-test ($t = 2.09$, df = 9, $P = 0.03$).

Replicate Pair and overall mean	Treatment	
	Control	Shaded
1	0	1
2	3	1
3	4	3
4	3	3
5	3	1
6	2	2
7	3	3
8	2	1
9	3	1
10	3	3
Mean	2.6	1.9

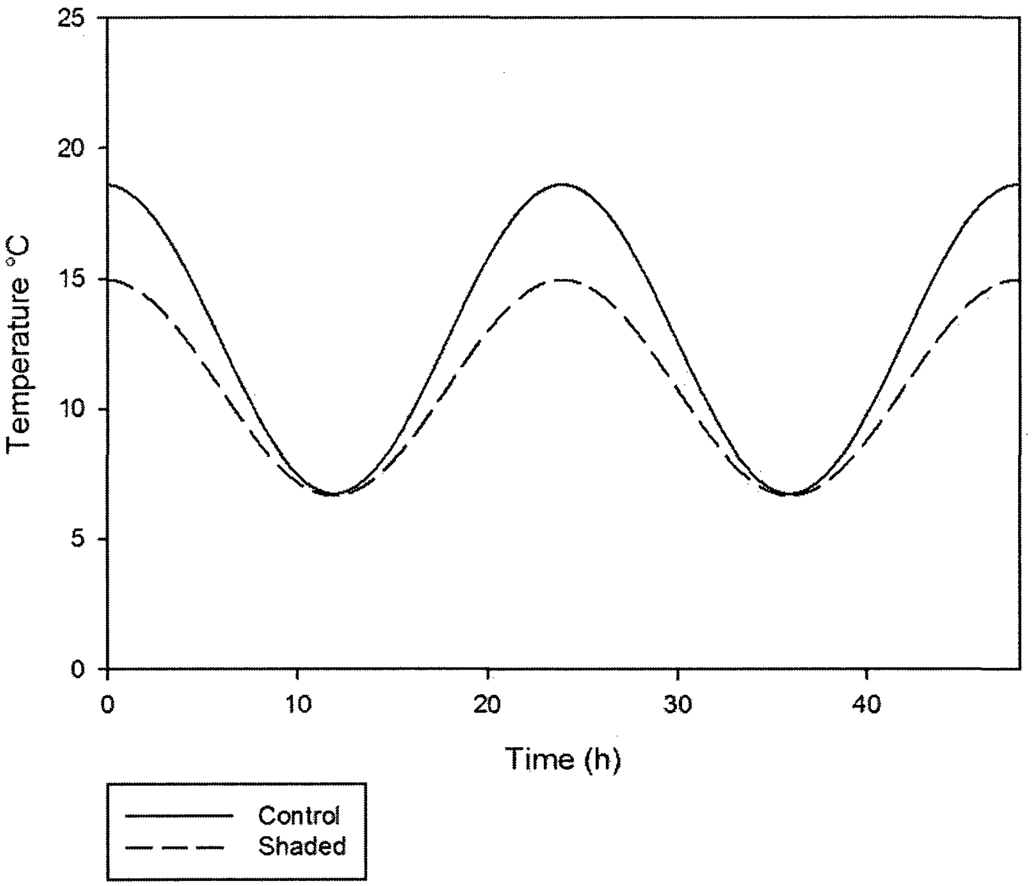

Figure 5.2. Sine modelled temperature profile derived from pooled temperature data collected over 42 days from 10 replicate pairs of control and shaded pieces of downed woody debris hosting colonies of *Leptothorax muscorum*. Forty eight hours of modelled data are shown here. See Table 5.1 for sine curve fit estimates.

controls, as determined from 95% confidence intervals. Mean temperatures of shaded pieces were 1.9 °C cooler than controls and one-half daily amplitudes were 1.8 °C lower (Table 5.1).

Shading of **Formica aserva** *colonies in stumps.*

No significant differences were found between the volumes (t = 1.03, df = 9, P = 0.33) or total surface area (t = 0.29, df = 9, P = 0.74) in contact with the air, of stumps assigned to the control or shaded treatments (Table 5.4). Shaded stumps lost their *F. aserva* colonies with only one exception, while 8 out of 10 control stumps retained their colonies over the 61 days of the experiment (t = 3.27, df = 9, P = 0.004) (Table 5.5). The one remaining colony in a shaded stump was also active in a stump immediately outside of the shading fence.

Sine modelled temperature profiles (Figure 5.3), examined between treatments, show statistically significant differences in mean daily and one-half mean daily amplitudes, as determined from 95% confidence intervals. Shaded stumps were lower in both cases. The mean temperature of shaded stumps was 12.1 °C ± 0.04 (SE), compared to 13.5 °C ± 0.04 (SE) for control stumps. One-half mean daily amplitudes were 2.6 °C ± 0.06 in shaded stumps as compared to 3.0 °C ± 0.06 in controls.

A comparison of stump and downed woody debris temperatures

Plotted temperature data for downed woody debris and stumps showed an unexpected difference between the two (Figure 5.4). Mean stump temperatures were significantly higher than those of DWD for both shaded and control treatments (Table 5.1), as determined from confidence intervals. Mean stump volumes (0.041 m^3 ± 0.011 (SE)) were not significantly

Table 5.4. Comparison of stump volumes and total surface area in contact with the air (m^2) assigned to the control and shaded treatments. Volumes and surface areas calculated as a cylinder. Means compared by 2 tailed *t*-test.

	Treatment		*t*	df	Probability
	Control	Shaded			
Mean volume (m^3 ± SE)	0.05 ± 0.02	0.03 ± 0.01	1.03	9	$P = 0.33$
Mean surface area (m^2 ± SE)	0.42 ± 0.10	0.37 ± 0.07	0.29	9	$P = 0.74$

Table 5.5. The number of colonies of *Formica aserva* present in stumps assigned to either control or shaded treatments. Colonies were counted when more than 100 workers were observed and larvae and/or pupae were present. Treatments compared by paired 1 tailed t-tests ($t = 3.27$, df = 9, $P = 0.004$).

Replicate Pair and overall mean	Treatment	
	Control	Shaded
1	1	0
2	1	0
3	1	0
4	1	0
5	1	0
6	1	0
7	0	1
8	1	0
9	0	0
10	1	0
Mean	0.8	0.1

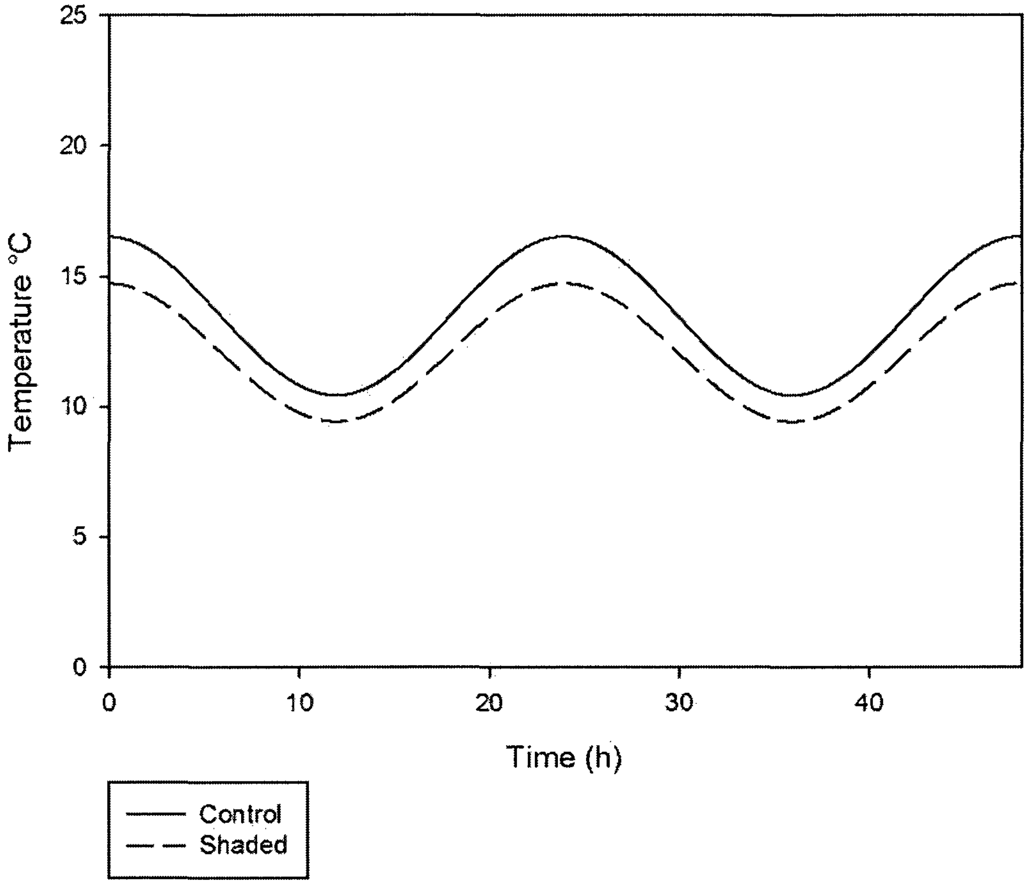

Figure 5.3. Sine modelled temperature profile derived from pooled temperature data collected over 42 days from 10 replicate pairs of control and shaded stumps hosting colonies of *Formica aserva*. Forty eight hours of modeled data are shown here. See Table 5.1 for sine curve fit estimates.

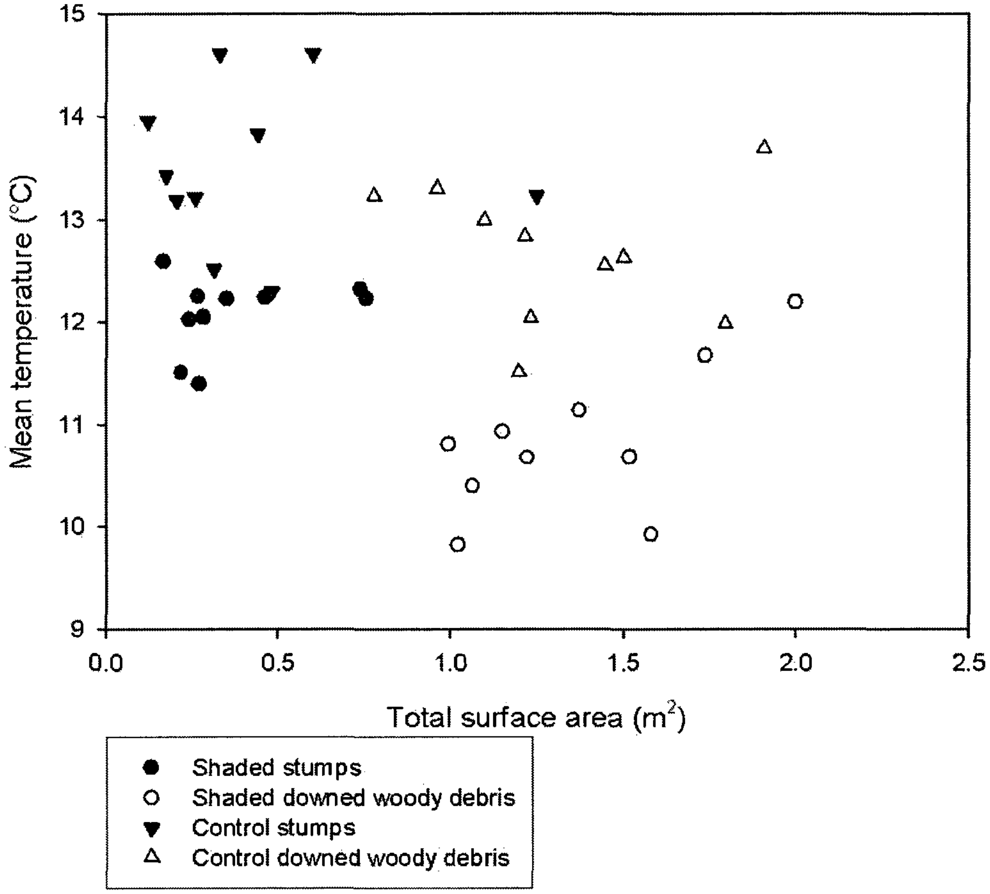

Figure 5.4. Relationship between total surface area in contact with the air and mean temperature in shaded and control stumps (n = 20) and downed woody debris (n = 20). Temperature data measured over 42 days.

different from DWD volumes (0.056 m^3 ± 0.006 (SE)) ($t = 1.5$, $df = 38$, $P = 0.255$), despite a significantly smaller mean surface area for stumps (0.39 m^2 ± 0.06 (SE)) as compared to DWD (1.34 m^2 ± 0.07 (SE)) ($t = 9.79$, $df = 38$, $P < 0.001$). Overall, control stumps were 0.8 °C warmer than control DWD while shaded stumps were approximately 1.3 °C warmer than shaded DWD.

