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Predatory hymenopteran assemblages in boreal Alaska: associations with forest composition and post-fire succession

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ABSTRACT

Changes to the fire regime in boreal Alaska are shifting the ratio of coniferous to deciduous dominance on the landscape. The increase in aspen and birch may have important effects on predatory hymenopteran assemblages by providing a source of extrafloral nectar and increasing prey availability. Furthermore, fire-induced changes in successional age alter habitat structure and microclimate in ways that may favor ants. This study is the first to characterize the influence of fire-related vegetation changes on boreal predatory hymenopteran assemblages. We compare the abundance, species richness, and composition of predatory hymenopteran assemblages among forests at different stages of succession and of varying post-fire tree species compositions. Ant assemblages were weakly related to forest composition, but ants were significantly more abundant and speciose in early-successional forests than in mid-late successional forests. In contrast, macropterous wasp morphospecies richness and abundance, and micropterous wasp abundance, were positively related to the basal area of aspen, but were not related to successional stage. The results suggest that shifts in boreal vegetation related to climate warming will result in changes to the predaceous insect community, with ants responding positively to disturbance and wasps responding positively to an increase in the representation of aspen on the landscape.

RÉSUMÉ

Les changements du régime des feux dans la forêt boréale de l'Alaska modifient le rapport de dominance des conifères vers les feuillus. L'augmentation du tremble et du bouleau pourrait avoir des effets importants sur les assemblages d'hyménoptères prédateurs en fournissant une source de nectar extrafloral et en augmentant la disponibilité des proies. De plus, les changements de stade successional des forêts induits par le feu modifient la structure de l'habitat et le microclimat, ce qui pourrait favoriser les fourmis. Cette étude est la première à caractériser l'influence des changements de végétation liés aux feux sur les assemblages d'hyménoptères prédateurs boréaux. Nous comparons l'abondance, la richesse spécifique et la composition des assemblages d'hyménoptères prédateurs de forêts à différents stades successionnels et de différentes compositions forestières après feu. Les assemblages de fourmis étaient faiblement liés à la composition forestière, mais leur abondance et leur richesse spécifique étaient significativement plus élevées dans les forêts de début de succession que dans les forêts de milieu de succession. En revanche, la richesse et l'abondance des morpho-espèces de guêpes macroptères et l'abondance des guêpes microptères étaient positivement liées à la surface terrière du tremble, mais n'étaient pas liées au stade successional. Les résultats suggèrent que les changements de la végétation boréale liés au réchauffement climatique entraîneront des changements dans la communauté d'insectes prédateurs, les fourmis réagissant positivement aux perturbations et les guêpes réagissant positivement à une représentation accrue du tremble dans le paysage.

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Introduction

The insect order Hymenoptera is exceptionally diverse, and its members are abundant throughout terrestrial ecosystems. Dominated by predaceous species, the Hymenoptera are ecologically important as regulators

of terrestrial ecosystem structure and function (LaSalle and Gauld 1991, 1993; LaSalle 1993; Forbes et al. 2018). Hymenoptera comprises several groups of important predators, including ants, social and solitary wasps, and parasitoid wasps (the latter of which function ecologically as predators (Doutt 1959) and are grouped as

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such herein). It is estimated to be the most species-rich order of animals, largely due to the diversity of parasitoid wasps, the vast majority of which have not yet been described (Forbes et al. 2018). Studies of insect trophic interactions in terrestrial systems have found that hymenopteran predators and parasitoids interact with more insect prey than any other predatory insect taxa, and are responsible for an estimated 57% of all insect predation (Schoenly 1990; LaSalle and Gauld 1991). Due to their disproportionately large effect on other trophic levels, several groups of hymenopterans have been identified as keystone species, notably members of the ants and parasitoid wasps (LaSalle and Gauld 1991, 1993).

