FORMICA INTEGROIDES OF SWAKUM MOUNTAIN:

A Qualitative and Quantitative Assessment and Narrative of *Formica* mounding behaviors influencing litter decomposition in a dry, interior Douglas-fir forest in British Columbia

by Adolpho J. Pati

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Abstract

Formica spp. mound construction is fundamental to northern forests as their activities govern and shape forest floor dynamics and litter decomposition. The interior Douglas-fir forest at Swakum Mountain contains a super colony of *Formica integroides* whose presence and monolithic structures dramatically demonstrate their impact on the landscape. Through a series of observations, natural and controlled experiments I examine the effects of *Formica* mounding on litter decomposition. The basic measurements of temperature, moisture, evolved CO₂, and mass loss reveal that *Formica* mounds buffer litter decomposition as Douglas-fir needles are carefully stacked, stockpiled, and assembled into thatch, where at the depth of ~ 8 cm thatch mass loss minimizes and begins to stabilize. The function of *Formica* mounding further exacerbates the prevailing arid conditions endemic to this forest type. Cotrufo's Microbial Efficiency-Matrix Stabilization (MEMS) framework sets forth a conceptual model where labile plant constituents are efficiently utilized by microbes and stabilized into soil organic matter (SOM). I integrate my findings within this framework while conceptualizing aspects of complexity theory as potential ecological drivers contributing to soil organic matter formation relating to *Formica* mounds.

Through natural and controlled experiments my overall objective is to describe and explain litter decomposition involving *Formica* spp. within an interior Douglas-fir forest. I have included descriptive observations, sketches, and photographs involving the forest floor and *Formica* spp. behaviors and ecology to provide a holistic perspective describing litter decomposition within this local forest type. The framework of scientific methodology combined with a novel approach, provides further empirical and qualitative support for the findings of my research.

Preface

This dissertation, all poetry, figures and sketches are original, unpublished, independent work by the author, Adolpho Pati, under the guidance, support and supervision of Cindy Prescott.

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Dedication

To the ants of Swakum Mountain as a source of inspiration to help me tell their story.

1 Introduction

Falling, Colliding, One-particle, -structure, -moment folds into the next. The loss of identity, purpose, direction. Coalescing amorphous forms: Engendering formlessness.

1.1 Overview

"Our intellect does not draw its laws from nature, but imposes its laws upon nature." - Kant

When considering the process of decomposition from the platforms of the forest floor, soil horizons, the rhizosphere, soil microbes, and fauna; the dynamic interconnectivity ^{16,31,72,174} ranges from a fine tether to a densely woven braid; contingent upon the mixing potential of the biota. Soil organic matter is derived from the interaction of plant detritus, dissolved organic matter, residues, exudates, faunal fecal deposition; soil minerals as related to texture, sorption, and complexing properties, with microbes. As defined by these scientific constructs, Kant's words strike a stark chord of truth. Over the past 30-40 years, soil scientists have purported a pathway of poly-condensation reactions, coupled to mineral complexing ^{100,205}, whereby the refractory end product of acid-unhyrdolyzable residue (AUR) found in humus, was thought to have provided a stable backbone for the oldest soil organic matter, based upon ex-situ alkaline extractions ^{35,120,121,185,186,187,205}. This perspective has not only proven to be incorrect, but fails to consider the significance of the soil biota output, while not fully addressing the issue of soil organic matter composition, stability, and longevity ^{35,120,121,205}.

Currently, reconsideration is being given to humus and soil organic matter formation as a non-fixed, by-product of evolved biological and ecological processes ^{31,35,120,121,174,205}, linking substrate to process while unraveling its elusive complexity where one only needs to glance underfoot to experience. What drives decomposition? Is it temperature, moisture, litter-quality, substrate, the microbial and soil faunal community or the interactions among all the aforementioned factors and perhaps a few other unknowns ³⁵.

Decomposition, distilled to its rarefied form, is the interaction of prevailing abiotic conditions with detritus and soil organic matter as linked to soil microbes and fauna giving the medium a unique signature and defining it as an ecosystem property ^{35,205}. In attempts to construct a working model

^{101,120}, fundamental elements have been defined: macro/micro-nutrients; structural C forms as labile, intermediate, recalcitrant; roles of organisms and key genetic pathways; abiotic factors such as temperature, moisture, soil texture; litter and litter quality ^{31,120,121,128,185,186,187,253}. The next logical step involves bridging the gaps between the known cornerstones to form a more complete, holistic perspective. In consideration of the inherent mutable nature of detritus and soil organic matter if baseline influences are in a constant and imperceptible state of flux, how do we approach and begin to identify the main causes driving decomposition? As we further examine microbial and faunal activities as integral to the process, it is useful to conceptualize, identify, and clarify the links, gaps, and specific roles significant to the overall process.

1.2 The Conundrum: Humus and Soil Organic Matter - An Evolving Conceptual Overview

The forest floor is a spatial-temporal accumulation dominated by plant biomass, which is a dynamic and heterogeneous interface between above- and below-ground communities ^{31,159,174,245}. The L horizon (characterized by accumulation of undecomposed plant litter), F horizon (below the L horizon characterized by accumulated partly decomposed organic matter) and H horizon (below the F horizon characterized by accumulated decomposed organic matter, structurally indiscernible) contain layers of accumulated detritus in various stages of decomposition based on mass loss and remnant structural integrity ^{50,156,180, 245}. Predominantly, the least decomposed, most structurally sound material is found within the L horizon; the most decomposed, least structurally sound, unidentifiable, and presumably, the oldest is found within the H horizon ^{159,174,245}.

The development of the H horizon has three defined pathways H₁₋₃ accumulation, types, prevailing abiotic conditions, and biota ⁷², premised on organic matter:

- H₁ accumulated detritus, inherent and residual, indicative of mor formation; degradative process under anoxic conditions
- H₂ polycondensation: polymerization of monomers, phenols, and aromatics (LMW compounds) forming macro-molecules by extracellular enzymes; complexing, the adsorption to clay particulates, and aggregation of soil organic matter with minerals; lignin, the AUR, forming "stable" refractory structures under aerobic conditions ^{120,121,128,185,186,187,205}
- H₃ Microbial neosynthesis: occurring within detritus, mucilaginous residues, fecal pellets, fine roots, and aggregates; rhizodeposition of labile-intermediate C forms which accumulate, polymerize, and mineralize via a microbial pathway (filter); microbial death; complexing and occlusion of soil organic matter to mineral surfaces, undergoing microbial catalysis ^{72,120,121,149}

Setting aside the H₁ pathway as an inherent property of northern boreal forests and re-evaluating H₂ pathway, contemporary research ^{35,120,121,156,179,180} supports a refined H₃ pathway as the main directive behind humus and soil organic matter formation. Based upon Hayes's observations of fungal inhabitation, Ponge's ecological succession of forest litter, Zhang's work on litter quality, and Mori's

more recent work of classifying and quantifying humus into fragments and material types, there is a more replete perspective that has quantified and identified the composition of humus whereby the H₃ pathway is the main catalyst of humus and soil organic matter formation ^{35,120,205}. The logical question as posited by Cotrufo: "What is the nexus between above-ground humus to below-ground soil organic matter formation" ³⁵? To further distill her thought: How does above-ground organic matter become integrated into the below-ground system then further transformed into soil organic matter? What are the mechanisms behind this transformation?

When conceptualizing detritus and the development of the organic horizons as a back-drop of temporally varied and layered source-materials, which degrade through inhabitation, shredding, fragmentation, and comminution, consideration needs to be made of the physical transformation and translocation linking detritus as a precursor to soil organic matter. Cotrufo's implied question not only serves as a critical departure point, but as a directive to identify, deconstruct and redefine the main components within the prevailing nexus.

My perspective of the components within her nexus includes:

- The inherent qualities and physical attributes of the soil
- Plant community influences:
 - Accumulation of detritus
 - Root expansion, deposition, and the rhizosphere
- Microbial and faunal influences

My proposed amendment to the MEMS framework ³⁵ includes the "mixing potential" as a qualitative description that ranges from a non-connective, limited mixed-state, to a highly connective, fully mixed state. The "mixing potential" connects organic to mineral horizons, which further considers biotic influences and their residual by-products. The "mixing potential" is directly orchestrated by fauna, microbes, root expansion ¹⁹ and deposition into soil horizons, framed within the intrinsic soil properties providing the connective network transferring detritus, dissolved organic matter (DOM) into the soil matrix ^{9,12,74,174,245}.

Detritus, when mixed into mineral horizons by soil fauna ¹⁵⁶, significantly contributes to soil organic matter ³⁵. The aforementioned biotic activities further amend the surrounding soil matrix, providing a linkage between detritus and soil organic matter. The biotic mechanisms of the C pathway, via rhizodeposition; the microbial activities of C uptake, mineralization, and turn-over; faunal fecal deposition and mixing potentially establishes ecological feed-back loops ^{31,174,179} that further amend soil properties while increasing soil heterogeneity, contributing to soil organic matter formation and stabilization ^{24,28,156,162,174,179,180,243}.

1.3 The Components

1.3.1 Soil Attributes - The Physical Framework

The list of soil properties that affect translocation of detritus and dissolved organic matter include: porosity, tortuosity, texture, water potential, compaction, bulk density, aggregation, sorptive, and complexing properties ^{50,75,245}. Singularly, these physical properties and their interactions are complex without considering the dynamic interplay of plant and microbial-derived organic matter and activities of the biota. Soil porosity provides a network of potentially inter-connective pore spaces that when connected, yield an infiltration potential, i.e., tortuosity, allowing for the translocation of detritus and dissolved organic matter. The downward movement of detritus and dissolved organic matter, from organic to mineral horizons, interacts, forming and contributing to the preexisting soil organic matter.

When comparing uniform compacted soils to textured non-compacted soils, tortuosity ranges from a few isolated pore spaces, to pore spaces variably sized and shaped that form an interconnective web, maximizing tortuosity while providing a full gamut of connectivity. With a greater infiltration of translocated dissolved organic matter and detritus, there is a potential increase of various covalent and ionic bonds due to additional surface exposure to the surrounding matrix ^{12,120,121,205}. The interactive nature of surfaces and the matrix composition adds to the complex dynamics of porosity and tortuosity. "Self-assemblage", sorption to clay surfaces and mineral complexes, and increased aggregation are the purported causes of soil organic matter stability and occlusion, notwithstanding the amphiphilic properties of the dissolved organic matter and detritus ^{120,121}.

When considering temporal influences from seasonal to accumulated millennia, a layering effect of residual deposition of detritus and dissolved organic matter would provide a wide range of labile to recalcitrant C and N sources, contributing to soil organic matter variability, imparting it with a unique signature, and establishing it as an ecosystem property ²⁰⁵.

1.3.2 Plant Community Contributions: The Forest Floor, Roots, and Rhizosphere

1.3.2.1 Forest Floor

The forest floor, from a spatial perspective, is a topical and surficial extension of the soil horizons comprised of accumulated detritus and organic matter (OM) in various stages of decay. Accumulated detritus as habitat, provides microvariability of temperature and moisture, extending niche potential for soil microbes and fauna ^{75,174}. The depth of detritus accumulation is contingent upon: litter senescence and the amount that falls at any given moment; early differential rates of decomposition established by litter quality indicated by lignin content ^{128,155,253}; seasonal abiotic factors of temperature and moisture 185,186,187 coupled to microbial and faunal presence and inhabitation ¹⁸⁰.

Setting aside the concept of ecological niche potential, upon further examination of accumulated plant source materials, i.e., litter and coarse woody debris (CWD), a heterogenic and spatially dynamic interior landscape emerges, which functionally links above- to below- ground systems 1,16,66,85,92,115,125,174,208

Litter and CWD in advanced decay stages, may functionally provide "empty chambers" for moisture absorption and retention ¹⁷⁴. Ideal moisture conditions are potentially maintained for longer durations promoting expanded physical ranges and extended metabolic periods for the microbial community ⁷⁵. Additionally, the lower bulk density of litter compared to compacted mineral soils, increases potential accessibility of soil organisms due to reduced physical resistance, while connecting the pore spaces, i.e., tortuosity, extending the continuity from organic to mineral horizons, thus increasing overall connectivity.

Undisturbed, the forest floor depth provides a variable habitat that houses soil microbes and fauna, provides C and N sources, and acts as a buffer from the prevailing climate. The surficial material undergoes more extreme abiotic stresses such as UV degradation, moistening and drying effects ^{9,13,33,40,71,119,135,154,155,158,164,170,172,188,228,232,241,252,253}, while deeper interred materials are physically less exposed to these extremes.

The complex interplay between space, functionality, and habitat creates a dynamic ecologic-temporal component that supersedes the perspective of litter decay as simply a matter of mass loss and CO₂ evolution.

1.3.2.2 Roots and Rhizosphere

Immobile, the growth of coarse, fine, and exploratory roots extend a plant's surface into direct contact with soil ^{135,228}. Exploratory roots elongate into unknown regions to capitalize upon potentially untapped resources as the rhizosphere undergoes periods of depletion. Hydrotropically directed root growth ^{228,232} and the additional development of root hairs facilitate the uptake of soil nutrients through increased surface area contact ²²⁸. Moreover, mycorrhizal associations indirectly extend the surface absorption potential further linking root systems to mineral soils and organic horizons.

Secondary development of adventitious roots found in tree species form a dense and pervasive "web-like" structure that tends to develop in nutrient-depleted soil types. This structure enables complete propriety over access, conservation, and recycling of localized resources. A combination of mass flow and diffusion drive nutrients towards root surfaces based upon the concentration gradient and nutrient diffusion coefficient of the individual nutrients ²²⁸. The root surface not only allows access of nutrients during growth phases, but also acts as a barrier if there is an excess concentration. When absorbed, nutrients are captured by apoplastic and symplastic pathways along a chemo-electro gradient ^{228,232}. Additionally, proton extrusion and exudates, i.e., ions, water, enzymes, mucilage, and degraded C-

based compounds that form organic acids, manipulate rhizosphere pH levels ^{33,141,228,241} while further promoting and stabilizing aggregation ^{72,105,159,245}.

Fine-root surfaces provide a dynamic interface for microbial activity and turnover stimulated by exudation. From regions of heightened microbial activity, considered "hotspots" ²³, exudates and plant biomass are released from living sources into the rhizosphere and detritusphere as fresh pulses of organic matter releasing labile C in the forms of monomeric sugars ^{129,164}. These C pulses stimulate microbial turnover, priming the preexisting soil organic matter, which further transforms and decomposes the developed soil organic matter ^{23,129,149,177}. Jones et al. propose four possible mechanisms which are driving exudation ¹⁰⁵. Although singularly applicable, when considering plant adaptability and genetic regulating mechanisms, all the proposed options seem simultaneously viable.

Root structural and functional longevity, from ephemeral to inveterate, root systems penetrate soil, facilitate nutrient and water uptake, and eventually decompose leaving remnant gaps and tongues of C and N in various age and qualities ²³. Accumulation of living and moribund fine roots and fungal hyphae, contribute significantly to detritus and soil organic matter when fully considering the temporal and spatial pervasiveness of the rhizosphere and mycorrhizosphere ¹⁵⁶. As remnant structures fully deteriorate, the emergent gaps and channels further contribute to bulk soil pore space and tortuosity.

As I sort through research and begin to unravel the complexity and dynamics of a single plant, I am riddled by the dense complexity of an entire evolved community and its unimaginable spatial and ecological interactions that are scarcely discernible even with current isotopic and imaging technologies. Embracing philosophical and aesthetic approaches coupled with imagination to inspire questions, while pragmatically utilizing current technologies and information, allows for alternate novel pathways to develop in efforts to unravel these questions.

1.3.3 The Microbes and Fauna

The spatial composition of a soil pedon is framed by the organic and mineral horizons, where each domain and aggregate falls within a range from isolation to fully connected and is, potentially, its own island immersed within the larger void of the bulk soil, forming a three-dimensional interior landscape ²³¹. Aggregates and rhizospheres, enriched with microbial life limited in motility, exposed within pore spaces and tortuous channels, are facilitated by water films and fauna serving as dispersal agents within the metacommunity ^{26,31,159,174}. The fauna sublimely inhabit their domain. A sensorial extension into their surroundings as evidenced by mucus-covered integuments, bristle-like extensions, inured casings, and in some cases limited pigmentation and vision ^{31,58,59,72,159} allowing for pre-scripted movement. Corporeal extension is intrinsic for the survival of soil organisms. Based on their temporal presence, they are innately linked to their environment via physical stimuli and through biochemical signals and inputs that orchestrate specific responses and metabolic activities ³¹.

Ponge's description of litter decay elegantly illustrates forest litter and detritus as a successionaltemporal habitat, implicitly linking humus formation to microbial and faunal activities as identified by fecal pellets, and physical-structural decay of litter ¹⁸⁰. Additionally, Mori et al. support these observations by quantifying the percentage of fecal pellets as a main source material within detritus and humus ¹⁵⁶.

The faunal trophic levels each have autonomous functionality while overall possessing an evolved interdependence as a community ^{31,104,141,230}. Microfauna serve as indicators of environmental conditions and community stability; the mesofauna as dominant dispersal agents, while the macrofauna have direct effects on soil structure by fragmenting, mixing, and re-distributing detritus and soil organic matter throughout the pedon ^{31,58,59,72,96,137,159,240}. The dualistic relation of bottom-up support and top-down controls collectively forms a self-regulating system ^{16,90,127,174,210,211}. Over extended periods of time, the range of organismal links forming networks increases adaptability of the entire system ^{26,230}, intimately embedding organism to community assemblage and structure, and to its prevailing environment ²⁶.

The individual actions of shredding, comminution, and fragmentation of detritus transforms and weakens decayed remnant plant structures which, when working in tandem with the microbial community, allows increased access and utilization of stored C and N sources. The MEMS framework ³⁵ is supported and enhanced through faunal activities by decreasing energetic costs of microbial acquisition to held nutrients and by extending dispersal ranges. The passage from gut to fecal pellets ^{31,82,96,103,137,143,185,186,187,237,243}, serves both as a microbial food source and an emergent micro-community; and as a residual by-product of the accumulated interactions of the microbial and faunal communities, linking detritus to soil organic matter, engendering the MEMS framework as tenable.

Carbon and N are tractable threads identifying various forms found within detritus and humus, tracing the flow throughout the soil food web. As labile forms deliver pulses, priming microbial metabolic activities ^{47,60,129}, the ability to identify various levels and connectors allows for a more replete picture linking detritus to soil organic matter formation and stability, while adding further definition to the MEMS framework.

1.4 Literature Review

what lies within and below; opaquely complex, profound in simplicity, impalpable to the senses, awaiting discovery....

1.4.1 Overview

The process of decomposition is the underlying, complex, and fundamental process that governs a forested ecosystem. Detritus is penetrated, comminuted, utilized, and re-distributed as smaller particles and nutrients amongst the macro, meso, and micro fauna, including the microbial and plant communities. How do red wood ants, also known as Formica sp., contribute to and what role do they play within this labyrinthine process? Formica sp. should be perceived as an organism or super-organisms rather than as a collective of individuals ^{49,151}.

"An organism is neither a thing nor a concept, but a continual flux or process, and hence forever changing and never completed," William Morton Wheeler¹⁵¹. The eloquence of Wheeler's description of ant communities is astute and well-studied. He tenders a contemporary view of what would otherwise be referred to as "biological organisms"; formidable living entities reduced to utilitarian forms. One may criticize his viewpoint as lofty as opposed to its strength of validity, as it is firmly ensconced in the most basic principles governing life: nutrition, reproduction, and protection ¹⁵¹.

Ants are the embodiment of adaptive plasticity, resilience, and idiosyncrasy, not only physically, but behaviorally ⁴⁹. These qualities allow for residency in some of the most inhospitable locations on the planet, giving them the functional status of "ecosystem engineer" and "key-stone species" ^{13,34,54,57,65,68,77}. Their status is due to their lasting and transformative affects over their physical environment (e.g., mounding and colonial activities) ^{4,46,105,153}, and their re-structuring of the above-ground invertebrate and plant community within their foraging territories ^{8,26,31,47,58,59,75,81,95,110,113,117,132,133,139}. As a formidable force expressed through an extended, temporal trajectory with a low-level biotic and abiotic disturbance regime, ant communities directly transform the soil structure based solely upon behavior and presence.

Why are wood ants significant? They preside both arboreally and terrestrially, tending aphids and scales for honeydew, a primary food source; and predate macro or meso fauna and developing larvae; holding an imperious rank within the above-ground invertebrate community ^{8,58,59,64,132,133,136}. While foraging for seeds containing fatty and protein-enriched elaiosomes, open meadow *Formica* sp. are secondary dispersal agents for myrmecophagous plants ²⁶. Many species of the group will construct colossal mounds or elaborate subterranean colonies stacking leaves, plant and light woody debris containing lichens, bryophytes, and resins ^{18,47}, while bio-perturbing and redistributing soil by carving extensive tunnels and belowground chambers ^{4,46,94,105}. When present, their foraging activities will re-structure the above-ground invertebrate community, and regulate the microbial community within the domain of their colony ^{8,31,51,58,59,105,132}, as part of the dynamic interwoven mesh known as decomposition (Appendix F, Fig. 67).

1.4.2 Decomposition in Northern Forests

The governing dynamics of litter decomposition as associated to soil fauna are: fragmentation, comminution, the redirecting of energetic and nutrient feedback loops that eventually go through the processes of mineralization and immobilization ^{19,146}. The process does not follow a direct linear progression, but rather a circuitous pathway of simultaneous actions, redundancies, and turnovers all elegantly based in the first law of thermodynamics - conservation of energy.

The process is largely driven by the plant community and the production of detritus in the form of organic materials (e.g., leaves, woody debris, and roots) ¹⁴⁹ acted upon by various factors such as, seasonal moisture, temperature, soil fauna and the microbial community's interactions. This is not to suggest the process is predictable or energetically homogeneous, but rather susceptible to various abiotic (e.g., fire, flooding, and freezing) and biotic (e.g., grazing, foraging, urination, defecation, and animal death) fluxes, that enrich and destroy, providing the dynamic texture that is endemic to the process.

The rate of decomposition for various organic materials characterized from litter bag experiments in North American and European forests ^{19,181,182,185,186}, demonstrates three, sequential seasonal rates:

- An initial, autumnal leaf loss marked by a rapid mass loss of litter, flushing the system with readily absorbable leachates
- A hibernal phase with a stilted rate of litter mass loss due to cold temperatures, indicated by diminished decomposition rates
- A vernal phase indicated by increased seasonal temperatures accelerating the remaining mass loss at increased rates of decomposition, then slowing as moisture content decreases¹⁹

These early experiments demonstrate mass loss due to decomposition, providing a departure point for later research to question and define the functional roles of the soil biota, litter quality, and interaction with substrates, and the mechanisms of nutrient transfer.

In later studies, litter diversity, quantity, stand age, substrate, moisture, temperature, and pH ¹⁹ become crucial considerations for identifying productive and unproductive systems ¹⁴⁶. Logically, with greater diversity of litter comes an increase of C sources, increased N and P availability, and an increase of other elemental sources (e.g., Ca, Mg, and K). The amount of litter as it relates to stand age or succession, contributes to thicker L, F, and H layers in older forest types. Depending on substrate alone, the retention and mobility of macronutrients (N, K, Ca, Mg, P, and S), in their ionic forms, will bind more closely to clay/silt particles and associate more freely amongst sand-dominated loams. Moisture increases the availability of nutrients to the microbial biota within the soil matrix by forming micro-films and promoting the stabilization of soil aggregates ¹⁹. Low pH levels (<5.5) will inhibit nutrient availability and uptake, or leach macronutrients from underlying substrates. Increased

temperatures accelerate the rate of decomposition due to increased mass loss driven by the increased metabolism, respiration (CO₂ release), and growth of the soil biota including plants and roots ^{19,109,110,121,122}. Sugars and starches are considered easily available labile energy sources; cellulose and hemi-cellulose are intermediate sources; and tannins, lignins, suberins and cutins rich in polyphenols containing long and complex C structures are considered recalcitrant sources ^{19,149}.

Wardle et al. ¹⁴⁹ further distinguish productive and unproductive ecosystems with the latter being more characteristic of northern forests, excluding the Northern Pacific Coast range. Comparatively, with its richer biota, the Northern Pacific Coast range is more indicative of an ecologically productive system due to a wet and temperate climate which gives rise to: a fully developed heterogenic forest floor; higher quality and greater litter quantities; and temporally diverse and fully developed stands ²⁴⁵. Their review examines the linkages between terrestrial and belowground systems. Upon further examination, characteristics of an unproductive system include:

- K-selected tree species (long-lived and highly adaptive) produce low-quality litter due to low N content and high concentrations of phenols, lignin, and structural carbohydrates
- L, F, H layers driven by fungal-based networks (Conversation with Elaine Ingham, Summer 2001; unreferenced)
- Increased numbers of enchytraeids with macro/micro arthropods (e.g., isopods, Diplopoda, Chilopoda, Collembola, and Acari)
- Soil processes marked by slower decomposition and mineralization, with high nutrient conservation, where "C sequestration is promoted" ¹⁴⁹

In advancing the perspective of decomposition, a more replete view includes the above and belowground systems, whereby the plant community drives the process by providing: nutrients in the form of detritus, the root structures supporting rhizospheric interactions, and C as the fuel for the process with the microbial and faunal communities working in tandem.

Suzanne Visser ¹⁴⁶ eloquently describes and functionally defines the actions to specific soil fauna. Comminution consists of three sizes (20-50 µm, 100-200 µm, 200-300 µm) of fragmented litter associated, respectively, with appropriately sized fauna: micro-arthropods; meso-arthropods; and earthworms or millipedes ¹⁴⁶. The soil fauna not only fragments the litter providing additional surface area to the microbial community, but "conditions" these particles (Class discussion with Cindy Prescott, spring 2008; unreferenced) for further "break-down". Conversely, some of these particles may pass undigested through these organism's guts with little conversion whatsoever (Class discussion with Cindy Prescott, spring 2009; unreferenced). The next treatment, grazing, there is "selective feeding of microbial tissue by the micro-fauna without extensive destruction of the resource" ¹⁴⁹. The grazer's role is fulfilled by the microbial-feeding nematodes and protozoa, whereas the enchytraeids, Collembola, and mites not only graze but often selectively feed on fungal thalli which may inhibit growth, while this feeding is also thought to accelerate decay due to faunal preferences for specific fungi ¹⁴⁹. The final stage includes the dispersal of fragments, in which these "inoculants" are seeded with microbial communities and then transferred by fecal pellets and castes, or where spores adhere to soil fauna and are dispersed throughout the system ¹⁴⁹. The study provides a comprehensive view which includes the microbial and faunal as active participants and begins to clarify functionality to members of the belowground communities.

J. F. Ponge's 1991 paper on the succession of Scotch pine needles by the microbial and faunal communities is one of the seminal papers on decomposition. Ponge classifies decomposition into four stages giving a highly resolved accounting of needle litter decomposition. The first two stages include specific, successional, fungal colonizers that appear to enter through stomatal and mesophyll cells, as evidenced visually by cellulose and hemi-cellulose discoloration and tissue disruption, accessing easy C sources ¹¹⁴. The tertiary stage is a significant and transitional period, where noticeable fragmentation (tunneling) occurs; where fecal pellets (oribatids) and cysts (nematodes) are present throughout the needle tissue; and where noticeable colonization of the tissue by the fauna and the microbial community is indicated by the removal of cytoplasm ¹¹⁴. The final stage is marked by noticeable blackening and significant deterioration of the cellular tissue and mycorrhizal presence; and distinctive mycelial growth within the hollowed cells of the needles ¹¹⁴. This paper provides a compelling depiction of the sequence of events behind decomposition, and a replete roster of the "players" driving the process.

Decomposition is a difficult process to discuss because of its complexity and often indistinguishable pathways. A reductionist approach embraces small facets of a complete picture, which involves intimately linked soil biota and abiotic elements that, when perceived collectively, defines the holistic process. Heikki Setälä introduces a contemporary framework that characterizes decomposition in fast and slow cycles ¹²⁹ that, perhaps, includes the recalcitrant C sequestration as the slowest cycle. The "fast cycle" occurs in the rhizosphere where root exudates supply easily accessible nutrients highly sought after by the microbial community for rapid turnover ¹²⁹. The "slow cycle" occurs in the L, F, H and A layers where detritus "breaks down" at a much slower rate, offering a more sustained nutrient pulse contingent upon nutrient mobilization in the soil food web ¹²⁹. The slower recalcitrant nutrient cycle, where nutrients are sequestered into non-decomposable forms (e.g., lignin) and remain intact depending on the presence of saprophytic fungi, substrate, temperature, and moisture. Setälä's framework provides a sophisticated example of this ecological interconnectivity, by defining the innerworkings of the overall process and interlinking these cycles.