Discussion

Ants in North America appear to utilize wood, rather than soil, as a nesting resource as climate becomes more continental, or as elevation or latitude increase (Higgins and Lindgren 2006). Thus, it is probable that the thermal properties of wood must be advantageous with poor environmental thermal conditions. Our hypothesis that woody debris (both downed woody debris and stumps) would be warmer than soil was supported by the data (Figure 5.1). The very cool soil mean temperature (11 °C), especially in combination with moisture which is typical of the biogeoclimatic zone and subzone (SBSmc) (Meidinger and Pojar 1991), likely do not provide adequate heat for ant colony survival, driving the selection of woody debris.

The most obvious thermal property of wood that would appear advantageous is its low specific heat (1.23 kJ^{-1} kg^{-1} C^{-1} at 25 °C), which would allow for rapid heat gain during the day (Wenzl 1963). This gain can occur conductively from air or soil, convectively from air, or through insolation from direct exposure to sunlight. It was our second hypothesis that the latter would be the most significant. The shading of nests in wood, despite resulting in a relatively modest reduction in mean temperature of approximately 1.5-2.0 °C in downed woody debris (DWD) (Table 5.3) and stumps (Table 5.6), elicited a significant negative response from both *Leptothorax muscorum* (Table 5.3) and *Formica aserva* (Table 5.5). This supports the hypothesis that these ants are dependent on insolation to meet thermal requirements. In addition, the stronger negative response to shading observed for *F. aserva* is consistent with earlier work (Chapter 3 and 4), in which *F. aserva* exhibited a greater sensitivity to advancing seral age, and thus declining ground temperature, as compared to *L. muscorum*.

Work in England (Pontin 1960) demonstrated a decreased survival rate for *Lasius flavus* (F.) and *L. niger* (L.) queens when they were placed in shaded field locations. In addition, *Myrmica* spp. ant larvae in European boreal forests were shown to require mean temperatures of at least 15 °C to develop normally (Elmes and Wardlaw 1983). Given that the mean temperature in control stumps was 13.5 °C and only 12.7 °C in control DWD between June and August, it suggests that the two ant species in this study are tolerant of cooler conditions than found by these authors for *Myrmica* spp. larvae, unless they are able to elevate localized temperatures within brood chambers. The paucity of ants nesting in the soil in the sub-boreal forests of this study, which, as noted, had a mean temperature of 11.0 °C, suggests that these ants must be very close to their thermal tolerance, that is, close to the minimum temperature needed to raise larvae, which is the most temperature sensitive life stage (Elmes and Wardlaw 1983).

Ants normally move their larvae and pupae during the day to maintain the best possible temperatures for growth (Vanderplank 1960; Roces and Núñez 1989). The small colonies of *L. muscorum* observed in this study are normally only found near the surface of the wood with galleries mostly parallel to the wood grain. Thus, they cannot always move deeper into the wood during the night to gain heat as surface temperatures drop. The larger colonies of *F. aserva* often extensively tunnel through their woody nesting medium, presumably allowing them to move both parallel to the wood surface but also more deeply into the wood to optimize thermal conditions. Thus, *F. aserva* should be able to maintain higher mean colony temperatures than *L. muscorum.* Despite this, *F. aserva* seems less tolerant of low temperatures.

Endogenous metabolic heat production has been documented to significantly raise nest temperatures in species of ants producing thatched nests (Horstmann and Schmid 1986; Rosengren et al. 1987). Thatching nest temperatures have been shown to abruptly rise in the spring to temperatures reaching 30 °C, despite snow and ice covering the nest (Rosengren et al. 1987). In addition, thatching ants have been shown to be able to control temperature amplitudes to avoid excessive heating or cooling by opening or closing, respectively, nest entrances to alter ventilation (Horstmann and Schmid 1986). No equivalent research, however, has been performed on wood-nesting ants. Although this experiment was not designed to assess endogenous heat production, the large colony sizes of *F. aserva* and extensive tunneling, might be expected to create a heat signature in the stump if endogenous heat production is high. In the single case of a shaded stump hosting *F. aserva* at the end of this experiment, there was no grossly discernable difference in the mean temperature recorded in that stump (12.0 °C) as compared to the other nine stumps from which *F. aserva* colonies had departed (mean 12.1 °C). Nor were mean temperatures lower in the two control stumps that were not hosting ants (mean 14.3 °C), as should be expected if heat is being generated endogenously, as compared to the eight that were hosting ants (mean 13.3 °C). Given this, it seems unlikely that *F. aserva* is generating endogenous heat, at least not at the scale that affects overall stump temperature. The temperature dataloggers would not, however, have been able to detect localized effects of endogenous heat production within just the brood chambers. Further, it is also unlikely that *L. muscorum* can generate significant metabolic heat given the minute size of these ants and the small colony sizes. Thus, these ants are likely dependent upon external heat sources, especially insolation.

The incidental observation, following the planned analysis for this study, that both control and shaded stumps have significantly higher mean temperatures as compared to DWD in the same treatment, merits mention. Given the equivalent volumes of stumps and DWD in this study, but despite the lower surface area of stumps (Figure 5.4), the higher mean temperature for stumps, suggests that factors other than insolation are also important. We suggest that the higher mean temperatures in stumps arise because the extensive contact of the stump and roots with the soil, maintains the stump at thermal equilibrium with the soil. Thermal gain through insolation, on the exposed stump surface, may displace the equilibrium, but maintains a higher minimum stump temperature at night as compared to downed woody debris that lacks such extensive contact with the soil. The hypothesis of thermal equilibrium is supported by the observation that mean minimum stump temperatures did not go below mean minimum soil temperatures, unlike DWD (Figure 5.1). It should be noted, however, that it might also be possible that despite all wood in this study being assigned to decay class 2, some biological differences may exist between DWD and stumps that enhances microbial metabolic heat and causes the stumps to be warmer. The thermal equilibrium hypothesis noted above could be tested more accurately by placing temperature dataloggers in the soil immediately adjacent to temperature monitored stumps.

The higher mean temperatures associated with stumps might also be hypothesized to have a positive biological affect, especially with respect to thermally constrained ants. Our data (Chapter 4) did not show a strong selction of stumps over downed woody debris as might be predicted if stumps are thermally advantageous. As stumps, however, in their abundant, current, anthropomorphic form (i.e., cut face, low height, initially decay free form), are a relatively recent resource in the forests of BC, it would seem unlikely that ants could have an evolved preference either for or against stumps. Large scale industrial logging in west-central BC only began in the mid-1960s (Hols 1999). Prior to this, the major disturbance element was wildfire (DeLong and Tanner 2006) which does not produce stumps in the form associated with logging. If stumps are advantageous thermally, a microevolutionary behavioural shift may arise in the future. If so, this could be tested by inoculating stumps and DWD with ant colonies, or other organisms, and assessing the length of the life cycle.

Summary

As hypothesized, woody debris offers a warmer nesting environment as compared to soil in the cool-moist forests of west-central BC. This resource may be considered a thermal refugia for ants and possibility other species that find cool moist soil inhospitable. In addition, a reduction in insolation, and consequent reduction in temperature, had a strong negative effect on ant colony utilization of wood. The response of *F. aserva* was more pronounced than that of *L. muscorum*, which was consistent with earlier observations that *F. aserva* disappeared from the ant community, in response to advancing seral age, at an earlier time than *L. muscorum*. Thus, the dependence upon insolation suggests that both species thrive under disturbance conditions where the canopy is removed. The finding that stumps had a higher mean temperature was unexpected but may suggest that this relatively new woody debris resource is a better nesting choice for ants. No preference, however, was noted in related studies and it is possible that this resource is new enough that ants have not developed a selective preference. The testing of colony development time in both DWD and stumps should answer this question.

Chapter 6. Synthesis

> "It appears … that the expression *animal life*, is nearly synonymous with the expression, *animal heat* … The grand necessity, then, for our bodies, is to keep warm, to keep the vital heat in us." Thoreau, *Walden's Pond* (1854).

When Thoreau (1854) was speaking of *heat* in the context of an animals' life, he was framing an argument for what he considered to be the most fundamental necessity of life to both humans and other animals. He was inductively reasoning from observations that clothing, shelter and food were necessary to human life, and the confluent principle he found from each was that of *heat*, or at least heat in the sense that might be used in the 19th century. Thoreau uses the word *heat* mostly in the sense of a state of matter. Today, the most appropriate term would be *temperature,* which refers to the average kinetic energy contained within an object (Giancoli 1991). *Heat*, in its modern form, is a process, and refers to the transfer of kinetic energy between two objects. As discussed in Chapter 5, this occurs through convection, conduction and radiation. Esoteric terminology aside, the findings of this dissertation would have been no surprise to Thoreau, as much of the results here consider the choices of habitat, shelter, and life-history colony founding strategies made by ants in a temperature-limited environment. The need for heat gain appears to be critical in making those choices.

Logistic regression, used to model ant presence or absence in the forests of this study highlighted these choices. Logistic regression is a multivariate maximum likelihood estimation technique designed to estimate dichotomous outcomes (Homer and Lemeshow 1989). Although there has been movement toward blending this technique with information-theoretic techniques such as the Akaike Information Criterion (AIC) (Rushton et al. 2004), the lack of *a priori* knowledge of the system being modelled argued against that approach and toward a stepwise regression. Model discrimination for 4 of the 5 most common species of ants, as estimated by the Receiver Operating Characteristic (ROC), ranged between 0.78 and 0.88, suggesting the models were 'confident' (Swets 1988). Overall the models identified seral age, some physical characteristics of woody debris, and the presence of other colonies of the same species, as variables associated with predicting ant presence or absence. All three are possibly related to the flux of heat.

Seral age, to an ant, is a proxy for temperature, and was a common significant variable in logistic regression modeling. The mean litter temperatures recorded in the 2-3 years post-harvest sites were the highest recorded for any post-harvest or non-harvested site in this study. Following this seral age, mean litter temperatures declined by approximately 1 °C (Chapter 3) with each increase in seral age examined in this dissertation. The mean litter temperatures were approximately 14 °C through June and August in the 2-3 years post-harvest sites. This mean temperature is above the general heuristic minimum for foraging ants of 10 °C (Hölldobler and Wilson 1990), but actually below the temperature considered a minimum for developing pupae (15 °C) in a north European species of *Myrmica* (Elmes and Wardlaw 1983). Despite this, the ant community appeared to thrive, at least over the first 13-15 years post-harvest when mean litter temperatures had declined to approximately 12 °C (Chapter 3) and mean control downed woody debris temperatures were approximately 13 °C (Chapter 5). Given that these temperatures are below those reported as the minimum needed for pupae (Elmes and Wardlaw 1983), it suggests that monitored temperatures are either an underestimate of the actual temperatures experienced by ants, or that the ants in these forests are highly adapted physiologically to tolerate lower temperatures. I suggest that while it is likely that ants seek out microhabitats that are warmer than those monitored in either the litter or woody debris, and that some limited metabolic heat may raise brood chamber temperatures (the generation of metabolic heat on a larger scale was not observed in these studies (Chapter 5)), that the temperature constrained environment evident in these forests would have created strong selective pressures on this ant fauna to adapt physiologically to cool conditions. Given the near complete absence of ants from non-harvested stands, and the response of ants to shading, which decreased mean nest temperatures by approximately 1.5 °C (Chapter 5), we can observe that cool temperatures are strongly selecting against the survival of this fauna. Cool temperatures in regenerating sub-boreal forests is a major stressor for ants and any adaptation to increasing tolerance should be rapidly selected for within the species.

An additional suite of variables that arose in the models related to nesting choice. Of the 17 species identified through all forms of sampling in my dissertation, 16 were either found in woody debris or known to use woody debris for nesting (Chapters 3 and 4). One pragmatic advantage of this relationship was that the localization of most of the ant fauna in woody debris allowed for absolute sampling techniques, per unit area, which was superior to only using relative abundance techniques (Chapter 2, Southwood and Henderson 2000). The fact that woody debris had higher temperatures than those recorded for the soil (Chapter 5), and likely had a lower moisture content typical of northern soils (Ballard 2000), especially post-harvest (Elliot et al. 1998; Mäkitalo and Hyvönen 2004), would seem to be the primary reasons for this choice.

With respect to the choice of specific characteristics associated with woody debris, there were no universal preferences evident across all species. Three of the five species showed a preference for larger pieces of wood and two species showed a preference for woody debris in decay class 3 and 4 as compared to decay class 2. Although wood of decay class 4 was uncommon, wood of decay class 2 and 3 was widely available making the use of later decay stages a genuine choice and likely a consequence of the easier access and ability to form galleries within this slightly softer wood.

The finding that stumps were warmer than downed woody debris was unexpected (Chapter 5). Although control downed woody debris had higher mean maximum temperatures, control stumps had higher overall mean temperatures. I hypothesize that this is due to a higher base temperature arising from stumps coming to thermal equilibrium with the soil when air temperatures are low, a hypothesis supported by the observation that stump temperatures did not go below soil temperatures. Further, if higher mean temperatures are more significant than higher mean maximum temperatures to the ants, this should be a superior nesting resource. Although two species (*F. aserva*, and *Myrmica alaskensis*) did appear to show a preference for stumps, while other species showed no preference, it may simply be that stump selection is arising from characteristics other than heat. My doubts relating to ant choice of stumps because of heat, are based on the fact that stumps are a relatively recent resource associated with anthropogenic activities in sub-boreal forests. If stumps are a better nesting resource, this should be testable by examining the rates of colony growth and the formation of reproductive ants within colonies between stumps and downed woody debris.