Despite the ecological importance of predatory hymenopterans, their relationships to habitat are not well documented within the boreal forest (Danks and Footitt 1989; Paquin and Coderre 1997; Bennett and Hobson 2009). The boreal forest is currently undergoing unprecedented changes due to rapid climate warming, which may affect how these functionally important organisms are distributed on the landscape. In interior Alaska, the boreal forest undergoes regular fire intervals of approximately 100 years, and is characterized by stable, conifer self-replacement succession cycles, where deciduous broadleaf species characterize earlier stages of post-fire succession (Johnstone et al. 2010a). However, over the last century, boreal warming has reduced snowpack and thawed permafrost, which in turn has influenced the boreal fire regime by increasing forest fire frequency, severity, and extent (Wendler and Shulski 2009; Johnstone et al. 2010a, 2010b; Shenoy et al. 2011; Schuur et al. 2015). Climate-driven changes to the boreal fire regime have facilitated hardwood persistence, including trembling aspen (*Populus tremuloides*) and Alaska birch (*Betula neoalaskana*), in forests that were historically dominated by coniferous black spruce (*Picea mariana*) (Johnstone 2005; Johnstone and Kasischke 2005; Johnstone et al. 2010a; Lindroth and St Clair 2013). This increase in aspen in the boreal forest could be particularly relevant to predatory hymenopterans. Aspen is highly palatable to herbivorous insects which serve as prey, and is one of few plants in the boreal forest that produces extrafloral nectar, both of which may influence arthropod community composition and trophic interactions (Heil 2015).

The foliage of hardwood species, such as aspen and birch, is poorly defended relative the foliage of coniferous species, such as black spruce (Bryant et al. 1983), and therefore may foster a robust prey base for predatory arthropods. In general, conifers tend to invest more in defensive compounds, such as resins, terpenes, and phenolic compounds, than hardwood species (Bryant et al. 1983). This makes them less preferred

by generalist herbivores (MacLean and Jensen 1985; Baraza et al. 2006), and as a result less palatable plants suffer less leaf damage (Coley et al. 1985; Herms and Matson 1992). Black spruce is exceptional in its tolerance for low-nitrogen levels and employs a variety of non-nitrogenous defenses, making it notably poor in quality for herbivores (Mattson 1980). Herbivores feeding under these conditions must have specialized means of avoiding dietary deficiencies, and suffer from prolonged generation times (Mattson 1980; Ode 2006). These observations suggest that coniferous forest generally provides fewer, less-diverse prey for predatory hymenopterans relative to hardwood forest (Poelman et al. 2008). While surveys of insect diversity across broadleaf versus conifer habitats are limited, there is evidence that some insect taxa are more abundant and species-rich in aspen stands than in conifer stands (Hughes et al. 2000; Simonson et al. 2001). Less palatable plants also facilitate anti-predator defense in herbivores that sequester plant toxins (Bowser 1990), which both reduces the herbivore's quality as prey and reduces the survivorship of their predators (Price et al. 1980; Ode 2006). These effects may be especially consequential for parasitoids of herbivores, which develop on or within their hosts. Prey quality affects not only the development of parasitoid wasps, but also their lifetime fecundity (reviewed in Jarvis et al. 2001). Therefore, we expect predatory hymenopteran abundance and richness to be low in black spruce stands relative to aspen and birch stands.

Another reason why forest composition is likely to influence predatory hymenopteran assemblages is that aspen produces extrafloral nectar, whereas birch and black spruce do not. Due to their constricted waists, adult ants, wasps, and parasitoid wasps cannot consume solid food, and subsist largely on plant nectars, honeydew, and prey haemolymph (Jarvis 1998). For many plant species, extrafloral nectar mediates an indirect plant defense by attracting and nourishing predatory hymenopterans, which then may harass, consume, or parasitize herbivorous arthropods on the plant (Bentley 1977; Wäckers et al. 2005; Heil 2015). In general, access to extrafloral nectar improves the performance, longevity, and fecundity of parasitoid wasps and ants (Wanner et al. 2006; Byk and Del-Claro 2011; Jamont et al. 2013), and may enhance top-down control of herbivores by enhancing predatory hymenopteran fitness and by aggregating hymenopteran predators near the nectar source (Tylianakis et al. 2004; Heimpel and Jarvis 2005; Wäckers et al. 2005). Because extrafloral nectar is an additional resource available to predatory hymenopterans, aspen stands may support a greater abundance of predatory hymenopterans than stands composed of other tree species. Additionally, the presence of a unique food

source provides additional niche space, which could increase the species richness of predatory hymenopterans (Gause 1934; Bluthgen and Feldhaar 2010). The influence of both extrafloral nectar and plant palatability may be especially pronounced in younger successional aspen stands for ants, because foliar resources, such as extrafloral nectar and foliar herbivorous prey, are more accessible to most ants on shorter, understory seedlings and saplings than on canopy-reaching trees.