Decomposition and the transformation of detritus into utilizable components by and for living organisms, is a profound process. The work of David Coleman, Elaine Ingham, Heikki Setälä and many others has provided inspiration for future research, which may include: further definition of the mechanisms behind the various rates of nutrient cycling as it relates to the entire process;

identification, evolutionary linkage, and further definition to functionally similar species including the points of exchange between functional groups, while further refining the overall process.

1.4.3 Red Wood Ants and Decomposition

Red wood ants, formally known as the Formica rufa group, are sometimes known for their large polydomous (inhabiting more than one nest), and polygynous (multiple egg-laying queens co-existing within one-several nests) ⁸⁷ colonies; and their prominent "thatched mounds" comprised mainly of leaf litter; light, woody debris; pine and fir needles. They are generalist foragers and predators that tend aphids and scales for honeydew, a stable C source ^{8,58,59,132,133,136}. When present within an ecosystem, they tend to be the dominant invertebrate species ²⁸. They possess a set of unique physiological attributes coupled to aggressive yet idiosyncratic behaviors; characteristics that are the driving forces behind this extensive group ⁴⁹. If unobstructed, they have the ability to shape the community structure and leave a lasting impression on the landscape ³⁴.

The physiological needs of red wood ants, as any living organism, are basic. Physical resilience and plasticity in behavior are the key attributes to their survival. Hölldobler and Wilson have named these as the "norm of reaction". The concept is based on the flexibility of responses of an individual organism, but due to the eusociality of ant species, it applies to the whole colony ⁴⁹. A few of the specialized organs and physical features include: the infrabuccal pocket, the crop, the metapleural gland, and the rectal papillae (Appendix F, Fig. 68).

The infrabuccal pocket is a cavity behind the labium within the head region of the digestive tract where wastes and debris collect into hardened pellets for later disposal ⁴⁹. The pellet that is formed in this pocket is significant to the attine group for transmission of fungi symbionts to nuptial females ^{67,117,125}. With reference to the Rufa group, these "waste" pellets form as a by-product of grooming and foraging activities, that, when dispensed of, may act as dispersal agents for the microbial community, in turn affecting soil aggregate formation, stability, and heterogeneity; particularly affecting soil quality and the belowground community structure.

The crop, also referred to as the "social stomach", is located in the post-petiolar region. This first segment of the gastro tract holds liquid food that can be later regurgitated for nest mates in their efforts to collect "booty" during foraging activities ⁴⁹. Foraging, predation, and trophallaxis are crucial for colonial stability and growth, as it reinforces and establishes an impetus for nest mates to assist in the collection of viable food sources for pupae and larvae within the developing colony. In so doing, they predate and forage expansive regions and, with assistance, are able to collect more and perhaps unwieldy prey, based on the nutrient needs of the queen(s) and developing broods. The refuse and discarded body parts are displaced outside and throughout the thatch, acting as potential enriching agents for decomposition ^{39,87}.

The metapleural gland, an essential organ intrinsic to colony survival unique to the Formicidae family, located in the lower alitrunk and upper petiolar region, contains specific biochemical compounds that act as anti-microbial agents. The gland is thought to have evolved as a protective mechanism for communal living ⁴⁹, due to easy transmission of pathogens from close contact and to the very nature of the medium that wood ants transport and manipulate detritus.

The rectal papillae, located in the lower post-petiolar region of the digestive tract, regulates and reabsorbs water ³⁰. This physiological attribute is especially vital for *Formica* sp. primarily because it provides them with a "foothold" enabling them to tolerate and survive in arid environments. From an evolutionary perspective, it is a provisional adaptive feature that may disallow less adaptive species to occupy niches within extreme environments. The fecal pellets produced in this papillae are highly concentrated and possible sources for soil enrichment of the below-ground microbial community potentially increasing aggregate stability and bulk density ^{39,87}.

Nest departures, nuptial rites, and the founding, ergonomic, and reproductive stages; this general sequence of events, initiated by the foundress, eventually leads to the establishment of a new colony and gives rise to mounding activities ⁴⁹.

Mounding behaviors are contingent upon species type, adaptive plasticity, colony size, seasonality, egg laying, and brood rearing. Mound construction consists of either smaller, shorter-lived excavated nests that resemble craters, identified as Type 1 mounds, or as a more prominent feature where thatch is incorporated and carefully stacked to form a mound, referred to as Type 2 mound ³¹. Bio-perturbation is a significant factor in mound construction for both types ^{4,46,105,153}. The mixing of organic and mineral layers of varying textures along with the addition of litter creates a heterogeneous mixture that increases soil porosity, aggregate stability, bulk density, drainage, and nutrient availability. During colony establishment, the mounded materials provide an organic matter sink, leaching valuable nutrients throughout the soil matrix ^{4,46,105,153}. There is a temporal loss of soil horizonation beneath the mound that is eventually regained after abandonment, but may have lasting effects on the local environment ⁴⁶.

From personal observations, Type 2 mounds can be as large as 2 meters in height and 5 meters in diameter, with construction preference for old stumps, snags, and felled trees of older, larger trees that structurally support larger mounds and provide the additional insulation and sustained periods of low-moisture levels necessary for brood rearing ⁴⁹, with the later having an indirect effect on decomposition. The exterior of the mound forms a dense, encrusted layer approximately 5-8 cm thick while the interior thatch mixture, resembling carrot cake, is drier and more porous in texture, allowing the nest to warm and cool at increased rates diurnally, but making it susceptible to ambient temperature extremes ^{38,45}. In addition, it allows for water drainage both laterally and vertically throughout the "formicarious pedon" ⁴⁶.

Formica spp. are poikilothermic and require insulation for survival. Mound temperature and moisture regulation are key for brood survival and major factors influencing decomposition; what Hölldobler and Wilson refer to as the "temperature - humidity envelope" ⁴⁹. Each ant species has a range of temperature and moisture that they are able to survive and successfully rear a brood in.

Based on forager's temperature and moisture sensitivity which establishes the parameters for the remaining colony, Northern *Formica* sp. tend to show a higher level of cold tolerance compared to Southern *Formica* sp. ^{87,37,41}. When comparing non-foraging workers to foragers, based on their adaptive behaviours of sunning, huddling, vertical egg movement, and venting, demonstrating internal mound regulation, external foragers that are exposed to ambient conditions are highly susceptible to moisture and temperature extremes ⁸⁷ (personal observations). Moreover, Horstmann's 1986 study of temperature and moisture regulation and brood-rearing behaviors in nests of *F. polyctena,* discovered a temperature optimum of 28-30 °C for inner chambers with a relative humidity determined by worker and pupae respiration to be between 85% - 95% based on structural nest manipulations and worker departures from mounds ⁹³.

The interior Douglas-fir forest provides a mosaic framework of micro-habitats ^{174,209,210}. The dry conditions of Swakum Mountain when coupled to *Formica* species micro-habitat specialization and resistance to desiccation ^{46,87}, provide adaptive mechanisms underlying the "temperature - moisture envelope" ⁸⁷. The warmer and drier conditions of Swakum Mountain due to its southern exposure, supports early seasonal *Formica* activity. External activity was noted in March 2010 where ambient air temperatures were ~ 8-10 °C and surface mound temperatures were ~ 15-17 °C demonstrating environmental micro-variability whereby *Formica* adaptive responses provide further evidence supporting the "temperature - moisture envelope" ^{46,87}.

Mound maintenance, stacking, and piling litter uphold these conditions by stabilizing humidity and creating a temperature gradient within the mound; both intrinsic to decomposition. Frouz and Finer further examined mound temperature and egg-laying, noting an increase in temperature during the laying period in wet and dry Type 2 mounds ³⁸. They do not describe the effects on decomposition, although one might infer from their findings that increased temperature and moisture will increase decomposition rates. Furthermore, with dry and wet nest types, moisture within the upper layer of the mound was higher compared to the interior ³⁸, suggesting that, with increased seasonal temperatures, a varied rate of decomposition may occur.

When nests are founded, location preference is given to southerly exposed areas due to increased insolation with slight coverage resembling an edge effect ^{27,54,130,131}. Southern-exposed mounds have a greater likelihood of receiving and retaining more heat, elevating nest temperatures earlier in the season, giving an ecological advantage for early brood rearing. This extends foraging and laying time and the seeking of prey based on the nutrient requirements of the emerging larvae, which also affects

early nuptial departure ⁴⁹. Early emergent behaviors include "sunning" when workers absorb sunlight and then re-enter the mound to transfer heat, thereby potentially raising the mound temperatures up to 20-30 °C higher then ambient temperatures, based on observations and estimated calculations ^{49,142}. For this temperature spike to be possible, worker populations must be greater than a million ⁴⁹.

Mounds tend to be drier ^{68,115} than the surrounding forest floor and soil, while temperatures are generally warmer and fluctuate at various depths within the mound ^{68,204}. Dry mounds tend to have a more uniform temperature over the entire surface area while moister mounds exhibit warmer temperatures at the top portion of the mound ⁶⁸. With periodic and seasonal windows of high moisture and increased temperatures that in turn affect decomposition rates, the prevailing drier conditions of the mound largely inhibits litter decomposition ^{44,62,204,242}. There are subtle monthly and seasonal fluctuations of increased moisture, especially after late fall and winter snowmelt, which affects the texture of the mound's crust layer (first 8 cm) and increases CO₂ emission rates ^{6,43,167,196,234}.

Formica spp. mounds are viable habitats for many soil invertebrates and nutrients. The myrmecophilous residents include: several earthworm species, nematodes, collembolas, oribatids, larval forms of dipteral species, protozoa, and other non-aggressive ant species ^{39,74,77,78,80,81,126}. The common thread for all of these species is their classification as microbi-detritivores, where their feeding tends to favor a bacterial-based food web ^{74,77,81}. Considering that belowground, forested ecosystems are usually fungal-dominated, an ant mound is an anomaly, adding compositional variance to the forest floor. Despite these findings, Laakso and Setälä were inconclusive with their premise that *Formica* spp. exert top-down control over the soil invertebrate community structure where their study showed minimal effect on select species ^{74,77,81}. Although, with the addition of macro-, meso-, and micro- invertebrates within a mound, the process of comminution lends itself to various fragment sizes and degrees of fragmentation; the primary action in decomposition ¹⁴⁶.

Although active mounds tend to contain less moisture then the peripheral forest floor and soils and have lower decomposition rates ^{23,38,45,86}, after abandonment, the mounds act as "leaky" nutrient sinks, leaching nutrients into the peripheral area and throughout the soil column, until a threshold of equilibrium occurs between the enriched, abandoned mound and its surroundings ^{46,67}. The material and the content of mounds possibly contains a woody core, soil, pine and fir needles, other leaf litter, woody debris, resin ^{18,84}, various bryophytes and lichens ⁴⁷, honeydew, invertebrate body parts, and various types of excrement ⁴³. This diverse base of materials provides a wide array of organic and inorganic compounds for energy utilization and mineralization for the detrital community ranging from quickly mineralized sources to long-standing lignin-based complexes.

The variety of soil nutrients and minerals includes: C, N, P, Ca²⁺, K⁺, Mg²⁺, and Na^{+ 23,39,44,67,86,110,140}. The typical properties of the three major soil nutrients, C, N, and P, within mounds are as follows:

- C Higher concentrations compared to adjacent soils: Depending on the form (sugars, carbohydrates, cellulose, lignin), quickly utilized and mineralized or more slowly broken-down; higher C:N ratio indicating slower decomposition ⁶³.
- N Inconsistent findings: In cases with more open areas containing grass species, higher concentrations were found in mounds while in other cases, concentrations were consistent with the adjacent area. Within "nutrient-poor mounds", lower concentrations were prevalent due to rapid uptake and mineralization by the microbial community. In some cases, N-fixing bacteria were present ^{22,23,39,132}.
- P Consistently higher: A greater variability of forms, ranging from readily utilized/mineralized to recalcitrant forms possibly due to foraging, prey and litter ^{39,43,63,67}.

Interesting research conducted by Bernhard Stadler and associates in 2005 and 2006 concerns red wood ants and their effects on the composition of detrital leachates ¹⁴⁰. Stadler's previous work had been based on red wood ant-aphid mutualisms and the effects on honeydew production; and the C and N enrichment of mounds nearer to honeydew production sites ^{132,133,136}. Through greenhouse experimentation, they found that the presence of Formica polydena on litter had significant effects on the composition of leachates, more so than leachates containing honeydew. The ant-mediated litter leachates contained an "increased aromaticity and complexity" of organic compounds along with microbial enzymatic activities that were significantly higher ¹⁴⁰. Though these were controlled laboratory experiments, the findings suggest that wood ants not only use the litter, but that they may have a significant role in the possible enzymatic conditioning of litter, ameliorating the breakdown within specific moisture and range of temperatures.

Another body of research has focused largely on CO_2 emissions from red wood ant mounds. The findings have reported greater emissions during summer phases coinciding with the reproductive and brood-tending stages, in addition to higher emissions during evening and night-time hours ^{24,104,121,123}. This information demonstrates the cyclic and dynamic equilibrium of natural systems.

1.4.4 Significance of Red Wood Ants

The process of decomposition and the biota performing the functional roles within the process are so intimately linked, that it is difficult to discuss one without addressing the other. The role of wood ants within this process not only embodies this concept but provides a complex dynamic framework for the process to occur.

As ecosystem engineers and bio-indicators of soil and forest health ^{54,80,88,138}, red wood ants not only serve a practical role to our needs, but they can possibly restore and revitalize soil and forest ecosystem functions. Red wood ants, as described, have the capabilities to transform ecosystems, though they too are greatly affected by their surroundings. Studies show that clear-cutting and highly degraded conditions drive red wood ants from their nests within a two-year time-span, inhibit

reproductive cycles-by predominately producing male alates, and cause an increased frequency of mound abandonment ^{27,82,130,131}.

The red wood ant-aphid mutualisms seem, potentially, to be harmful to the tree species involved, but under closer examination, they may balance the potential damage by predating and eliminating more damaging defoliators and non-myrmecophilous aphid species ^{8,58,59,60}. Ohashi et al. found increased fine root and root biomass densities below mounds compared to the surrounding mineral soil. Levels of N, Ca, K, P, S, Mg, Zn, Cu were also higher within below-mound root systems ¹¹⁰.

Maurice Maeterlinck presents a romantic yet deferential description of ants as "selfless" ⁸⁹, based on the premise of possessing a "social stomach" ⁴⁹. According to Maeterlinck, since humans do not possess this physiological attribute, we can only be "selfless" cerebrally, not truly in a corporeal sense like ants. Notwithstanding the bond between mother and child acquired during nursing, his awareness begins to draw attention to kinship recognition and alternative forms of bonding in other species; providing a better understanding of the subtle behaviors driving ant eusociality ⁸⁹. Depending on species, behavioral plasticity, environmental conditions, and colony size, red wood ants can become a formidable force - an organism of fragile beginnings, yet, through inextinguishable persistence, an irreconcilable force of nature.

1.5 Soil Organic Matter, Wood Ants, and Their Dwellings

The bioperturbative activities of wood ants (Formica spp.) as ecosystem engineers ^{52,102,108,140,250} in northern forests directly influences soil organic matter through the mixing and translocation of decayed litter into intricate mound structures that extend into the mineral horizons, which likely provides an enriched soil environment driving soil organic matter formation ^{6,74,248}.

Ecosystem engineers, as described by Clive Jones, are "...directly or indirectly modulating the available resources to other species by causing physical changes in biotic and abiotic features in maintaining or creating habitats" ⁷⁴. Depending upon their foraging and mound-building habits, wood ants will transform soil conditions; shape the plant, invertebrate, and microbial communities; and, if undisturbed for extended time spans, will sculpt an entire landscape through their livelihood, mound abandonment, and re-colonization ⁷⁴.

The mound structure in its entirety may extend up to 2 meters above and below ground ^{6,43,63,68,117,152,217} (Fig. 1), with the excavated and selectively sized clay and silt particulates redistributed and incorporated into subterraneous tunnels and chambers and above-mound surfaces for additional structural support and protection from erosion ^{6,74,108,163}.



Figure 1 "Perfect Mound" extending 2 meters above ground.

The translocation and mixing of detritus into mineral horizons increases the likelihood of the further development of soil organic matter. Putting detritus in direct contact with clay surfaces substantially increases the possibility of aggregation and occlusion endemic to soil organic matter properties. Research by Wardle et al. strongly supports that the presence of *Formica* sp. over extended periods (\geq 13 years) will promote a bacterial-based food web ²⁴⁴, thus implying a linkage to the MEMS framework. Stadler's research on aphid honeydew enrichment near mounds coupled with his later findings that ant-mediated litter leachates contain "increased aromaticity and complexity" ^{218,219,220,221} associated with microbial enzymatic properties, both support the "priming affect" ^{23,129,149,177} and the MEMS framework associated with soil organic matter formation. In a recent study, leafcutter ant nests in the tropical rain forests and the Patagonian Steppes were found to be enriched sites for soil organic matter and internal dump sites holding up to two orders higher in microbial populations compared to the surrounding soil ²¹⁷; the tropical forested nests exhibited elevated levels of CO₂ emissions that indicated decreased residence time of soil organic matter ²¹⁷.

Moreover, the earlier findings by Ohashi et al. of increased fine roots, root biomass, and associated increased nutrients below mounds ¹⁶⁸ provides further evidence of a microbial pathway driving soil organic matter formation. Active mounds tend to exhibit drier conditions compared to surrounding bulk soils, reducing decomposition, possibly inhibiting soil organic matter formation, but the storage of litter provides an enriched "temporally protracted sink" ^{65,163,234} as mounds are abandoned and moisture conditions become more suited for soil organic matter formation ^{68,86,115,194}.

Formica mounds are morphologically systematized into five general types ranging from expansive, indeterminate, parabolic ellipsoids to monolithic, rigorously defined paraboloids (Figs. 2-6) (personal observations).



Figure 2 Type 1 mound. The "dome" is stacked litter collected from the surrounding forest floor, while the stump-core is a structural support for the mounded thatch and inner habitation chambers for the *Formica* sp.



Figure 3 Type 2 mound. Downed trees serve as structural support for mounded thatch.



Figure 4 Type 3 mound. Snags provide a protective shell and support the thatch stacked within the hollowed interior.



Figure 5 Type 4 "Pancake" mound. Wide diameter with a flat, minimal height. This type was encountered once in my research; largely containing clay, gravel, and sand. The dark hatching in the lower sketch indicates added exterior thatch as observed during the second field season.



Figure 6 Type 5 mounds. Secondary structures of thatch accumulation, indicated by the darker hatching, were observed at locations with single or several large mounds. These structures contain less thatch, but qualitatively possess the diagonal stacking and cells of air space as primary mounds.

At locations with large primary mounds (Figs. 1,7-9), the fifth type, secondary indeterminate mound-like structures serving as bivouacs are established throughout deposits of CWD. The shape physically describes the colony's societal and reproductive requirements as adaptively shaped by environmental stresses, associating form to function ¹⁶⁵. Mounds are often located on south-facing slopes, in areas that have a characteristic "edge effect" ^{36,44,88,110,113,144,194,204}, and are elevated-above the forest floor as the surface area maximizes insulative capacities while encouraging water run-off ^{6,83,88,94,99,109,144,204}. Hölldobler and Wilson refer to this function as a "temperature - humidity envelope" ⁸⁷: a self-regulating mechanism of maintaining a constant temperature and moisture level in an effort to rear a successful brood. Throughout the larval-pupae stage, attendants continually monitor and transfer the broods vertically within the mound to maintain ideal temperature and moisture ranges for successful maturations ⁸⁷. From a singular perspective, the formicary ⁷⁴ is reduced solely to a utilitarian structure, but when holistically viewed, is considered a dwelling: a protective safe-place that extends the temporal survival of the species ²³³; while on a landscape level, the remnant structure profoundly imprints upon the landscape long after the colony collapses, by amending and transforming the intrinsic soil properties ^{115,125,163,207,248}.



Figure 7 Type 1 large mound - "Kim's Big-Bad..."



Figure 8 Type 2 large mound - "Sleeping Dragon"



Figure 9 Type 3 large mound - "Kandy Kane"

The construction "style" and form of a mound is that of an externalized deterministic structure based on the adaptive plasticity of the *Formica* sp. as observed by the various forms, range and usage of forest-based materials. By deeply embedding itself into the overall community structure and the prevailing environment, the adaptive response and co-evolution of the *Formica* sp. strongly supports the ecological "tangled nature evolutionary model" ^{21,193}. To further the notion of "tangled nature evolution", the next level of application may exert itself through community restructuring. As *Formica* sp. inhabit an area evinced by the presence of selective above and below ground invertebrates, and by a woody plant community ^{41,94,110,244}, their occupancy tethered to colony growth and population density, over extended periods, demonstrates the strength of this concept and their influence over the forest floor ecosystem ²⁴⁴. The Formicary construction, from both an architectural and biological perspective ¹⁶⁵, adheres to principles of logical or functional design.

Comparing the active-mound construction of carefully stacked needles to that of accumulated, nonsorted, and compacted litter on the forest floor, the achievement of highly maintained internal pore space, i.e. porosity ⁷⁴, is evident from the multitude of perforations and the overall mound volume ^{74,165}. Functionally, the perforations provide ingress and egress for workers, and dually, serve to maintain the delicate temperature and humidity balance allowing for efficacious heating, cooling, and ventilation of the internal chambers. The compacted crust observed on the forest floor is an endemic attribute of the outer 5-8 cm of the mound ⁷⁴. The encrustment, composed of thatched needles interlaced with silt and clay particulates, is considered a protective outer sheath from direct rainfall and erosion ^{74,204}. Although the outer encrustment may appear to be an environmental artifact caused by moistening and drying abiotic factors, the incorporation of selectively sized and types of soil particulates provides strong evidence that the "crust" is innate to the overall construction ^{74,204}.

Commonly, the mounds found within the interior Douglas-fir forests are composed of stumps (Figs. 2,7,10), downed logs (Figs. 3,8), accumulated CWD (Figs. 6,11), or a snags acting as internal or external means of support (Figs. 4,9). At the Pancake mound, I observed no evidence of an external woody structure and little evidence of incorporated litter. Only a single large opening overarching a large excavated area of soil particulates resembling a pancake (Fig. 5). The other remaining types contain interiors comprised predominately of senesced Douglas-fir needles collected from the surrounding forest floor with inner chambers carved into the woody core or below it (Figs. 12-14), threaded (Figs. 15-17) and nested with thatch which most likely serves as insulation. As the collected litter accumulates, it is meticulously placed and stacked diagonally, externally forming the emergent structure of a mound, representing an exosomatic extension of the colony itself ¹⁶⁵.


Figure 10 Type 1 mound with exposed stump. *Formica* sp. sunning, threading, and stacking litter.



Figure 11 CWD. In the foreground, abiotic accumulation of litter at the bases of interior Douglas-firs forming flattened mounds.



Figure 12 Excavated woody core. From the stump of a Type 1 abandoned mound



Figure 13 A close up of inner carved chambers. From a Type 1 Formica mound



Figure 14 Carved inner chambers. Note the specs of white rot formation.



Figure 15 *F. integroides* worker carrying a senesced interior Douglas-fir needle to be "threaded" into a Type 2 mound



Figure 16 *F. integroides* worker, assisted by a nest-mate, carrying an interior Douglas-fir needle to be threaded into a Type 2 mound structure



Figure 17 F. integroides workers threading interior Douglas-fir needles into Type 2 mounds

Given that wood ants are poikilothermic, the need for sunning is one of the many possible mechanisms for thermoregulation in which the colony survives seasonal cold temperature shifts ^{37,73,87}. As the heat is collected and stored within their dark bodies, they coalesce within the inner chambers to warm the incubating vernal brood ⁸⁷ giving them an ecological foothold for early emergence over other invertebrate species ¹¹⁰. During the spring, at several mounds found at the NE edge of the area (Fig. 18), I observed a re-location of thatch within the mound, forming an inverted conical-shaped divot extending from the mounds surface into the interior. The red wood-ants gathered within the divot, sunned themselves, and then re-stacked and filled the conic void with the suspected translocated thatch (Figs. 19, 20).



Figure 18 Aerial view of study area. Red "hatching" indicating location of venting activities at the NE edge of the study area.



Figure 19 A large conical shaped vent. "Perfect Mound" with *F. integroides* sunning during late February to early March 2010.



Figure 20 "Perfect Mound" vent located at the top quarter on the west side facing a forest gap.

1.6 Formica Mounds: Structure and Composition

At first glance, one might consider the mound as a pile of decomposed needles amassed into a "compost heap" ^{62,139}. This utilitarian perspective gives little consideration to the construction, variability, and utilization of the materials. Microscopically, the variance and heterogeneity of the materials becomes evident: various needle lengths, coloration representing the different decay classes, soil particulates; micro-particulates of wood and needles; intertwining threads of mycelia enshrouding the needles with pitting, dark-spots, and melanization which strongly supports saprotrophic fungi colonization (Figs. 21-23). Both Hayes's and Ponge's observations on litter decomposition ^{81,82,156,180} support my observations through their descriptions and characterization of litter decomposition, while further associating the various fungal groups and quantification of the process. When scrutinized, the thatch composition not only reveals its intrinsic heterogeneity, but also provides a context and a natural historic overview of the colony.



Figure 21 Decomposed litter from an active mound. Intact, fragmented melanized needles; wood particles and particulates; and mycelia



Figure 22 Dissecting microscopic perspective of thatch from active mounds



Figure 23 Dissecting microscopic perspective. Details of the particulate encased needles from collected thatch comprised of fragmented wood and needle litter, soil particulates, and mycelium.

Northern forests tend to be dominated by K-selected tree and plant species that endemically produce low-quality litter containing high concentrations of phenols, lignin, and structural carbohydrates with a low N content and a high C:N ratio ^{174,184,185}. The *Formica integroides* mounds near Merritt predominately contain senesced litter, generally of one type interior Douglas-fir (*Pseudotsuga menziesii var. glauca*) (Fig. 24) providing it with a specific C signature. Other source materials include: leaf litter and fine roots from saskatoon (*Amelanchier alnifolia*), yarrow (*Achillea millefolium*), nodding onion (*Allium cernuum*), common juniper (*Juniperus communis*); decayed logs, stumps, snags, and accumulated large pieces of CWD in later decay stages.



Figure 24 Interior Douglas-fir needle thatch at various decomposition stages from an active mound. Notice the organic matter below the thatched material

Why do *Formica* construct mounds of senesced and decayed needles? Perhaps for insulation or as a possible vehicle for increased moisture retention that has an increased heat-holding capacity while conversely possessing the trait of rapid drying, promoting ventilation, which benefits early brood rearing in spring ^{87,204}. The use of "green litter" not only contains more moisture, but also labile C sources as photosynthates which encourage microbial degradation ²¹⁷. In northern boreal forests, this potentially threatens the well-being of colonies as they are highly susceptible to fungal-driven decomposition ^{81,82,180,243,244}. The exoskeletons of ants contain chitin, a recalcitrant C. In seasonal higher moisture levels coupled to cooler temperatures, ants will be in a state of shock or "cold-coma" ³⁷ where abiotic conditions favor colonizing saprotrophic, mycorrhizal, and parasitic fungi potentially utilizing their stunted bodies as a viable C source.

Formica mounds tend to possess a higher content of C and N in the form of litter compared to the surrounding forest floor and soil, coupled with greater porosity and a lower bulk density ^{6,125,163,145}. The soil below mounds are enriched in organic matter compared to surrounding bulk soils (Fig. 25), reflecting above-ground accumulation and mixing of litter ^{125,138,139}. The carbon is predominantly

derived from lignin (AUR) based compounds (vanillyl and syringyl phenols (VSC)) along with plantbased cellulosic polysaccharides ¹²⁵.



Figure 25 Lichen and bryophyte atop melanized needle thatch from an abandoned mound. Encrustment of the litter occurs during hibernal phase at un-disturbed active and abandoned mounds due to abiotic stresses as evidenced from the compacted thatch above. Note the crumbly texture and a darkened brown-coloration of the Oh and A horizons.