The enigma throughout this dissertation has been *F. neorufibarbis*. This species was the only species that did not demonstrate a unimodal abundance distribution across seral ages, peak in abundance in the 13-15 yr post-harvest plots, or show more than one significant association in the logistic regression model. I hypothesize that this is likely due to the parasitic nest founding strategy of *F. aserva*. *Formica aserva* is known to parasitize *F. neorufibarbis* during nest founding which may explain why *F. aserva* is not found in the earliest seral ages, before *F. neorufibarbis* colonies are established. Further it may explain why the peak in abundance of *F. aserva* is associated with a decline in *F. neorufibarbis* colonies and why the *F. neorufibarbis* population slightly rebounds after cool seral conditions cause a decline in *F. aserva* colonies (Chapter 5). Finally, F. *aserva* may displace *F. neorufibarbis* from its preferred woody debris choices for nesting, resulting in different woody debris associations for *F. neorufibarbis* pre- and post-parasitism. This may explain why no woody debris characteristics were found to be significant for this species.

Although utilization of woody debris was high for the ant species followed in this study, it is not possible to ascertain what constitutes minimum woody debris requirements. This study was constrained to examine woody debris choice based on pre-existing options following normal harvesting operations. Not all decay classes were equally abundant nor were all size ranges. In particular, large pieces of woody debris were seldom present. It is not possible to know if certain species are absent from the stands of this study because of the lack of appropriate woody debris resources. For example, other species of *Camponotus* may exist in the landscape but might require larger pieces of woody debris than those available in these post-harvest stands. A lack of replicated burned stands of sufficient size to allow installation of plots within the study area landscape blocked my ability to examine the ant fauna associated with large volumes of woody debris created by natural disturbance. As a consequence, it is unknown if ants will simply choose the best of the options available, even if they are sub-optimal, or continue to search until a minimum is located. *Camponotus* spp.

queens are frequently found in very small pieces of wood (personal observation), indicating that carpenter ants do the former.

Although the clear effect of declining temperatures on ant communities was evident with seral age, woody debris, as noted, was not a controlled variable. As a consequence, the response of the ant fauna to a complete loss of this resource could not be ascertained. It seems reasonable, however, that the complete removal or destruction (e.g., by crushing) of woody debris would have a dramatic effect upon the ant fauna. The apparent absence of any ants directly nesting in the soil (Chapter 3) suggests that few ants would be able to colonize post-harvest forest sites depleted of woody debris. This would then presumably and unpredictably affect the stand level invertebrate community given the role of ants as major predators of invertebrates (McNeil et al. 1978; Skinner 1980), and reduce food available to myrmecophagous birds (Torgersen and Bull 1995; Elchuk and Wiebe 2002) and bears (Raine and Kansas 1990; Elgmork and Unander 1999).

Recently, there has been a move in the forestry scientific community away from considering woody debris as unsalvaged waste (Maser et al. 1979) and toward an appreciation that this resource plays important roles both forest ecological processes (Maser et al. 1994, Stevens 1997, Lofroth 1998) and as habitat for many species (Keisker 2000). Low volumes of woody debris post-harvest have been shown to affect biodiversity. In Sweden, a lack of woody debris has contributed to the red-listing of 542 wood-dependent invertebrates (Jonsell et al. 1998). This has led to one recommendation that dead wood retention following harvesting increase by at least 50% in Sweden before 2010 (Ehnström 2001). Despite this, there are currently no clear guidelines for woody debris management that are not superseded by other management objectives. Further, the bio-energy industry is placing a new value on this resource, potentially greatly reducing post-harvest woody debris volumes in the future. Without guidelines in place it is possible that we will follow the example of Sweden.

The last broadly shared logistic model variable was that relating to the presence of other colonies of the same species within 50 m^2. Although the connection of this variable to temperature may not be readily apparent, it is likely there. The clustering of ant colonies may be indicative of colony budding, a mechanism of colony founding in polygynous ants most common in habitats with cold winters (Rosengren et al. 1993), or polydomy (Hansen and Klotz 2005), the formation of satellite nest colonies that seem to be an adaptation for the same purpose. Four of the five common ant species found in sub-boreal forests were polygynous and the fifth, *Camponotus herculeanus*, which is usually monogynous, is normally polydomous. High mortality rates for solitary queens during cold winters have been documented (Heinze et al. 1996). Physical crowding of individuals in nests has been shown to reduce the mortality of ants near the centre, however (Heinze et al. 1996). Hence, mortality from heat loss during the winter may have shaped a significant aspect of ant life history strategies in cold sub-boreal forests.

Although thermal pressures have made many demands upon ants, current anthropogenic changes to the forests have been largely beneficial, from the perspective of an ant. The complete removal of the canopy during clearcut harvesting, clustering of harvested blocks, post-harvest woody debris volumes, and climate change may all be generally beneficial to ants. Clearcut harvesting, now the most common form of disturbance in the sub-boreal forests of BC (DeLong and Tanner 1996), completely removes the canopy and increases surface temperatures, a factor beneficial to ants. The closely packed cutblocks also make dispersal easier. Heavy machinery operation over the cutblocks crush and splinter wood (Higgins and Lindgren 2006), improving nesting access for small species (e.g., *Leptothorax* spp.), but possibly destroying it for others (e.g., *Camponotus* spp.). Further, it is less likely that this wood will persist for as long as undamaged wood. Finally, as noted earlier, the creation of stumps may provide a resource thermally advantageous for ant colony growth. Examples of where harvesting may be detrimental to the ant community would include the large scale removal of all living biomass which draws up the water table (Sun et al. 2001) and the few pieces of large woody debris that remain on a post-harvest stand. It is in the latter case where harvesting operations most deviate from emulating natural disturbances. A comparison of regenerating naturally disturbed forests to anthropogenic forests would be informative. Overall, however, I suggest that ants appear to benefit from harvesting operations.

Harvesting may not be the only anthropogenic process to alter the ecosystem in favor of ants. For a taxon as thermophilic as the ants, climate change is also likely to be largely beneficial although species assemblages would be expected to change. The BC Ministry of the Environment report on climate change (MOE 2007) indicates that summer temperatures in the Smithers area, close to Houston, the focal point of this study, have been increasing 0.14 °C per decade since 1950 (note: this was not statistically significant at $\alpha = 0.05$ although larger increases noted for winter, spring and mean annual temperatures were significant). This suggests an increase of almost 1 °C in summer temperatures since 1950, and the report estimates additional temperature increases of 2-3 °C by 2050, although these latter temperatures are mostly associated with winter. It is not possible to determine if climate change to date has altered the ant fauna of these forests as no historical data on ant communities are available. Given the historically cooler climate, lack of harvesting, and the narrow thermal window for *Formica aserva*, however, it is possible that this ant was uncommon or absent 60 years ago. With increasing temperature, it is likely that new ant species will be introduced into the area, most likely species described for the Prince George area (Lindgren and MacIsaac 2002), which is connected to Houston by the Highway 16 corridor. Environment Canada climate records for Prince George indicate a current mean temperature in June, July, and August 1 °C warmer than Topley, which is the nearest federal weather station to Houston (14.5 °C versus 13.5 °C). This small temperature difference has been shown repeatedly in this dissertation to be significant to the ant community.

Given the relationship between the sub-boreal ant community and temperature developed in this dissertation, ants may have some utility as indicators of climate change. Andersen (1999) described ideal bioindicators as species-rich, functionally important, sensitive to environmental fluctuations, reliable and easy to identify. The ant community in the sub-boreal forests where my research was conducted are functionally important (e.g., as food for vertebrates and in pest control), have been shown in this dissertation to be sensitive to fluctuations in temperature (see Chapter 5), and are reliable (see Figure 3.1). Where they are less ideal are in species richness, the ease of identification, and, in my opinion, in sampling. The interpretation of data relating to ant community structure, derived from sampling, has been shown here to be complex, and requires a clear identification of objectives to ensure the best approach is used. Although it is tempting to advocate for a continuation of the primary sampling technique used in this dissertation, i.e., unit area sampling of CWD, I suspect that while new introductions to the area may increase CWD ant biodiversity, the most significant change will be the arrival of new soil nesting species.

Slight increases in soil temperatures from climate change, combined with lower soil moisture that may arise a few years into seral regeneration, may allow species nesting under rocks or those building thatch mounds to establish. How these will interact with the current community is unknown, but it may introduce more general competition into these forests. Given this, the use of pitfall traps within these forests to detect the arrival of soil nesting ants will most likely be the best methodology for detecting a shift in climate fundamental enough to restructure these communities.

It is my hope that this dissertation provides a foundation for continued research on ants in BC. Although the ant community in this study appears to be strongly influenced by temperature, many of the patterns and relationships here may be applicable to ant communities in southern BC, they may be temporally shifted. In addition, the finding that woody debris acts as a form of thermal refugia for ants in these cool moist forests, is an observation that may have broader value. Taxa other than ants, may be residing only in woody debris. Their discovery and their relationships to ecosystem processes in the forests of BC are yet to be established.

References

Abenspergtraun M, Steven D. 1995. The effects of pitfall trap diameter on ant species richness (Hymenoptera: Formicidae) and other species composition of the catch in a semi-arid eucalypt woodland. Australian Journal of Ecology. 20:282-7.

Adis J. 1979. Problems of interpreting arthropod sampling with pitfall traps. Zoologischer Anzeiger. 202:177-84.

Agosti D, Majer JD, Alonso L, Schultz TR, editors. 2000. Ants: Standard methods for measuring and monitoring biodiversity. Washington, DC: Smithsonian Institution Press. 280 p.

Akre RD, Hansen LD, Myhre EA. 1994. Colony size and polygyny in carpenter ants (Hymenoptera:Formicidae). Journal of the Kansas Entomological Society. 67:1-9.

Alinvi O, Bohlin J, Ball JP. 2008. Interspecific competition among ants in the boreal forest: Testing predictions from a linear hierarchial competition model. Insectes Sociaux. 55:1-11.

Andersen AN. 1995. A classification of Australian ant communities, based on functional-groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography. 22:15-29.

Anderson AN. 1997. Functional groups and patterns of organization in North American ant communities: a comparison to Australia. Journal of Biogeography. 24:433-60.

Andersen AN. 1999. My bioindicator or yours? Making the selection. Journal of Insect Conservation. 3:61-4.

Andersen AN, Hoffman BD, Muller WJ, Griffiths AD. 2002. Using ants as bioindicators in land management: Simplifying assessment of ant community responses. Journal of Applied Ecology. 39:8-17.

Ballard TM. 2000. Impacts of forest management on northern forest soils. Forest Ecology and Management. 133:37-42.

Beal FEL. 1911. Food of the woodpeckers of the United States. United States Department of Agriculture, Biological Survey Bulletin. 37:1-64.

Beckwith RC, Bull EL. 1985. Scat analysis of the arthropod component of pileated woodpecker diet. The Murrelet. 66:90-2.

Béique R, Francoeur A. 1968. Les fourmis d'une pessière à *Cladonia*. II. Étude quantitative d'une pessière naturelle. Revue d'Ecologie et de Biologie du Sol. 3:523-31.

Bestelmeyer BL. 2000. A multi-scale perspective on ant diversity in semiarid landscapes [dissertation]. [Fort Collins (CO)]: Colorado State University. 237 p.

Bestelmeyer BT, Agosti D, Alonso L, Brandao CRF, Brown WL, Delabie J, Silvestre R. 2000. Field techniques for the study of ground-dwelling ants. In: Agosti D, Majer JD, Alonso L, Schultz TR, editors. Ants: Standard methods for measuring and monitoring biodiversity. Washington, DC: Smithsonian Institution Press. p. 122-44.

Billeck I. 2001. Density dependence and colony growth in the ant species *Formica neorufibarbis*. Journal of Animal Ecology. 70:895-905.

Billeck I. 2003. Worker demography in the ant *Formica neorufibarbis*. Ecological Entomology. 28:139-44.

Blacker NC. 1992. Some ants (Hymenoptera: Formicidae) from southern Vancouver Island, British Columbia. Journal of the Entomological Society of BC. 89:3-12.

Blades DCA, Maier CW. 1996. A survey of grassland and montane arthropods collected in the southern Okanagan region of British Columbia. Journal of the Entomological Society of BC. 93:49-73.

Bolton B, Alpert G, Ward PS, Naskrecki P. 2006. Bolton's catalogue of the ants of the world [CD-ROM]. Cambridge, MA: Harvard University Press.

Bono JM, Blatrix R, Antolin MF, Herbers JM. 2007. Pirate ants (*Polyergus breviceps*) and sympatric hosts (*Formica occulta* and *Formica* sp. cf. *argentea*): host specificity and coevolutionary dynamics. Biological Journal of the Linnean Society. 91:565-72.