Alterations to forest age structure in the boreal forest is likely to have additional effects on predatory hymenopterans, independent of the effects of tree species composition. Climate-induced increases in forest fire frequency increase the representation of early-successional habitat on the landscape. A forest's post-fire successional age is most likely to affect predatory hymenopteran assemblages through its influence on microclimate and structural niche space. The open canopies of early-successional forests allow insolation to warm the soil. As forests age, the canopy shades the understory, cooling the soil (Hart and Chen 2008; Chen and Robinson 2015). Warmer temperatures increase ant foraging and development rates (Finnegan 1973; Kipyatkov and Lopatina 2015). Thus early-successional forests likely benefit ant abundance and species richness, due to the reduced canopy cover and warmer soil temperatures (Chen and Robinson 2015). The assemblage patterns of wasps over successional time are even less well known than those of ants. In broadleaf forests of Japan, parasitoids of herbivores decrease in abundance over successional time, as understory vegetation is shaded by taller, woody species; however, parasitoids of detritivores increase in abundance over successional time as leaf-litter mass increases (Maleque et al. 2010). Evidence from temperate forests has shown that stand basal area is positively related to the species richness of parasitoid communities, perhaps due to the diversity of microhabitats and hosts provided by mature trees (Giovanni et al. 2015). In boreal Alaska, we predict that the structural complexity and buildup of organic matter in more mature successional forests will support more abundant and species-rich assemblages of wasps.

In this study our goal was to characterize how tree species composition and successional stage affect predatory hymenopteran assemblages (*sensu* Stroud et al. 2005) in post-fire boreal forests of interior Alaska. Specifically, we had two objectives. First, we investigated whether aspen stands support a greater abundance and richness of predatory hymenopterans than birch or black spruce stands. Second, we investigated whether earlier and later successional stages support different assemblage compositions of predatory hymenopterans. To test this, we characterize associations between predatory hymenopteran

abundance, species richness, and assemblage composition in forests that vary in their tree species composition and time since last burn. To rule out potentially confounding underlying microclimate factors, environmental data are also compared among forest habitats and correlated to predatory hymenopteran metrics.

Materials and methods

Study sites

We sampled 29 study sites from the Bonanza Creek (BNZ) Long-Term Ecological Research (LTER) regional site network (RSN) based on their age and current forest composition (Bonanza Creek LTER 2018). The study sites were located along major road systems within a 2.3 million ha area of interior Alaska centered around Fairbanks, AK (Figure 1). Each study site covered 1200 m² (30 m x 40 m). Prior to the most recent burn, all sites were dominated by black spruce forest. However, the forests that have regenerated since the most recent fire vary in their aspen, birch, and black spruce compositions, which could potentially indicate differences in successional trajectory. Sites were characterized by the BNZ LTER as 'young,' 'intermediate,' or 'mature' age class based on the date of the last burn. A total of 13 young sites were sampled, of which seven resulted from the Dall City fires (burned in 2004) and six from the Boundary fire (2004). The 12 intermediate sites sampled consisted of six sites from the Gerstle River fire (1947), three sites from the Murphy Dome fire (1958), one site from the Goldstream fire (1966), and two sites from the Wickersham Dome fire (1971). The four mature sites burned prior to available records, but estimated burn periods range within 1800 and 1930. Common tree species at all sites include black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg), trembling aspen (*Populus tremuloides* Michx), and Alaska birch (*Betula neoalaskana* Sarg.); less common species include white spruce (*Picea glauca* (Moench) Voss), tamarack (*Larix laricina* (Du Roi) K. Koch), and balsam poplar (*Populus balsamifera* L.). All tree species were identified by the Bonanza Creek LTER. The study sites include both aspen-abundant and aspen-poor forest compositions within each age class except mature. The BNZ LTER RSN only contains mature black spruce sites, because sites were chosen with the purpose of understanding changes that may occur in the 'typical' boreal black spruce relay succession, and hardwood persistence is a relatively recent phenomena in boreal Alaska (Bonanza Creek LTER 2018).