Lisette Lenoir ^{138,139,140} found "hot-spots" in *Formica* mounds containing higher C:N. N as inorganic forms (NH₄) perhaps from excrement and wastes, with an overall higher C content compared to the surrounding forest floor. In her experiments measuring C and N mineralization and immobilization of thatch and forest floor materials at 15% and 60% water holding-capacity (WHC), she found higher C mineralization and net N immobilization in thatch compared to forest floor litter. Conversely, Domisch et al. ¹⁶⁷ found lower rates of C and N mineralization and significantly less mass loss of "litter-bag" needles within mounds compared to those measured on the forest floor at "*in situ*" moisture levels Domisch et al. ¹⁶⁷ concluded that active mounds serve as "cold spots" of nutrient storage until abandonment, at which time the mound changes to a "hot-spot" for mineralization as the microbial and plant communities re-colonize the remnant sites. Ants also directly change the C pathway through accumulation and stockpiling of litter as thatch and indirectly as the honeydew throughfall runoff from obligate aphid attendance, potentially priming the soil microbial community ^{218,219,220,221}.

The prevailing question of this study is, "What happens to thatched-needle litter within *Formica* mounds and how does this differ from needle litter not associated with *Formica* mounds found on the forest floor? Before embarking on measurements and experiments to specifically address this question, I familiarized myself with the ants, their activities and the ecosystem. My initial observations were made during the *Formica* spp. annual active period from July to November 2008, these observations were incorporated into the larger body of observations made during the field experimentation in 2009-2012. My field observations are intrinsic to the identification and development of my methods.

1.7 Field Observations



Figure 26 Interior Douglas-fir / Ponderosa Pine Forest

This section is separated into three seasonal periods with the omission of mid-winter. As temperatures drop in late fall, stemming the preconceived notion of *Formica* spp. inactivity, one may question why I would make observations prior to their aestivation. Several reasons come to mind: to survey the structure and boundary of the mounds within their respective locations, to take notice of the subtle nuances in their behaviors which became apparent during the seasonal transition periods, not to mention the annoyance of thousands of red wood ants covering my body during their active periods.

1.7.1 Summer / Fall 2008, Summer 2009

Unknowing... origins of a beginning

The mounds are located in a disturbed interior Douglas-fir open mosaic-forest ecosystem in British Columbia, approximately 8 km northeast of Merritt. The dominate tree species are Interior Douglas-fir (*Pseudotsuga menziesii* subsp. glauca) and Ponderosa Pine (*Pinus ponderosa*) along with an array of shrubby plants: Saskatoon serviceberry (*Amelanchier alnifolia*), common juniper (*Juniperus communis*), and mixed sages such as rabbit brush (*Ericameria nauseosa* var. *nauseosa*) and fringed sagebrush or prairie sagewort (*Artemisia frigida*). Other species include various native and invasive grasses: bluebunch wheatgrass (*Pseudoroegneria spicata* ssp. *spicata*), timothy (*Phleum pratense*), alfalfa (*Medicago sativa*), quackgrass (*Elymus repens*), and spotted knapweed (*Centaurea biebersteinii*), a local dominate invasive, with a scattering of native Asters throughout the landscape (See Appendix B).

Arriving at my first observation area "Point of Origin", I noticed a large blackened mushroom, possibly a honey mushroom (*Armillaria mellea*)⁴, located on the lower branches of a Douglas-fir tree, where, I assume, an overzealous chipmunk was storing its cache for later consumption. On two occasions (October 2008 and July 2009) following a cool, wet period and a dense mid-summer downpour, I noticed and attempted to collect mushroom specimens, but failed to successfully deliver and perform laboratory analyses on them. I recently learned that this group of mushrooms plays an important, functional role in the decomposition of woody debris.

The predominant identified ant species *Formica integroides* are from the *Formica rufa* group (See Appendix A), a group known for their thatched mounds, large colonies, and aggressive behaviors. Anatomically, the *Formica rufa* group is distinguished by a prominent mesonotum with a smaller sized epinotum found within the alitrunk and upper petiole region of their bodies. The final identifying feature of the *F. integroides* species and subspecies is the notable erect hairs growing within an occipital ridge located at the top of their heads, above and behind their eyes and extending along the scape of their head (Fig. 27).



Figure 27 Formica integroides (left lateral view). Missing an antenna and three legs

Based on their woody, structural framework, the *Formica* mounds are comprised of four predominant types: stumps, downed trees and woody debris, hollowed snags from burns, and "pancake" mounds that lack both thatch and woody structural support. The mounds contain a variety of senesced litter, predominantly Douglas-fir needles. The remaining portion of litter includes decayed *P. ponderosa* needles, small twigs, stipules, scales from both cones and bark, and mineral soil dominated by sand and clays particulates heterogeneously mixed throughout the lower portion of the mound. The bio-perturbation of materials, as well as the mixed O-A_{hu} horizons, are significant indicators that *F. integroides* inhabit the aboveground, stumps or downed-wood and thatched portions, and their domain extends downward into carved chambers and sinuous pathways belowground specifically noted in the "pancake" mound type.

In the more classic "mound" shape, the thatch material is stacked within or built around a "woody core" (e.g., a stump or within a hollowed snag). The thatch serves as a protective thermoregulatory insulating barrier for the inner chambers, provides for multiple entrances and exits for litter collection

and increasingly efficacious as a protection mechanism against intruders. The thatch also provides a suitably dry habitat for other organisms such as mites (*Acari*) and springtails (*Collembola*) (See Appendix A, Section C).

Over time, from weathering and with few physical disturbances, the external thatch becomes a compacted, continuous, encrusted layer approximately 8 cm in depth (Fig. 28).



Figure 28 Active mound with exposed top crust layer, interior thatch, and an enriched Oh - A interface.

The internal thatch medium is less compacted, more aerated, and drier in comparison with the encrusted layer. The "stump" type mounds are threaded with dry, senesced Douglas-fir needles throughout the carved and hollowed channels and crevices of the woody protective shell (Figs. 15-17). Perhaps this provides added security for the newly tended brood and further insulation from freezing during the winter months. I witnessed *Formica* sp. withdrawing into the stumps during the warmest period of the day in summer, and carrying larvae encasements away from the mound by exiting through the top and side crevices of the stumps, felled trees, and logs.

The observed mounds range from 50 cm high and 1-2 m wide to over 1 m high and 400-500 cm wide. The distribution of mounds is in a "clumping" configuration where a single colony has 3-5 polydomous mounds within an area of 0.5-30 m. The mounds range from an elevation of 882-1073 m along a W- to-E diagonal. Wind potentially plays a significant role in the area, possibly dispersing alates from the higher elevations, downwind to lower elevations.

Once a colony is fully established, there is a scant needle and small woody debris remaining on the ground surface within their domain. It appears that 70-80% of the fallen needle litter was imported to the mounds. Measuring the amount of litter within the mound provides a record of the type, amount, and age of the litter present. Mound size, the acquisition of seasonal thatch, and the number of individual layers within the mound can be used to estimate a colony's lifespan.

Upon discovering a large mound named "The Snag" near the "Point of Origin", I followed an active pathway for approximately 500 m in a NW to SE direction down a slope and across three satellite communities before reaching the largest community within "The Snag." If a colony's population becomes large enough to expand into other satellite colonies, the corridors between the mounds become formidable pathways. These pathways are an easy and direct connection between mounds, but what is the significance of remaining connected to the initial founding nest? Perhaps this is a protective dispersal mechanism to ensure a satellite community's success. If this community cannot attain or maintain an autonomous status possibly due to various disturbances, the remaining colony has the option to return to the initial or to other satellite mounds.

The cast of mound-disturbers includes woodpeckers, grouse, cattle, deer, big horn sheep, and the most notorious - the brown bear. The *Picidae* and *Phasianidae* families generally disturb mounds by feeding off larvae and workers and by the occasional dust bath when mound activities are low. The *Cervidae* and *Bovidae* will bed near the mounds and either trample or walk through active mounds during cooler, less active periods (e.g., the cooler nights of late fall and winter). The *Ursidae* pose the most formidable threat to the colonies by frequency and level of disturbances. I observed on several occasions, the aftermath of such disturbances with notable, specific measurements at two mounds. During the 2008 summer season, two mounds had holes dug to depths of 20-50 cm, with diameters of 2 m and 4 m, while a third disturbance recorded between July and mid-August 2009, had several smaller, peripheral, shallow holes around the edges and on top of the largest mound in the study. The disturbances and the evoked damage coupled to the sheer tenacity of the brown bear was notably impressive; moreover, so was the rapidity of recovery by the *Formica* sp.

In early July 2008 at "Open Meadow", a minor disturbance left materials splayed out around the area with a medium-sized hole within the thatch. The thatch measured 10-15 cm below the stump core. By the end of my field season in late October 2008, the thatch had been built up, not just to the top of the stump, but was stacked approximately 3 cm on top of the stump. Another noticeable build-up after a more severe disturbance occurred at "Kandy Kane" where a sizeable mound was built within a snag. In August 2008, a section of the snag was torn off and the thatch was displaced around the area. At this time, I placed a stick on top of the thatch, inside the snag. When I returned the following July, not

only was the stick still in place, but the material was stacked 50 cm above the stick. Perhaps, the ability to recover is contingent upon colony size, available materials, the plasticity and resilience of the *Formica* sp., and the low frequency of high-impact disturbances. These attacks may be just random, aggressive acts of feeding or carefully cued attacks, predicated on pheromonal signals emanating from the queens to their workers during egg-laying or larval-tending periods. The bears may be able to hone in on these biochemical signals specifically at these times. This is plausible given the specificity of the holes from the two separate infractions. The depth and size of the holes are distinct, exposing the roots of the stumps - an unequivocal attempt to locate something in the inner chambers of the mound. The rich nutritive protein source the larvae provide for a bear may provide enough of a driving impetus for a bear to expend the energy needed to endure multiple, aggressive *Formica* attacks.

A few notable quirky behaviors of *F. integroides* include sunning, aphid tending, and mound abandonment. I witnessed the sunning during a warm, sunny period in late August 2008. The *Formica* sp. were gathered around an entrance hole on the "The Snag." The visual was quite odd. They appeared to position themselves, ritualistically, around an unseen deity as they were all circled around a small hole in the snag. The most curious aspect was to observe them in complete stillness. This behavior was quite odd to me until I read in Hölldobler and Wilson's "The Ants", about ants sunning themselves in early spring and returning to the mound interior to warm the brood. As ants are poikilothermic, their reliance on an external heat source becomes crucial. This behavioral adaptation also permits early brooding of their young, giving them an early feeding advantage over other predatorial invertebrate species. Perhaps this group was sunning to return inside to warm their section of the mound. Due to their locale, the area of the mound may have been more vulnerable to the elements, especially wind and rain.

I became acquainted with aphid tending at the "Point of Origin" — my first exposure to ant behaviors. The situation included aphids on Quaking Aspen (*Populus tremuloides*) as they were shifting and cleaning their flock. Later, at this same location, I observed a far stranger behavior during what I believe was a first encounter and attempt at a newly formed association with a recently landed winged aphid. The ant lurked over the landed aphid while stroking and soothing the aphid with the front two sets of tarsi on its ventral side. The moment was oddly still with these two invertebrates in a complete state of other-awareness.

My quandaries during the first season regarding colony size, proximity to one another, and the means of nutritional support, were answered during the second season. The questions were why and how could there be such large colonies so closely situated without any apparent nutritional support? The first season I could not find their tended aphids. Where were they hiding them? After reading that aphids tend to reside on the bottom of branches, I began my pursuit. At "Perfect Mound", I identified a scrappy looking Douglas-fir, climbed 10-15 m to the top by following an ant trail, and found their flock

under the end of a yellowed branch. I applied this climbing technique to several of my other active mound locations, successfully discovering their honeydew sources. I was successful in collecting specimens, which I believe to be either aphids or common woolly adelgids (*Adelges cooleyi*). Other food sources include unassociated aphids, tussock moths and the most frequently observed summertime prey favorites - spruce budworm moths.

The tending of aphids creates a cascade effect involving other species and behaviors while possibly establishing other subsidiary cycles within the ecological fabric. For example, while *Formica* sp. are tending to aphids on *P. tremuloides*, leaf miners take advantage of the situation and feed off the new foliage of the already infested sapling. The disturbance, providing it is minor, evokes the sapling to produce more sugars, increasing shoot production and photosynthates while increasing the need of greater nutrient uptake thereby producing more fine roots to compensate for the added expenditure. Although the disturbance temporarily impedes the sapling's growth when the seasonal infestation ceases, the sapling is able to reallocate its resources for growth while benefiting from additional fine roots ^{218,219}.

Another observed potential mini-cycle, is aphid-tending on young Douglas-firs, which causes stunted growth, early senescence of needles, and bursts of morphologically smaller needles. Not only was the honeydew collected, but also the senesced needles. Due to aphid feeding activities, the needles prematurely (2-3 yrs.) senesce and eventually fall perhaps to be collected and incorporated as litter in mounds. Individually this may be novel, but on a longer endured temporal and expanded physical scale, it would transform the surrounding landscape.

A final observed behavior from my study that requires further inquiry is mound abandonment. From the current literature, it is explained by inadequate overstorey coverage, perhaps due to clear-cutting the vicinity. In the case of "Fork in the Road", this explanation is not applicable. I had the fortune to witness the mound in full operation during my 2008 season, but found in my 2009 season that it was an abandoned "ghost town". The mound was without extensive coverage, but on the edge of a denser covered area. There was no evidence of disturbance and the mound was without notable variation. My only thought was that there were not enough food resources, but that the mound was situated close enough to more enclosed canopy for possible aphid-tending. The unusual query that stemmed from this anomaly led me to the nearby "Pancake Colony" which, to my surprise, now contained surface thatch and had grown in size since October 2009 (Fig. 5). Could the former colony members of "Fork in the Road" have joined the "Pancake Colony?" What were the reasons for the abandonment? The behavior is reminiscent of North American beavers moving downstream to establish and then abandon lodges only to return to the lodges several years later. Do Formica follow the same trend? Perhaps the lack of resources or intense competition for resources with sister colonies having less overstorey coverage, leads to re-assimilation to larger sister colonies that would tender a greater rate of success.

Based on my field observations, I have speculated about the elements of a successful, large, endured colony: aggressive and highly plastic behaviors of the *Formica* sp.; increased overstorey coverage alleviating abiotic stresses (e.g., temperature, wind, seasonal rain, and snow); a solid base of food resources that is rich in prey and aphids; the appropriate age and species of trees for litter and hosting aphids; the presence of snags, downed logs and stumps for structural mound support; a low-level disturbance regime; and finally, a large enough worker population to compensate and recover from possible harsh winter conditions to bolster increasing colony populations.

1.7.2 Fall 2009

Within stillness — much is learned

The final rush of activity from the early warm temperatures of fall has now been arrested to a few insignificant twitches by strayed individual workers that are seemingly "frozen" on the peripheral confines of the outer-thatch; an example of ecological cost for the trait of poikilothermy. The days of activity are numbered in the fall for a worker ant. As ambient temperatures drop, if she does not arrive within the protected inner chambers of the mound where warmer temperatures are generated by the amassed bodies of her sisters, she may perish from exposure to the elements or become a food source for a foraging grouse or a slow-growing saprotroph.

As I explored the mounds, the frenzied activity has been transformed into complete stillness with a surficial covering of Douglas-fir needles across the landscape. I am now able to view and admire the splendor of the mound structure. The self-organizing activities of collecting and carrying senesced needles to be later stacked and threaded throughout the inner woody chambers provided by a downed log, snag or stump are repeated innumerable times by siblings and future siblings until an organic structure evolves rising 1-3 m in height; all based on the physical framework and the populace of workers of the colony.

My initial observations include the obvious scattering and accumulation of senesced and fresh Douglas-fir needles, downed twigs, and branches at each of the mounds provide an impression of demarcated territory and an indication of the amount of required activity necessary to maintain the physical structure of each of the mounds (Fig. 29). The summer's verisimilitude of "no litter accumulation" does not hold true in the fall. Although marginal in a singular isolated context, one could imagine that without the *Formica* sp. activity, litter accumulation may be significant over longer expanses of time.



Figure 29 "Mother / Father" Type 1 mounds. Clear demarcation and close proximity of large mounds and colonies displayed

Within a two-dimensional framework based upon seasonality and temperature, the downed litter and woody debris from fall to late spring provides the soil with essential structural heterogeneity and a seasonal pulse of carbon and nutrients intrinsic to the remaining soil biota and microbial community. *Formica* sp. litter collecting is most prevalent from late spring through early fall, tapering off through the fall, thereby punctuating winter forest-floor accumulation. The unequivocal reduction of *Formica* sp. activity is apparent throughout the winter and early spring, although occasional subtle activities during this period have been observed such as sunning (Fig. 30) and "mound venting" (Figs. 19, 20).



Figure 30 *F. integroides* sunning on top of an exposed stump. Activity occurs anytime from late October through April during the cold season on the occasional warm, sunny day.

The majority of the litter collected and incorporated into the mounds is golden-brown Douglas-fir needles (Fig. 31), which indicates a preference to senesced litter rather than fresh green litter based on the availability of both types. The litter incorporated is structurally intact and appears to be at least 6 to 12 months old; the labile components have been released and possibly utilized as a carbon source, respired as CO₂, or have otherwise been photo-oxidized.



Figure 31 Surficial golden-brown, newly senesced Douglas-fir litter. Contrasting deeper interred litter with Ponderosa pine needles scattered throughout.

Using Ponge's classification of litter degradation, I examined the mound thatch and Oh - A_{hu} interface at the edge and the base of the mounds to estimate the decomposition stages of the incorporated litter and the types of litter found within the mound. As previously mentioned, the majority of the litter is comprised of browned senesced Douglas-fir needles with minor portions of twigs, fir cones and parts, needle stipules, bark chips, and an occasional branch.

Assessing the moisture content of the outer 4 cm, it was evident that the dampest layer was the exterior thatch. I have named this "crust layer" based on its compressed and contained qualities. I imagine the outer-litter has acquired this encrusted quality based upon its constant exposure to the elements mainly: sunlight, precipitation, temperature, and wind. The function of this layer to a colony may be both as an immediate protective buffer and as an absorbent sponge. The thatch itself was intact and darker in color where it was damp, suggesting that it is in Ponge's 2nd to early 3rd stage decomposition class.

The next layer is the "interior thatch" (Figs. 32, 33), which is considerably less dense and moist compared to the "crust layer".



Figure 32 Interior thatch from an active mound. Note the varying textures, compaction, air-spaces, mycelium, and particulate accumulation on individual needles



Figure 33 Interior thatch from an active mound.

This layer contains the majority of the aboveground thatch; comprised of mostly 3rd stage decomposed needles, with an increase in small woody debris in addition to fragmented and possibly comminuted particulates attached to and encasing the needles. The forms of the needles are clearly intact, with evidence of partial fragmentation on the ends and throughout the body of the needles. It was clear that this layer did not receive a direct feed of fresh litter, based on coloration of the needles and the infrequency of fresh litter. Per handful, there was a higher occurrence of particulates, small twigs and stipules. The fragmented woody debris serves as an indicator of the staying power and resistance to decomposition. The interior could be viewed as a depository whereby the upper comminuted materials may have filtered from the above layers, and holds the largest portion of bulk thatch within the mound.

The final examined layer was the organic-mineral interface at the base of each mound. I collected material from the mound surface at 8 cm and greater in depth, and approximately 10 cm towards the center of the mound. The majority of the material was no longer recognizable in form; all needle structure was lost. The coloration was a rich brown at the moist areas, and it was less dense than the peripheral soil samples (Fig. 34). There was increased mixing of clay and sand aggregates, but this was only apparent in the layer that was in direct contact with the soil (Fig. 35). This layer contained particulates and a large portion of fine and coarse roots.



Figure 34 Organic and humic matter interred from below the center of an abandoned mound.



Figure 35 Mixed thatch and soil at the Oh - A_{hu} horizons located at the edge of an active mound. Note the encrusted thatch, darker coloration and texture.

Overall, five mounds had seedlings on the crust layer with additional moss and lichen growth on exposed stump and woody debris surfaces, possibly due to increased insolation and decreased *Formica* sp. activity. At two of the mounds, saprotrophic fruiting bodies were growing at the base of the mounds; specimens were collected and later identified.

Upon closer examination the belowground conditions of a remnant stump at an inactive mound contained lighter soil whereby appropriated litter and wood degradation possibly amended the soil bulk density and texture. The soil beneath the mound was not compacted and was thoroughly mixed with clay and sand, lacking the distinctive layers apparent in peripheral non-amended soil. I was able to disinter the mound to approximately 50 cm without a trowel, indicating minimal compaction. The amended soil was rich in decomposed litter, possessing an aerated and flaky quality (Fig. 24).

Regarding the stump and its larger-bodied roots, there were several carved chambers in the dead sapwood strewn with brown needles and located in the above-ground portion of the stump. The once deeply embedded caverns were used, perhaps, as protective incubation chambers for broods. The carved-out chambers would allow easier and greater access by colonizing saprotrophs, accessing potential untapped carbon sources. My observations sparked a possible scenario: as a colony collapses, it continues to contribute to the surrounding above and below ground communities by

increasing the structural heterogeneity of the physical landscape and by releasing and allowing increased access to carbon sources that would have otherwise been retained in an active mound.

A pattern observed for mounds located on a slope is the general displacement of materials into the surrounding area. When mounds are abandoned or unmaintained during the cooler months, erosion of the mound can occur. This also holds true for active mounds, but especially mounds that have been abandoned. Aeolian forces, heavy and directed precipitation, snowmelt, and gravity are all likely forces contributing to the structural collapse of a mound. The activity of stacking thatch directly contributes to the maintenance of the mound structure.

The gradual fragmentation and disintegration of stacked needles eventually forms particulates. The small woody debris, decomposing at a slower rate, does not lose its structural integrity, but acts as intermediate reinforcement for the organic structure of the mound, thus retaining its functionality as a communal dwelling. The maintenance of the crust layer prevents moisture absorption into the mound while the slope encourages surficial run-off and protects from further degradation of the interior thatch. As mounds are abandoned, natural weathering gradually returns the thatch to the forest floor surface to be processed by the biota and to undergo further physical and chemical degradation. The direct threat to a mound's structural integrity is not only anthropogenic or by large-bodied animals, but by imperceptible abiotic forces throughout time.

1.7.3 Spring 2010

Awareness,

Crisp spring air, reluctantly taken-in. New perceptions fostered, thinly veiled thoughts awakened. Momentary understanding...

It had been an unseasonably dry, warm winter. The mounds, partially frozen, glistened in the spring sun. Exposed colonies at higher elevations experienced an earlier annual snowmelt. Building in volition, the workers were congregating in preparation for the vernal collection and hunt. Relating to Tony Dixon's research on aphid ecology, the mark of a potentially warmer drier season may be indicated by the adaptive response of fall apteras. Employing one of their many reproductive strategies, aphids lay a series of eggs on the under-side of terminal branch needles, thereby ensuring an early foothold for emerging instars by securing potential food sources. The tactic of early emergence, locating viable food sources without energy expenditure, and the added protection of workers, sets up an elegant mutualistic strategy, fundamental to successful populations. Adelgid presence was indicated based on the non-descript, milky, webbed pouches hanging from the terminal buds of over-head Douglas-firs. From personal dialogues with Babita Bains, adelgids that employ this type of egg-laying strategy are poor dispersers, are commonly *Formica* sp. attended, and are often found within the same area as aphids and other invertebrate opportunists; all evidential support of a local population. I observed aphid and adelgid infestations with *Formica* sp. attendance and monitoring of these branches. If the branches were disturbed, the *Formica* sp. would drop and attack the unwanted intruder: namely me. This tendered support to the theory of early emergence and early reproductive strategies employed by invertebrate populations, in this case benefiting the local *Formica* and aphid populations.

Another fascinating behavior, referred to earlier as "mound venting" (Figs. 19, 20), was observed at several mounds located on the NE section of the study area, during a warming period in late February. The behavior included relocation of interior thatch and carving out smooth, conical-shaped indentations approximately 8 cm wide and 12-14 cm deep, with the apex towards the mound center. The "heating-vents" were centrally located on the sunny-side of the mound. The colony huddled and basked within the sunlit entrenchment retreating to the interior of the mound before sunset, corporally delivering the gathered heat to the inner chambers, thereby potentially raising and maintaining warmer temperatures for the emerging brood. What was observed is perhaps an adaptive response referred to as "sunning" which further supports their ecological advantage over other species. Amazingly, no sooner than the warming period faded, the conical indentations were filled. In this case, the assumption of non-activity during winter months does not hold true.

After observing the filled-in depressions, my perspective of the mounds began to shift. The mounds could be viewed as procured, miniature, self-organizing systems. Along an uninterrupted trajectory of time, the system could potentially become self-sustaining, accumulatively transforming the landscape. Mounds will differ in temperature and moisture based on location, position with respect to slope aspect, canopy closure, and soil type thereby producing variable microclimates at each location. On a landscape scale, this variability would contribute to physical and temporal heterogeneity.

A mound's structural vulnerability is acted upon by both abiotic and biotic disturbances: direct precipitation, fire, wind, UV exposure, snow accumulation and snowmelt, bear attacks, ungulate trampling, and fowl dust-bathing all directly contribute to erosion and indirectly, to increased structural heterogeneity of the local terrestrial scale. Other considerations regarding mound erosion include severity, frequency, type, and combination of disturbances. For example, both bear attacks and snowmelt amend and transform the peripheral landscape, but do so quite differently. The bear attacks tend to be abrupt and structurally destructive, displacing large portions of mound materials, creating a diverse environment unlike snowmelt which gently compresses and displaces mound thatch which extending the edges gradually and continuously into the surrounding area. The bear attacks tend to

create a multi-tiered discontinuous effect while the opposite holds true for snowmelt; each contributing to spatial heterogeneity in two contrasting modes.

After one or more disturbances of varying magnitude, how quickly or how does a colony recover? Does recovery depend on the timing of the disturbance? Does the size and population of the colony influence recovery rates? Do frequent disturbances allow the remnant populace enough time to recover, or are these the main causes of nest abandonment? Answering these questions requires an understanding of the intrinsic plasticity of individual *Formica* sp., and the extension of this awareness to the colony's behaviors.

As a colony is established, it has the potential for growth based on: resource availability, the nature of the species, adaptability, behavioral resiliency regarding disturbance, and "tight-fittedness" to its environment. Recovery is highly probable when a population exhibits multiple resilient characteristics tethered to abundant resources, i.e., a population considerable in numbers and comprised of distinctive size classes (polymorphism); possession of several egg-laying queens (polygyny); aggressive behaviors; plentiful food resources (honey-dew and invertebrate prey); and readily available large CWD (e.g., stumps, downed logs, snags). If a large disturbance or a series of disturbances ensues before a certain threshold of establishment is attained, nest abandonment and colony collapse will follow.

In the aftermath of such disturbances, abandonment appears imminent, but, if the entire area is occupied by a sizeable core community, the disturbance becomes incidental and may even act as a secondary dispersal agent, again demonstrating the behavioral plasticity and resilience of the ants.

Another set of observations supports the notion of the colony's behavioral plasticity; in one season a mound was completely abandoned and then the following season re-inhabited while at another mound the opposite occurred; this triggered a re-evaluation of preconceptions regarding *Formica* sp. inhabitation and abandonment.

In both accounts of the abandonment and re-inhabitation scenario, there were large core communities nearby, perhaps fostering and buffering the newly emergent communities. Employing the tactic, "When all else fails, we can always return home", the pressure for colony establishment and autonomy is greatly minimized based on the ecological principle of kin-relatedness. When *Formica* sp. dominance is exerted over the above-ground community by means of aphid attendance, they indirectly promote opportunistic invertebrate species as prey which contributes to stunted tree-growth, and promotes early needle senescence, demonstrating a pervasive influence over the local community. With dominance, the need for colonial autonomy becomes an arbitrary concept as the entire area becomes an extension of the primary colony, or in Hölldobler and Wilson's words: a "supercolony." Understanding what the concept means from a physical perspective, challenges the

notion of disturbance as a terminal event; rather it represents the mere redistribution and dispersal of materials and colonists.

The opposite still holds true for alated queens establishing emergent colonies located at the forest edges; the struggle to establish autonomy is strongly prevalent. The observed species, due to their inherently aggressive and adaptive nature, are intrinsically well suited for this disturbed environment. During this period, after visiting Monck Provincial Park, I began to understand the extent of disturbance and the impact at the study area, perhaps contributing to the lack of ant diversity and old-growth trees. The minor disturbances to the mounds were abiotic and biotic, but the more destructive were anthropogenically rooted. How does a forest recover from extensive clear-cutting and bull-dozing? According to Jan Frouz's work ⁶⁶, with a certain amount of overstorey coverage reducing edge effects, *Formica* sp. recover. However, without sufficient resources, even the most resilient species will be challenged and the scarred landscape will possess only a smattering of small, residual, and frequently abandoned mounds.