Borgelt A, New TR. 2005. Pitfall trapping for ants (Hymenoptera, Formicidae) in mesic Australia: The influence of trap diameter. Journal of Insect Conservation. 9:219-21.

Brady NC, Weil RR. 2002. The nature and properties of soils. 13th ed. New Jersey, NY: Prentice-Hall. 960 p.

Brian MV, Hibble J, Stradling DJ. 1965. Ant pattern and density in a southern English heath. Journal of Animal Ecology. 34:545-55.

Brown JH, Reichman OJ, Davidson DW. 1979. Granivory in desert ecosystems. Annual Review of Ecology, Evolution, and Systematics. 10:201-27.

Buckell ER. 1927. An annotated list of the ants of British Columbia. Proceedings of the Entomological Society of BC. 24:30-4.

Buckell ER. 1932. A list of the ants of British Columbia. Proceedings of the Entomological Society of BC. 29:22-5.

Campbell RW, Torgersen TR, Srivastava N. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. Forest Science. 29:779-90.

[CCAC] Canada Council on Animal Care. 2005. Guidelines Program. [cited on 2009 Jul 10]. Available from: http://www.ccac.ca/en/CCAC_Programs/Guidelines_Policies/ gublurb.htm.

Carlson CE, Campbell RW, Theroux LJ, Egan TH. 1984. Ants and birds reduce western spruce budworm feeding injury to small Douglas-fir and western larch in Montana. Forest Ecology and Management. 9:185-92.

Crdá X, Retana J, Cros S. 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. Journal of Animal Ecology. 66:363-74.

Cherix D, Chautems D, Fletcher DJC, Fortelius W, Gris G, Keller L, Passera L, Rosengren R, Vargo EL, Walter F. 1991. Alternative reproductive strategies in *Formica lugubris* Zett. Ethnology Ecology and Evolution, Special Issue. 1:61-6.

Cherrett JM. 1968. The foraging behavior of *Atta cephalotes* L. (Hymenoptera: Formicidae). Journal of Animal Ecology. 37:387-403.

Ciarniello LM, Boyce MS, Heard DC, Seip DR. 2007. Components of grizzly bear habitat selection: Density, habitats, roads, and mortality. Journal of Wildlife Management. 71:1446-57.

Clements FE. 1916. Plant succession: An analysis of the development of vegetation. Washington, DC: Carnegie Institute of Washington. Publication No 242. 512 p.

Cloudsley-Thompson JL. 1956. The effect of rock cover on the diurnal range of microclimatic conditions. The Entomologist. 89:213-5.

Coenen-Staβ D, Schaarschmidt B, Lamprecht I. 1980. Temperature distribution and calorimetric determination of heat production in the nest of the wood ant, *Formica polyctena* (Hymenoptera: Formicidae). Ecology. 61:238-44.

Colwell RK. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8. Persistent URL <purl.oclc.org/estimates>.

Connell JH, Slayter RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist. 111:1119-1144.

Contreras MA, Chung W, Jones G. 2008. Applying ant colony optimization metaheuristic to solve forest transportation planning problems with side constraints. Canadian Journal of Forest Research. 38:2896-910.

Cook JE. 1996. Implications of modern successional theory for habitat typing: A review. Forest Science. 42:67-75.

DeLong SC, Tanner D. 1996. Managing the pattern of forest harvest: lessons from wildfire. Biodiversity and Conservation. 5:1191-205.

Dorigo M and Gambardella LM. 1997. Ant colonies for the travelling salesman problem. BioSystems. 43:73-81.

Drury W, Nisbet I. 1973. Succession. Journal of the Arnold Arboretum. 54:331-68.

Dulsskii GM, Putyatina TS. 2004. Dynamics of ant communities in the course of pine forest regeneration after felling. Zoologichesky Zhurnal. 83:61-70.

Dunn RR, Parker CR, Sanders NJ. 2007. Temporal patterns of diversity: Assessing the biotic and abiotic controls on ant assemblages. Biological Journal of the Linnean Society. 91:191-201.

Ehnström B. 2001. Leaving dead wood for insects in boreal forests - Suggestions for the Future. Scandinavian Journal of Forest Research. Suppl. 3:91-8.

Elchuk CL, Wiebe KL. 2002. Food and predation risk as factors related to foraging locations of northern flicker. The Wilson Bulletin. 114:349-57.

Elgmork K, Unander S. 1999. Brown bear use of ant mounds in Scandinavia. Ursus. 10:269-74.

Elliot JA, Toth BM, Granger RJ, Pomeroy JW. 1998. Soil moisture storage in mature and replanted sub-humid boreal forest stands. Canadian Journal of Soil Science. 78:17-27.

Elmes GW, Keller L. 1993. Distribution and ecology of queen numbers in ants of the genus *Myrmica*. In: Keller L, editor. Queen number and sociality in insects. Oxford, Oxfordshire: Oxford University Press. p. 294-307.

Elmes GW, Wardlaw JC. 1983. A comparison of the effect of temperature on the development of large hibernated larvae of four species of *Myrmica* (Hymenoptera: Formicidae). Insectes Sociaux. 30:106-18.

Elmes GW, Wardlaw JC, Nielsen MG, Kipyatkov VE, Lopatina EB, Radchenko AG, Barr B. 1999. Site latitude influences on respiration rate, fat content and the ability of worker ants to rear larvae: A comparison of *Myrmica rubra* (Hymenoptera: Formicidae) populations over their European range. European Journal of Entomology. 96:117-24.

Errand C, Fresneau D, Heinze J, Francoeur A, Lenoir A. 1997. Social organization in the guest-ant *Formicoxenus provancheri*. Ethology. 103:149-59.

Finnegan RJ. 1974. Ants as predators of forest pests. Entomophaga, Mémoire Hons Série Numéro. 7:53-9.

Fischer-Blass B, Heinze J, Foitzik S. 2006. Microsatellite analysis reveals strong but differential impact of a social parasite on its two host species. Molecular Ecology. 15:863-72.

Fisher BL. 1999. Improving inventory efficiency: A case study of leaf-litter ant diversity in Madagascar. Ecological Applications. 9:714-31.

Fittkau EJ, Klinge H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica. 5:2-14.

Francoeur A. 1973. Révision taxonomique des espèces néarctiques du group *fusca*, genre *Formica* (Formicidae: Hymenoptera). Mémoires de la Societé Entomologique du Québec. 3:1-316.

Francoeur A. 1983. The ant fauna near the tree-line in northern Quebec. Nordicana. 47:177-80.

Francoeur A. 1997. Ants (Hymenoptera: Formicidae) of the Yukon. In: Danks HV, Downes JA, editors. Insects of the Yukon. Ottawa, ON: Biological Survey of Canada (Terrestrial Arthropods). p. 901-10.

Francoeur A. 2001. Les fourmis de la forêt boréale du Québec (Formicidae, Hymenoptera). La Société Provancher d'Histoire Naturelle Du Canada. 125:108-14.

Fridman J, Walheim M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. Forest Ecology and Management. 131:23-36.

Frouz J, Holec M, Kalcik J. 2003. The effect of *Lasius niger* (Hymenoptera, Formicidae) ant nest on selected soil chemical properties. Pedobiologia. 47:205-12.

Giancoli DC. 1991. Physics, 3rd ed. Prentice-Hall Canada Inc. Toronto. 962p.

Gleason HA. 1917. The structure and development of plant association. Bulletin of the Torrey Botanical Club. 44:463-81.

Gorn SN, Gorb EV, Punttila P. 2000. Effects of redispersal of seeds by ants on the vegetation pattern in a deciduous forest: A case study. Acta Oecologica. 21:293-301.

Green GW, Sullivan CR. 1950. Ants attacking larvae of the forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Lasiocampidae). Canadian Entomologist. 82:194-5.

Greenslade P, Greenslade PJM. 1971. The use of baits and preservatives in pitfall traps. Journal of the Australian Entomological Society. 10:253-60.

Greenslade PJM. 1973. Sampling ants with pitfall traps: Digging-in effects. Insectes Sociaux. 20:343-53.

Gregg RE. 1963. The ants of Colorado with reference to their ecology, taxonomy, and geographic distribution. Boulder, CO: University of Colorado Press. 792 p.

Gregg RE. 1972. The northward distribution of ants in North America. Canadian Entomologist. 104:1073-91.

Haines BL. 1978. Element and energy flows through colonies of the leaf-cutting ant, Atta colombica, in Panama. Biotropica. 10:270-7.

Hamburg HV, Andersen AN, Meyer WJ, Robertson HG. 2004. Ant community development on rehabilitated ash dams in the South African Highveld. Restoration Ecology. 12:552-8.

Hansen LD, Klotz JH. 2005. Carpenter ants of the United States and Canada. Ithaca, NY: Comstock Publishing Associates. 204 p.

Hatler DF. 1972. Food habits of black bears in interior Alaska. The Canadian Field Naturalist. 86:17-31.

Heinze J. 1993a. Life histories of subarctic ants. Arctic. 46:354-8.

Heinze J. 1993b. Habitat structure, dispersal strategies and queen number in two boreal *Leptothorax* species. Oecologia. 96:32-9.

Heinze J. 1994. Genetic colony and population structure of the ant *Leptothorax* cf. *muscorum*. Canadian Journal of Zoology. 72:1477-80.

Heinze J, Hölldobler B. 1994. Ants in the cold. Memorabilia Zoologica. 48:99-108.

Heinze J, Stahl M, Hölldobler B. 1996. Ecophysiology of hibernation in boreal *Leptothorax* ants (Hymenoptera: Formicidae). Ecoscience. 3:429-35.

Heithaus ER. 1981. Seed predation by rodents in three ant-dispersed plants. Ecology. 62:136-45.

Heron JM. 2001. The effects of grazing on ant (Hymenoptera: Formicidae) diversity the south Okanagan grasslands [M.Sc. Thesis]. [Vancouver (BC)]: University of British Columbia. 98 p.

Higgins R, Lindgren BS. 2006. The fine scale physical attributes of coarse woody debris and effects of surrounding stand structure on its utilization by ants (Hymenoptera: Formicidae) in British Columbia, Canada. In: Grove SJ, Hanula JL, editors. Insect biodiversity and dead wood: Proceedings of a symposium for the 22nd International Congress of Entomology. 2004. Southern Research Station, U.S. Department of Agriculture Forest Service. p. 67-74

Higgins RJ, Lindgren BS. 2009. The ants of British Columbia (Hymenoptera: Formicidae) [Internet]. In: Klinkenberg B, editor. 2009. E-Fauna BC: Electronic Atlas of the Wildlife of BC. Vancouver: Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia. [updated 2009 Jan 18; cited 2009 Aug 15]. Available from www.efauna.bc.ca.

Hillel D. 2004. Introduction to environmental soil physics. Maryland Heights, MO: Elsevier Academic Press. 497 p.

Hölldobler B, Wilson EO. 1990. The ants. Cambridge, MA: The Belknap Press of Harvard University Press. 732 p.

Hölldobler B, Wilson EO. 2009. The superorganism: The beauty, elegance, and strangeness of insect societies. New York, NY: W.W. Norton & Company. 522 p.

Hols G. 1999. Marks of a century: a history of Houston, BC, 1900-2000. Houston BC: District of Houston. 296 p.

Homer DW, Lemeshow S. 1989. Applied logistic regression. John-Wiley and Sons. Toronto.

Horstmann K, Schmid H. 1986. Temperature regulation in nests of the wood ant, *Formica polyctena* (Hymenoptera: Formicidae). Entomologia Generalis. 11:229-36.

Irwin LL, Hammond FM. 1985. Managing black bear habitats for food items in Wyoming. Wildlife Society Bulletin. 13:477-83.

Jonsell M, Weslien J, Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation. 7:749-64.

Jonsson BG, Kruys N, editors. 2001. Ecology of woody debris in boreal forests. Ecological Bulletins 49. 283 p.

Jurgensen MF, Storer AJ, Risch AC. 2005. Red wood ants in North America. Annales Zoologici Fennici. 42:235-42.

Kaspari M. 2005. Global energy gradients and size in colonial organisms: Worker mass and worker number in ant colonies. Proceedings of the National Academy of Sciences. 102:5079-83.

Kaspari M, Weiser MD. 1999. The size-grain hypothesis and interspecific scaling in ants. Functional Ecology. 13:530-8.

Kaveh A, Azar BF, Talatahari S. 2008. Ant colony optimization for the design of space trusses. International Journal of Space Trusses. 23:167-81.

Keisker DG. 2000. Types of wildlife trees and coarse woody debris required by wildlife of north central British Columbia. Ministry of Forests Research Program. Working Paper #50. 92 p.

Kéry M, Schmidt BR. 2008. Imperfect detection and its consequences for conservation. Community Ecology. 9: 207-16.

Kilpeläinen J, Punttila P, Sundström L, Niemelä P, Finér L. 2005. Forest stand structure, site type and distribution of ant mounds in boreal forests in Finland in the 1950s. Annales Zoologici Fennici. 42:243-58.

King JR, Porter SD. 2005. Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. Environmental Entomology. 34:1566-78.