Because site choice was constrained by the availability of accessible, burned areas, spatial aggregation of sites within age classes was unavoidable. On average, more recent burns were located at higher latitudes than

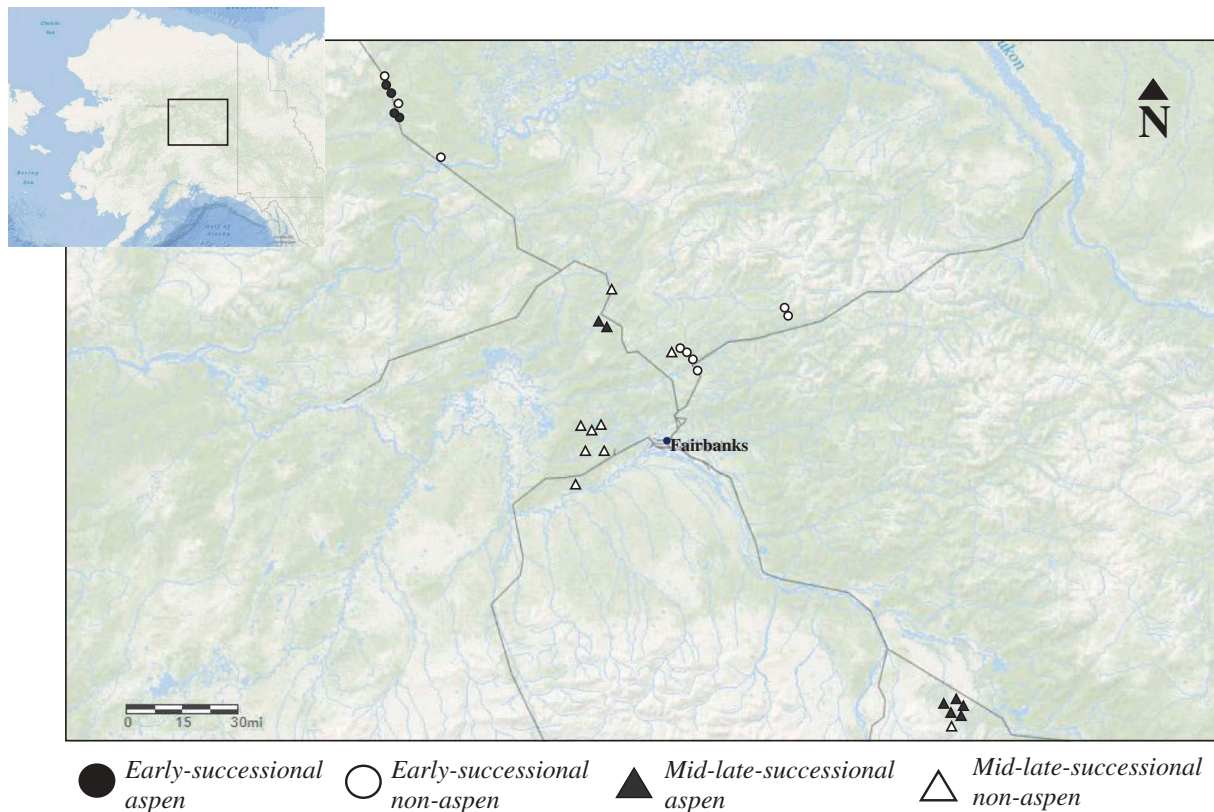


Figure 1. Map of 29 LTER study sites located throughout interior Alaska. Each site is represented by a point, indicating its forest composition and successional stage. Represented are 4 ‘early-successional aspen’ sites, 9 ‘early-successional non-aspen’, 7 ‘mid-late successional aspen’, and 9 ‘mid-late successional non-aspen’.

older burns. This spatial aggregation could influence the hymenopteran community in two ways. First, the area sampled could differ from the regional set of habitats of similar age within interior Alaska, which could influence predatory hymenopteran assemblages through bottom-up processes. Second, while we expected forest composition and successional age to exert influence over predatory hymenopteran assemblages, patterns detected in their assemblage composition may actually be driven by underlying environmental factors that are spatially autocorrelated and associated with elevation and latitude. To address the first issue, we employed a permuted subsampling test to compare the environmental conditions of the study sites to a broader set of regional LTER sites. To address the second, we tested for correlations between spatial variables (latitude, longitude, and elevation) and site environmental variables, and then compared predatory hymenopteran assemblage metrics directly to spatial variables. After conducting and interpreting these analyses, we found no evidence of spatial confounding among site categories. A thorough explanation of how we tested this issue can be found in Supplemental materials 1.