In my research, I noticed several large downed firs and a few standing old-growth trees. As I investigated the O layer (Figs. 36-38), I noted similarities of forest floor litter to that of the crust thatch of the mounds.



Figure 36 Litter accumulation below a ponderosa pine, forming a flat mound shape.



Figure 37 The O horizon. Accumulation and decomposition of woody debris at approximately 8 cm deep.



Figure 38 Organic matter containing bark, twigs, stipules, wood shreds, melanized needles, and mycelium.

The L layer possessed: a crust 8 cm deep at the deepest point (Fig. 39) (usually at the base of a Douglas-fir tree), thinning of the litter as it extended away from the base to a depth of 2-3 cm at the edges, mycelial growth apparent throughout the litter with fruiting bodies below (Figs. 33, 40) while occasionally perforating the surface, and a dry outer 2 cm and a moister layer beneath which permeated into the H layer. As I collected samples from the mounded thatch in the spring, I noticed a similar pattern within the crust layer of the mounds; dry for the first 2-3 cm then dampness extending into the interior thatch. As discussed earlier from Hölldobler and Wilson's research, perhaps the observed moisture was contributing to the "moisture / temperature envelope" required for the emerging brood.



Figure 39 Encrusted needle litter. At the edge of a mound under an interior Douglas-fir stand at a depth of approximately 5-7 cm.



Figure 40 Mycelium and asexual sporing bodies at the surface of the encrusted L layer.

The drying occurs at the surface encrusting the top 2-3 cm of thatch, while retaining moisture and heat of the underlying thatch which slowly evaporates, supporting the needs of the spring brood while temporally supporting the conditions for mycelial growth. As the warmth increases in duration and intensity throughout the spring, complete drying of the above-ground thatch occurs without deep penetration into the drier woody core. By slowly wicking the remaining moisture away from the core, the moisture level necessary for larvae incubation is maintained.

During the spring collection, the concept of a self-sustaining community emerged. Beginning with large landscape-shaping disturbances, anthropogenic or natural, it is conceivable that woody cores are potentially available for future nests. As CWD decays and is further acted upon by moisture, temperature, UV degradation, and saprotrophic fungi, the stage is set for later colonization (See Appendix C). To facilitate this endeavor, the basic requirement is an intact stand, which provides adequate coverage, litter, and a C source capable of supporting aphid and invertebrate populations.

As *Formica* sp. body mass increases, proportionately, so does their need for nitrogen extracted in trace amounts from honeydew and invertebrates. The increased sequestering of greater amounts of honeydew eventually short-circuits the carbon that would otherwise potentially leak into the below-ground rhizosphere. As the trees are denied substantial carbon, "hanger- on" opportunistic

invertebrate species add to the degradation scenario, stunting the growth of the firs and leading, inevitably, to the early senescence of needles which are conveniently linked to mound construction.

One may have the impression that the cycle induced by *Formica* sp. potentially degrades the local habitat, but Bernard Stadler's studies of ant and aphid interactions, support the "short circuiting" theory in that the throughfall enriched with saccharides from the leachates directly feeds the below-ground microbial community²²⁰.

Within the labyrinthine channels of the decayed wood, the foundress will begin to rear her first brood, in an effort to establish a formicarium. If successful, morphologically diverse workers will collect, hunt, and protect the burgeoning colony. If there are few disturbances, the emerging colony will begin to grow in strength and stature, asserting their dominance over the invertebrate and forest floor communities. As the colony grows, the mound becomes increasingly susceptible to structural damage. To an unrelenting bear, the colony becomes a possible protein source rich with fresh larvae being the object of pursuit. Interring and severing the mound, the bear dismantles and flays the contents onto the surroundings. The dismembered woody portions and tufts of thatch lay detached, waiting for re-construction or perhaps autonomous development with this event serving as a secondary dispersal agent. Meanwhile, the remaining colonists repair the accrued damage and with mettle, continue to carve out a lasting position within the ecological framework, whereby the cycle continues, having enduring effects over the entire landscape.

1.8 Thesis Objective

The decay rate of *Pseudotsuga menziesii* var. *glauca* needles on the forest floor in dry interior Dougfir forests has been estimated ^{73,185,186,253}. However, since much of the needle litter is incorporated into *Formica* sp. mounds as thatch, more exacting questions are raised: "Does the decay rate of Douglasfir needle thatch differ from that of needle litter on the surrounding forest floor? Does *Formica* mounding stimulate or inhibit needle litter decomposition?" I address these research questions by comparing decay rates of interred thatched-needle litter in mounds with that of Douglas-fir needle litter on the forest floor.

The decay rates are quantified by measuring and comparing:

- Evolved CO₂ from mound and forest floor materials: surface and interior thatch, wood, soil, and comparable materials from the surrounding forest floor
- Mass loss of needles collected from various depths in thatch and the surrounding forest floor

From my data of mound sizes, distribution, and estimated thatch amounts, I compare the decay rate of needle litter within thatch to that of needle litter on the forest floor. I further assess environmental conditions of temperature and moisture and litter chemistry (%C, %N, C:N) in each material to explore the underlying causes of any differences in decay rates.

2 Methods

2.1 Site Description

The study area was located in an interior Douglas-fir forest in the Very Dry Hot Interior Douglas-fir (IDFxh) subzone at lower elevations, grading into the Dry Cool Interior Douglas-fir (IDFdk) subzone at higher elevations on the southern face of Swakum Mountain, approximately 10 km NNE of Merritt, B.C. (Fig. 41). The 37 mounds were located on leased lands belonging to the Nikola Valley and Poole Ranches, which were contiguous to Crown lands and zoned for multi-purpose usage, i.e., commercial logging and open rangeland. Throughout the entire study, observations were made on *Formica* sp. mounding, feeding, and other characteristic behaviors; as were mound distributions and disturbance events. Of the 37 mounds, 19 were used only for observation while the remaining 18 were used for observation, measurements and material collection. The distance between the two mounds furthest apart was approximately 1.4 km. The mounds were located 840 - 1100 m a.s.l.



Figure 41 Aerial view of study area ~ 10-13 km NE of Merritt, B.C.

The seral forest formed a mosaic,^{3,174,211} (Conversation with S Simard; Vancouver (BC); unreferenced) with remnant old-growth trees of interior Douglas-fir (*Pseudotsuga menziesii* var. glauca) and ponderosa pines (Pinus ponderosa). Plant associates included: guaking aspen (Populus tremuloides), Saskatoon serviceberry (Amelanchier alnifolia), bluebunch wheatgrass (Pseudoroegneria spicata), yarrow (Achillea millefolium), and arrowleaf balsamroot (Balsamorhiza sagittata) 61,70,91,160,172

The average annual precipitation and temperature extremes for the four preceding years (2004-2007), and the study period (2008-2010) are given below 29 :

Table 1 Average Precipitation and Temperature extremes for 2004-2010				
	Units			
Avg. Annual Precipitation	273 mm			
Avg. Annual Snowfall	62 cm			
Annual Temperature:				
Lowest	-33 °C (Dec '08)			
Highest	39 °C (Aug '04, Jul '06)			

The average precipitation and temperature extremes for just July, November, and May for the four preceding years (2004-2007), and the study period (2008-2010) were ²⁹:

Extremes for 2004-2010							
Month	Average of 7-months Temperatures (°C)			Monthly Precipitation Average (mm)			
	Min	Мах	Average	Total			
July	12°	30°	20°	14			
Nov	-2°	6°	2°	40			
Мау	5°	20°	13°	31			

Table 2 Average Precipitation and Temperature and	
Extremes for 2004-2010	

Soil formation was initiated from Pleistocene de-glaciation events as evidenced by non-sorted, nonstratified remnant glacial till ^{69,70}, and the local soil orders have been classified as Eutric Brunisol and Regosol²⁵¹. The recent set of natural and anthropogenic disturbances that influenced the Swakum Mountain forest ecosystem were: mountain pine beetle (Dendroctonus ponderosae) and western spruce budworm (Choristoneura occidentalis) infestations; fire in 2005; extensive commercial logging from 1961-1969,^{101,251} (Conversation with Jerry Sanders. Merritt BC; unreferenced.); low- elevation

clear-cut for rangeland restoration January to May 2009; and annual grazing prior to and throughout the study period.

2.2 Observation Methods

Beginning in July 2008 and continuing through December 2012 I documented my seasonal observations, describing occurrences and events at the study area. 37 mounds were studied in detail, while an additional 50 mounds were observed within the entire study area. The 37 mounds were classified by type: Type 1 (25), Type 2 (7), Type 3 (4), and Type 4 (1). My observations were inspired by cited literature and the summer and fall 2008 field observations. My process was organically derived, drawing me to observe known and to discover a few unknown *Formica* behaviors which further enrich and support my results.

2.3 Mound Locations and Measurements

2.3.1 Study Area Survey and Mapping

I surveyed the area in July to September 2008. The study area was mapped and GPS coordinates recorded using a GarminTM 72 hand held GPS unit. The 37 mounds were classified into four types (Figs. 2-4, Appendix F, Fig. 69) based upon the woody structure supporting the thatch. Initially, 10 Type 1 mounds of similar size were randomly selected from the known mounds and measured for temperature, and litter samples collected for moisture and CO_2 evolution experiments. An additional 9 mounds were measured for mound growth, and from the large mounds of Types 1, 2, and 3, 500-800 grams of Douglas-fir needles were collected for the 100-needle decomposition sequence experiment.

2.3.2 Mound Size and Area of Influence

The mound heights were measured from the highest point using a metal measuring rod marked in 10cm denominations. The long and short sides were marked then measured with a 30-m DBH tape that was staked on one end. Initially, Type 1 mounds (Fig. 2) were measured in July 2009 and remeasured in November 2009, May 2010, and November 2010. In addition, the mounds used for the 100-needle experiment which included Types 2 and 3 (Figs. 3, 4), were measured in May 2010 and re-measured in November 2010.

In the November 2010 period the area of influence, with respect to litter coverage, was estimated by measuring the distance to the furthest Douglas-fir tree from the center of each mound. I estimated the percent needle litter cover by surveying the entire circumference of the forest floor surrounding each mound (determined by the furthest tree), divided the mound-area into 45° slices and noted which
slices contained freshly fallen litter. From that information I estimated a fraction of litter coverage for each mound-area. Where there was fresh litter, I measured its depth.

2.3.3 Large Woody Debris Measurements

I measured the remnant core stumps (Type 1), downed logs (Type 2), and snags (Type 3) within mounds with a metal measuring rod. When stumps were visible, I directly measured the height and diameter. When the stump was interred in thatch, I probed to find the base and top, measured the height, then slid the rod across the top surface of the stump probing for the opposite edge, and then measured the diameter. For downed logs, I measured the diameter directly; the length was defined by the mounded thatch surrounding the log. For snags, I measured the highest point of thatch relative to the supporting snag, the interior diameter of empty space, and the thickness of the remaining shell.

2.3.4 Ambient, Forest Floor, and Mound Temperatures

Temperatures were taken with a Checktemp 1 Pocket Thermometer from Hanna Instruments at all mounds on a single day during July 2009, November 2009, and May 2010 at Type 1 mounds. These days were selected to measure seasonal temperature extremes and *Formica* influence on thatch during spring brood rearing. The temperatures taken were ambient air, soil at the organic-mineral interface (~ 4-6 cm deep and ~ 4 m from the edge of the mound), crust thatch (~2-4 cm deep near the mound top), interior thatch (within mound > 8 cm deep), below and at the edge of the mound at ~ 4-6 cm deep (Appendix F, Fig. 70).

2.4 Specimen and Material Collection

2.4.1 Formica sp. and Invertebrate Collection

By hand, I collected *Formica* sp. workers and aphids from mounds and *Formica* influenced Douglasfir trees, and other invertebrates from the thatched litter samples and stored them in 75% ethanol solution. Plant and fungal species were collected and dried; selected fungal spore prints were made; and all were later identified.

2.4.2 Material Collection

With a trowel, I collected 500-800-gram samples of: needle litter, CWD, and soil 4-8 meters from the edge of the mound; thatch from various depths (crust at ~ 2-4 cm and interior at > 8cm); exposed decayed wood from the top of the mounds; and soil from mounds and below mounds, to test for differences in: seasonal moisture content; needle mass; %C, %N, C:N of needles and thatch; and evolved CO_2 . The initial study area included Type 1 mounds (Fig. 42), where the stump was interred, or ~ 90% covered with thatch. The *Formica* mounds were active at some point, and then remained

active throughout the study. The control areas contained naturally mounded Douglas-fir needles and CWD, free of *Formica* sp. activity and disturbance.



Figure 42 An example of Type 1 mound - "Open-meadow"

The collection periods were July 2009, November 2009, and May 2010. Materials were collected from the ten Type 1 mounds. The control samples consisted of three types of material: CWD, needle litter from the forest floor, and soil from the Oh - A interface collected at a depth of ~ 4-6 cm. Each material type was collected from three locations.

The sample materials from the study area included: CWD from the stump core, thatch from the external crust layer (collected at < 8 cm), inner thatch from within the mound (collected at > 8 cm), and the soil from the Oh - A interface (collected at the edge and below the mound at a depth of ~ 4-6 cm). Samples were placed in large, labeled zip-lock plastic bags, stored overnight in coolers, transported to a cold storage unit, and held at ~ 3.5 °C for < 2 weeks before drying.

2.4.3 100 Needles Collection for Mass Loss Studies

In November 2009 I collected 500-800 grams of Douglas-fir needles from the forest floor and thatch from ten of the largest *Formica* mounds of Types 1, 2, and 3, which conceivably contained the greatest amounts of thatch, largely composed of Douglas-fir needle litter. The needles and thatch

were classified based on coloration and placement (Figs. 43 a/b to 46 a/b). The needles were collected from the forest floor below two old, large, remnant *P. menziesii* trees, on the surface, and within the organic-mineral layer; and from the surrounding forest floor of large *Formica* sp. mounds, and the thatch from the surface and within the mounds (Fig. 47, Table 3).



Figure 43 a/b Newly senesced litter. Collected from the area surrounding an active mound. (length in cm)



Figure 44 a/b Exterior crust thatch. Collected from the surface of an active mound. (length in cm)



Figure 45 a/b Interior thatch at a depth of ~ 8 cm. Collected from an active mound. (length in cm)



Figure 46 a/b Interior thatch at a depth > 8 cm. Collected from an active mound. (length in cm)



Figure 47 100 needle samples, milled for EA analysis. Taken from various geographic locations of an active mound.

After collection, needles and thatch were stored in labeled zip-top plastic bags and held overnight at ~ 3.5 °C for < 2 weeks prior to processing.

Samples	Needle/Thatch Coloration - Placement - Depth							
Forest Floor:								
Needles beneath remnant old-growth interior Douglas-fir trees; having a maximum 8cm organic layer	Golden needles; on the forest floor; on the surface	Light-medium brown needles; on forest floor; at < 1 cm	Brown-dark brown needles, on forest floor; at 8 cm	N/A; no litter present; > 8cm at the A horizon				
Mounds : Thatch from large, Type 1-3 mounds	Golden needles; on forest floor surrounding mounds; on the surface	light-medium brown thatch; on the mound surface: < 1cm	brown-dark brown thatch; within the mound; at 8 cm	dominated by dark brown thatch; within the mound; > 8 cm				

Table 3 Color Description, Placement, and Depth of Needles and Thatch

2.5 Laboratory Procedures

2.5.1 Sample Drying

Both procedures for calculating percent moisture content, and measuring the C:N, required drying. Using the Gravimetric method,^{12,20} I pre-heated the drying oven to 72 °C (Fischer Scientific® Isotemp® oven 700 series); recorded the weight of the plates, and then recorded the initial weight of the plate including the sample before drying (Fischer Scientific® Balance S40152).

Samples were dried for 48 h, removed from the drying oven, immediately re-weighed and the final weights recorded, and then returned to the oven. Samples were re-checked at both 72 and 96 hours to ensure that no additional moisture loss occurred. The procedure was applied to all material types for each of the collection periods of July 2009, November 2009, and May 2010; and to the needles and thatch for the 100 needle mass loss experiment.

2.5.2 100 Needles Weight and Volume for Decomposition Sequence

The collected Douglas-fir needles were located at the forest floor surface, mound surface (< 1 cm depth), and at two depths within the mounds (8 cm and > 8 cm respectively) (Table 3). Needle coloration and depth within the forest floor and mounds were used as an approximation of age. Freshly fallen, golden-brown senesced needles on the forest floor were estimated to be 1-2 months old, thatch from the mound surface (< 1 cm) was incorporated into the mound 1-2 years earlier, thatch at 8 cm to be 6-8 years old, while thatch at > 8 cm is 9-15 years or older depending upon interred depth, disturbances and worker population growth rates.

I counted out 100 Douglas-fir needles from samples for each of the mound locations (forest floor, mound surface, at 8 cm, and > 8 cm); and forest floor locations (surface, 1 cm, and 8 cm), using the

following criteria: intact needle, of average length and width relative to all the needles in the individual sample. The lengths and widths of the needles were measured where an average length and width was calculated for each sample. The needles were weighed and dried using the sample drying method as mentioned above. The dried weight of 100 needles for each mound location was then measured and put into a decomposition sequence. After the drying was completed, the needles were dusted with a small, fine-haired paint brush, removing all particulates from each individual sample weighed and stored at room temperature for later C and N analysis.

I estimated the volume of each 100-needle sample by placing the 100 needles into a 50-mL graduated beaker (± 5% error). I rotated and gently tapped the beaker to settle the needles, reducing the air space in the sample. I then recorded the approximate volume.

2.5.3 Carbon and Nitrogen Analysis of 100 Needles

After drying and weighing, samples were ground using a Wiley® Mill with a 40-mesh sieve, and the particulates from the dusted samples were sifted through a 500-micron mesh sieve (Laboratory Sieve Endecotts®, Ltd.). Each individual sample of 100 needles was ground into a homogeneous mixture re-bagged and stored at room temperature (Fig. 47) for ~ 48 hours. I weighed out 2.0 mg \pm 0.2 mg, of the homogenous sample, onto a Sartorius® microbalance (Sartorius® model M2P, accurate to 0.001 mg), packed the samples into combustible tin capsules, and stored at room temperature overnight.

2.5.4 Elemental Analyzer Procedure

The elemental analyzer (Elementar® vario EL cube) was operated by Alice Chang in the CNN mode using the methods referenced in ²³⁶. The combustion and reduction temperatures were 950 °C and 600 °C respectively. The carrier gas was He with a pulse of O_2 injected at the moment of sample combustion. The sample gases were carried into the reduction reactor where NOX from sample was reduced into elemental N₂. The H₂O vapor was removed with the drying trap. The remaining CO₂ and N₂ were separated by a CO₂ absorbent trap which allowed the N₂ to reach the thermal conductivity detector (TCD) first. The CO₂ trap was heated to 215 °C allowing the released CO₂ to reach the TCD. The gas emitted from the sample created a pulse as a disturbance with respect to the He reference flow. This pulse was converted into an electrical signal that was translated by the software producing a peak directly proportional to the amount of C and N within the sample. Based on the calibration standard (acetanilide), of known C and N percentages, the software determined the C and N percentages in the gas samples and I converted this to mg using the sample dry weights. Mess 3 served as the certified external control.

2.5.5 CO₂ Evolution Sample Preparation and Incubation

The three material types were used from the collection periods of: July 2009, November 2009, and May 2010. The controls were CWD, Douglas-fir needle litter from the forest floor, and soil from the Oh - A interface. The samples were from Type 1 mounds containing: CWD from the inner stump, crust thatch taken from at ~ 4 cm depth, interior thatch taken from > 8 cm depth, and a soil mixture from the Oh - A interface at approximately 4-6 cm beneath and at the edge of the mound. I separated the controls and samples taken from the Oh - A interface into two groups: unfiltered and filtered with 500 micron mesh sieve (Laboratory Sieve Endecotts®, Ltd.). The filter separated out gravel, remnant litter, course and fine roots.

The 500-mL incubation chambers (Mason jars), were washed in hot soapy water, rinsed with deionized (DI) water, rinsed with 90% ethanol, rinsed again with DI water, and then air dried. The incubation storage space was cleaned with 90% ethanol. I measured the three material types into ~ 50 mL samples. When necessary, I broke up woody debris into 3-5 cm pieces. I weighed (Denver Instruments® XL-3100) the empty incubation chambers, added the samples, and re-weighed the incubation chamber plus the sample, covered them with 4x4 perforated Fischer® weighing paper, and incubated them at room temperature (21-23 °C) for 10-14 days (standard reference). By adding DI water, the initial weight was maintained every day for 4 days, and then every other day for the remaining days of the incubation period. The DI water was evenly distributed directly onto the samples using a micro-pipette. On the final day of incubation, the samples were re-weighed and brought to their initial weight.

I added moisture to the dry July 2009 samples to determine if increased moisture would affect the rate of evolved CO₂. I repeated the incubation process on the samples by increasing and maintaining the moisture content for an additional 10-14 days. Through observation and measurement of moisture content of May 2010 samples and earlier testing of July 2009 materials, I determined an appropriate increase of moisture to be: 20% Oa, 50% litter and thatch, 90% woody debris, for the final incubation.

In preparation for the CO₂ evolution experiment, I prepared the 5.9 mL Exetainers® by replacing the worn rubber seals, inserted silicon septa ^{99,197}, evacuated the containers to -1 atm (Edward Pirani 50 instrument), and stored them upside down until the material samples were incubated ^{100,101,98,173}, (Personal conversations with Rob Guy, Forest Sciences Department, UBC, Vancouver (BC); Rachhpal Jassal, Land and Food Systems, UBC, Vancouver (BC)).

Prior to taking the gas samples, all the materials were re-weighed, and if necessary, DI water added, ensuring that the initial weight was maintained. The incubation chambers were sealed with air-tight lids with rubber septums and gas samples were drawn from each chamber at time initial (t_i) and at time final (t_i). Incubation time was determined by prior experimentation and recommendations by Dr. Rachhpal Jassal. The incubation time was based on the maximum rate of change in the CO₂

concentration as determined from earlier experimentation. The maximum evolved CO_2 for litter/thatch and organic-mineral interface was between 0 and 20 minutes, and for CWD between 0 and 60 minutes.

For each gas sample, I mixed and withdrew the gases from the chamber with a sterile 20 mL BD® syringe with a $25_G 1\frac{1}{2}$ " needle. The t_i and t_f gas samples were both ~ 15 mL. This volume was determined from my prior low-level CO₂ concentration experiments in efforts to minimize external CO₂ contamination to the samples (Based on suggestions from personal conversations with Paul Rachhpal).

The Exetainers® holding the gas samples were stored overnight while the gas chromatograph (Trace Gas GC HP5890 II Series) was started and initialized for a minimum of 6 hours, stabilizing the carrier gas flow (He), the flow of H_2 thru the methanizer (Sri Instruments Model 510), and the FID (flame ionization detector) and temperature of the oven.

2.5.6 Gas Chromatograph Procedure

Approximately 5 mL gas samples were injected into the injector port, transferred through the valves and sampling loops by the Ultra 0 compressed air, mixed with the carrier gas (He ultra-high purity 5.0), transported through the stainless steel packed column (HSA 80/100 12' long, 2 mm I.D., 1/8" O.D.), inside the oven at a temperature of 80 °C, delivered to the methanizer where the CO₂ was converted to methane by the injected H₂ ultra high purity 5.0 gas at a temperature of 375 °C. After transport through the methanizer, the gas continued into the FID at a temperature of 300 °C utilizing the destructive method, burning / ionizing organic compounds. The ECD (electron capture detector) was not used for these measurements.

After initializing the gas chromatograph in accordance with the SOP developed by Kazu Ishimaru ⁹⁷, the oven, inlet A (FID inlet line), and detector A temperatures were measured: 80 °C, 80 °C, and 300 °C, respectively. When using the external methanizer unit, the sample temperature was increased to 375 °C then lowered to 300 °C upon entering the FID. The required flow of the carrier gas (He) was ~ 35 mL/min, the compressed air was set to 45-50 PSI at the tank. When measured with the flow meter into the gas chromatograph (Universal digital gas flow meter Agilent Technologies ADM 1000), it required a 450 mL/min flow rate. The flow of H₂ into the methanizer was 25 mL/min and requiring an additional 25 mL/min through the FID resulting in a total 50 mL/min flow rate for H₂. The combined flow rate of the compressed air, He, and H₂ was ~ 535 mL/min.

To establish a mean flow rate, the procedure required bracketing the pressure vs. flow relationship using the CO₂ methods provided by the Chem Station System software. The software then determined a new flow equation for each run. The FID ionized the sample creating a disturbance to the overall flow rate. This disturbance was translated into an electrical impulse creating a peak by

which the software integrated the area under the sample peak calculating the amount of CO₂ in each sample.

2.5.7 Internal Standards and Samples

The internal standard of pure CO₂ (99.99%) was determined by distillations based on the volume of pure CO₂ divided by the total volume of gas in the chamber.

The flasks (148 mL) were flushed with pure N₂ gas and sealed with rubber stoppers. Using a sterile, 10 mL BD® syringe with a 26_G 1/2 designated for each gas, 2 distillations were made. The first distillation was made, by taking a set volume of pure CO₂ and injecting it into the first flask and immediately sealing it. The gas was then mixed within the flask by flushing the syringe three times. On the fourth draw a set volume pulled and injected into a 2nd flask, mixed as mentioned before, ~ 15 mL withdrawn then injected into an Exetainer®. Using a pressured syringe (Vici Pressure-Lok® Precision Analytical syringe), I withdrew an ~ 5 mL sample from the Exetainer®, sealed off the syringe, removed the needle, attached the syringe to the gas chromatograph injector port, and injected the sample into the gas chromatograph. This was performed throughout the duration of each run.

The set of internal standards used, which included 2-4 replicates for each standard, were: 178.0 ppm CO₂, 434.6 ppm CO₂, 772.8 ppm CO₂, 1018.8 ppm CO₂, 1273.2 ppm CO₂.

During the preliminary tests and runs, internal control samples and outside air samples were injected into the gas chromatograph throughout the duration of each run. The outdoor samples provided a relative known (~ 350-385 ppm [CO₂]) utilized as a check point for measuring consistency during each of the runs. Preliminary tests included contamination and incubation experiments performed in November to Dec 2009 and repeated in May to Jun 2010. The experimental samples were run from July to August 2010. Additional Exetainers® were evacuated and stored in case of unforeseen sampling errors (e.g., manual errors while injecting CO₂ samples into the gas chromatograph), faulty Exetainer® lids, external CO₂ contamination to Exetainers®. Sample moisture content within the incubation chambers was also maintained throughout the gas chromatograph run until the each testing period for the experiment was completed.

2.6 Calculations

The moisture content using gravimetric methods was measured in % mass loss in grams using the equation:

Where W_1 was the initial weight of the sample before drying (g) and W_F was the final weight of the sample weight after drying (g).

This equation was also used for the "100 needle" and EA sample moisture content.

Elemental Analyzer

The software integrated the area below the curve which then calculated the sample C and N weights. The equations used for %C and %N:

$$C_{s} / T_{s} * 100 = %C$$

 $N_{s} / T_{s} * 100 = %N$

Where C_s and N_s are the sample weights of C and N, respectively, and T_s is the total sample weight (mg).

The C:N was calculated using the %C divided by the %N of each sample.

CO₂ Evolution

Moisture addition to July 2009 samples

The weight of additional water needed to maintain the moisture content of samples at 20%, 60%, and 90% of the original weight was calculated using this equation:

 $D_W - DS_W = H_2O W_A$

 D_W was the desired weight of the sample material (g), DS_W was the dried weight of the sample material (g), and H_2OW_A was the weight of water added to the sample material (g).

ppm

The area below the curve (A) was calculated by the software. I derived a regression line from my internal standards, giving a slope (m) and a y-intercept (\pm b). The equation used to determine the ppm at time zero (ppm₀) and time final (ppm_F) was:

 $(A/1000) * (m \pm b) = ppm$

CO₂ Evolution

 CO_2 evolution (E_p), (µmol/g min) was calculated using the following equation:

 $E_p = \rho * (V / W) * (dc/dt)$

rho (ρ)

rho (ρ) was derived from the density of dry air / molecular mass of air ¹⁰¹, (Personal conversation with Rachhpal Jassal, Land and Food Systems, UBC, Vancouver (BC)). The molecular mass of air ~ 44.0249 (mol m⁻³), V was the volume of the incubation chamber (m³), W was the weight of the sample (g), and dc/dt was the Δ [CO₂] from t₀-t_f (min).