Kipyatkov VE, Lopatina EB. 2002. Reaction norm in response to temperature may change to adapt rapid brood development to boreal and subarctic climates in *Myrmica* ants (Hymenoptera: Formicidae). European Journal of Entomology. 99:197-208.

Kipyatkov VE, Lopatina EB, Imamgaliev AA, Shirokova LA. 2004. Effect of temperature on rearing of the first brood by the founder females of the ant *Lasius niger* (Hymenoptera, Formicidae): Latitude-dependant variability of the response norm. Journal of Evolutionary Biochemistry and Physiology. 40:165-75.

Knowlton GF, Roberts RS, Wood SL. 1946. Birds feeding on ants in Utah. Journal of Economic Entomology. 39:547-8.

Koivula M, Kotze DJ, Hiisivuori L, Rita H. 2003. Pitfall trap efficiency: Do trap size, collecting fluid and vegetation structure matter? Entomologica Fennica. 14:1-14.

Kronauer DJC, Schöning C, Vilhelmsen LB, Boosma JJ. 2007. A molecular phylogeny of *Dorylus* army ants provides evidence for multiple evolutionary transitions in foraging niche. BMC Evolutionary Biology [Internet]. [cited 2009 Jul 1]; 7:56. Available from http://www.biomedcentral.com/1471-2148/7/56.

Kusnezov N. 1957. Numbers of species of ants in faunae of different latitudes. Evolution. 11:298-9.

Lafleur B, Parsons FJ, Bradley RL, Francoeur A. 2006. Ground-nesting ant assemblages and their relationship to habitat factors along a chronosequence postfire-regenerated lichen-spruce woodland. Environmental Entomology. 35:1515-24.

Laine KJ, Niemelä P. 1980. The influence of ants on the survival of mountain birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. Oecologia. 47:39-42.

Lang A. 2000. The pitfalls of pitfalls: a comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in arable land. Journal of Pest Science. 73:99-106.

Laurent P. 1917. Collecting insects by the aid of molasses traps. Entomological News. 28:81-2.

Lemieux JP, Lindgren BS. 1999. A pitfall trap for large-scale trapping of Carabidae: Comparison against conventional design, using two different preservatives. Pedobiologia. 43:245-53.

Lindgren BS, MacIsaac AM. 2002. A preliminary study of ant diversity and of ant dependence on dead wood in central interior British Columbia. In: Shea PJ, Laudenslayer WF Jr, Valentine B, Weatherspoon CP, Lisle TE, editors. Proceedings of the symposium on the ecology and management of dead wood in western forests. Symposium on the ecology and management of dead wood in western forests; Nov 2-4 1999; Reno, NV. Albany, CA: USDA Forest Service. Gen. Tech. Rep. PSW-18. p. 111-19.

Lindsey PA, Skinner JD. 2001. Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. Journal of Arid Environments. 48:551-68.

Littlewood NA, Young MR. 2008. A habitat suitability model for the narrow-headed ant, *Formica exsecta*, evaluated against independent data. Insect Conservation and Diversity. 1:108-13.

Lofroth E. 1998. The dead wood cycle. In:Voller J, Harrison S, editors. Conservation biology principles for forested landscapes.Vancouver, BC: UBC Press. p. 185-214.

MacKenzie DI. 2005. What are the issues with presence-absence data for wildlife managers? Journal of Wildlife Management. 69:849-60.

Magurran AE. 1988. Ecological diversity and its measurement. Princeton, NJ: Princeton University Press. 179 p.

Mäkitalo K, Hyvönen J. 2004. Late-summer soil water content on clear-cut reforestation areas two decades after site preparation in Finnish Lapland. Forest Ecology and Management. 189:57-75.

[MBI] Mallinckrodt Baker Inc. 2008a. Propylene Glycol. Material Safety Data Sheet. [cited 2009 Jun 01]. Available from:http://www.jtbaker.com/msds/ englishhtml/p6928.htm.

[MBI] Mallinckrodt Baker Inc. 2008b. Ethylene Glycol. Material Safety Data Sheet. [cited 2009 Jun 01Available from: http://www.jtbaker.com/msds/ englishhtml/E5125.htm.

Mao CX, Colwell RK, Chang J. 2005. Estimating the species accumulation curve using mixtures. Biometrics. 61:433-41.

Martelli MG, Ward MM, Fraser AM. 2004. Ant diversity sampling on the southern Cumberland plateau: A comparison of litter sifting and pitfall trapping. Southeastern Naturalist. 3:113-26.

Maser C, Anderson RG, Cromack K Jr, Williams JT, Martin RE. 1979. Dead and Down Woody Material. In: Thomas JW, technical editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USA: USDA Forest Service agricultural handbook No. 553. p. 78-95.

Maser C, Cline SP, Cromack K Jr, Trappe JM, Hansen E. 1994. What we know about large trees that fall to the forest floor. Pacific Northwest Station: General technical report. 229:25-46.

McCook LJ. 1994. Understanding ecological community succession: Causal models and theories, a review. Vegetatio. 111:115-147.

McCune B, Mefford MJ. 1999. PC-ORD: Multivariate analysis of ecological data, Version 5 [CD-ROM]. Gleneden Beach, OR: MjM Software Design.

McIver JD, Yandell K. 1998. Honeydew harvest in the western thatching ant. American Entomologist. 44:30-5.

McIver JD, Torgersen TR, Cimon NJ. 1997. A supercolony of the thatch ant *Formica obscuripes* Forel (Hymenoptera: Formicidae) from the Blue Mountains of Oregon. Northwest Science. 71:18-29.

McNeil JN, Delisle J, Finnegan RJ. 1978. Seasonal predatory activity of the introduced red wood ant, Formica lugubris at Valcartier, Quebec, in 1976. Canadian Entomologist. 110:85-90.

Meidinger DV, Pojar J, editors. 1991. Ecosystems of British Columbia. Victoria, BC: BC Ministry of Forests. Special Report Series No. 6. 330 p.

Menard S. 2002. Applied logistic regression analysis, 2nd ed. Thousand Oaks, CA: Sage Publications Inc. 111 p.

[MOE] Ministry of the Environment. 2007. Environmental trends in British Columbia: 2007:Climate Change. British Columbia, Ministry of the Environment [Accessed 2009 June17]. Available from: http://www.env.gov.bc.ca/soe/et07/04_climate_change/technical_paper/climate_change.pdf.

Mori A, Moli FL. 1998. Mating behavior and colony founding of the slave-making ant *Formica sanguinea* (Hymenoptera: Formicidae). Journal of Insect Behavior. 11: 235-45.

Naumann K, Preston WB, Ayre GL. 1999. An annotated checklist of the ants (Hymenoptera: Formicidae) of British Columbia. Journal of the Entomological Society of BC. 96: 29-68.

Nielsen GR. 1986. The spatial distribution of wood-nesting ants in the central coast range of Oregon [dissertation]. [Corvallis (OR)]: Oregon State University. 102 p.

Nielsen MG, Elmes GW, Kipyatkov VE. 1999. Respiratory Q10 varies between populations of two species of *Myrmica* ants according to the latitude of their site. Journal of Insect Physiology. 45:559-64.

Nkem JN. 2000. The impact of ant bioturbation and foraging activities on surrounding soil properties. Pedobiologia. 44:609-21.

Nordlander G. 1987. A method for trapping *Hylobius abietis* (L.) with a standardized bait and its potential for forecasting seeding damage. Scandinavian Journal of Forest Research. 2:199-213.

Noyce KV, Kannowski PB, Riggs MR. 1997. Black bears as ant-eaters: Seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal of Zoology. 75:1671-86.

Oliver TH, Leather SR, Cook JM. 2008. Macroevolutionary patterns in the origin of mutualisms involving ants. Journal of Evolutionary Biology. 21:1597-608.

Olson DM. 1991. A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a tropical wet forest, Costa Rica. Biotropica. 23:166-72.

Osborn F, Goitia W, Cabrera M, Jaffé K. 1999. Ants, plants, and butterflies as diversity indicators: Comparisons between strata at six forest sites in Venezuela. Studies of Neotropical Fauna and Environment. 34:59-64.

Parr CL, Chown SL. 2001. Inventory and bioindicator sampling: Testing pitfall and Winkler methods with ants in a South African savanna. Journal of Insect Conservation. 5:27-36.

Pearce JL, Schuurman D, Barber KN, Larrivee M, Venier LA, McKee J, McKenney D. 2005. Pitfall trap designs to maximize invertebrate captures and minimize captures of nontarget vertebrates. Canadian Entomologist. 137:233-50.

Petal J. 1980. Ant populations, their regulation and effect on soil in meadows. Ekologia Polska. 28:297-326.

Petersen B. 1977. Pollination by ants in the alpine tundra of Colorado. Transactions of the Illinois State Academy of Science. 70:348-55.

Phillips ID, Cobb TP. 2005. Effects of habitat structure and lid transparency on pitfall catches. Environmental Entomology. 34:875-82.

Pickett TA. 1976. Succession: An evolutionary interpretation. The American Naturalist. 110:107-19.

Pontin AJ. 1960. Field experiments on colony foundation by *Lasius niger* (L.) and *L. flavus* (F.) (Hymenoptera: Formicidae). Insectes Sociaux. 7:227-30.

Porter SD. 2005. A simple design for a rain-resistant pitfall trap. Insectes Sociaux. 52:1-3.

Punttila P. 1996. Succession, forest fragmentation, and the distribution of wood ants. Oikos. 75:291-8.

Punttila P, Haila Y. 1996. Colonisation of a burned forest by ants in the southern Finnish boreal forest. Silva Fennica. 60:421-35.

Punttila P, Haila Y, Niemelä J, Pajunen T. 1994. Ant communites in fragments of old-growth tiaga and managed surroundings. Annales Zoologici Fennici. 31:131-44.

Punttila P, Haila Y, Pajunen T, Tukia H. 1991. Colonisation of clearcut forests by ants in the southern Finnish taiga: A quantitative survey. Oikos. 61:250-62.

Punttila P, Haila Y, Tukia H. 1996. Ant communities in taiga clearcuts: habitat effects and species interactions. Ecography. 19:16-28.

Raine RM, Kansas JL. 1990. Black bear seasonal food habits and distribution by elevation in Banff national park, Alberta. International Conference on Bear Research and Management 8:297-304.

Redford KH. 1987. Ants and termites as food: patterns of mammalian myrmecophagy. 349-393. In: Genoways HH. editor. Current Mammology. New York, NY: Plenum Press. 540 p.

Redford KH, Dorea JG. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. Journal of Zoology, London. 203:385-95.

Risch AC, Jurgensen MF, Schutz M, Page-Dumroese DS. 2005. The contribution of red wood ants to soil C and N pools and CO2 emissions in subalpine forests. Ecology. 86:419-30.

Roces F, Núñez JA. 1989. Brood translocation and circadian variation of temperature preference in the ant Camponotus mus. Oecologia. 81:33-7.

Romero H, Jaffe K. 1989. A comparison of methods for sampling ants in savannas. Biotropica. 21:348-52.

Rosengren R, Fortelius W, Lindström K, Luther A. 1987. Phenology and causation of nest heating and thermoregulation in red wood ants of the *Formica-rufa* group studied in coniferous forest habitats in southern Finland. Annales Zoologici Fennici. 24:147-55.

Rosengren R, Sundström L, Fortelius W. 1993. Monogyny and polygyny in *Formica* ants: The result of alternative dispersal tactics. In: Keller L, editor. Queen number and sociality in insects. Oxford, Oxforshire: Oxford University Press. 308-33.

Rushton SP, Omerod SJ, Kerby G. 2004. New paradigms for modelling species-distributions? Journal of Applied Ecology 41:193-200.

Russell RH, Nolan JW, Woody NA, Anderson G. 1979. A study of the grizzly bear in Jasper National Park 1975-1978. A report to the Canadian Wildlife Service, Edmonton, Alberta. 136 p.

Sanders CJ. 1972. Seasonal and daily activity patterns of carpenter ants in northwestern Ontario. Canadian Entomologist. 104:1681-7.

Sanders NJ, Lessard J, Fitzpatrick MC, Dunn RR. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology & Biogeography. 16:640-9.

Savolainen R, Deslippe RJ. 1996. Slave addition increases sexual production of the facultative slave-making ant *Formica subnuda*. Behavioural Ecology and Sociobiology. 38:145-8.

Savolainen R, Deslippe RJ. 2001. Facultative and obligate slave making in *Formica* ants. Naturwissenschaften. 88:347-50.

Savolainen R, Seppä P. 1996. Genetic relatedness among worker nestmates of three formicine slave-making ants. Insectes Sociaux. 43:31-6.

Savolainen R, Vepsäläinen K. 1988. A competition hierarchy among boreal ants: Impact on resource partitioning and community structure. Oikos. 51:135-55.

Savolainen R, Vepsäläinen K. 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. Oikos. 56:3-16.

Savolainen R, Vepsäläinen K, Wuorenrinne H. 1989. Ant assemblages in the tiaga biome:Testing the role of territorial wood ants. Oecologia. 81:481-6.