Predatory hymenopteran collection

To assess predatory hymenopteran species richness, abundance, and assemblage composition, arthropods were sampled three times at each site during the growing season using two methods. Arthropods were sampled from the ground surface with pitfall traps; 12 pitfall traps were placed at 10 m intervals within a 20 m by 30 m grid per sampling period at each site. Pitfall traps were constructed from 200 mL cups with a 6-cm diameter opening containing approximately 75 mL of a pre-diluted propylene glycol solution (20% propylene glycol, 20% glycerin, 60% deionized water: Splash brand RV & Marine Antifreeze). A pinch of bittering agent (denatonium benzoate) was added to discourage bear interest. Each pitfall trap was placed in the soil so that the upper edge of the trap was flush with the ground surface, and a foam plate was suspended 3 cm above the trap to prevent rain water from entering and overflowing the trap. Pitfall traps remained in the field for seven days per sampling period. In order to capture variation in assemblages across the growing season, each site was sampled once in each of the months of June, July, and August for a total of three trapping periods per site. Most sampling was conducted in

2014, however for some sites additional sampling was necessary, which was conducted in 2015.

Predatory hymenopterans were also sampled from vegetation via sweep netting. Sweep sampling took place once during each pitfall-sampling period (total of three sweep samples per site), on the same day as pitfall trap placement unless it was raining, in which case sweep sampling was delayed until pitfall collection seven days later. Sweep sampling consisted of 100 sweeps per site, approximately one half to one meter above the ground surface.

Predatory hymenopteran identification

Ants were identified to the species level using a variety of published sources (Francoeur 1997; Ellison et al. 2012; Glasier et al. 2013; AntWeb 2014), personal communications with Dr. Rob Higgins (Thompson Rivers University, BC, Canada, 2014–2016), and by comparison to museum specimens at the University of Alaska Museum Insect Collection.

Wasps were identified to the lowest taxonomic level possible using Goulet and Huber (1993). Most groups were identified to family, with the exception of several groups that were identified to subfamily (Braconidae, Cynipoidea, Diaprioidea, Platygastroidea, and Vespoidea) and one group to superfamily (Chalcidoidea). The same literature source was used to determine the known feeding habits of each taxonomic group of wasps, in order to validate that wasp taxa were arthropod predators or parasitoids during one or more stages of their lives (all phytophagous groups were excluded). Because the wasp taxa of the region are poorly described, wasps were grouped based on morphology into presumed species (hereafter ‘morphospecies’). Morphological characteristics used to define morphospecies included, but were not limited to: color, shape, size, pubescence, texture, or articulation, of the body (mesosoma/metasoma), wings, antennae, face, eyes, legs, or mouthparts. When possible, male wasps were given the same morphospecies identification as their respective female wasps; however, if male wasps were too morphologically dissimilar to associate with a female wasp, then they were excluded from analyses to avoid overestimating morphospecies richness. Additionally, a few wasp specimens that were too damaged to accurately identify were also excluded from analyses. Hymenopteran voucher specimens were donated to the University of Alaska Museum Insect Collection for long-term preservation (accession number: UAM-2017.10-Wenninger-Ento).

Forest characteristics

To assess tree species composition and structure, the overstory and understory basal area of each tree species (m^2/ha)

was quantified at each site. As per BNZ LTER specifications (as used in Hollingsworth et al. (2010)), overstory trees were defined as individuals with a diameter at breast height (dbh) of at least 2.5 cm (breast height = 1.37 m). For overstory trees, the dbh was used to calculate basal area. Understory individuals were defined as all tree seedlings and saplings with a dbh smaller than 2.5 cm or a total height shorter than 1.37 m. For these smaller individuals, basal area was estimated from the diameter at the base of the stem. At the intermediate sites, every overstory tree dbh was measured in 2013 by the BNZ LTER (Van Cleave et al. 2015). Understory seedlings/saplings at all sites, and overstory trees at the young sites, were measured on two, 2-by-30 m transects per site, and these basal areas were used to estimate basal area across the entire site.