One way ANOVA analyses and General Linear Models were used in the statistical analysis for: temperature, moisture, and evolved CO_2 ; ANOVA analyses were used in the mass loss experiments. Linear and polynomial regressions were used in the moisture and evolved CO_2 analysis and the mass loss decomposition sequences. Paired T-tests were used in evolved CO_2 re-moistening experiment. All statistical analyses were performed using mini-tab 16 with an alpha level of ≤ 0.05 for ANOVA analyses.

3 Results

3.1 Temperature

Temperatures were measured at the ten Type 1 mounds at each location on the three occasions. AM/PM temperatures were averaged and are shown in Fig. 48. Although there were minimal variations between types on each occasion, in November crust thatch and ambient soil had the lowest mean temperatures, while in May ambient air and crust thatch mean temperatures were higher than the interior thatch, ambient soil, and below-mound soil.



Figure 48 Mean temperatures of ambient and mound materials. Black bars represent temperature range of the ambient and mounded material type.

	Ambient Air	Crust Thatch	Interior Thatch	Ambient Soil	Below-Mound Soil
July 2009	± 1.2°	± 1.3°	± 1.1°	± 0.7°	± 0.9°
Nov 2009	± 0.2°	± 0.2°	± 0.2°	± 0.2°	± 0.2°
May 2010	± 0.9°	± 1.3°	± 0.7°	± 0.8°	± 0.4°

The date of temperature measure was the dominant factor contributing to the significance of the data (Table 4). The General Linear Model with the factor of date alone, showed significance with a *p*-value of 0.014 while the R^2 and adjusted R^2 values for the model were 97.51% and 96.63%. Other significant interactions with date included: time of measurement (AM/PM), location with respect to mounds, and mounds- with *p*-values of 0.000, 0.000, and 0.010 respectively (Table 4). Other significant interactions included time (with both location and mound) with *p*-values of 0.000 and 0.018 (Table 4). Overall, interior thatch displayed the lowest temperature in May when compared to the crusted thatch and the ambient air temperatures (Fig. 48).

Source	df	Seq SS	Adj SS	Adj MS	<i>F</i> ratio	<i>p</i> -value
Date ¹	2	28135.86	27522.14	13761.07	35.97	0.014
AM/PM (time) ²	1	1496.96	1497.93	1497.93	4.36	0.169
Date*AM/PM	2	705.21	685.58	342.79	166.27	0.000
Location ³	4	377.20	373.31	93.33	2.11	0.172
Date*Location	8	356.77	355.00	44.38	11.65	0.000
Mound ⁴	9	224.20	223.84	24.87	2.31	0.068
Date*Mound	18	114.85	114.85	6.38	3.10	0.010
AM/PM*Location	4	100.33	106.35	26.59	6.98	0.000
AM/PM*Mound	9	59.50	58.08	6.45	3.14	0.018
Date*AM/PM*Mound	18	36.90	36.90	2.05	0.54	0.937
Error	212	807.68	807.68	3.81		
Total	287	32415.46				

 Table 4 General Linear Model results for ambient and mounded material temperatures

 $(R^2 = 97.51\%, adjusted R^2 = 96.63\%)$

¹ Dates included July 2009, November 2009, and May 2010.

² AM and PM refer to the time of measurements.

³ Location¹ refers to where at the mound the temperature was measured.

⁴ Mound refers to the geographic location of the colony.

In the six AM/PM one-way ANOVA analyses for mean temperatures, there were significant differences amongst locations in all time blocks (Table 5). November AM, May AM, and May PM demonstrated a three-tier pattern with the strongest relationship for the series evidenced by the May PM block ($R^2 = 64.18\%$, adjusted $R^2 = 60.85\%$).

Table 5 a-c One-way ANOVA analyses for AM/PM time blocks for each period ^{1,2} (a) July 2009

АМ								F	PM		
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value	Source	DF	SS	MS	F ratio	<i>p</i> -value
Location	4	93.86	23.46	5.01	0.002	Location	4	185.51	46.38	4.81	0.003
Error	44	206.00	4.68			Error	44	424.39	9.65		
Total	48	299.86				Total	48	609.89			
(D ² 04 0	<u> </u>	r , , , , , , , , , , , , , , , , , , ,	05 000	()		(D ² 00 4	00/	" · · · D ²	04.000	()	

 $(R^2 = 31.30\%, adjusted R^2 = 25.06\%)$

 $(R^2 = 30.42\%, adjusted R^2 = 24.09\%)$

(b) Nov 2009

АМ								I	PM		
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value	Source	DF	SS	MS	F ratio	<i>p</i> -value
Location	4	19.657	4.914	6.93	0.000	Location	4	13.296	3.324	4.44	0.004
Error	42	29.798	0.709			Error	42	31.432	0.748		
Total	46	49.455				Total	46	44.729			
(R2 = 39.7	75%, a	djusted R2	2 = 34.01	%)		$(R^2 = 29.7)$	'3%, a	djusted R ²	= 23.03	%)	

(R2 = 39.75%, adjusted R2 = 34.01%)

(c) May 2010

АМ							l	PM			
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value	Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Location	4	123.38	30.85	4.95	0.002	Location	4	437.84	109.46	19.26	0.000
Error	43	267.91	6.23			Error	43	244.37	5.68		
Total	47	391.30				Total	47	682.20			
(D ² 04 5	.00/ -	alterna al D2	05 4 00			(D ² 04.4	00/ -			· \	

 $(R^2 = 31.53\%, adjusted R^2 = 25.16\%)$ $(R^2 = 64.18\%, adjusted R^2 = 60.85\%)$

 1 α = 0.0083 using the Bonferroni correction. All tests used Tukey's 95% Simultaneous Confidence Intervals.

 2 N = 10 for all ambient and mounded material types with the exception of the crust thatch type which varied between periods: N = 9, N = 7, N = 8, for July, November, and May respectively.

Ambient soil and below-mound soil temperatures tended to be lower than ambient air in both July 2009 and May 2010, which contrasted with November 2009 temperatures when below-mound soils (AM) were warmer than ambient and mounded materials and similar to ambient air and interior thatch in the PM (Figs. 48, 49). Compared to the mound crust, the interior thatch was warmer in November (AM & PM) and cooler in May (AM & PM) indicating a temperature differential of mounded litter materials creating a buffering effect within the mound (Figs. 48, & 49). The differences between July and November AM and PM were not significant even though July and November "book-ended" the temperature extremes. In May, mean temperature differences were significant between groups (pvalue = 0.00, R^2 = 36.77%, adjusted R^2 = 30.89%) (Table 6). Smaller temperature differences occurred in below-mound soil relative to ambient soil and interior thatch in May (AM) (Figs. 49, 50). The temperature differences between material types became pronounced during May (PM) as afternoon temperatures tended to increase (Fig. 50). In Figure 50, the difference between AM & PM

ambient air temperature showed the greatest variance (~ 13 °C), while the mounded materials variance was much less, ranging from ~ 1 °C for below-mound soil to ~ 7 °C for interior thatch (Fig. 50). Additionally, there was a significant difference between material types (Fig. 50) where crust thatch was the warmest for the May block (Fig. 49) and was significantly different from both interior thatch and below-mound soil (Fig. 50), further indicating a temperature buffering effect of mounded materials.



Material Type

Figure 49 Mean temperatures of ambient and mounded materials for AM and PM for the three periods. Black bars indicate temperature ranges of the varied material types and unlike letters indicate significant temperature differences of material type during AM and PM.

	Ambient Air	Crust Thatch	Interior Thatch	Ambient Soil	Below-Mound Soil				
July 2009 AM / PM	± 1.0° / ± 0.5°	± 0.7° / ± 0.8°	± 0.6° / ±1.4°	± 0.6° / ± 0.7°	± 0.4° / ± 1.2°				
Nov 2009 AM / PM	± 0.03° / ± 0.3°	± 0.2° / ± 0.4°	± 0.3° / ± 0.2°	± 0.2° / ± 0.3°	± 0.3° / ± 0.3°				
May 2010 AM / PM	± 1.1° / ± 0.5°	± 1.2° / ± 1.5°	± 0.8° / ± 0.7°	± 0.3° / ± 0.7°	± 0.4° / ± 0.5°				

Standard Error (for Figure 49)

Table 6 One-way ANOVA analysis of AM/PM temperature differencesfor ambient and material typesMay 2010 2							
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value		
Location	4	182.46	45.62	6.25	0.000		
Error	43	313.70	7.30				
Total	47	496.16					

 $(R^2 = 36.77\%, adjusted R^2 = 30.89\%)$

 1 N = 10 for all groups with the exception of crusted thatch where N = 8.

² Using Tukey's 95% Simultaneous Confidence Intervals



Ambient Air & Material Types

Figure 50 Mean differences of AM/PM temperatures for May 2010. Black bars indicate range of temperature differences between AM and PM and unlike letters indicate significant temperature differences between AM and PM.

Standard	Error (f	or Figure	50)
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	Ambient Air	Crust Thatch	Interior Thatch	Ambient Soil	Below-Mound Soil
May 2010	± 1.4°	± 0.8°	± 0.9°	± 0.6°	± 0.2°

3.2 Moisture

The General Linear Model for moisture indicated a significant effect of time (date) and a significant interaction between date and material type (*p*-value = 0.012, and P = 0.000) (Table 7). The mean moisture content for the various material types was lowest (< 10%) in July with a ~ 14% variance in the mound crust and mound wood (Fig. 51). In July, the inner thatch was slightly drier than the litter and mound crust while mound wood and below-mound soil were moister than their respective forest floor types (Fig. 51). In November, both mounded thatch types were considerably drier than litter while mounded wood and wood exhibited the same characteristic relationship (Fig. 51). In May, although there was not a significant difference in moisture content between the various mounded materials, a similar relationship occurred in the thatched and below-mound soil types (Fig. 51), indicating a moisture buffering effect of the mound.

 Table 7 General Linear Model for moisture with collection times (date),
 geographic location of mounds (mound), and materials (type)

DF	Seq SS	Adj SS	Adj MS	F ratio	<i>p-</i> value
2	1.820667	1.938912	0.969456	10.61	0.012
9	0.106422	0.089059	0.009895	1.38	0.268
18	0.087180	0.129269	0.007182	0.77	0.724
3	0.374794	0.384995	0.128332	1.35	0.345
6	0.571704	0.571704	0.095284	10.26	0.000
73	0.678222	0.678222	0.009291		
111	3.638989				
	DF 2 9 18 3 6 73 111	DFSeq SS21.82066790.106422180.08718030.37479460.571704730.6782221113.638989	DFSeq SSAdj SS21.8206671.93891290.1064220.089059180.0871800.12926930.3747940.38499560.5717040.571704730.6782220.6782221113.638989	DFSeq SSAdj SSAdj MS21.8206671.9389120.96945690.1064220.0890590.009895180.0871800.1292690.00718230.3747940.3849950.12833260.5717040.5717040.095284730.6782220.6782220.0092911113.638989	DFSeq SSAdj SSAdj MSF ratio21.8206671.9389120.96945610.6190.1064220.0890590.0098951.38180.0871800.1292690.0071820.7730.3747940.3849950.1283321.3560.5717040.5717040.09528410.26730.6782220.6782220.0092911111113.638989

 $(R^2 = 81.36\%, adjusted R^2 = 71.66\%)$





Mean moisture content of mound material types during the three periods. Black bars represent range of moisture content of the various material types and unlike letters indicate significant differences between mounded material types.

	Crust Thatch	Interior Thatch	Mound Wood	Below-Mound Soil
July 2009	± 1.9%	± 0.5%	± 1.3%	± 0.5%
Nov 2009	± 1.4%	± 4.3%	± 4.9%	± 2.1%
May 2010	± 3.2%	± 2.8%	± 5.4%	± 2.3%

*The three forest floor types: litter, wood, and soil are composite samples from areas uninhabited by *Formica* sp. containing CWD, Douglas-fir needles, and soil from the O/Ae horizon.

Comparing November to May, the moisture content for forest floor litter and wood was considerably wetter with May levels having dropped by 75-85% (Fig. 51). When compared to their respective mounded material types, the more exposed types (mound crust and mound wood) had a moisture decrease of approximately 45% and 26% while the inner thatch and below-mound soil types maintained very similar moisture levels throughout the two periods (Fig. 51).

The one-way ANOVA analyses indicated significant differences between mounded material types in July and November (*p*-values of 0.016 and 0.000 respectively) (Table 8 a-c). Crust and inner thatch materials were not significantly different in July, but were significant in November (Fig. 51). Mounded wood, although a different material, had the same moisture content as the mound crust in both periods (Fig. 51). In July and November, the below-mound soil was the driest of all mounded material types. However in May, the moisture content was the same as November and moister than the mound crust (Fig. 51).

Although there were significant differences among mounded material types in July and November (Table 8), forest floor materials were not included in the one-way ANOVA analyses as moisture contents were based on a single composite sample collected from uninhabited locations in the study area (Fig. 51). Overall there was a clear tendency for moisture content of the mounded thatch (crust and interior) to be consistently lower than forest floor litter. Moreover, the same tendency was evidenced by the remaining material types (wood, soil), thereby associating drier material to mounds (Fig. 51).

Table 8 a-c	One-way	ANOVA	analyses	for the	various	mounded
material typ	es ¹					

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(a) Jui 2009					
Source	DF	SS	MS	F ratio	<i>p-</i> value
Material Types	3	0.01255	0.00418	3.99	0.016
Error	33	0.03462	0.00105		
Total	36	0.04717			

 $(R^2 = 26.60\%, adjusted R^2 = 19.92\%)$

(b) Nov 2009 ²					
Source	DF	SS	MS	F ratio	<i>p-</i> value
Material Types	3	0.8378	0.2793	21.48	0.000
Error	33	0.4290	0.0130		
Total	36	1.2667			

 $(R^2 = 66.14\%, adjusted R^2 = 63.06\%)$

(c) May 2010 ²					
Source	DF	SS	MS	F ratio	<i>p-</i> value
Material Types	3	0.0701	0.0234	1.83	0.160
Error	34	0.4343	0.0128		
Total	37	0.5044			

 1 N = 10 for all material types with the exception of mound crust thatch

where N =7 for July and Nov and N = 8 for May.

² All tables are using Tukey's 95% Simultaneous Confidence Intervals

With the exclusion of the July 2009 data, an amended General Linear Model indicated a single interaction between date and the mounded material types (p-value = 0.00) (Table 9).

Source	DF	Seq SS	Adj SS	Adj MS	F ratio	<i>p-</i> value
Date:(Nov, May)	1	0.56012	0.69758	0.69758	4.48	0.125
Mounds	9	0.10156	0.08308	0.00923	0.71	0.691
Date*Mounds	9	0.07304	0.11695	0.01299	0.96	0.482
Types	3	0.45777	0.47382	0.15794	0.99	0.502
Date*Types	3	0.47714	0.47714	0.15905	11.78	0.000
Error	49	0.66165	0.66165	0.01350		
Total	74	2.33127				

Table 9 Amended General Linear Model for moisture content in Nov 2009 and May 2010

 $(R^2 = 71.62\%, adjusted R^2 = 57.14\%)$

All mounded materials showed significant differences in moisture content between the three periods (Table 10), peaking in November for most material types (Fig. 52). The mound crust and interior thatch reached their maximum moisture levels in November. By May, the crust had dried to a similar level as July while the interior thatch maintained a moisture level similar to that of November (Fig. 52).

 Table 10 a-d
 One-way ANOVA analyses of mounded material types

(a)					
Source	DF	SS	MS	F ratio	<i>p-</i> value
Crust Thatch	2	0.97045	0.48522	112.38	0.000
Error	19	0.08204	0.00432		
Total	21	1.05249			

 $(R^2 = 92.21\%, adjusted R^2 = 91.38\%)$

(b)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p-</i> value
Interior Thatch	2	0.30232	0.15116	17.39	0.000
Error	27	0.23475	0.00869		
Total	29	0.53707			

 $(R^2 = 56.29\%, adjusted R^2 = 53.05\%)$

(c)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p-</i> value
Wood	2	0.9396	0.4698	25.88	0.000
Error	27	0.4901	0.0182		
Total	29	1.4297			

 $(R^2 = 65.72\%, adjusted R^2 = 63.18\%)$

(d)					
Source	DF	SS	MS	F ratio	<i>p</i> -value
Below Mound Soil	2	0.14528	0.07264	21.55	0.000
Error	27	0.09100	0.00337		
Total	29	0.23628			

 $(R^2 = 61.49\%, adjusted R^2 = 58.63\%)$

 1 N = 10 for all types with the exception of July 2009 and Nov 2009 where N = 7 and May 2010 N = 8. 2 All tables are using Tukey's 95% Simultaneous Confidence Intervals



Figure 52 Mean moisture content of the various forest floor and mounded material types for the three periods. Different letters indicate significant differences within each material type between the three collection dates.

The forest floor soil steadily increased in moisture, peaking in May, while the below-mound soil plateaued at the same level in November and May (Fig. 52). For the three material types, mounding had a buffering effect on moisture by lowering peak levels relative to their respective forest-floor correlates (Fig. 52).

3.3 CO₂ Evolution

The General Linear Model for CO_2 evolution indicated a significant effect of date and a significant interaction between date and material type (P= 0.002, P= 0.000) (Table 11). For all occasions, the highest level of CO_2 was produced by the forest floor litter and thatch types (Fig. 53). Materials collected in November generated the highest levels of CO_2 while those collected in July produced the lowest.

Table 11 General Linear Model for CO₂ evolution of the various forest floor and mounded material types

Source	DF	Seq SS	Adj SS	Adj MS	<i>F</i> ratio	<i>p</i> -value
Date	2	0.0006110	0.0005216	0.0002608	9.20	0.002
type	8	0.0006036	0.0006098	0.0000762	2.15	0.092
Date*type	16	0.0005686	0.0005686	0.0000355	5.65	0.000
Error	151	0.0009490	0.0009490	0.0000063		
Total	177	0.0027322				

 $(R^2 = 65.27\%, adjusted R^2 = 59.28\%)$





Standard Error	(for Figuro	521
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	Forest Floor Litter	Crust Thatch	Interior Thatch	Forest Floor Wood	Mound Wood	Forest Floor Soil	Below-Mound Soil	Forest Floor Sifted Soil	Below-Mound Sifted Soil
July 2009	± .48	±.30	± .35	± .27	±.08	±.18	±.09	±.11	±.11
Nov 2009	± 4.68	±.72	± 1.16	±.75	±.68	± 1.03	±.23	±.12	±.33
May 2010	± 1.62	± 1.62	± 1.20	±.81	± 1.75	±.10	±.33	±.06	±.33

The one-way ANOVA analyses (Table 12) indicated a significant difference of CO_2 levels for the various materials in both November and May (P=0.000, P=0.036). November forest floor litter was significantly greater than the mounded thatches and showed the greatest variance among material types for that period. Wood and soil types, although not significantly different from their respective forest floor materials, showed significant differences between crust thatch, mounded wood, and soil types when compared to the various mounded materials (Fig. 53).

Table 12 a-d One-way ANOVA analyses for evolved CO_2 of the various material types 1

(a) Jul 2009					
Source	DF	SS	MS	<i>F</i> ratio	<i>p-</i> value
Material Types	8	0.0000061	0.000008	2.03	0.061
Error	50	0.0000188	0.0000004		
Total	58	0.0000250			
(b) Nov 2009					
Source	DF	SS	MS	F ratio	<i>p</i> -value
Material Types	8	0.0009551	0.0001194	17.56	0.000

0.0003400

0.0012952

0.000068

 $(R^2 = 73.75\%, adjusted R^2 = 69.55\%)$

50

58

Error

Total

(c) May 2010					
Source	DF	SS	MS	F ratio	<i>p-</i> value
Material Types	8	0.0002109	0.0000264	2.28	0.036
Error	51	0.0005902	0.0000116		
Total	59	0.0008011			

 $(R^2 = 26.33\%, adjusted R^2 = 14.77\%)$

¹ All tables are using Tukey's 95% Simultaneous Confidence Intervals

The materials collected in May generated lower, yet similar mean levels of CO_2 compared to November although there were large variances among mounded thatch and wooded types (Fig. 53). Interior thatch produced the highest concentrations of CO_2 , followed by mounded wood, forest floor litter, crust, and soil. The various materials did not show significant differences with their respective forest floor materials, but comparing the various mounded materials, there was a significant difference between interior thatch to that of the below-mound sifted soil (Fig. 53).

The one-way ANOVA analyses for the evolved CO_2 of the various material types for the three occasions were significant for most materials, except for forest floor soil (Tables 13-15). The forest floor and below mound sieved and non-sieved soil groups tended to generate much lower levels of CO_2 compared to the other material types (Fig. 54). Comparing evolved CO_2 levels for the three

occasions, most material types (with the exception of below-mound sifted soil), peaked in November, while below-mound sifted soil peaked in May (Fig. 54).

Table 13 a-c One-way ANOVA analyses of CO_2 evolved from Forest Floor Litter and Thatch types during the three periods ¹

(a)					
Source	DF	SS	MS	F ratio	<i>p</i> -value
Forest Floor Litter	2	0.0004423	0.0002211	8.92	0.016
Error	6	0.0001487	0.0000248		
Total	8	0.0005909			

 $(R^2 = 74.84\%, adjusted R^2 = 66.45\%)$

(b)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Crust Thatch	2	0.0002954	0.0001477	16.28	0.000
Error	19	0.0001723	0.0000091		
Total	21	0.0004677			

 $(R^2 = 63.15\%, adjusted R2 = 59.28\%)$

(c)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Interior Thatch	2	0.0002127	0.0001063	11.00	0.000
Error	27	0.0002610	0.0000097		
Total	29	0.0004736			

(R² = 44.90%, adjusted R2 = 40.82%)

¹ All tables are using Tukey's 95% Simultaneous Confidence Intervals

Table 14 a-b One-way ANOVA analyses of CO₂ evolved from Forest Floor Wood and Mound Wood during the three periods ¹

(a)					
Source	DF	SS	MS	F ratio	<i>p</i> -value
Forest Floor Wood	2	0.0000145	0.0000072	5.57	0.043
Error	6	0.0000078	0.0000013		
Total	8	0.0000222			
0		0			

 $(R^2 = 65.01\%, adjusted R^2 = 53.34\%)$

(b)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Mound Wood	2	0.0001764	0.0000882	7.52	0.003
Error	27	0.0003166	0.0000117		
Total	29	0.0004930			

 $(R^2 = 35.77\%, adjusted R^2 = 31.02\%)$

¹ All tables are using Tukey's 95% Simultaneous Confidence Intervals

Table 15 a-d One-way ANOVA analyses of CO ₂ evolved from Forest F	looi
Soil and Below-Mound Soil types during the three periods ¹	

(a)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Forest Floor Soil	2	0.0000066	0.0000033	2.99	0.125
Error	6	0.0000066	0.0000011		
Total	8	0.0000133			

(b)					
Source	DF	SS	MS	F ratio	<i>p</i> -value
Below Mound Soil	2	0.0000139	0.0000069	12.08	0.000
Error	27	0.0000155	0.0000006		
Total	29	0.0000294			

 $(R^2 = 47.22\%, adjusted R^2 = 43.31\%)$

(c)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Forest Floor Sifted Soil	2	0.0000054	0.0000027	88.65	0.000
Error	6	0.0000002	0.0000000		
Total	8	0.0000056			

 $(R^2 = 96.73\%, adjusted R^2 = 95.64\%)$

(d)					
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Below Mound Sifted Soil	2	0.0000108	0.0000054	7.17	0.003
Error	27	0.0000203	0.0000008		
Total	29	0.0000311			

 $(R^2 = 34.68\%, adjusted R^2 = 29.84\%)$

¹ All tables are using Tukey's 95% Simultaneous Confidence Intervals



Figure 54 Evolved CO_2 from various forest floor material types. Different letters indicate significant differences within each material type between the three collection dates.

Complementary to the moisture results, there was a tendency for CO_2 levels to peak in November and to be consistently lower than their respective forest floor types, with the exception of belowmound sifted soil which peaked in May, and mound wood which produced higher CO_2 levels than forest-floor wood (Fig. 54). CO_2 evolved from interior thatch plateaued in November and May, which paralleled the moisture content (Fig. 54). As previously mentioned, mound wood generated higher CO_2 levels in November and produced only slightly less in May (Fig. 54). The CO2 evolved from below-mound soil types increased in November and leveled out in May, while below-mound sifted soil marginally increased in May (Fig. 54). CO_2 evolved from forest-floor sifted soil steadily increased and peaked in May, unlike the other soil types, but showed the same pattern as moisture content of forest-floor soil (Figs. 52, 54). Mounding had a buffering effect on CO_2 production in thatch and below-mound soil types, lowering peak CO_2 levels and leveling out CO_2 production in November and May.

The relationship between moisture content and CO_2 generation (Fig. 55 a-j) showed significant associations for most material types with the exception of forest-floor soil. The Pearson's coefficient (r_p), demonstrated a strong correlation between moisture and CO_2 generation (values > 0.5) for all materials, indicating a strong relationship (Fig. 55 a-j). For most of the forest-floor materials, the slope values were comparable and consistent to their mounded counterparts. Among the various types, forest-floor litter and corresponding thatch types had the largest R^2 and adjusted R^2 values (Fig. 55 ad) and slope values (m = ~ 0.0216-0.0294). Wood and soil types showed weaker correlations (Fig. 55 e-j). These linear regressions have demonstrated that CO_2 generation was strongly associated to moisture content for mounded and forest-floor materials.



Figure 55 b









Figure 55 e

Figure 55 f



Figure 55 g





Figure 55 a-j Evolved CO₂ regression analysis for various forest floor mounded material types. The forest floor types are composite samples from areas uninhabited by *Formica* sp. Solid circles (•) represent the remoistened July 2009 samples, open circles (•) represent all untreated samples.

The General Linear Model of CO_2 evolution for July 2009 (control) and moistened samples denote a significant difference between controls and moistened samples (P=0.00), the various material types (P=0.00), and a significant interaction between material type and control/moistened samples (P=0.000) (Table 16).

Source	DF	Seq SS	Adj SS	Adj MS	<i>F</i> ratio	<i>p</i> -value
Samples (controls/moistened)	1	0.0017712	0.0011449	0.0011449	76.30	0.000
Material type	8	0.0010172	0.0010172	0.0001272	8.47	0.000
Samples*type	8	0.0008398	0.0008398	0.0001050	7.00	0.000
Error	100	0.0015006	0.0015006	0.0000150		
Total	117	0.0051288				

Table 16 General Linear Model for CO₂ evolution from control and moistened samples.

 $(R^2 = 70.74\%, adjusted R^2 = 65.77\%)$

The paired T-test has further pinpointed the significant differences among each material type (Table 17). Despite greater levels of CO_2 generated from all the moistened types (Fig. 56), significant differences were noted only from mounded material types (Table 17).




	Controls /						
Material Type	Moistened	Ν	Mean	Std Dev	Std Error	T value	<i>p</i> -value
Forest Floor Litter	С	3	0.000980	0.000830	0.000480	-2.37	0.141
	Μ	3	0.012930	0.009540	0.005510		
Crust Thatch	С	7	0.001240	0.000780	0.000300	-4.49	0.004
	М	7	0.016540	0.009340	0.003530		
Interior Thatch	С	10	0.000970	0.001090	0.000350	-8.99	0.000
	М	10	0.013150	0.004370	0.001380		
Forest Floor Wood	С	3	0.000580	0.000460	0.000270	-1.55	0.260
	М	3	0.008920	0.009760	0.005630		
Mound Wood	С	10	0.000470	0.000250	0.000080	-5.94	0.000
	М	10	0.012060	0.006230	0.001970		
Forest Floor Soil	С	3	0.000517	0.000313	0.000181	-1.82	0.210
	М	3	0.001161	0.000359	0.000207		
Below Mound Soil	С	10	0.000420	0.000276	0.000087	-3.64	0.005
	М	10	0.003202	0.002345	0.000742		
Forest Floor Sifted Soil	С	3	0.000216	0.000190	0.000109	-1.45	0.283
	М	3	0.001051	0.000834	0.000481		
Below Mound Sifted Soil	С	10	0.000361	0.000349	0.000111	-4.75	0.001
	М	10	0.002276	0.001233	0.000390		

Table 17 Paired T-test results for evolved CO₂ from control and moistened material types

Unexpectedly, during the experiment as July thatch types were moistened, sprouting of seeds within the samples occurred thereby necessitating an impromptu measurement and analysis. The one-way ANOVA for July control thatch types and moistened sprouted thatch indicated a significant difference (P = 0.00) (Table 18).