Schlick-Steiner BC, Steiner FM, Moder K, Bruckner A, Fiedler K, Christian E. 2006. Assessing ant assemblages: pitfall trapping versus nest counting (Hymenoptera: Formicidae). Insectes Sociaux. 53:274-81.

Schowalter TD, Zhang YL, Rykken JJ. 2003. Litter invertebrate responses to variable density thinning in western Washington forest. Ecological Applications. 13:1204-11.

Seal JN, Tschinkel WR. 2007. Complexity in an obligate mutualism: do fungus-gardening ants know what makes their garden grow. Behavioral Ecology and Sociobiology. 61:1151-60.

Seppä P, Sundström L, Punttila P. 1995. Facultative polygyny and habitat succession in boreal ants. Biological Journal of the Linnean Society. 56:533-51.

Sharplin J. 1966. Annotated list of the Formicidae (Hymenoptera) of central and southern Alberta. Quaestiones Entomologicae. 2:243-53.

[SigmaPlot]. ©2008, SigmaPlot 11 [CD ROM]. San Jose, CA. Systat Software Inc.

Simberloff DS, Wilson EO. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology. 50:278-96.

Skinner GJ. 1980. The feeding habits of the wood-ant, *Formica rufa* (Hymenoptera: Formicidae), in limestone woodland in north-west England. Journal of Animal Ecology. 49:417-33.

Soberón J, Llorente J. 1993. The use of species accumulation functions for the prediction of species richness. Conservation Biology. 7:480-8.

Southwood TRE, Henderson PA. 2000. Ecological Methods, 3rd ed. Oxford, Oxfordshire: Blackwell Science Ltd. 575 p.

Spence JR, Niemelä JK. 1994. Sampling carabid assemblages with pitfall traps: The madness and the method. The Canadian Entomologist. 126:881-94.

[STATA]. ©1985-2007. Stata Intercooled 9.2 [CD-ROM]. College Station, TX: Statacorp LP.

Stathers RJ, Spittlehouse DL. 1990. Forest soil temperature manual. BC: Government of Canada. Report FRDA 130. 47 p.

[SAS] Statistical Analysis Software. ©2002-2008. SAS 9.1 [CD-ROM]. Cary, North Carolina: SAS Institute Inc.

Steinitz O, Heller J, Tsoar A, Rotem D, Kadmon R. 2005. Predicting regional patterns of similarity in species compositions for conservation planning. Conservation Biology. 19:1978-88.

Stevens V. 1997. The ecological role of coarse woody debris: An overview of the ecological importance of CWD in BC forests. Research Branch, B.C. Ministry of Forests,Victoria BC. Working Paper 30. 26 p.

Steventon D. 2002. Historic disturbance regimes of the Morice and Lakes Timber Supply Areas. Working Paper. Victoria, BC: BC Ministry of Forests, Prince Rupert Forest Region. 16 p.

Stille M. 1996. Queen/worker thorax volume ratios and nest-founding strategies in ants. Oecophylla. 105:87-93.

Sun GZ, McNulty SG, Shepard JP, Amatya DM, Riekerk H, Comerford NB, Skaggs W, Swift L Jr. 2001. Effects of timber management on the hydrology of wetland forests in the southern United States. Forest Ecology and Management. 143:227-36.

Swenson JE, Jansson A, Riig R, Sandegren F. 1999. Bears and ants:Myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology. 77:551-61.

Swets JA. 1988. Measuring the accuracy of diagnostic systems. Science. 4857:1285-93.

Tesař M, Šír M, Krejča M, Váchal J. 2008. Influence of vegetation cover on air and soil temperatures in the Šumava Mts. (Czech Republic). In: Brilly M, Bonacci O, Nachtnebel PH, Szolgay J, Balint G, editors. XXIVth Conference of the Danubian Countries on the Hydrological Forecasting and Hydrological Bases of Water Management; 2-4 June 2008; Bled, Slovenia. IOP Conference Series: Earth and Environmental Science 4. p. 1-7.

Thomas ML. 2002. Nest site selection and longevity in the Ponerine ant *Rhytidoponera metallica* (Hymenoptera, Formicidae). Insectes Sociaux. 49:147-52.

Tisch EL. 1961. Seasonal food habits of the black bear in the whitefish range of northwestern Montana [M.Sc. Thesis]. [Bozeman MT]: Montana State University. 108 p.

Tiwari MK, Dashora Y, Kumar S, Shankar R. 2006. Ant colony optimization to select the best process plan in an automated manufacturing environment. Proceedings of the Institution of Mechanical Engineers, Part B: Journal of Engineering Manufacture. 220:1457-72.

Torgersen TR, Bull EV. 1995. Down logs as habitat for forest dwelling ants-the primary prey of pileated woodpeckers in northeastern Oregon. Northwest Science. 69:294-303.

Torgersen TR, Mason RR. 1987. Predation on egg masses of Douglas-fir tussock moth. Environmental Entomology. 16:90-3.

Torgersen TT, Bull EV. 1995. Down logs as habitat for forest dwelling ants-the primary prey of pileated woodpeckers in northeastern Oregon. Northwest Science. 69:294-303.

Van Pelt A. 1963. High altitude ants of the southern Blue Ridge. American Midland Naturalist. 69:205-23.

Vanderplank FL. 1960. The bionomics and ecology of the red tree ant, *Oecophylla* sp., and its relationship to the coconut bug, *Pseudotheratpus wayi* (Corediae). Journal of Animal Ecology. 29:15-33.

Vanderwoude C, Andersen NA, House, A. P. N. 1997. Ant-communities as bio-indicators in relation to fire management of spotted gum (Eucalyptus:Maculata) forests in south-east Queensland. Memoirs of the Museum of Victoria. 56:671-5.

Vogt JT, Harsh DK. 2003. A simple device to assist with pitfall trap sampling. Florida Entomologist. 26:94-5.

Vojta CD. 2005. Old dog, new tricks: Innovations with presence-absence information. Journal of Wildlife Management. 69:845-8.

Wagner D, Brown MJF, Gordon DM. 1997. Harvester ant nests, soil biota and soil chemistry. Oecologia. 112:232-6.

Walthur BA, Martin J-L. 2001. Species richness estimation of bird communities: How to control for sampling effort? Ibis. 143:413-9.

Wang C, Strazanac J, Butler L. 2001a. Association between ants (Hymenoptera: Formicidae) and habitat characteristics in oak-dominated mixed forests. Environmental Entomology 30:842-8.

Wang C, Strazanac J, Butler L. 2001b. A comparison of pitfall traps with bait traps for studying leaf litter ant communities. Journal of Economic Entomology. 94:761-5.

Watts MJ, Worner SP. 2008. Comparing ensemble and cascaded neural networks that combine biotic and abiotic variables to predict insect species distributions. Ecological Informatics. 3:354-66.

Way MJ, Khoo KC. 1992. Role of ants in pest management. Annual Review of Entomology. 37:479-503.

Wenzl HFJ. 1963. The chemical technology of wood. New York, NY: Academic Press. 692 p.

Wheeler GC, Wheeler J. 1963. The ants of North Dakota. Grand Forks, ND: The University of North Dakota Press. 326 p.

Wheeler GC, Wheeler J. 1986. The ants of Nevada. Los Angeles, CA: Natural History Museum of Los Angeles County. 138 p.

Whittaker JB, Warrington S. 1985. An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) III. effects on tree growth. Journal of Applied Ecology. 22:797-811.

Wilson EO. 1971. The insect societies. Cambridge, MA: Belknap Press of Harvard University Press. 548 p.

Wilson EO. 1987. Causes of ecological success: The case of the ants. Journal of Animal Ecology. 56:1-9.

Wilson EO, Hunt GLJ. 1966. Habitat selection by the queens of two field-dwelling species of ants. Ecology. 47:485-7.

Woodcock BA. 2005. Pitfall trapping in ecological studies. In: Leather SR, Lawton JH, Likens GE, editors. Insect sampling in forest ecosystems. Malden, MA: Blackwell Scientific Ltd. 37 p.

Work TT, Buddle CM, Korinus M. 2002. Pitfall trap size and capture of three taxa of litter-dwelling arthropods: Implications for biodiversity studies. Environmental Entomology. 31: 438-48.

Worner SP, Gevrey M. 2006. Modelling global insect pest assemblages to determine risk of invasion. Journal of Applied Ecology. 43:858-67.

Wu J, Wong HR. 1987. Colonization of lodgepole pine stumps by ants (Hymenoptera: Formicidae). The Canadian Entomologist. 119:397-8.

Appendix I. Dates of pitfall trap and mini-Winkler sampling in 13-15 year post-harvest stands (pine-leading, sub-boreal spruce biogeoclimatic zone, moist-cold subzone, variant 2 (SBSmc2) (Meidinger and Pojar1991)) near Houston, BC.

Site Name	Pitfall Traps Set One	Pitfall Traps Set Two	Mini-Winklers Set One	Mini-Winklers Set Two
Topley	30-Jun-04	03-Aug-04	23-Jul-04	05-Aug-04
Fenton Creek	30-Jun-04	05-Aug-04	22-Jul-04	16-Aug-04
Nadina West	22-Jun-04	08-Aug-04	22-Jul-04	08-Aug-04

Appendix II. Dates of coarse woody debris, pitfall trap and mini-Winkler sampling in five seral ages of forest (pine-leading, sub-boreal spruce biogeoclimatic zone, moist-cold subzone, variant 2 (SBSmc2) (Meidinger and Pojar1991)) near Houston, BC from 2003-2005.

Years post-harvest	Site Name	CWD Transect One	CWD Transect Two	Pitfall Traps Set One	Pitfall Traps Set Two	Mini-Winklers Set One	Mini-Winklers Set Two
2-3	Chisholm	11-Jul-05	06-Aug-05	12-Jun-05	02-Aug-05	25-Jul-05	06-Aug-05
2-3	Nadina South	22-Jun-05 24-Jun-05	03-Aug-05	28-Jun-05	02-Aug-05	19-Jul-05	09-Aug-05
2-3	Pimpernel	25-Jul-05	06-Aug-05	08-Jul-05	02-Aug-05	24-Jul-05	07-Aug-05
8-10	Decker	07-Jun-03	23-Jul-03	20-Jun-03	27-July-03	20-Jun-03	27-Jul-03
8-10	Tanglechain	16-Jun-03	24-Jul-03	08-Jun-03	28-Jul-03	18-Jun-03	14-Aug-03
8-10	Nadina West	25-Jun-03	25-Jul-03	19-Jun-05	25-Jul-03	19-Jun-03	25-Jul-03
8-10	Nadina East	17-Jun-03	22-Jul-03	21-Jun-03	26-Jul-03	12-Jun-03	26-Jul-03
13-15	Topley	11-Jun-04	09-Jul-04	30-Jun-04	03-Aug-04	23-Jul-04	03-Aug-04
13-15	Fenton Creek	13-Jun-04	19-Jul-04	30-Jun-04	05-Aug-04	22-Jul-04	16-Aug-04
13-15	Nadina West	22-Jun-04	06-Jul-04	22-Jun-04	08-Aug-04	22-Jul-04	08-Aug-04
23-25	Pimpernel	26-Jun-04	07-Jul-04	07-Jul-04	05-Aug-04	26-Jun-04	25-Jul-04
23-25	Tatsha	28-Jun-04	12-Jul-04	12-Jul-04	07-Aug-04	24-Aug-04	18-Aug-04
Non-harvested	Decker	03-Jun-03	23-Jul-03	20-Jun-03	27-Jul-03	09-Jul-03	23-Jul-03
Non-harvested	Tanglechain	23-Jun-03	13-Aug-03	18-Jun-03	03-Jul-03	18-Jun-03	14-Aug-03
Non-harvested	Nadina West	06-Jun-03	21-Jul-03	19-Jun-03	25-Jul-03	25-Jun-03	21-Jul-03
Non-harvested	Nadina East	26-Jun-03 07-Jul-03	26-Jul-03	21-Jun-03	26-Jul-03	24-Jun-03	22-Jul-03

Appendix III: An inventory of the ants of this dissertation with natural history annotations relating to the most common species.

Sub-family Formicinae

The subfamily Formicinae comprise some of the ants most familiar to people living in temperate regions of the world, including carpenter ants and red wood ants. Most are medium (5-8 mm) or large ants (≥8 mm) and are common in forests, grasslands and urban environments. Many members of this taxon tend honeydew excreting insects for a substantial portion of their diet. This sub-family is characterized by the replacement of a sting by a round, often nozzle-like acid-secreting opening called the acidopore, and a single scale-like petiole (an isolated segment between the alitrunk and abdomen) (Hölldobler and Wilson 1990). The most common genera are *Camponotus*, *Formica*, and *Lasius*.

Camponotus (Camponotus) herculeanus (Linnaeus)

Camponotus herculeanus (Figure III.1) is a medium to large ant, notably polymorphic, with minors and majors ranging in size from 6-13 mm (Hansen and Klotz 2005). This species is considered to be circumpolar up to the treeline and is found in the north-eastern United States, as well as along the Rocky Mountains in the western United States, down to Mexico (Hansen and Klotz 2005). Where it is largely absent in North America it appears to be replaced by *C. pennsylvanicus*.