 Table 18 One-way ANOVA analysis for July thatch and moistened sprouted thatch types 1

Source	Df	SS	MS	<i>F</i> ratio	<i>p-</i> value
Control/Moistened Sprouted Thatch	2	0.0014576	0.0007288	55.17	0.000
Error	25	0.0003302	0.0000132		
Total	27	0.0017878			

(R2 = 81.53%, adjusted R2 = 80.05%)

¹ Using Tukey's 95% Simultaneous Confidence Intervals

The mean CO_2 levels for the various control and moistened materials were highest among litter and thatch, followed by wood and soil types (Fig. 56). Litter, thatch, and wood types have shown greater variances among materials (Fig. 56). The close relationship between evolved CO_2 and moisture was also evident when comparing controls and moistened samples from the July collection (Fig. 56).

3.4 100 Needles: Weight, Size, Carbon and Nitrogen Contents

After drying, weighing, and measuring 100 intact Douglas-fir needles from each location of the selected 10 large mounds (Types 1-3) were used to produce decomposition sequences based on mean weight and a combination of mean weight and mean surface area (Figs. 57, 58).







Figure 58 Decomposition sequence based on the mean weights/mean surface area of 100 needles collected from various depths within mounds. Regression is represented as a polynomial function and unlike letters indicate significant differences in between mounded locations.

One-way ANOVA analyses for mound-associated litter and thatch indicated significant differences in 100-needle weight among mound locations, whereas C:N ratios did not differ (Table 19 a-d).

Table 19 a-e 100 needle one-way ANOVA analyses¹

(a) Mean Weights of mound-associated litter and thatch						
Source	DF	SS	MS	F ratio	<i>p</i> -value	
Mean Weights	3	0.40732	0.13577	27.91	0.000	
Error	36	0.17515	0.00487			
Total	39	0.58248				

(R-Sq = 69.93% R-Sq(adj) = 67.42%)

(b)	Mean Weights /	¹ mean surface area of mound-associated litter and thatch	
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Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
Mean Weights / Mean Surface Area	3	0.0000497	0.0000166	29.04	0.000
Error	36	0.0000205	0.000006		
Total	39	0.0000702			

(R-Sq = 70.76% R-Sq(adj) = 68.32%)

Table 19 a-e (cont.)

(c) C content ² of mound-associated litter and thatch							
Source	DF	SS	MS	F ratio	<i>p</i> -value		
C content	3	0.04959	0.01653	10.45	0.000		
Error	36	0.05695	0.00158				
Total	39	0.10654					

(R-Sq = 46.55% R-Sq(adj) = 42.09%)

² Based on 2 mg homogeneous samples

. ,					
Source	DF	SS	MS	F ratio	<i>p</i> -value
N content	3	0.0000998	0.0000333	5.46	0.003
Error	36	0.0002194	0.0000061		
Total	39	0.0003192			

(R-Sq = 31.27% R-Sq(adj) = 25.54%)

² Based on 2 mg homogeneous samples

(0) 0.11							
Source	DF	SS	MS	<i>F</i> ratio	P-value		
C:N	3	285.9	95.3	2.00	0.132		
Error	36	1717.0	47.7				
Total	39	2002.9					

(R-Sq = 14.28% R-Sq(adj) = 7.13%)

¹ Using Tukey's 95% Simultaneous Confidence Intervals

² Based on 2 mg homogeneous samples

This simple analysis revealed a significant decreasing "stepwise" sequence in needle weights, weight/mean surface area, and C content between surficial mound-associated needles and thatched-needles interred within mounds (Table 20). Tukey's tests for weight and weight/mean surface area indicated significant differences between senesced needles on the mound surface and thatched-needles found at > 8 cm inside the mound (Table 20), representing a decomposition sequence related to depth and thus, presumably, age. Comparing the decomposition sequence for weight, weight / mean surface area, and C content, tests indicated significant relationships of non-contiguous groupings (Table 20) suggesting decreasing rates of mass loss from "older" thatched needles at ≥ 8 cm within mounds. Nitrogen content was significantly lower in thatch from the mound surface compared to contiguous materials (senesced and inside mound at 8 cm), but did differ from thatched needles at > 8 cm (Table 20 a-b).

 Table 20 a-b
 Tukey's HSD test of selected decomposition attributes

 of mound-associated needles and thatch of the 100-needle
 decomposition sequence ¹

(a) Results - Details				
Test	Senesced on forest floor	Mound surface < 1 cm	Inside mound ~ 8 cm	Inside mound > 8 cm
Mean Weights				
Mean	0.79915	0.65394	0.57218	0.53699
Std Dev	0.09043	0.05042	0.05422	0.07617
Mean Weights / mean surface area				
Mean	0.008670	0.007245	0.006056	0.005891
Std Dev	0.000928	0.000898	0.000384	0.000681
C Content ²				
Mean	0.9948	0.9891	0.9422	0.9091
Std Dev	0.0316	0.0463	0.0451	0.0339
N Content ²				
Mean	0.022385	0.018135	0.021249	0.019960
Std Dev	0.002279	0.001739	0.002982	0.002696
C:N ratio ²				
Mean	45.970	52.425	46.253	46.593
Std Dev	7.149	5.799	8.100	6.359

 1 N = 10 for each location

²Based on 2 mg homogeneous sample for each location

(b) Results - Su	Immary
------------------	--------

Location	Senesced on forest floor	Mound surface < 1 cm	Inside mound ~ 8 cm	Inside mound > 8 cm		
Mean Weights	а	b	bc	с		
Mean Weights /						
Mean Surface						
Area	а	b	С	С		
C Content ²	а	ab	bc	С		
N Content ²	а	b	а	ab		
C:N ²	- 3	-	-	-		

 1 N = 10 for each location 2 Based on 2 mg homogeneous sample for each location 3 No significant difference

The following ANOVA analyses (Table 21 a-d) of mound-associated needles and thatch, included particulates comprised of: fragmented needles, mycelium, soil particles, ligneous fibers, and varied organic matter, adhering and encasing thatched-needles from ~ 8 cm and > 8 cm. The ANOVA

analyses denoted significant differences in weights, C content, and C:N ratios. With the addition of particulates, the analysis demonstrated a significant decrease (by approximately half), for weights, C content, and C:N ratios, thereby disparately grouping particulates from their respective litter and thatched-needle counterparts (Table 22 a-b). Tukey's HSD test for weight analysis again indicated a stepwise pattern, showing significant differences between senesced litter, thatched needles, and particulates (Table 19 a-b) while the C content and C:N ratios showed the same group relationships (Table 19 a-b).

Table 21 a-d 100-needle one-way ANOVA¹

(a) Mean Weight of mound-associated litter and thatch including particulates							
Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value		
Mean Weights	5	2.1175	0.4235	27.35	0.000		
Error	54	0.8362	0.0155				
Total	59	2.9537					

(R-Sq = 71.69% R-Sq(adj) = 69.07%)

(b) C content ²	of mound-associated litter and thatch including particulates

Source	DF	SS	MS	F ratio	<i>p</i> -value
C content	5	3.5289	0.7058	70.41	0.000
Error	54	0.5413	0.0100		
Total	59	4.0702			

(R-Sq = 86.70% R-Sq(adj) = 85.47%)

² Based on 2 mg homogeneous samples

(c) N content 2 of mound-associated litter and thatch including particulates							
Source	DF	SS	MS	F ratio	<i>p</i> -value		
N content	5	0.0001611	0.0000322	2.26	0.061		

0.0000142

59 (R-Sq = 17.32% R-Sq(adj) = 9.66%)

54

Error

Total

² Based on 2 mg homogeneous samples

(d)	C:N ²	of mound	-associated	litter ar	nd thatch	including	particulates
-----	------------------	----------	-------------	-----------	-----------	-----------	--------------

0.0007689

0.0009300

Source	DF	SS	MS	F ratio	<i>p</i> -value
C:N	5	7445.4	1489.1	33.09	0.000
Error	54	2429.7	45.0		
Total	59	9875.1			

(R-Sq = 75.40% R-Sq(adj) = 73.12%)

² Based on 2 mg homogeneous samples

¹ Using Tukey's 95% Simultaneous Confidence Intervals

Table 22 a-b Tukey's HSD test for selected decomposition attributes of mound-associated needles, thatch, and particulates ¹

(a) Results - Detail

. /						
Test	Senesced on forest floor	Mound surface < 1 cm	Inside mound ~ 8 cm	Inside mound > 8 cm	Particulates ~ 8 cm	Particulates > 8 cm
Mean Weights						
Mean	.7992	.6539	.5700	.5370	.3200	.2500
Std Dev	.0904	.0504	.0542	.0762	.1687	.2121
C Content ²						
Mean	.9948	.9891	.9422	.9091	.4259	.4715
Std Dev	.0316	.0463	.0451	.0339	.1574	.1704
N Content ²						
Mean	.022385	.018135	.021249	.019960	.018117	.018483
Std Dev	.002279	.001739	.002982	.002696	.004859	.006120
C:N ratio ²						
Mean	45.970	52.425	46.253	46.593	23.703	25.634
Std Dev	7.149	5.799	8.100	6.359	6.632	5.933

 1 N = 10 for each location

² Based on 2 mg homogeneous samples for each location

(b) Results - Summary								
Location	Senesced on forest floor	Mound surface < 1 cm	Inside mound ~ 8 cm	Inside mound > 8 cm	Particulates ~ 8 cm	Particulates > 8 cm		
Mean Weights	a a	ab	b	b	С	С		
C Content ²	а	а	а	а	b	b		
N Content ²	_ 3	-	-	-	-	-		
C:N ²	а	а	а	а	b	b		

 1 N = 10 for each location 2 Based on 2 mg homogeneous samples for each location 3 No significant difference

Figures 59 and 60 illustrate a decomposition sequence of the forest-floor litter (not associated with mounds) as a proximate representation analogous to that of the mound-associated litter and thatched needles (Figs. 57, 58). Combined decomposition sequences (Figs. 61, 62) indicate continuous mass loss from litter on the forest floor while thatched-needles harbored within mounds at depths of 8 cm and > 8 cm, retained similar weights.



Figure 59 Decomposition sequence based on the mean weights of 100 needles collected from various depths of the forest floor. The regression line represents an estimated decomposition rate of litter expressed as a polynomial function.



Figure 60 Decomposition sequence based on the mean weights of 100 needles collected from various depths of the forest floor. The regression line represents an estimated decomposition rate of litter expressed as a polynomial function.



Figure 61 Decomposition sequence based on the mean weights of 100 needles collected from various depths in the forest floor and mounds. The regression lines represent the estimated rate of decomposition of needles on the forest floor (solid line) and within mounded thatch (dashed line).



Figure 62 Decomposition sequence based on the mean weights and mean surface area of 100 needles collected from various depths in the forest floor and mounds. The regression lines represent the estimated rate of decomposition of needles on the forest floor (solid line) and within mounded thatch (dashed line).

The remaining ANOVA analyses reported in Table 23 a-e shows significant differences in forest-floor litter and mounded needle-thatch in the measured attributes, with the exception of N content (Table 23 d).

Table 23 a-e 100 needle one-way ANOVA for mound-associated litter and thatch, forest-floor litter, including particulates $^{\rm 1}$

(a) Weight ²						
Source	DF	SS	MS	F ratio	<i>p</i> -value	
Mean Weights	9	2.6062	0.2896	19.02	0.000	
Error	58	0.8832	0.0152			
Total	67	3.4893				

(R-Sq = 74.69% R-Sq(adj) = 70.76%)

² Based on 2 mg homogeneous samples

(b) Weight / mean surface area					
Source	DF	SS	MS	F ratio	<i>p</i> -value
Mean Weights/Mean Surface	6	0.000763	0 0000127	23.16	0.000
Error	39	0.0000703	0.00000127	23.10	0.000
Total	45	0.0000977			

(R-Sq = 78.09% R-Sq(adj) = 74.72%)

(c) (C con	tent 2	

Source	DF	SS	MS	<i>F</i> ratio	<i>p</i> -value
C content	9	3.7801	0.4200	40.16	0.000
Error	58	0.6066	0.0105		
Total	67	4.3867			

(R-Sq = 86.17% R-Sq(adj) = 84.03%)

² Based on 2mg homogeneous samples

(d) N content²

Source	DF	SS	MS	F ratio	<i>p</i> -value
N content	9	0.0002677	0.0000297	1.99	0.056
Error	58	0.0008650	0.0000149		
Total	67	0.0011327			

(R-Sq = 23.63% R-Sq(adj) = 11.78%)

² Based on 2 mg homogeneous samples

Table 23 a-e (cont.)										
(e) C:N ²										
Source	DF	SS	MS	F ratio	<i>p</i> -value					
C:N	9	9436.2	1048.5	24.81	0.000					
Error	58	2450.9	42.3							
Total	67	11887.1								

Table 22 a. a. (aant)

(R-Sq = 79.38% R-Sq(adj) = 76.18%)

² Based on 2 mg homogeneous samples

¹ Using Tukey's 95% Simultaneous Confidence Intervals

The Tukey's HSD tests (Table 24) for weight and weight/mean surface area indicated significant differences between non-contiguous types, with the exception of forest-floor particulates, but comparable relationships between mound-associated needles and thatch to forest-floor needles. C content of mounded materials indicated a significant decrease for particulates, but a non-significant decrease relative to the forest-floor counterpart (Table 24). Carbon content of the forest-floor particulates was slightly greater than particulates found within mounds (Table 24 a-b). C:N ratios of mound types denoted a significant difference between needle, thatched-needles types, and particulates while the forest floor C:N ratios indicated a significant difference between needles from < 1 cm and ~ 8 cm and particulates to needles from both senesced and < 1 cm (Table 24 a-b).

A cross-comparison of C:N ratios between mound-associated materials and that of the forest floor largely indicated similar groupings among respective needle, thatch, and particulate types with the exception of forest-floor needles from ~ 8 cm which shared a non-significant grouping with both needles from > 8 cm and forest-floor particulates (Table 21 a-b). The overall results of the 100needles analysis clearly demonstrated a buffering effect of mounding on decomposition of thatched needles and a significant decrease in weight and C content of particulates compared to intact needles.

Table 24 a-b Tukey's HSD tests of mound-associated needles and thatch, forest floor litter, including particulates

(a) Results - Detail

Mound associated needles and thatch ¹							Forest Floor needles (without mounds) ²			
Location	Senesced on forest floor	Surface < 1 cm	Inside ~ 8 cm	Inside > 8 cm	Particulates ~ 8 cm	Particulates > 8 cm	Senesced	< 1 cm	~ 8 cm	Particulates ~ 8 cm
Weight										
Mean	.7992	.6539	.5722	.5370	.3200	.2500	.9111	.6569	.4769	.2500
Std Dev	.0904	.0504	.0542	.0762	.1687	.2121	.0279	.0078	.0341	.2121
Mean Weights / Mean Surface Area										
Mean	.008670	.007244	.006056	.005891	_3	-	.010154	.007244	.005180	-
Std Dev	.000928	.000898	.000384	.00681	-	-	.000648	.000648	.000211	-
C Content ⁴										
Mean	.9948	.9891	.9422	.9091	.4259	.4715	1.0252	.9835	.9096	.6405
Std Dev	.0316	.0463	.0451	.0339	.1574	.1704	.0058	.0698	.0038	.2457
N Content ⁴										
Mean	.022385	.018135	.021249	.019960	.018117	.018483	.018504	.015390	.022209	.024919
Std Dev	.002279	.001739	.002982	.002696	.004859	.006120	.000428	.001529	.002202	.009419
C:N ⁴										
Mean	45.970	52.425	46.253	46.593	23.703	25.634	55.421	63.994	41.148	25.675
Std Dev	7.149	5.799	8.100	6.359	6.632	5.933	1.597	1.821	3.907	.156

 1 N = 10 for each mound location

 2 N = 2 for each forest floor location

³No available data

⁴ Based on 2 mg homogeneous samples for each location

((b)	Results ·	- Summarv
	,	results	Guinnary

	1											
	Mound associated needles and thatch $^{\scriptscriptstyle \perp}$							Forest Floor needles (without mounds) ²				
Location	Senesced on forest floor	Surface < 1 cm	Inside ~ 8 cm	Inside > 8 cm	Particulates ~ 8 cm	Particulates > 8 cm	Senesced	< 1 cm	~ 8 cm	Particulates ~ 8 cm		
Mean Weights	а	ab	b	bc	d	d	а	ab	bcd	cd		
Mean Weights / Mean Surface Area	ab	с	d	d	_3	-	а	bcd	d	-		
C Content ⁴	а	а	а	а	С	с	а	а	ab	bc		
N Content ⁴	5	•	•	•				•	•			
C:N ⁴	b	ab	b	b	d	cd	ab	а	bc	cd		

 $r_{\rm N}$ r_{\rm

⁵ No significant difference

4 Discussion

An illusory veil distinguishing one from other. A perceived thread separating connecting intertwining the you, and the I, from the world. Questions agitating "the mix". Chaos? Knowledge? A Momentary truth? Glimmering; forgotten.

Collected, transported, then stacked, needle litter defined as thatch, when assimilated into *Formica* mounds; the mound structure becomes a physical metaphor for the conceptual framework of decomposition within the interior Douglas-fir forest. The defining measurable abiotic factors of decomposition are: temperature, moisture, CO₂ evolution, and mass loss; elegantly framing the underlying biotic influences of the *Formica* spp. The adaptive physiological and behavioral responses to environmental stresses establish a unique ecology, idiosyncratically expressed by the interaction. The concept of tangled nature evolution between organism and environment demonstrates a profound seamlessness of in-situ adaptations whereby *Formica* spp. within this specific environmental context champion ^{26,104}. The seamless thread between the biota and abiotic influences are demarcated by adaptive-responses, which are defined by the random interactions of set environmental factors, together, fueling the evolutionary process.

The innate plasticity of *Formica* spp. has endured prior to the Pleistocene epoch ⁸⁷ evinced by physiological and behavioral adaptations to cold temperatures through mechanisms such as cold hardiness, fluid evacuation enabling freeze resistance and tolerance ³⁷; mound construction, and huddling ⁸⁷. Adaptations to primary abiotic stresses emerge as successful responses to environmental cues, ensuring their survivability. The *Formica* mound serves as a "dwelling"; insulating, protecting, and ensuring early brood development, giving an ecological foothold over other ant and invertebrate species. From an ecosystem perspective, the thatch contained within active mounds is buffered from further decomposition as it has limited exposure to moisture. The seminal, collective, inner-workings of the small directly affecting the larger whole are another example demonstrating the profound interconnectivity of natural evolving systems.

4.1 Temperature & Moisture

The interior Douglas-fir forest is a patchy mosaic of temporally mixed-open stands also containing Ponderosa Pine, Cottonwood, and Quaking aspen with intermittent expanses of grassland ^{174,210,211}, (Conversation with S Simard; Vancouver (BC); unreferenced). The unique mosaic quality of the interior Douglas-fir forest is also contingent upon seasonal abiotic variability of temperature and precipitation. Temperatures range from sub-zero to 40 °C that, when coupled with low levels of annual rainfall and snow accumulation (Tables 1, 2), not only support this forest type, but are the baseline attributes governing the system. The obvious seasonal extremes obscure the subtle and the often unpredictable abiotic variability of spring and fall. Within those transitional seasons, the known singularities of summer and winter become frayed when a warm fall day unexpectedly erodes into inhospitable coldness, or conversely, when winter's crispness is broken by unseasonable periods of warmth. The forest floor also reflects this notion of a patchy mosaic: structurally, by the accumulation of litter, CWD, and the mounded thatch of *Formica* spp.; temporally, by the various stages of decomposition of these materials.

4.2 Temperature

The behavioral adaptation of *Formica* spp. as evinced through mound construction of vertical and diagonal stacked senesced needles extends above the forest floor, buffering decomposition while insulating the inner brooding chambers of northern *Formica* spp. The temperature variation from the outer thatch layers to ambient air temperatures is similar in summer and in late-fall-winter during the seasonal temperature extremes, but in spring, as moderate temperatures tend to gradually increase, a gradated pattern emerges within the mounded materials, demonstrating a temperature variance based on depth within the mound (Figs. 48, 49, May 2010).

Despite the increased temperatures and daylight hours of spring, snowmelt is delayed and protracted at higher elevations and in mid-elevation glacial carved valleys due to colder and more variable temperatures. At these mounds in late April through May, the Formica colonies emerge slowly whereby external activity is not always visible. The thatch and below-mound soil undergo a temperature differential between AM and PM hours. The crust at ~ 8 °C and the interior thatch and below-mound soil ~ 3 °C where the interior thatch demonstrates a greater differential compared with the below-mound soil, thus providing insulation to the inner brooding chambers and buffering the interior litter.

May through October is the generalized active period for *Formica* spp. which includes tasks of: brood tending, litter collection, hunting, and scavenging that often overshadow and remotely linked to thatch decomposition. Throughout the summer, forest-floor litter is incorporated as thatch into the mound structure. Moreover, the larger colonies will construct secondary mounds and "low-rise" bivouacs

which extend the physical boundaries and the conceptual notion of monodomy and polydomy by providing workers and foragers with yet another physical extension to larger established-primary mounds. The senesced golden-brown litter is then threaded into the mound structure. In summer through late fall the temperatures of the crust and interior thatch are comparable to ambient air temperatures due to the highly aerated nature of the mound structure. As fall temperatures decrease towards freezing, less thatch is collected as *Formica* spp. activity is greatly diminished and they retreat and amass within the inner chambers, while the stragglers remain in the crust and interior thatch layers in a state of cold coma until the spring thaw.

Much of the literature regarding temperature of red wood ant mounds ^{6,19,43,44,63,68,140,165,196,204} generalize that mound temperatures are higher than ambient temperatures, based on: thatch insulative properties, location under partial overstorey coverage, and the prevailing slope aspect ¹⁹⁴. This generalization may hold true within other forest types during Formica spp. active periods, but it does not completely hold true within the Douglas-fir forest on Swakum Mountain. For example in July 2009 the mean ambient temperatures and the above ground thatch materials fell within a narrow range between ~ 25 °C and ~ 29 °C book-ended by ambient soil and ambient air where the belowmound soil was 1 degree below the range. November 2009 mean ambient temperatures were similar to mounded material mean temperatures with all ambient and material types falling within a 2-degree range. In May 2010 ambient mean temperatures were higher than that in all mounded material types. The larger Formica spp. mounds were more than 2 meters in stature and comprised of vertical and diagonal stacked needles promoting aeration. The biogenic structure gualitatively falls between the two ambient temperature types of air and soil; as thatch is neither air or fully developed soil organic matter or soil but litter of a particular age that possesses a unique thermal property that lies somewhere between the ambient field temperatures. Other studies have only narrowly considered temperatures during Formica spp. active periods which clearly demonstrated temperature differentials based on mound type and position within the mound ^{63,68,194}, but the overall comparison was to the surrounding forest floor or soil horizons.

When evaluating AM and PM temperatures for May, a similar pattern in the AM becomes more distinct at a higher temperature differential during the PM. Setting aside the obvious hot and cold extremes of July and November, the emergent pattern in May shows a 3-tiered distinction where the external crust showed the greatest differential while the deeper layers of interior thatch and below mound soil showed lesser degrees of differentiation (Figs. 49, 50).

For future consideration I would recommend additional testing days with earlier am, midday, and later PM readings throughout the month and over a 3-year period. Regardless, with the exception of July 2009, the mean temperatures of ambient and mounded materials were within close proximity of the seven-year average for that month, whereby July 2009 was closer to the maximum average value. A final consideration would be to include temperatures of inner brooding chambers using a non-invasive

approach as to develop a more replete survey for mounds during selected months to then eventually link the findings annually.

4.3 Moisture

Interior Douglas-fir forests are moisture-limited systems, receiving a large portion of annual moisture from snowmelt (Table 1). Largely, my data supports previous findings of thatch tending to be drier than the surrounding forest floor; however, these findings do not support a drier tendency for the remaining material types compared to their respective forest-floor complements. Mound wood tends to be drier in November and below-mound soil in May (Fig. 51). The buffering effect is most distinct in November (Fig. 51) as the exposed crust and mound wood hold similar amounts of moisture, furthermore the exposed woody cores absorb and retain more moisture and dry at a slower rate than thatch.

As expected, July had low mean moisture levels ranging from 2-8% (Fig. 52); with the mounded materials holding slightly higher levels of moisture than their respective forest-floor types. Furthermore, crust and mound wood contained a broad range of moisture (4-18%) (Fig. 51) indicating: mound and material type variability; and differential losses which on a localized scale supports the endemic variability of the interior Douglas-fir forest. When collecting the materials that July, there were periodic thunder showers dampening the exposed mounded wood and crust which contributed to the moisture range of exposed mounded materials. Despite the prevailing arid summer conditions, there was an unexpected wider range among the assorted material types.

The November results reveal an increase of moisture content greater than 100% for forest floor litter and wood compared to July (Fig. 52). The moisture retention of late fall-winter as indicated by November becomes a crucial "sink" for the biota as the interior Douglas-fir forest becomes increasingly drier throughout the late spring and summer. As mentioned earlier, the moisture content of the mounded materials form a distinct 3-tiered pattern aka "buffering effect" (Fig. 51, Nov 2009). The range of moisture content for crust is very narrow (Fig. 51) showing a consistency among the various mounds, while the mound wood had a wider range of moisture levels. During the November collection there was a physically evident discontinuity among samples. At certain mounds the upper portions of the stump-core were exposed while at others the stumps were completely interred by thatch, indicating a discontinuity among individual and differing samples alike. Another concern was destructive sampling of the stump, which if rendered, would have left the colony vulnerable. To minimize damage I only selected the most exposed and surficial portions of the stump.

In May, the lingering presence of snow at higher elevations and valleys indicated slower melting when compared to mounds at lower elevations and mounds with greater sun exposure; in turn, affecting moisture content of the various forest floor and mounded materials. Both the forest-floor litter and soil

showed the highest level of moisture among the sampling groups while the mean moisture content of the mound materials ranged between 14% and 22%. Interestingly, the crust showed the lowest amount of moisture at 14% indicating rapid drying from the November moisture level at ~ 55 % (Fig. 52). Interior thatch absorbed moisture from the crust and dried more slowly where in November the moisture content was at ~ 30% and ~ 22% by May (Fig. 52). The "sealing in" of absorbed moisture by the crust layer is crucial to emerging broods as water has a high intrinsic heat capacity. Another unforeseen result was in the below-mound soil from November and May when the moisture content was approximately the same at ~ 18%, indicating equal amount absorption and loss between the two months and perhaps throughout that 6-month period. The mean moisture content for mound wood was the highest among the mounded types at ~ 25% and similar to the interior thatch. Despite the wide range of moisture in the mounded wood samples (as explained above), the mean moisture content of mound wood was very similar to that of the forest floor, indicating similarities in exposed woody cores in Type 1 mounds to that of the forest-floor wood.

For future consideration and improvement with my sampling technique I would not coalesce forest floor materials into a single composite sample as it is statistically is untestable; despite the error, the composite samples provide an accurate physical and temporal representation of forest floor. Another bias in my sampling methods was collecting the mound wood from Type 1 mounds, as previously mentioned. Lastly, a more rigorous sample collection with several readings at various locations and levels within the mound and the surrounding area, monthly during the course of a year, would provide an annual depiction of moisture content of mounded and forest floor materials.

The mound structure itself provides a natural-organic shape that promotes water run-off with internal constructed chambers and macro-pores promoting percolation and ventilation of the structure ^{6,17,68,74,163,248.} The placement of mounds under partial overstorey coverage and on southern-faced slopes 194,195 promotes protection and insolation which abets in moisture regulation 63. The use of decayed CWD and needle litter that possess intrinsic absorptive properties for both moisture and sunlight, permit rapid drying and malleable usage of materials that prove beneficial to colony longevity.

4.4 Temperature and Moisture in Forest floor Litter and Formica spp. Mounds

Decomposition is the complex interaction of several factors where temperature and moisture provide a fundamental relation within the process. Deconstructing this relationship within the ecological context of the interior Douglas-fir forest floor, notwithstanding *Formica* spp. mounding activities, reveals a unique seasonal interplay between these abiotic factors. A simplified overview within the prevailing framework of low annual levels of precipitation is largely defined by: hot-dry summers and cold-damp winters. A narrow window for potential increased rates of decomposition occurs in late summer-fall and spring-early summer (Fig. 63).



Figure 63 Temperature - Precipitation and Formica spp. Activity

- Orange and Blue lines represent mean monthly temperature (°C) and total precipitation (mm) for the period 2005-2013.
- The vertical highlighted areas are periods of potential increased decomposition rates indicated by heightened CO₂ levels ^{185,253}
- The horizontal red bars indicate levels of Formica spp. activity:
 - The bottom line represents a "huddled" inactive estivated state
 - The middle line represents periods of low intermittent medium activity levels within mounds with periods of visible external activity
 - The top line represents the high active period with visible external and internal mound activity ⁴⁶

September demarcates an end to the dry summer and beginning of a period of increased precipitation and increasingly cooler temperatures. In xeric conditions (< 20%), decomposition is uninhibited at temperatures above 10 °C which most likely occurs during late morning - afternoon. In late April through June, moisture from snowmelt and precipitation coupled with longer daylight hours sustaining increasingly warmer temperatures also supports favorable conditions for decomposition. Temperature cannot be considered singularly as decomposition also requires ~ 30% moisture ^{185,253}, which is a limiting factor within the interior Douglas-fir forest. Annual mean precipitation is ~ 273 mm (Table 1), most of which falls between October and January, with a minor secondary pulse from April to early June (Fig. 63). Consideration should not only be given to the amount of precipitation from any single storm event but the amount accrued over the two periods of October-January and April-June. Likewise, cold temperatures support surface and sub-surface formation and ice packs thus preventing

evaporation and promoting moisture retention within the arid landscape. Despite the prevailing seasonal trends there are uncharacteristic gaps such as: the aforementioned summer thundershowers or pockets of warm temperatures during winter stimulating microbial activity and promoting early seasonal melt.

Senesced needle litter and decomposed CWD are highly absorptive materials which further contribute to the spatial and temporal heterogeneity of the interior Douglas-fir forest. Senesced litter potentially holds more than 100% moisture while CWD holds more than 300% moisture (personal experimentation). As supported by the data in Figure 51, the retention of moisture by these forest floor materials, or more pointedly, the non-solar exposed layers and regions of these materials provide ephemeral moisture "sinks", extending durations of increased moisture levels which are beneficial to emerging plants (personal observations) and microbes ^{86,115,221,244}. The needle litter of the interior Douglas-fir forests accumulates to a signature maximum depth of ~ 8 cm under stands and single old-growth interior Douglas-firs while intermittent Islands of accumulated CWD further provide potential "moisture pockets" of varied gradients which provide water sources vital within this moisture-limited forest system.

Natural mounding of forest floor litter is apparent (Figs. 11, 36, 37); diversely sourced, low-lying, indeterminately shaped and distributed. The compacted crust encases a non-aerated sub-stratum, distinguishing the abiotic-derived mound formation from a biogenic constructed *Formica* mound ²⁰⁴ (Figs. 35, 39). The primary *Formica* mounds are: highly-defined, carefully constructed with select needle litter that is stacked and interwoven; the thatch has an aerated quality, while the overriding form and materials lack an inherent randomness compared to that of a "natural" mounded litter accumulation.

The sheltered thatch contained within the defined *Formica* mounds promotes run-off, insolation, aeration and drainage due to diagonal stacking ^{74,94}. The overall construction acts as a moisture buffer, limiting ambient exposure and surface area contact with soil organisms, which is unlike the diffuse, random, non-sorted accumulated scattering of forest floor litter. Additionally, the selected needles are largely devoid of labile photosynthates which further limits microbial attack based on source availability and type.

The presence of saprotrophic fungi was duly noted and specimens collected during the two periods of increased decomposition (Fig. 63) which provides supportive evidence of the main group of decomposers. *Formica* spp. mounds are not immune to saprotrophs. Sporocarps (LBMs) and mycelium were found throughout the crust layer while evidence of white and brown rot within the woody core; likewise fungal evidence was also found at the mound areas on the surrounding forest floor litter and CWD. In an informal Substrate Induced Respiration (SIR) experiment, I also found evidence of increased respiration on mound wood at 23 °C at sustained and increased moisture

levels with added chitin at 90 days incubation time, indicating presence of slow-growing microbes under more ideal conditions. As moisture and litter quality are the prevailing factors limiting decomposition within the interior Douglas-fir forest ^{185,253} likewise, the absence of activity of a broad and diverse-ranged microbial consortium within *Formica* mounds; mound size and shape, coupled to brief periods of increased moisture; all contributing factors inhibiting litter decay.

Low moisture, seasonal cold temperatures, qualitatively poor litter, and microbial constraints coupled to *Formica* spp. mounding inhibit litter decomposition in the interior Douglas-fir forests. Singularly, these factors stand alone, but it is the adaptive interplay between organism and environment that weaves an ecological fabric underpinning this process. When integrating *Formica* spp. adaptive behavioral and physiological responses into the decomposition process, the parameters regarding moisture and temperature further reduce decomposition.

Formica spp. adaptivity allows a seamless fit into their environment providing strong support to tangled nature evolution ^{26,104}. Formica spp. morphological, physiological and behavioral adaptive plasticity not only challenge the notion of speciation as a "fixed" trajectory, but their mutability challenges the concept that adaptation works in an either/or scenario, i.e., a generalist or specialist. A few noteworthy examples of morphological, physiological, and behavioral plasticity include: workers in developed colonies that vary physically and have various sized mandibles; rectal palpae and coldadaptation mechanisms governing water retention and evacuation essential in semi-arid and cold environments; within a single-defined species there is a "range" of polygyny and polydomy which in part is based upon proximity within northern ranges (which also applies to brooding capacity and dvnamics) ^{37,41,87,118}. Adaptively, *Formica* spp. inhabit a wide northern and southern geographical range and depending on location, will be specifically adapted to cold or hot temperature extremes with a general overall adaptation to desiccation ^{37,41,87}. Under this same either/or adaptation scenario, this concept could be further challenged, as when F. integroides are isolated with limited resources they construct a singular nest and employ a flighted nuptial dispersal. With abundant resources they construct multiple nests, terrestrially inhabiting the same nest, or possibly establishing another nest in close proximity. A more comprehensive perspective would embrace the potential range of specialization of certain traits while book-ending the extremes within a species or group.

Larger colonies within northern ranges have higher rates of survival than smaller colonies of similar species118. Kipyatkov's research based upon brood adaptations and behaviors falls under the catchment of brood-rearing capacity. If during an annual cycle a colony has a rapidly developing summer brood and slowly developing hibernal brood or several early and rapidly developing broods, there will be a higher probability of survival, leading to increased population of workers which in turn supports colony survival. When connecting brood-rearing capacities to the concept of several closely-related queens, a "multi-temporal brooding sequence" emerges. The addition of more workers coupled to increased longevity theoretically extends a colony's livelihood, capacity, and duration. The

importance of maintaining a vital and morphologically diverse worker populace is intrinsic to a colony's survival. As the task-driven engine of a colony, the extension of the lives of the workers will have a profound effect on colony size, decreasing energy expenditure on population maintenance, in effect ensuring greater numbers. Through my observations, each large mound seemed intrinsically linked to other nearby large mounds while the entire study area was part of a localized "super colony". Localized meaning: each of the major mounds was geographically isolated and as separate colony size increases (indicated by polydomy), the chance of any singular disturbance to any one mound causing disbandment or collapse, does not detrimentally threaten the "super-colony".

How does growth and a sustainable *Formica* worker population connect to litter decomposition? Through the "hard-wired" dogged behavior of litter collection.

The task of workers is entrenched in: maintenance, defense, collection, growth, assemblage, and manipulation of thatch. Collected litter that is stacked and interwoven into thatch (Fig. 17) has given *Formica* spp. an eco-behavioral adaptation capitalizing on available materials that insulate and protect them over winter. Spring venting (Figs. 19, 20), through thatch manipulation, allows for excess moisture release by sun exposure, and corporeal heat absorption of workers within the conical depression i.e. "protective sunning", are pieces of physical evidence of adaptations linked to successfully brood-rearing. The large mounds within a "super colony" (See Appendix D) equate to increased proportions of litter as thatch that is protected, tended to, maintained and manipulated, to ensure survivability. The "buffering effect" is an artifact of survival behavior which secondarily affects litter decomposition by maintaining lower moisture levels in an already moisture-limited context. The defining thread of adaptive responses by organisms within their environment is a dynamic, non-static interplay producing a unique permutation that through time becomes an endemic characteristic of that system.

4.5 CO₂ Evolution of Forest Floor and Mounded Materials

Respired CO_2 is a biotic residual produced by living organisms, intimating life stage, activity level, food sources, and environmental stresses. Biogenically-constructed dwellings that are both part of an environment, yet self-contained by their inherent properties, pose an array of questions, whereby *Formica* mounds are a prime example. The impressive body of work on litter decomposition and respiration of *Formica* mounds by Ohashi et al. ^{43,44,54,109,114-116,165-168} until now, has only considered the whole package while not teasing apart *Formica* respiration from that of their habitation as combined CO_2 levels of nest litter and *Formica* respiration are seemingly non-significant. This approach has also been appropriated by others authors such as Sousa and her work on tropical ant species ²¹⁷. Deconstructing potential CO_2 evolution by defining the separate components in a non-hierarchical domain provides definition to each component while considering the inter-connectivity of the whole. Dreyer's 1932 paper on *Formica* respiration ⁴⁶ provides an explicit description of the

effects of temperature on respiration. The information when extrapolated is significant in teasing apart the contribution of *Formica* respiration from that of thatch, which provides a stepping-stone for examining the subtle interplay between these components.

The interior Douglas-fir forest is moisture-limited with two potentially broad, annual periods (Fig. 63) of increased decomposition. The insulative and aerated quality of thatch when collectively assembled into a mound structure promotes run-off and infiltration while buffering the interred thatch. Colony survivability is directly linked to adaptability, source material availability, recuperation from disturbances, and high population numbers within northern climates. *Formica* spp. not only construct and maintain the structural integrity of the mound but select senesced needle litter, that upon eventual abandonment, later contributes to humic and soil organic matter formation. The visual evidence of mycorrhizae and saproptrophs within the forest floor and *Formica* mounds at Swakum Mountain provides support to a fungal-based food web driving decomposition within the interior Douglas-fir forest. In a study by David Wardle et al. 2011 on red wood ant exclusion, their research further supports this notion whereby in year 6 of the study, sites without *Formica* spp. promoted a bacterial-based food web in the larger context of a fungal-based food web within a forested system ²⁴⁴. As moisture is the main driving force within this northern forest type, the microbial consortium contains a range of r-K selected species such as; rapidly growing LBMs to slow-latent saprotrophs within decayed wood.

The interior Douglas-fir forest floor is a template for litter decomposition where moisture is a fundamental driver in the process. The temporal pathway of C, as forest litter, begins as an evolved solid form acted upon by extraneous forces; eventually decomposing into a preservable thread of C. Senesced needle litter is the first stage of decomposition whereas in advanced decay stages microbes utilize the remaining C skeleton and further transform the C into CO₂. Abiotically derived mounds and *Formica* mounds alike develop a crust approximately 8 cm deep, where the crust "buffers" the interred thatch from moisture and temperature, thereby inhibiting decomposition.

Overall, the November 2009 samples yielded the highest levels of potential evolved CO_2 for the three testing periods; with forest-floor litter producing the greatest, followed by: crust, interior thatch, woody materials, then by the soil types (Fig. 53). Within the context of the interior Douglas-fir forest from May through June, CO_2 levels are likely to reach their annual maximum in level and duration as moisture and temperature conditions are conducive for decomposition. By mid to late June, as temperature increases and moisture content decreases, evolved CO_2 drops to minimal levels by July as materials are in their driest state. In summer, precipitation from seasonal periodic thunder-showers stimulates microbial activity thus producing intermittent fluxes of CO_2 (i.e. "the birch effect") ⁷². Incidentally, the Formica high-active period coincides at this time indicated by needle collection, mound building, aphid tending, and brood-rearing activities (Fig. 63). This is followed by a brief window of heightened CO_2 evolution in September, providing there is sufficient moisture. As temperatures continue to

decrease to freezing in October to November, which also has the highest precipitation, CO₂ evolution and decomposition are minimal, as is Formica activity (Fig. 63).

The low levels of evolved CO₂ in soil samples for all sampling periods indicate low microbial activity; where decayed litter/thatch and both wood types have higher levels of evolved CO₂ further supporting a strong saprotrophic presence in these material types. The accumulation of needle litter and CWD in the interior Douglas-fir forest floor forms low-rising irregular shaped mounds which contrasts with the distinct *Formica* mounds; both harboring saprotrophs, while creating a patchy mosaic landscape. The forest-floor landscape possesses intermittent and isolated mounds that are tenuously linked by corridors of accumulated litter. When associated to MacArthur's classic ecological theories on dispersal, the mounds act as microbial sources and the corridors as pathways for growth interconnecting the forest-floor microbial community. *Formica* translocation of senesced litter ^{156,180} (personal observations) while *Formica* mounds are potential saprotrophic sinks contributing to interior Douglas-fir forest floor ecology and physically by increasing spatial heterogeneity ^{43,115,195,250}. The decaying litter has a unique signature based on its type, quality, senesced state, and CO₂ evolution. The decayed materials restrict microbial r-selected opportunists, leaving staid saprotrophic K-selected organisms to dominate and access these materials as their prime sources.

The drop or leveling-off pattern in ex-situ evolved CO_2 in May 2010 compared to November 2009 (Figs. 53, 54) indicated by: forest floor needle litter, wood, soil, and crust thatch; "leveling-off" by: interior thatch, mounded wood, and mounded soil types; with the exception of sifted forest floor soil as it increased in May. As CO_2 levels are intimately linked to moisture content within the context of the interior Douglas-fir forest, there is a noticeable similarity in these two patterns types as demonstrated by Figures 52, 54. Exposed forest floor materials tend to dry and lose moisture more readily than interred mounded materials that are buffered from direct insolation and aeolian effects. The crust shields the interior thatch; the exposed decayed mound wood innately retains moisture and is also protected and insulated by the thatch; while the entire structure shields the below-mound soil from moisture. With reference to *Formica* brood behaviors, as the crust dries it seals in the absorbed moisture of the interred thatch and mound wood which becomes crucial for heat retention for emerging broods ^{87,204}.

The results of the July 2009 moistening experiment (Fig. 56), notwithstanding the obvious increase of CO₂, adds further support that moisture is the main abiotic driver while also demonstrating that *Formica* mounds "buffer" interred materials (See Appendix D Table 65) further inhibiting decomposition.

Likewise, litter and thatch materials evolved similar mean levels of CO₂; while crust and the emergent sprouted thatch group produced the highest evolved CO₂ levels in the July 2009 moistening

experiment (Fig. 56). The sprouted thatch group unexpectedly developed under the increased moisture regime from various thatch types due to ideal conditions and the dispersal of peripheral seeds and/or myrmecochory (dispersal of seeds by ants⁸⁷). The high mean generated CO₂ and wide variation in CO₂ evolution of the crust indicates a microbial patchiness harbored within the material. Although the crust is temporally diverse, holding the largest proportion of newly imported goldenbrown litter, this alone does not explain heightened CO₂ levels. Associating the intermittent pockets of hyphae (Fig 21) enduring the prevailing dry conditions when coupled to brief periods of moisture, accounts for a "sit and wait" strategy for microbes which provides an explanation for the disparate evolved CO₂ levels. The mound wood, to a lesser degree, also showed a broad range and a higher mean for potential evolved CO₂. When associated with prior documentation (Figs. 12-14, SIR (Substrate Induced Respiration) informal experiment, personal field observations) there is a strong body of evidence that mounds harbor saprotrophs such as white and brown rot fungi, which employ a "sit and wait" strategy until conditions become more ideal. The significance of evolved CO₂ from mound materials is not myopically based on inflated CO₂ levels alone but the interactions of materials and organisms within the mounds driving the process.

4.6 100 Needles: Mass loss Decomposition Sequence

The life span of a Douglas-fir needle is delineated from an emerging bud where mass gradually accrues, to senescence where it is lost, but traceable by a C thread. The biotic pathway of C from CO₂ to organic matter provides a physical continuum where the self-assemblage of C backbones in organic matter is elemental. Photosynthates range from simple linear structures as labile C sources to large complex cellulose-lignin based frameworks that are essential for tree growth, maintenance and support. As senesced litterfall structurally unravels and decomposes, indicated by mass loss, it releases and extends utilizable remnant C to the forest floor and soil communities.

The 100-needle experiment employs the litter-bag method concept, without the use of litter bags, to support the notion that *Formica* mounds inhibit litter decay within the interior Douglas-fir forests. What does the mass loss of forest floor needles and mounded thatch describe? From a reductionist viewpoint, it describes the weight differentials between the varying depths of needle litter and thatch (Figs. 61, 62). From a holistic ecological stance, which includes the reductionist perspective, it describes the underlying abiotic and biotic interactions driving the weight differences over time. The measure of mass loss at various depths is a comprehensive temporal representation that provides numerical depiction of these interactions.

A larger ecological context of *Formica* inhabitation within the interior Douglas-fir forest begins when incipient colonies within their northern ranges are ensconced in a seemingly infinite resource base (e.g., needles; CWD; predated invertebrates and aphid mutualisms providing protein and carbohydrate sources). The larger ecological context also includes *Formica* spp. aggressive and

eusocial behaviors, innate plasticity, and adaptability framed within a low-disturbance regime. Considering this entire context, the concept of tangled nature evolution is played out ^{26,104} as the environment impresses constrictions upon newly emigrated species inciting inherent, adaptive responses for survival. Furthermore, when considering expanses of time, the once disjointed conglomeration of emigrants, now an integrated community shape and condition their environment, skewing the boundary of organism and environment. *Formica* spp. within the tangled context are a keystone species ^{8,36,94} that provide a self-contained, exemplary representation of this concept. Throughout the first three years, a newly forming isolate colony is vulnerable until a foothold is established. For the next 5-15 years, predicated by environmental limitations, the colony undergoes an intermediate growth phase until a self-maintaining populace is attained ^{2,87}.

During the early and intermediate phases, establishment of the mound's inner-core and protective thatch structure is critical for mound growth, contiguous with population ^{8,114,165,197,215,216}. If resources continue to be abundant and eusocial behaviors of polygyny and polydomy are engaged, the next phase of mound budding and "super colony" status emerges, where needle collection is seminal.

The collection of needles as it relates to mound size, growth, and location, provides an approximate time line for senesced thatch. Yellow-green needle-fall approximately 3-5 years, begins to decompose as photosynthates are respired or absorbed by early microbial colonizers. In 4-6 months, the needles change in coloration to golden-brown and are selectively incorporated into mounds (Figs. 43-48). The crust layer at < 1 cm is approximately 5-7 years and is an amalgamation (Fig. 43) of fresh thatch with the previous season's collection denoted by the dark spots of early-stage melanization. The forest-floor litter and mounds at depths of ~ 8 cm and thatch > 8 cm (~ 8-10 years and > 10 years respectively), are fully melanized, becoming increasingly uniform dark brown (Figs. 45-47). The projected timeline may be compressed or extended depending on factors affecting needle collection: material availability, number of queens affecting worker populations within a single mound, and large disturbance events. As fresh litter and top layers of thatch are colonized by microbes, a continuum of additional litter-fall or incorporated needles as thatch supersedes the earlier top layers, increasing the depths of the Douglas-fir forest floor to ~ 8 cm and mounds to 8 cm and greater. The categorical shift of decayed to senesced in *Formica* mounds occurs at ~ 8 cm where thatch is predominately buffered from moisture creating suboptimal levels limiting further microbial degradation.

What the simple analysis and figures reveal (Table 20 a-b, Figs. 57, 58) is a general pattern of weight and C loss across all groupings. Once needles are incorporated into the mound thatch a diminishing pattern emerges where contiguous groupings are not significantly different, but alternating groups are. Forest floor litter mass loss is significantly different than mound surface crust thatch while the crust thatch is significantly different than deeper interred thatch. A tapering and levelling-off of weight occurs at ~ 8 cm where weights at 8 cm or greater are not significantly different. This levelling-off of weights indicates a buffering of thatch contained within mounds that suspends mass loss. The C content of forest floor litter and thatch also reflects a similar diminishing pattern throughout (Tables 20, 22, and 24 a-b).

The C content of the golden-brown forest floor needles and the mounded < 1 cm thatch, although not showing significant differences, is greater; the < 1 cm thatch is largely comprised of golden-brown needles. N content tended to have low, similar values across all groups. The forest floor needles were the highest in N content, with the < 1 cm having the least and showing significantly lower values when compared to its contiguous groupings. This is likely due to the general low quality of Douglas-fir needles as the organic matter and soil in these forest types tend to be N deficient ^{3,174,245}.

As decaying needle litter and senesced thatch decomposes and structurally collapses, particulates form, adhere to, and encase the surrounding needles and thatch. Microscopically, the particulates are comprised of wood shreds and fibers, mycelium, and soil. The continual stresses of wetting and drying; UV and microbial degradation; Formica manipulation; and the inherent delicacy of the material itself, over time, collectively contribute to particulate formation with the surficial layers being the most susceptible. Individually, the particulates are seemingly inconsequential, but when examining the forest floor and mounded materials, needles, and thatch found at ~ 8 cm and greater, they had considerable amounts of adhered particulates encasing their structures. After particulate removal, the forest-floor litter at 8 cm and interior thatch at 8 cm and greater was lighter in weight than forest-floor litter and crust thatch, but the total mass of needles and adhered particulates remained nearly constant across locations. Adhered particulates not only increase the weights of interred litter and thatch, but also inhibit direct contact of microbes and hyphae, preventing further structural deterioration and incorporation with developed organic matter or soil organic matter. Within the context of the ANOVA analyses and Tukey's HSD results, the inclusion of particulates as separate groups substantially weights the tests by minimizing the subtle differences between locations, as their mean values are considerably lower when compared to all testing groups (Table 22 a-b). This inclusion produced two significant differences between contiguous groupings of the forest floor materials and three significant differences among contiguous groupings of mounded materials. Singularly, these tests flatly assign values perhaps lessening their qualitative import, but within the context of Formica mounds and abiotic mounded needle litter in the interior Douglas-fir forest, fragmentation and adhesion are critical intermediate steps within decomposition and senescence: filtering and impeding direct absorption into the soil matrix providing further details and possibly protracting these processes.

The comparison of forest floor litter to mounded thatch indicated a general increased rate of mass loss where initial rates diminished at < 1cm and a distinct boundary was evident between the Oh and A horizons at ~ 8 cm depth (Figs. 59, 60, 39). The study area was largely devoid of mature, developed stands of interior Douglas-firs that, when present, predominately contained *Formica* mounds. The paucity of mature trees prevented litter accumulation and abiotic mounding that defines

a developed O horizon by and large limiting the chances to record data from the forest floor (Figs. 59, 60). Based on Prescott's 2005 findings and observations from litter-bag experiments in Ponderosa Pine forests ²⁵³, my own observations, and given the xeric conditions, one would assume a slow rate of mass loss establishing a thick-crusty O horizon, providing there were no fires ^{182,253}. Rather, what was observed was a patchy forest floor mosaic with intermittent grassy sections contrasted by dry barren areas with a non-developed O horizon; rare, mature stands with an ~ 8 cm litter depth at the deepest point; and more pointedly, large imposing *Formica* mounds. *Formica* needle collection strips the forest floor of needle litter which then takes on an increasingly stark quality that coincides with active periods. As fall is characterized by shorter days and cooler temperatures, litter begins to thinly accumulate where *Formica* activities are minimal (Fig. 63). The low to mid-elevation mounds in the study area were also disturbed by clear-cutting and grazing where barren expanses of forest floor were considerable and an increase in grasses was prominent.

Compiling the forest floor with the mounded thatch data created a high variance over-shadowing the significant weight and C differences among groups. This is largely contributed by the low weight and C content of the particulates from the forest floor litter and mounded thatch (Table 24 a-b). The ANOVA analyses and Tukey's HSD test revealed in the weight/surface area category, a non-significant difference between the at 8 cm and > 8 cm groups indicating a leveling and a cessation of mass loss at 8 cm for mounded thatch. When comparing C content of mounded thatch across contingent groupings (Table 24 a), although not significant, once incorporated into the mound there was a mean mass loss of ~ 0.04 mg between groups indicating an even rate in C loss before reaching the possible 20% remaining threshold ¹⁵⁵ where C loss is further minimized or suspended due to mound buffering. Another interesting point was the common N content decrease for both mounded and forest floor groups at < 1 cm thereby increasing C:N for this layer. Associating this slight drop in N content with my observations of mycelium and LBMs, perhaps there is an intermittent, consistent loss of remaining N in thatch and litter within the 1-cm depth due to fungal uptake.

The 100-needle experiment supports the assertion that when forest-floor needles are integrated into thatch of prevailing *Formica* mounded structures, needle litter is buffered from abiotic stresses of moistening and extreme drying, establishing conditions that are sub-optimal for further microbial degradation. A diminishing trend of mass loss and C content occurs where non-contiguous groups form an alternating pattern of significant differences. A "leveling" off of and abeyance of weight and C loss occurs when needle-thatch at an approximate depth of 8 cm and greater, is sheltered within *Formica* mounds thereby suspending decomposition and then categorizing thatch as senesced. Particulates comprised of senesced litter, soil, hyphae, and wood adhere and encase thatch further limiting contact with soil mineral surfaces protracting the integration into organic matter and soil organic matter and soil aggregation.

Mass loss in Douglas-fir forest litter and thatch in Formica mounds incites a few lingering questions:

- How many years will thatch remain in a suspended, buffered state before it fully decomposes?
- Is the remaining mass and C content of thatch contained in *Formica* mounds greater than the CIDET ¹⁸⁵ findings of ~ 25% where various litter types converge?
- How long will the remaining mass of thatch remain ~ 25% before convergence and before any further mass loss? Will it collapse into a singular non-differential point? At this point, is it considered humus or developed organic matter?

5 Conclusion

Formica needle litter collection begins as a repetition of spatial patterns on the forest floor weaving a physical-temporal fabric, expressed through the transformation of individual needles stacked and threaded into thatch. As thatch is constructed and accumulated a mound emerges conceivably developing into a series of monolithic structures architecturally transforming the interior Douglas-fir forest floor into a spatially rich landscape. *Formica* mounds are the organic interaction and culmination of all of these processes that do not only pervade physically, but on ecological and landscape levels. The properties of the minute are non-transferable to the large, but ironically, are seminal to these imposing biogenic structures.

In addressing my original hypotheses, "Does the decay rate of Douglas-fir needle thatch vary to that of needles on the surrounding forest floor?" and "Does Formica mounding stimulate or inhibit needle litter decomposition?", the decay rate of Douglas-fir thatched needle litter within Formicas mounds is reduced compared to the needle litter on the surrounding forest floor as Formica mounding of needle litter inhibits decomposition. My research has demonstrated that *Formica* mounding within the interior Douglas-fir forests establishes a buffering effect over mounded thatch that, when coupled to low moisture, poor litter quality, and limited microbial activity, further inhibits decomposition, suspending mounded thatch in a senesced state. When forest floor litter is present, it tends to be found in areas without Formica spp., occurring in patchy, thin regions with a tendency of the O layer to not exceed a depth of 8 cm and with a distinct boundary between Oh and A horizons. In the presence of Formica spp., litter-thatch is found within formidably sized mounds and contains much of the needle-litter that would otherwise be accumulated and dispersed on the forest floor. Based on observations and natural experiments, a buffering effect of Formica mounds was noted for temperature in May 2010 and moisture content in July 2009 and November 2009 during seasonal moisture extremes. Likewise, when compared to the forest floor, Formica mounds shelter litter-thatch during seasonal extremes further emphasizing buffering. In my CO_2 evolution experiments, an increase in CO_2 was noted in November 2009 and during the re-moistening experiment of July 2009 indicating a moisture-limited system. Seasonal moisture and temperature increases produce higher evolved CO₂ levels, demonstrating that moisture is a major influential component driving decomposition within the interior Douglas-fir forest. The suspension of mass loss of needle litter contained within mounds at depths of 8 cm and greater further supports my assertion that Formica mounds in the interior Douglas-fir forest buffer and inhibit litter decomposition.

When examining Cotrufo's MEMS framework as the primary driver behind soil organic matter formation, further consideration and integration should be given to the underlying supportive abiotic and biotic platforms of:

· Forest floor physical, spatial, temporal dynamics and heterogeneity

- Plant community's above and below ground contributions: litter diversity and quality, CWD, and rhizosphere / mycosphere deposition
- Faunal litter degradation and manipulation, fecal deposition, microbial translocation and seeding

With this additional detailing, a more refined, comprehensive framework of interconnectivity emerges, which is vital to understanding ecological systems (Fig. 64).

As ecosystem engineers, *Formica* spp. and their biogenic structures provide an interface to the above and below ground systems acting as a precursory filter to the MEMS. By gathering needles, forest floor litter, and carving chambers into decayed CWD and mineral horizons for mound construction, *Formica* inherently demonstrate a high mixing potential contributing to humus and soil organic matter formation. When active, mounds are a sink of C, organic matter, and soil organic matter. Upon abandonment, as the structure collapses, a transfer of content and source to sink status occurs where thatch mixes into the Oh and A horizons, adding to organic matter and soil organic matter.