As is typical for polymorphic species, *C. herculeanus* is normally monogynous. Multiple queens have been identified in some nests but they had clearly defined internal territories within the nests (Hölldobler 1962). Laboratory cultures, initiated with multiple queens, maintained a polygynous but territorial internal nest structure only for a few months or years before queens attacked each other reducing the nest to a monogynous nature. It has

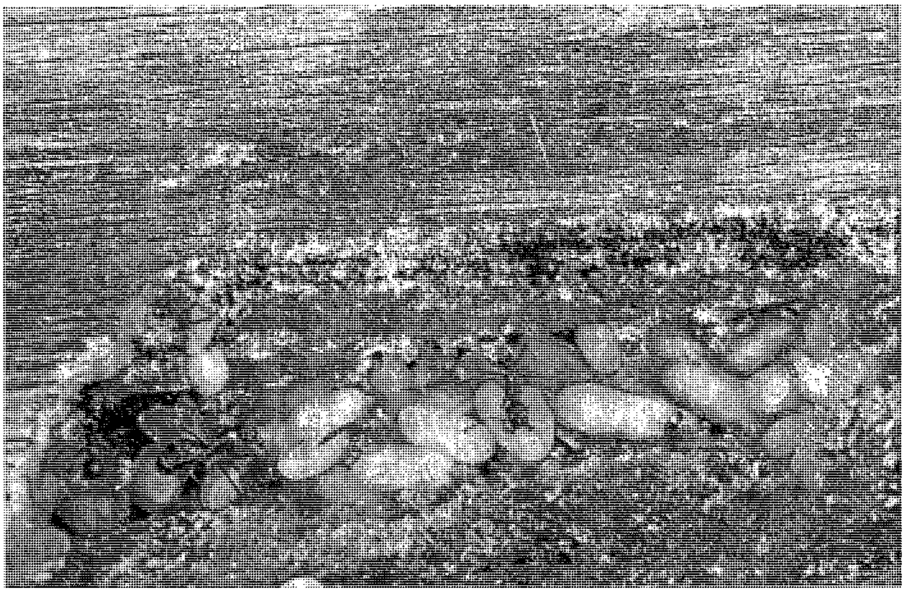

Figure III.1. A *Camponotus herculeanus* nest with workers and pupae exposed in an opened nest within woody debris. Approximate worker length is 9 mm. Photo taken in a 15-yr post-harvest site approximately 50 km south of Houston on 10 July, 2005. Photo credit: R. Higgins.

been reported from laboratory observations, that queens can live in excess of 10 yr (Holldobler and Wilson 1990).

As is typical for many species in this large genus, *Camponotus herculeanus* normally nests in woody debris, hence the common generic name 'carpenter ants.' Rare colonies have been reported in soil, however (Francoeur 1983). Mature colonies may range in size from 3,000 to 12,000 workers and some consider this species a major cause of structural damage in buildings throughout its range (Hansen and Klotz 2005). Established colonies will normally form satellite colonies throughout their territory in which larvae and pupae may be raised, making it difficult to distinguish between the natal and satellite colonies. It has been reported that this species is nocturnal (Hansen and Klotz 2005), although this may reflect a preference for cool conditions. We have certainly observed this species actively foraging during the day.

Reproductives are normally maintained within the nest over the winter, unlike most species which do not begin to lay reproductive eggs in the spring. This allows *C. herculeanus* to initiate mating flights early in the year (e.g., late May or early June) (Sanders 1970). It was reported that 50-75% of solitary queens die during hibernation over the first winter (Heinze and Hölldobler 1994).

Camponotus herculeanus is omnivorous, frequently tending aphids (especially giant conifer aphids, *Cinara* spp. in British Columbia) for their energy-rich honey-dew, but also predaceous upon forest arthropods. Nests of *C. herculeanus* are frequently targeted for food by black and grizzly bears in BC (unpublished personal observations).

Other species of *Camponotus* collected in this study include:

Camponotus noveboracensis (Fitch), (Location-Houston);

Camponotus modoc Wheeler W.M., (Location-Knife Creek).

Formica aserva Forel **(formerly *F. subnuda* Emery)**

Formica aserva (Figure III.2) is a medium to large ant, 6-9 mm long, that belongs to the *Formica sanguinea* species-group (Naumann et al. 1999). It is aggressive and when a nest is disturbed, workers will quickly swarm, bite and spray formic acid. While four species within this species group are recorded in British Columbia (Naumann et al. 1999), *F. aserva*, is by far the most common. Superficially, however, this ant is similar in coloration and size to several members of the *F. rufa* species-group, the so-called 'red wood ants,' of which, many are common throughout British Columbia.

Formica aserva is only known from North America where its distribution is described as ranging across the continent, including the Yukon and Alaska (Creighton 1950). It was not discovered in Churchill (Gregg 1972) unlike the other four species described in this Appendix. Specimens have also been described from Washington and California at both high and low elevations (Ward 2009), but Coovert (2005) notes that he does not believe it occurs in Ohio. Thus, the distribution of this species appears to be northern, short of the treeline, across Canada, and extending south into western United States.

Formica aserva forms colonies in a variety of locations. This species has been described as nesting in "mineral and organic matter, in heavy or open deciduous and coniferous woods, or in fully exposed biotypes such as pasture (Francoeur 1983)." It is commonly found nesting in woody debris, where it may or may not pile thatching around the wood (Talbot 1985). Colony sizes were estimated at 3,000-4,000 (Savolainen and Deslippe 1996).

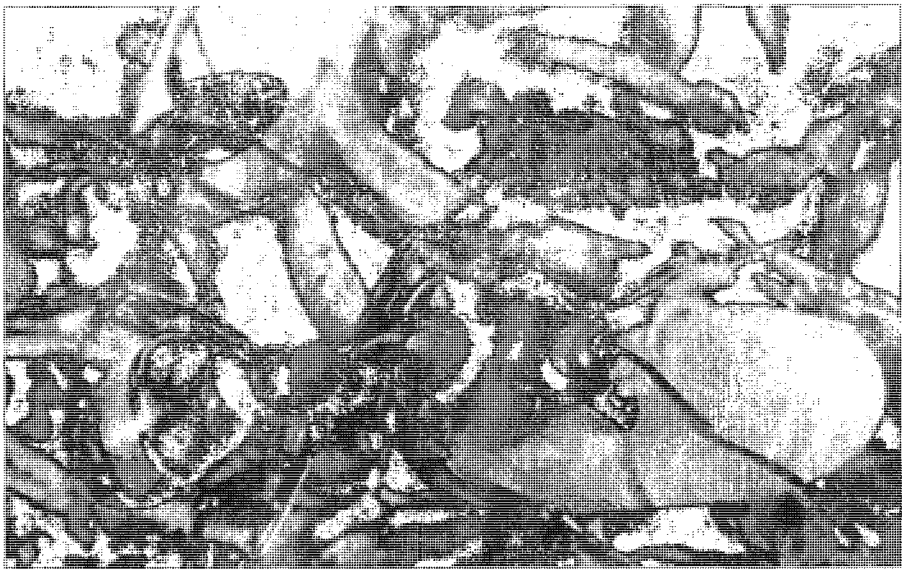

Figure III.2. *Formica aserva* workers moving pupae in a newly opened nest. Estimated worker length approximately 8 mm. Photo taken in a 15-yr post-harvest site approximately 50 km south of Houston on 09 July, 2005. Photo credit: R. Higgins.

Members of the *F. sanguinea* species-group are characterized by parasitic dependent nest founding (Hölldobler and Wilson 1990). This form of nest founding involves the queen invading the nest of another species, normally a member of the *F. fusca* species-group, killing the native queen or queens, and then beginning to lay eggs that will be tended and fed as they develop into larvae by the parasitized species. *Formica aserva* is known to parasitize *Formica neorufibarbis* Emery, *F. subaenescens* Emery, *F. argentea* Wheeler, and *F. fusca* L. (Wheeler GC and Wheeler J 1963; Francoeur 1983).

Facultative slave taking is also characteristic of this species-group. This behaviour involves established *F. sanguinea* species-group nests attacking the nests of other species (again, normally members of the *F. fusca* species-group), killing any workers attempting to defend the nest, and then carrying away pupae to their own nest. These pupae eclose in the *F. sanguinea* species-group nest and then begin to work for the slave-taking species. Detailed descriptions of slave raids initiated by *F. sanguinea subintegra* have been made (Talbot and Kennedy 1940). It is generally thought, however, that once *F. aserva* has established a nest it does not continue to engage in slave-raids as frequently as other members of this species-group. It has been noted that the Dufour's gland, a 'propaganda' gland used to secrete pheromones inducing panic among attacked species, is smaller in *F. aserva* than in other members of the *F. sanguinea* species-group (Savolainen and Deslippe 2001).

Like *C. herculeanus*, *Formica aserva* is omnivorous, tending aphids or preying upon forest arthropods. Nests of *F. aserva* are frequently targeted for food by black and grizzly bears in BC (unpublished pers. obs.).

While *F. aserva* is the only member of the *Formica sanguinea* species group collected in the work for this dissertation, it is easily mistaken for members of the *Formica rufa* species group with which it shares similar coloration and size. Members of the *Formica rufa* species group collected in this dissertation include:

Formica dakotensis Emery (Location-Houston. This is the first identification of this species in British Columbia),

Formica obscuripes Forel (Location-Becher's Prairie),

Formica obscuriventris Mayr (Location-Houston),

Formica oreas Wheeler W.M. (Location-Knife Creek).

Formica neorufibarbis Emery

Formica neorufibarbis (Figure III.3) is a medium sized ant, approximately 5-6 mm in length. It is a common member of the *Formica fusca* species-group, and is often encountered in urban environments.

This species is reported as broadly distributed throughout North America (Wheeler GC and Wheeler J 1986). It is known from northern Alaska to northern Newfoundland but also found as far south as New Mexico, Arizona and California. It was reported in Churchill, Manitoba (Gregg 1972), and reported as common at the treeline (Francoeur 1983). This species was identified in northern sandy soils and in open spruce-lichen forests (Francoeur 1983). It has been suggested that *F. podzolica* replaces *F. neorufibarbis* in similar habitats farther south (Francoeur 1983).

Although colonies in northern Quebec were reported as consisting of a few hundred individuals (Francoeur 1983), colonies in Colorado were reported as reaching 21,000 workers (Billeck 2001). In both locations, however, the colonies were normally polygynous. In North Dakota it was reported that all colonies were in woody debris (Wheeler GC and Wheeler J 1963). Francoeur (1983) reports finding this species only occasionally in wood, with most colonies under stones or in sandy terraces, although his work was at the treeline.

Pupae of this species are commonly taken away to become slaves within the nests of facultative or obligate slave-taking species (e.g., *F. aserva*, *Polyergus breviceps* Emery). *Formica neorufibarbis* is reported as seldom aggressive with other species of ants and does not defend its territory (Billeck 2001).

The diet of *Formica neorufibarbis* is similar to that of *C. herculeanus* and *F. aserva,* including predation (personal observations and Figure III.3).

Figure III.3. A *Formica neorufibarbis* worker dragging a, still living, carabid beetle, *Synuchus impunctatus* (Say). Approximate worker length is 6 mm. Photo taken in a 10-yr post-harvest site approximately 75 km north-east of Houston on 07 July, 2005. Photo credit: R. Higgins.

There are many species within the *Formica fusca* species group to which this ant belongs, however its coloration is fairly unique, similar only to *Formica subpolita* which has a much glossier integument. Most other members of this species group lack reddish coloration, and are mostly black or black/brown. Other members of this species group collected for this dissertation include:

Formica accreta Francoeur (Location-Houston);
Formica argentea Wheeler W.M. (Location-Knife Creek, Houston);
Formica fusca Linnaeus (Location-Knife Creek, Houston);
Formica hewitti Wheeler (Location-Houston);
Formica podzolica Francoeur (Location-Knife Creek);
Formica subpolita Mayr (Location-Becher's Prairie).

The genera *Lasius* and *Polyergus* are closely related to *Formica* but easily distinguished either microscopically or to an experienced observer. Species of these genera collected during the work for this dissertation include:

Lasius alienus (Foerster), (Location-Houston);
Lasius crypticus Wilson, (Location-Becher's Prairie);
Lasius pallitarsis (Provancher), (Location-Houston);
Polyergus breviceps Emery, (Location-Houston).

Sub-family Myrmicinae

Members of this sub-family are typically smaller, both shorter and thinner, and form smaller colonies than most members of the sub-family Formicinae. They range in size from 3-7mm with colonies of perhaps a few dozen to a few hundred individuals. The Myrmicinae are characterized by the possession of a sting, although it is too small in most species in British Columbia to break the human epidermis. They also possess two isolated petioles (as opposed to one in the Formicinae) between the alitrunk and abdomen (Hölldobler and Wilson 1990). Common genera are *Leptothorax* and *Myrmica.*

Leptothorax muscorum **(Nylander)**

Leptothorax muscorum (Figure III.4) is considered a species complex that is circumpolar (Heinze et al. 1996). While some authors consider this species in Canada as *L. canadensis,* (Brown 1955, Heinze et al. 1996) this combination is not officially recognized (Bolton et al. 2006). Unfortunately, no comprehensive keys exist for the identification of species within this genus in Canada. Four species are listed as occurring in BC but that would almost certainly be an underestimate (Naumann et al. 1999).