The interior landscape of the MEMS houses other soil ecological concepts such as priming effect and home field advantage that are intrinsic properties of the MEMS. The inner workings of ephemeral labile C utilization priming the microbial community to further degrade latent recalcitrant sources ^{23,120,121,129,201,205,224}, or "localized" species degrading litter at a ~ 7-10% increased efficiency ^{5,134,183,185,239}. Additionally, the identification of enzymes as indicators of microbial groups and abiotic stresses¹³ serves to refine and provide further detail to the MEMS framework.

Conceptually linking *Formica* mounds, behaviors, and ecology to the MEMS establishes a co-existing interconnected platform which filters, establishes limitations, and is a source for the MEMS in the context of the interior Douglas-fir forest. The *Formica* platform includes physical manipulation of forest floor materials, a community restructuring, and a qualitative imprint, which, over time, reshapes and restructures the surrounding landscape. Bernard Stadler's 2005-2006 work on aphid and *Formica* mutualisms in honey dew collection, research on mound abandonment and increased forest floor mineralization by Domisch et al. (2008), and Frouz's analyses (1997, 2005, and 2008) of increased P and N of active and abandoned mounds, all provide support to *Formica* contributions to forest floor enrichment and linkage to priming effects. Due to litter stacking and organic matter accumulation, *Formica* mounds tend to favor particular microbial groups ^{44,244}. The mound structure in the interior Douglas-fir forest not only serves as a physical deterrent which further limits moisture within thatch, but inhibits microbial activity and full community expression. The low quality of interior Douglas-fir litter, a major component of thatch, leads logically to the assertion that local microbes would be best suited to inhabit, degrade, and utilize the remaining nutrients, which links to the concept of "home field" advantage ^{183,5}.

Connecting the tangled nature model with the MEMS provides a co-evolutionary environmental community approach by incorporating a temporal trajectory to the MEMS model which considers the evolving system holistically. As connectivity increases, the system gains greater resiliency by possessing discrete channels and networks compensating for various abiotic stresses and disturbances. The innate resiliency of *Formica* spp. is not only a common shared thread to a developed MEMS model, but, within the interior Douglas-fir forest, provides a broad adaptive platform supporting systematic resiliency and their presence. Over extended durations, *Formica* shape and structure the landscape and community dynamics ^{43,115,195,250}.

An undisturbed interior Douglas-fir forest houses several invertebrates including a broad range of ant species. The interior Douglas-fir forest at Swakum Mountain is highly disturbed and singularly dominated by *Formica integroides*. Surprisingly, the forest and *Formica* are highly resilient and not only survive, but the forest system is shaped and tailored to the *Formica*. Active mounds not only increase forest floor spatial heterogeneity ⁶⁵, but retain and protract C as a sink evinced through mass loss. *Formica* presence in harvested, grazed, and highly disturbed locations with a minimal forest structure, having their basic requirements met, i.e., low percentage of canopy cover, aphids, CWD and litter, could restore the interior Douglas-fir forest productivity within a reduced capacity.

My research supports the findings that active *Formica* mounds tend to be drier with greater porosity when compared to forest floor litter ^{44,63,68,140} due to *Formica* thatch construction and maintenance which supports the over-all mound structure. My findings also support Kipyatkov's and Hölldobler's and Wilson's findings that maintenance and building activities are accomplished by a large diverse worker populations ^{87,118} which is further linked to temperature and moisture regulation of broods and mounded materials i.e., vertical movement of larvae within the mound chambers, sunning as a means of insolation capture ⁸⁷, and venting to release excess moisture within the mound (personal observations). The underlying success of *Formica* spp. in northern ranges is mainly determined by large populations ¹¹⁸ supported by their intrinsic physiological and behavioral adaptive plasticity.

With periodic and seasonal windows of high moisture and increased temperatures that temporarily increase decomposition rates, my findings support the assertions that drier mound conditions will inhibit litter decomposition ^{62,204,242}. Senesced needle-litter in the interior Douglas-fir forest during summer months tends to be dry and when interred within *Formica* mounds, is further harbored from abiotic stresses of moistening and drying, UV degradation and microbial degradation. My findings reveal, within the context of the moisture-limited interior Douglas-fir forest at Swakum Mountain, that *Formica* mounding inhibits and suspends decomposition while the mounds remain active, which is different than the findings of Domisch et al. ⁴⁴.

The novelty of my approach utilizes a combination of: qualitative observations, natural and controlled scientific methodologies; conceptual, deconstructive, and imaginative processes which forms a rounded and holistic perspective; which I leave to you, the reader, to receive as you will.

The inner, subtle, and seemingly unnoticed workings of the small provide support to the whole as exemplified by *Formica* within forested systems. By gaining understanding of the under-belly of the minute we are then able to better understand the placement, importance, and connection to the larger ecosystem. When embarking on this journey I never imagined that I would begin to perceive through the lens of such wildly different sentient creatures. For my future endeavors, I hope never to lose this new-found awareness.

Released; open-space or chaos? Frenzied gatherings, directionless,

I am carried away...

downward,

alone.

Crawling into darkness; all is obscure all is unknown.....AP



Figure 64 Sketches A-C: Interconnective abiotic / biotic conceptual framework of a forest system

Ellipsis and circles - biotic / abiotic physical and qualitative platforms

• Includes: organisms or various plant and animal communities including community based ecological properties examples; plant based organic matter; innate environmental qualities such as: climate, erosion, disturbance types and regime, geologic origins/contributions

Lines and dashed lines - energetic, physical, and qualitative connections linking platforms

Blue arrow - downward movement of ecosystem's matter: organic matter, dissolved organic matter, and soil organic matter

• As solid matter deposition occurs on forest-floor and below-grounds energetically, becoming increasingly inert, requiring higher Activation energy (Ea) **Orange arrows -** gaseous exchange: respired CO₂, O₂, UV oxidative degradation

• Higher entropic value; escaping physical / structural system

Brown Arrow

• Innate geologic / soil-mineral / ground H₂O attributes and contributions supporting the system

As time increases arrows broaden and connectivity increases depending on platform establishment within the system and context of community structure representing an overall accumulation effect. Platforms become more complex forming nexuses, expanding and containing ephemeral sections indicated by dashed boundaries. Some contain nested platforms and color regions representing specie or community expression based on abiotic stresses affecting survivability of individuals and selected members within a community. As potential connectivity increases as does greater complexity indicated by more gaseous exchanges (number / type). Model based on: Cotrufo's MEMS, food-webs, Cascade effect, and complexity theory

6 Afterword

The train, imperceptible transit across a temporal landscape; unconscious steady-rhythmic progression. Momentarily, a lapse, a break; stepping-off and -on again subtly holding its own rhythm. Each re-entry possesses a strange-unfamiliar quality, as the train itself seems different. Awareness of rapid forward trajectory speeding with determined certainty, apparent, clear. overwhelming... Will it ever stop?

One of the underlying metaphors of the opening poem is the lapse and compression of time as moments slip by, potentially unnoticed. This notion has played a significant part of my life while writing this paper. Does disclosure of personal experience through poetic metaphors have any significance to a scientific document? Imagination is the source of process, where process accesses one's creativity. In communicating ideas through a personal and creative context, the reader not only gains access to the author's perspective, but insight into their process.

The sketches and remaining poems within this paper are not meant as decorative pieces demonstrating my abilities, but an offering of myself openly through the work, with the intention that they will provide the reader with greater insight into the subject matter while providing a more replete perspective.

I have come to understand that my process is not the achievement of multiple publications, financial gain, or peer status, but the commitment to a process and revealing oneself through the work, be it writing a thesis or sweeping floors. The work presented herein is intimate to me and is the culmination of my individual efforts and the understandings attained through personal experience melded with the information and support of others.

As my experiences have been drawn from physical labor, philosophic, artistic, and scientific backgrounds, I find the arbitrary branding of any one specific interest or job to be an artificial construct that is heavily weighted by many. The sources of imagination, in part, are a product of one's experiences, creativity, and perceptions as imagination provides the fuel underpinning process. The misconceptions that all art is creative or scientific research is purely analytical, are very limited perceptions and often are the projections of the questioner. For example, for a dancer the work can often be physically utilitarian and without much creativity, while a researcher may need to create a novel methodology, or develop an alternative perspective in analyzing data, which requires imagination.

Having had many disparate feelings throughout this process, I realized that emotions are part of the process that when compassionately accessed, inform the process. In my attempts to expand my own knowledge, I stumbled across the writings of Jacob Bronowski, finding resonance and inspiration with his perspectives. In his documentary "The Ascent of Man", he speaks passionately about absolute truth while drawing upon his own personal experiences. Not only does the moment reveal individual bravery, but also by offering his experience, he provides a thread of deeper understanding, knowledge and wisdom.

His compassionate view of mans' endeavors through science, art, and philosophy as a creative impulse, I find echo true through the fertile void of our common collective and individual imaginations. This newly discovered awareness not only provided me with a sense of fellowship, but veneration of my predecessors' and colleagues' endeavors and encouragement of my own vision and creative pursuits.

My concern is that the current disregard for process, which is seminal to "free-thinking", will become further marginalized and eventually extinct, while being dominated by corporate paradigms that skew our sense of knowledge and truth. Corporatization, as solely motivated by materialism, provides only a singular perspective. Truth and knowledge require, and are products of, multiple perspectives and approaches, not singular perspectives and approaches providing only a verisimilitude of truth and knowledge while emitting a misleading air of completeness and absolutism. The imposing threat on academic institutions by corporate paradigms, directly upbraids process-based knowledge by dogmatically attaching materialistic gain to academic outcomes. Certainly, outcomes are fundamental, but they are only part of an entire process. The beneficial contribution that a corporate paradigm tenders is valuing the outcomes and the ability to make immediate use and implementations based on acquired information.

Unknowingly, are we racing towards a pending certainty or slowly suffocating by our own determination and apathetic unawareness? This, of course, is a rhetorical question, but the metaphor and imagery is provocative and demonstrative of engaging the imagination. The challenges I present
to myself I also pose to our academic community: stretching our imaginations, developing and utilizing new abilities, refining perceptions, questioning current paradigms, and ultimately, the source and acquisition of knowledge. As the sciences, arts, and philosophy are, in part, derived from the common spring of our imaginations, I wonder as we refine and extend our perceptions, will they transform the current body of knowledge, and will they supersede it, or just continue adding to it?

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Appendices

Appendix A: Collected Invertebrate Species

a) Ant species 55,247

Identified Ant Species	Number of identified specimens without size distinction	Number of identified specimens < 3 mm in length	Number of identified specimens 3-6 mm in length	Number of identified specimens <=7 mm in length			
Formica integroides	-	32	33	40			
Polyergus breviceps	3	-	-	-			
Camponotus noveboracensis	1	-	-	-			
Formica fusca	1	-	-	-			

Total of collected and identified ant species = 110

Note: Specimen identification advisement by:

- Ant species Robert Higgins, PhD., Allan Vyse, PhD.
- Aphids Cho Kai
- Spruce budworm Suzi Lavelle, PhD

b) Identified Aphids in Cinara group ¹⁶⁹

Identified Species (Aptera form)					
Ciniara pseudotaxifoliae or Ciniara pseudotsutae*	20 specimens collected / observed				
Adelgid cooleyi**	Collected 4-7 terminal buds which contained signature features (e.g., webbing, fuzzy cocoon- like growth) and commonly observed these features at the mounds.				
* Closely related species. More information is peeded to distinguish species					

* Closely related species. More information is needed to distinguish species.

** Identified by Cho Kai Chan, Babita Bains

c) Identified Other Species ^{31,159}

Spruce budworm moth (Choristoneura	3 - collected
occidentalis)*	5 - observed in field
Specimens found within thatch	
Rotifera	2 - observed in thatch
Collembola or Acari	5 - observed in thatch
Pseudoscorpion	1 - observed in thatch
* Identified by Dr. Currie Levellee	

Identified by Dr. Suzie Lavallee

Appendix B: Plant Species Identified in the Field

			Latin Family
Common Name	Latin Name	Group	Name
Ponderosa pine	Pinus ponderosa	tree	Pinaceae
Trembling aspen	Populus tremuloides	tree	Salicaceae
Cottonwood	Populus trichocarpa	tree	Salicaceae
Interior Douglas-fir	Pseudotsuga menziesii subsp. glauca	tree	Pinaceae
Saskatoon	Amelanchier alnifolia	shrub	Rosaceae
Kinnikinnick	Arctostaphylos uva-ursi	shrub	Ericaceae
Common juniper	Juniperus communis	shrub	Cupressaceae
Choke cherry	Prunus virginiana	shrub	Rosaceae
Wood rose / Baldhip rose	Rosa gymnocarpa	shrub	Rosaceae
Woods' rose	Rosa woodsii	shrub	Rosaceae
Yarrow	Achillea millefolium	flower	Asteraceae
Nodding onion	Allium cernuum	flower	Alliaceae
Pasture sage	Artemisia frigida	flower	Asteraceae
Tufted white prairie aster	Aster ericoides	flower	Asteraceae
Arrow-leaved balsam root	Balsamorhiza sagittata	flower	Asteraceae
Hoary cress	Cardaria draba	flower	Brassicaceae
Pallid Indian paintbrush	Castilleja pallescens	flower	Scrophulariaceae
Sulphur Indian paintbrush	Castilleja sulphurea	flower	Scrophulariaceae
Thompson's Indian paintbrush	Castilleja thompsonii	flower	Scrophulariaceae
Diffuse knapweed	Centaurea diffusa	flower	Asteraceae
Spotted knapweed	Centaurea stoebe L.	flower	Asteraceae
Hoary false yarrow	Chaenactis douglasii	flower	Asteraceae
Common rabbitbrush	Chrysothamnus nauseosus	flower	Asteraceae
Canada thistle	Cirsium arvense	flower	Asteraceae
Edible thistle	Cirsium edule	flower	Asteraceae
Narrow-leaved collomia	Collomia linearis	flower	Polemoniaceae
Slender hawksbeard	Crepis atribarba	flower	Asteraceae
Showy daisy	Erigeron speciosus	flower	Asteraceae
Parsnip-flower wild buckwheat	Eriogonum heracleoides	flower	Polemoniaceae
Sticky geranium	Geranium viscosissimum	flower	Geraniaceae
Baby's breath	Gypsophila paniculata	flower	Caryophyllaceae
Pursh's silky lupine	Lupinus sericeus	flower	Fabaceae
Sulphur lupine	Lupinus sulphureus	flower	Fabaceae
Alfalfa	Medicago sativa L.	flower	Fabaceae
Yellow owl's clover	Orthocarpus luteus	flower	Scrophulariaceae
Silky phacelia	Phacelia sericea	flower	Hydrophyllaceae
Russian knapweed	Rhaponticum repens	flower	Asteraceae
Yellow rattle	Rhinanthus minor	flower	Scrophulariaceae
Black-eyed Susan	Rudbeckia hirta L.	flower	Asteraceae
Woolly groundsel	Senecio canus	flower	Asteraceae
Common groundsel	Senecio vulgaris	flower	Asteraceae
Common mullein	Verbascum thapsus	flower	Scrophulariaceae
Crested wheatgrass	Agropyron cristatum	grass	Poaceae
Cheatgrass	Bromus tectorum	grass	Poaceae
Poverty oat grass	Danthonia spicata	grass	Poaceae
Giant wild rye	Elymus cinereus	grass	Poaceae
Quackgrass	Elytrigia repens	grass	Poaceae
Timothy-grass	Phleum pratense	grass	Poaceae
Alkali bluegrass	Poa juncifolia	grass	Poaceae
Bluebunch wheatgrass	Pseudoroegneria spicata	grass	Poaceae

Appendix C: Saprotrophic / Ectomycorrhizal Fungi

Season of Collection	Identified Samples
Fall 2009	Xeromphalina
	Clitocybe
	Mycena
	Psathyrella
Spring 2010	Morchella elata
	Clitocybe
	Psathyrella
November 2010	Russula
	Lactarius
	Phaelolus
	Hygrophoropsis
	Inocybe
	Agrocybe

"LBM" - Little Black Mushrooms (woody decomposers)

Note: Specimen identification advisement by:

• Mary Berbee, PhD.



Appendix D: Mound Growth and Estimated C and N in Thatch and Litter

Figure 65 Mound Growth During Active Phase

Describes mound growth during *Formica* active phase (May - Sept). The numbers below the X-axis are the *Formica* mound numbers found in Tables 25 a-d. Type 1 mounds are the solid bars, Type 2 mounds are the heavy diagonal pattern, and Type 3 mounds are the light diagonal pattern. s - located on steep slope; b - bear disturbance. $\pm 0.05 \text{ m}^3$ error bar.



- Abandoned then re-inhabited over the final 6 month period
- Active for 10 months over a 16 month period
- Active for 6 months and measured in the final 6 month period

Note:

* Mound 1 consists of two separate physical structures that, due to proximity (~ 15 cm), is considered a single colony.

Table 25 a-d Mound area and volumes for weight, C, and N values

<i>Formica</i> mounds	May 10 mound area (m ²)	May 10 mound vol (m ³)	Nov 10 mound area (m ²)	Nov 10 mound vol (m ³)	Entire area surrounding mound (m ²)
1	64.4	6.5	72.3	7.8	858.8
2	64.2	7.9	69.6	11.2	306.1
3	89.3	12.0	92.7	12.4	1345.3
4	74.2	9.3	81.2	11.4	795.9
5	46.6	5.5	65.4	8.3	1519.0
6	36.3	3.7	41.8	4.3	631.1
7	66.1	5.0	69.8	5.6	538.3
8	34.0	5.4	37.6	6.5	1128.4
9	33.8	4.6	60.4	8.1	1153.1
10	96.4	6.4	97.7	7.3	426.7
Mean	60.5	6.6	68.9	8.3	870.3
11 *	0	0	58.8	1.6	88.2
12 *	0	0	155.1	4.1	265.9

(a) Selected Formica mounds area and volumes

(b) Estimated needle, thatch, and particulates surrounding and inside select mounds; Estimated K value based on senesced goldenbrown litter outside mound / mounded thatch at each mound area.

<i>Formica</i> mounds	est. needle weight surrounding mound (kg)	est. needle weight w/i mound (kg)	est. needle + part. weight w/i mound (kg)	total est. weight at mound (kg)	est. total needle weight / mound area (g/m ²)	est. total needle + particulate weight / mound area (g/m ²)	est. total needle weight outside mound (g/m ²)	est. total needle weight inside mound (g/m ²)	est. total needle + particulate weight inside mound (g/m ²)	est. K value at mound
1	187.59	235.89	324.78	512.37	493.1	596.6	218.4	274.7	378.2	0.58
2	73.72	687.52	1,874.53	1,948.25	2486.8	6364.4	240.8	2246.0	6123.6	0.04
3	319.70	1,417.49	1,944.73	2,264.43	1291.3	1683.2	237.6	1053.6	1445.5	0.16
4	193.60	976.39	1,424.92	1,618.52	1469.9	2033.5	243.2	1226.7	1790.2	0.14
5	253.03	492.92	915.23	1,168.26	491.1	769.1	166.6	324.5	602.5	0.28
6	138.81	400.24	477.38	616.19	854.2	976.4	220.0	634.2	756.4	0.29
7	63.58	496.04	582.75	646.32	1039.6	1200.6	118.1	921.5	1082.5	0.11
8	261.61	489.22	581.71	843.32	665.4	747.4	231.8	433.6	515.5	0.45
9	201.08	340.51	452.05	653.13	469.7	566.4	174.4	295.3	392.0	0.44
10	46.39	594.20	822.24	868.64	1501.4	2035.9	108.7	1392.6	1927.1	0.06
Mean	173.91	613.04	940.03	1,113.94	1076.2	1697.3	196.0	880.3	1501.4	0.25
11*	0.0	148.63	258.45	258.45	1684.2	2928.7	0.0	0.0	0.0	
12*	0.0	183.28	214.31	214.31	689.3	805.9	0.0	0.0	0.0	

					est. Total				
					C needles	est. Total C			
					+ thatch	needles			est. C w/i
			est. C of		at each	thatch +			mound at
	est. C	est. C of	needles +		mound /	particulates at	est. C	est. C w/i	each location
	surrounding	needles w/i	part. w/i	est. total C	mound	each mound /	surrounding	each	(thatch +
Formica	mound	mound	mounds	at mound	area	mound area	mound	mound	particulates)
mounds	(kg)	(kg)	(kg)	(kg)	(g/m²)	(g/m²)	(g/m²)	(g/m²)	(g/m²)
1	82.01	111.07	132.32	214.33	224.8	249.6	95.5	129.3	154.1
2	35.59	266.61	382.91	418.50	987.2	1367.1	116.3	870.9	1250.9
3	145.92	620.07	714.13	860.05	569.4	639.3	108.5	460.9	530.8
4	88.30	438.06	520.67	608.98	661.3	765.1	110.9	550.4	654.2
5	119.39	223.87	369.72	489.10	226.0	322.0	78.6	147.4	243.4
6	65.09	184.60	207.90	272.99	395.6	432.6	103.1	292.5	329.4
7	30.36	226.98	238.94	269.30	478.0	500.3	56.4	421.6	443.9
8	123.92	222.28	253.74	377.67	306.8	334.7	109.8	197.0	224.9
9	96.56	157.62	185.99	282.54	220.4	245.0	83.7	136.7	161.3
10	22.50	263.56	305.50	328.00	670.4	768.8	52.7	617.7	716.0
Mean	80.96	271.47	331.18	412.15	474.0	562.4	91.6	382.4	470.9
11*	0.0	65.50	90.12	90.12	742.2	1021.2	0.0	0.0	0.0
12*	0.0	84.17	96.81	96.81	316.5	364.1	0.0	0.0	0.0

(c) Estimated C in litter, thatch, and particulates surrounding and inside select mounds.

(d) Estimated N in litter, thatch, and particulates surrounding and inside select mounds.

<i>Formica</i> mounds	est. N surrounding mound (kg)	est. N of needles w/i mound (kg)	est. N of needles + part. w/i mounds (kg)	est. total N at mound (kg)	est. Total N at each mound / mound area (g/m ²)	est. Total N at mound + particulates (g/m ²)	est. N surrounding mound (g/m ²)	est. N w/i each mound at each (g/m ²)	est. N w/i mound at each location + particulates (g/m ²)
1	2.18	2.34	3.20	5.38	5.3	6.3	2.5	2.7	3.7
2	0.79	7.90	13.61	14.40	28.4	47.0	2.6	25.8	44.5
3	3.49	15.25	19.52	23.01	13.9	17.1	2.6	11.3	14.5
4	2.02	9.49	13.02	15.04	14.5	18.9	2.5	11.9	16.4
5	2.92	4.97	9.05	11.96	5.2	7.9	1.9	3.3	6.0
6	1.59	3.72	4.42	6.01	8.4	9.5	2.5	5.9	7.0
7	0.53	4.00	4.63	5.16	8.4	9.6	1.0	7.4	8.6
8	2.60	5.11	6.49	9.09	6.8	8.1	2.3	4.5	5.8
9	2.08	3.03	4.14	6.23	4.4	5.4	1.8	2.6	3.6
10	0.46	5.52	7.07	7.53	14.0	17.7	1.1	12.9	16.6
Mean	1.87	6.13	8.52	10.38	10.9	14.7	2.1	8.8	12.7
11*	0.0	1.42	2.37	2.37	16.1	26.8	0.0	0.0	0.0
12*	0.0	2.07	2.52	2.52	7.8	9.5	0.0	0.0	0.0

The same set of equations was used for both C and N, substituting N for C.

The estimated C and N (g) within thatch and litter for each mound was extrapolated using the collected data in proportions, and determining the unknown value (x) for each proportion. M represents the variables C and N as the same extrapolation was applied to both variables. The series of proportions used to calculate total C and N:

$$\begin{split} \mathbf{M}_{t} / S_{t} &= x\mathbf{M}_{t100} / W_{t100} \\ x\mathbf{M}_{t100} / V_{t100} &= x\mathbf{M}_{tm} / V_{tm} ; \\ \mathbf{M}_{om} / S_{om} &= x\mathbf{M}_{100Nom} / W_{100Nom} \\ x\mathbf{M}_{100Nom} / V_{100Nom} &= xT\mathbf{M}_{Nom} / TV_{Nom} ; \\ (x\mathbf{M}_{tm} / V_{tm}) + (x T\mathbf{M}_{Nom} / TV_{Nom}) &= T_{est}.\mathbf{M} \\ A_{s} &= \pi r^{2} \\ T_{est}.\mathbf{M} / A_{s} &= T\mathbf{M}_{F} \end{split}$$

 \mathbf{M}_{t} was the weight of C or N in the thatch (g), S_t was the 0.002 sample of thatch (g), x \mathbf{M}_{t100} was the calculated estimate of C or N in 100 needles of thatch (g), and W_{t100} was the weight of 100 needles of thatch (g); V_{t100} was the volume of 100 needles of thatch (m³), x \mathbf{M}_{tm} was the calculated C or N of thatch in mounds (g), and V_{tm} was the calculated total volume of thatch in mounds (m³).

 \mathbf{M}_{om} was the weight of C or N in the sample of needles (g), S_{om} was the 0.002 sample of needles (g), $\mathbf{x}\mathbf{M}_{100Nom}$ was the calculated estimate of C or N of 100 needles, and W_{100Nom} was the weight of 100 needles (g); V_{100Nom} was the volume of 100 needles (m³), $\mathbf{x}T\mathbf{M}_{Nom}$ was the calculated estimate of total C or N in needles (g), TV_{Nom} was the calculated estimate volume of needles (m³).

 $T_{est.}M$ was the total estimated C or N for each mound, A_s was the area surrounding each mound; finally TM_F was the total estimate of C or N in and surrounding the mound respectively as thatch and needles for each mound area (g/m²).

Appendix E: Estimation of Formica spp. Mound density within study area

To estimate mound density I first subtracted any recently harvested and open large grazed areas from the contiguous forest, as these would not be inhabited by *Formica* spp. I then randomly situated 20 1-m-wide transects (4,800 m2) within the contiguous forest. Any mounded thatch that intersected with the transects was measured: long side (Ls), short side (Ss), and height(H).



Figure 66 Transects and unmarked road in study area. Black stars represent the 20 transects. Red circles and lines represent an unmarked road in the study area.

Table 26 a-cMound density Estimates(a) Study area and transects

total est. of forest in study area m ²	length of transects m ²	total length of all transects m ²	% area of transects of study area
1,261,800	240	4,800	0.38%

(b) Estimated low - high of mounded thatch of study area

est. mean vol. of single thatch mound (m ³)	est.net mound thatch of transects (m ³)	est. % of thatch in a single mound in study area	total est. mound thatch (total number mound thatch / mean contribution of thatch) (m ³)	total est. mound thatch (total est of thatch vol / est mean vol of a mound) (m ³)	total estimate of mound thatch (prob.sum) (m ³)
1.18	237	0.07%	272,290	273,322	322,520

(c) Estimated area of mounded thatch within study area

mean length of single thatch mound (m)	% single thatch mound length in study area	est. volume mounded thatch of transects (m ³)	total est. mounded thatch area of study area (m ²)
2.80	0.05%	673	375,145*

* The estimated total area of *Formica* spp. mounds in the study area is 375,145, which represents $\sim 30\%$ of the estimated study area.

Equations

P_j=(2L*r_m)/A_t v_j/p_j

- P_{j} = probability of encountering mounded thatch
- L = length of transect (m²) = 240
- $\texttt{r}_{_\texttt{m}}$ = radius of mounded thatch within transects
- A_t = total study area (m²)
- v_{j} = individual mounded thatch volume (m³)
- $p_{\ j}~$ = individual probability of encountering mounded thatch

Appendix F: Formica Diagrams and Mound Temperature Locations



Figure 67 *Formica* spp. basic life cycle of a worker.

Spring broods mature in three instar stages within the inner mound chambers for approximately 4 months. When mature workers emerge from the mound, their duties includes: aphid tending, litter and prey collection, nest guarding, and scouting the trees and forest floor for additional resources. The workers life is approximately 2-5 years.



Figure 68 Specialized organs in *Formica* spp.

Organs supporting eusociality (crop - social stomach and metapleural gland), desiccation resistance (malpighian tubes and rectal papillae), and efficient waste removal (infra-buccal pocket).



Figure 69 *Formica* mounds within the study area. 37 mounds of Types 1-4 were measured and observed during the study. Orange diamonds represent the *Formica* mounds. Red circles and lines represent an unmarked road in the study area.



Figure 70 Examples of temperature locations taken at and around a mound.