Workers of this minute species are seldom greater than 5 mm in length, usually 2.5-3.5 mm. Colonies are small, usually consisting of a few dozen workers (Heinze 1993a), although some nest populations can reach 100 or more (Francoeur 1983). The boreal *Leptothorax* spp. are considered to be usually polygynous (i.e., multiple queens), with both nest founding by single and multiple queens as well as the later acceptance of additional queens (secondary polygyny) into established nests (Heinze 1993b). Secondary queen acceptance, however, may not always be successful, as illustrated (Figure III.4), where *Leptothorax muscorum* workers encountered by the author were found to be killing a queen on the surface of a piece of downed woody debris.

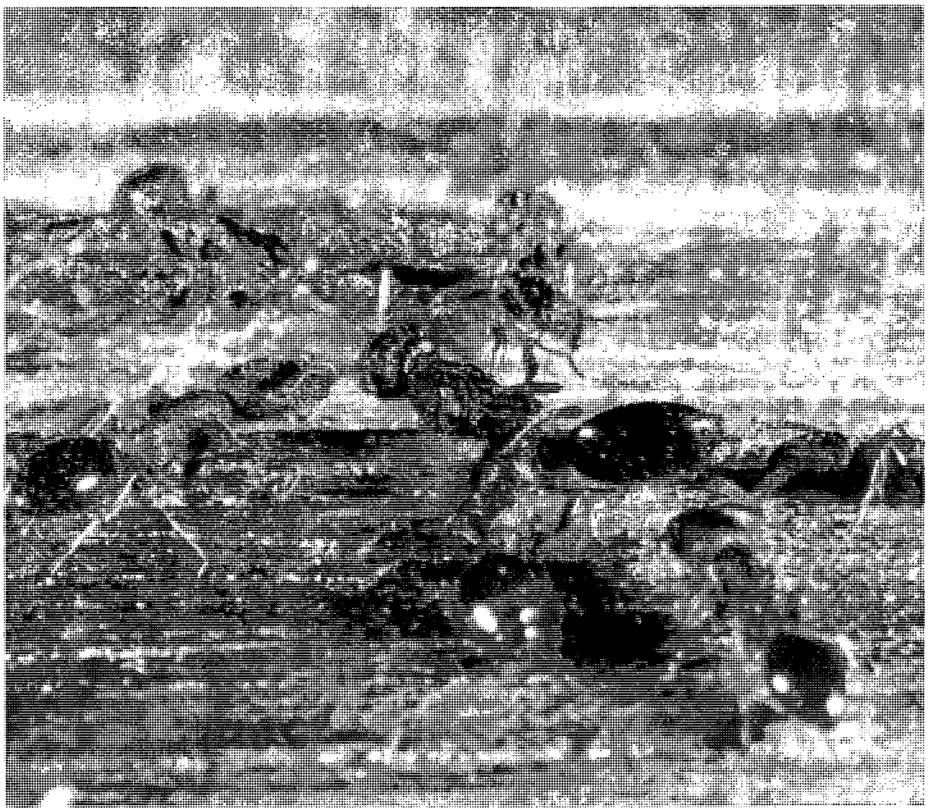

Figure III.4. *Leptothorax muscorum* workers killing a queen on the surface of a piece of downed woody debris. Photo taken in a 15-yr post-harvest stand approximately 50 km south of Houston on 03 August, 2005. Estimated worker length is approximately 4 mm. Photo credit: R. Higgins.

Leptothorax muscorum is described as nesting in almost any type of woody debris, ranging from twigs to large pieces of coarse woody debris (Francoeur (983). We have found this species in twigs similar in size to a pencil as well as under rocks, directly in the soil in warm grasslands.

The most northerly location at which it has been located is at Kidluit Bay, Richards Island NWT (69 32'N 133 47'W) (Brown 1955). It was also described in Churchill, Manitoba (Gregg 1972) and has been associated with cold conditions (Wheeler GC and Wheeler J 1986). While many ant species move into the ground during the winter, this species remains within woody debris (Heinze et al. 1996). When temperatures within nests overwintering in Russia were monitored, outside temperatures dropped to a nadir of -57 °C, while nest temperatures did not drop below -25 °C because of snow cover (Berman et al. 1982). Laboratory work indicated that permanent damage to hibernating larvae did not occur until temperatures reached -41°C.

Reproductive alates (i.e., winged queens and males) were observed on July 19th in New Hampshire (Brown 1955).

We could find no records indicating preferred food resources. Presumably it feeds upon microarthropods or small arthropod eggs in woody debris or forest litter. It is recorded as being occasionally found in proximity to *C. herculeanus* and *F. neorufibarbis* (Wheeler GC and Wheeler J 1986) which may suggest it steals food from these species.

Of the ants collected during the course of this dissertation, *L. muscorum* is the smallest and rarely confused with other genera. This genus, however, is in need of taxonomic revision.

Myrmica alaskensis Wheeler W.M. (formerly *M. kuschei*)

Myrmica alaskensis (Figure III.5) is a thin, small to medium sized ant (5-6 mm) that has seldom been mentioned in the literature. This may be the result of inadequate and incomplete species keys available for this genus. Francoeur (1983), after examining material collected by Gregg (1972) in Churchill, Manitoba, reported that Gregg misidentified this ant as *M. brevinodis*. It is unclear how many identifications of *M. brevinodis* (now recognized as *M. incompleta*) (Bolton et al. 2006) might be *M. alaskensis*. The publication, "The Ants of the Idaho National Laboratory," make no attempt to identify this taxon below the level of genus (Clark and Blom 2005).

This species is reported as present in moist boreal forests across North America from Labrador to Alaska (Francoeur 1983). Its nests are described as occurring in "organic and mineral soil, within a small hummock of *Polytrichum* spp. or dead wood, such as decaying stumps covered by mosses," (Francoeur 1983). It is not reported in the Ants of North Dakota (Wheeler GC and Wheeler J 1963), the Ants of Nevada (Wheeler GC and Wheeler J 1986), the Ants of Ohio (Coovert 2005), and the AntWeb website (Ward 2009) at the University of California, only records this species in Alaska, suggesting this is a cool climate specialist.

Myrmica spp. ants have been extensively examined in Europe and are generally considered polygynous (Elmes and Wardlaw 1993). Extensive work on the adaptations of members of this genus, although not *M. alaskensis*, to cool climates, has been performed on the Russian fauna by V.E. Kipyatkov.

We could find no records indicating preferred food resources. As with *Leptothorax muscorum*, this species is most likely feeding upon microarthropods or small arthropod eggs.

Figure III.5. A *Myrmica alaskensis* worker moving a larva in a recently opened nest within woody debris. Approximate worker length is 5 mm. Photo taken in a 15-yr post-harvest site approximately 50 km south of Houston on 09 July, 2005. Photo credit: R. Higgins.

Species within this genus are taxonomically challenging. Other species within this genera that were collected during the course of the work for this dissertation include:

Myrmica crassirugis Francoeur, (Location-Becher's Prairie) (Note: the taxonomic description of this species made use, in part, of the specimens collected in this work (Franceour 2007)).

Myrmica incompleta Provancher, (Location-Houston);

Myrmica fracticornis Forel, (Location-Knife Creek, Houston).

This genus does have a similar appearance to the genus *Aphaenogaster* although the shape of the alitrunk is distinctly different. The only member of this latter genus to be collected by sampling for this dissertation was:

Aphaenogaster occidentalis (Emery), (Location-Knife Creek).

Sub-family Dolichoderinae

In British Columbia only two species belong to this sub-family, *Tapinoma sessile* (Say) (Figure III.6) and *Liometopum luctuosum* Wheeler,W.M. In the samples collected for this dissertation only *Tapinoma sessile* was identified, at both the Knife Creek and Becher`s Prairie sites. While this sub-family is often referred to as the Dominant Dolichoderinae by myrmecologists working in the tropics and sub-tropics, it is clearly not a dominant sub-family in BC and is largely replaced by the Formicinae. In the course of this study, *Tapinoma sessile*, a minute ant (2.5-4 mm) was identified nesting in twigs, at the base of bunchgrass, under rocks and within cattle dung. A common name for this species is odorous house ant. As implied, it is a frequent house pest, infesting residential and commercial kitchens, noted for forming narrow foraging columns toward any food source.

Members of this sub-family are characterized by a slit-like opening at the end of the gaster and a reduced petiole that attaches ventrally to the abdomen (Hölldobler and Wilson 1990).

Figure III.6. *Tapinoma sessile* moving larvae within a nest. Approximate worker size 3.5 mm. Photo taken in the Williams Lake river valley, 20 April, 2005. Photo credit: R. Higgins.

Appendix III: References

Berman DI, Zhigulskaya ZA, Leirikh AN. 1982. Ecology of Leptothorax muscorum (Hymenoptera: Formicidae) in the upper Indighirka Basin. Zoologichesky Zhurnal. 61:1509-1517.

Billeck I. 2001. Density dependence and colony growth in the ant species Formica neorufibarbis. Journal of Animal Ecology 70:895-905.

Bolton B, Alpert G, Ward PS, Naskrecki P. 2006. [CD]. Bolton's catalogue of ants of the world 1758-2005. Harvard University Press.

Brown WL. 1955. The ant Leptothorax muscorum (Nylander) in North America. Entomological News 66:40-43.

Clark WH, Blom PE. 2005. The ants of the Idaho National Laboratory. Sociobiology 49(2):1-127.

Coovert GA. 2005. The ants of Ohio (Hymneoptera: Formicidae). Bulletin of the Ohio biological survey: New series 15(2). 196p.

Creighton WS. 1950. The ants of North America. Bulletin of the Museum of Comparative Zoology at Harvard College. Cambridge, Mass. Vol 104. 585 p.

Elmes GW, Wardlaw JC. 1983. A comparison of the effect of temperature on the development of large hibernated larvae of four species of Myrmica (Hym. Formicidae). Insectes Sociaux 30:106-18.

Francoeur A. 1983. The ant fauna near the tree-line in northern Québec. Nordicana 47:177-80.

Francoeur A. 2007. The Myrmica punctiventris and M. crassirugus species groups in the Neartic region. In: Snelling RR, Fisher BL, Ward PS, editors. Advances in ant systematic (Hymenoptera: Formicidae: Homage to E.O. Wilson – 50 years of contributions. Memoirs of the American Entomological Institute 80:153-185.

Gregg RE. 1972. The northward distribution of ants in North America. Canadian Entomologist 104:1073-91.

Hansen LD, Klotz JH. 2005. Carpenter ants of the United States and Canada. Comstock Publishing Associates, Ithaca. 204 p.

Heinze J. 1993. Habitat structure, dispersal strategies and queen number in two boreal Leptothorax species. Oecologia 96:32-9.

Heinze J, Hölldobler B. 1994. Ants in the cold. Memorabilia Zoologica 48:99-108.

Heinze J, Stahl M, Hölldobler B. 1996. Ecophysiology of hibernation in boreal Leptothorax ants (Hymenoptera: Formicidae). Ecoscience 3(4):429-35.

Holldobler B. 1962. Zur frage der oligogynie bei Camponotus lignipderda Latr. Und Camponotus herculeanus L. (Hym. Formicidae). Zeitschrift fuer Angewandte Entomologie. 49:337-352.

Hölldobler B, Wilson EO. 1990. The ants. Cambridge, Massachusetts: The Belknap Press of Harvard University Press. 732 p.

Naumann K, Preston WB, Ayrse GL. 1999. An annotated checklist of the ants (Hymenoptera: Formicidae) of British Columbia. Journal of the Entomological Society of British Columbia 96:29-68.

Sanders CJ. 1972. Seasonal and daily activity patterns of carpenter ants in northwestern Ontario. Canadian Entomologist 104:1681-7.

Savolainen R, Deslippe RJ. 1996. Slave addition increases sexual production of the facultative slave-making ant Formica subnuda. Behavioural Ecology and Sociobiology 38:145-8.

Savolainen R, Deslippe RJ. 2001. Facultative and obligate slave making in Formica ants. Naturwissenschaften 88:347-50.

Talbot M, Kennedy CH. 1940. The slave-making ant, *Formica sanguinea subintegra* Emery, its raids, nuptial flights and nest structure. Annals of Entomological Society of America Vol XXX111:560-577.

Talbot M. 1985. The slave-making ant *Formica gynocrates* (Hymenoptera: Formicidae). Great Lakes Entomologist 18(3):103-112.

Ward P. 2009. [Internet resource]. Antweb. California Academy of Sciences. Available from: www.antweb.org. Accessed June 12, 2009.

Wheeler GC, Wheeler J. 1963. The ants of North Dakota. The University of North Dakota Press. 326 p.

Wheeler GC, Wheeler J. 1986. The ants of Nevada. Natural History Musuem of Los Angeles County. 138 p.