Environmental variables

Environmental variables assessed at each site included slope, aspect, elevation, percent canopy cover, soil moisture potential, and soil temperature (mean and minimum). Slope (degrees), aspect (degrees, corrected for declination), and elevation (m) were retrieved from the ‘Bonanza Creek LTER Data Catalog’ (Bonanza Creek LTER 2014) (Johnstone and Hollingsworth 2013). Percent canopy cover was measured with a convex spherical densiometer in the late summer or early autumn of 2014 or 2015. Sites were characterized as the average canopy cover of four measurements (one in each cardinal direction) at each of six randomly selected locations within each plot. Soil moisture potential was categorized on a scale ranging from xeric (dry, category one) to subhygric (wet, category six) based on site topography, permafrost extent, and soil texture (Johnstone et al. 2008). Young sites were assessed in 2008, intermediate sites in 2011, and mature in 2001 by BNZ LTER. Because the factors affecting potential moisture are relatively slow to change, the BNZ LTER data were still considered accurate, despite the time passed since the last measurements were taken. Soil temperature during the growing season was measured at three locations per plot and 10 cm depth using SmartButton temperature sensors (ACR Systems, Vancouver, Canada). Temperature measurements were taken every four hours between 3 June 2015 and 11 September 2015 and averaged across time and location within each plot.

Data analysis: predatory hymenopteran richness and abundance

Predatory hymenopteran assemblages were characterized by species (or morphospecies) richness and

abundance. Data collected from pitfall and sweep sampling methods were combined at each site across all three sampling periods. Ants were analyzed separately from wasps. Furthermore, we distinguished between wasp taxa that were likely to be flight-capable and had access to aboveground plant resources, such as extrafloral nectar and foliar herbivorous prey, and predominantly litter-dwelling adapted taxa with reduced flight capabilities, which were unlikely to access foliar resources. Wasps were categorized as ‘macropterous’: taxa with fully developed wings that reach at least as far as the posterior end of the metasoma, or ‘micropterous’: apterous and brachypterous taxa. In this study, we did not differentiate between social and solitary wasps, nor parasitoids and true predators, because virtually all wasps collected were solitary parasitoids.

Because ants live in colonies, it cannot be assumed that individual pitfall captures of ants were independent events. For instance, nests that were closer to pitfall traps may have inflated the estimate of abundance if many ants fell in that trap simply due to its proximity to the nest; a nest of the same size farther from the pitfall trap at a site may have collected relatively fewer ants (Gotelli et al. 2011). To adjust for this, the ant abundance from pitfall traps was calculated on a sample basis, where the abundance was based on the number of traps that ants of each species were caught in at a site, rather than the raw number of individual ants caught in those traps (Longino et al. 2002; Gotelli et al. 2011). Ant abundance values at each site were calculated using this occurrence-based method, which better approximates colony abundance.

Data analysis: predatory hymenopterans and their relationship to tree composition

To assess relationships between predatory hymenopteran assemblages and forest characteristics, we used a multimodel inference approach. Using model selection following multiple regression, we assessed whether the assemblage richness and abundance of ants, macropterous wasps, and micropterous wasps could be explained by the understory and overstory basal areas of aspen, birch, and black spruce (Burnham and Anderson 2002). All assemblage metrics were calculated from combined pitfall and sweep data within sites. Model selection and analyses were performed in RStudio version 1.0.136, R version 3.3.3. Before conducting model selection, a full model of all forest predictor variables (basal areas of aspen understory, aspen overstory, birch understory, birch overstory, black spruce understory, and black spruce overstory) was

first run for each hymenopteran assemblage metric, and this full model was used to verify that the data met the assumptions of linear multiple regression. In order to meet the assumptions, of the model, ant richness and abundance were natural-logarithm transformed, and micropterous and macropterous wasp abundances were square-root transformed. There was no evidence of multicollinearity among the predictor variables (all VIF values <2).

Model selection was performed on each predatory hymenopteran assemblage metric by use of an all-subsets routine, ranking all 64 possible models (every combination of the 6 forest predictor variables, plus the null model which includes only an intercept) in descending order by weighted AICc (Akaike Information Criterion, corrected for small sample sizes). A confidence set of models was selected from the full set of models by descending through the AICc weight-ranked models, retaining all models in which the AICc weights cumulatively summed to ≤ 0.95 (Burnham and Anderson 2002; Symonds and Moussalli 2011). From this confidence set, model-averaged parameter coefficients were derived and weighted by AICc. The parameter coefficients were averaged across only those models that included that predictor (aka ‘conditional parameter coefficients’) (Symonds and Moussalli 2011). Coefficients are reported with 85% confidence intervals, which are appropriate under this multimodel inferential framework (Arnold 2010).

To assess overall model fit, we report R^2 , adjusted R^2 , F statistics, and Cohen’s f^2 measure of effect size (based on the adjusted R^2 value) for each full model of predatory hymenopteran assemblage metrics (Supplemental materials 2). Because the model selection procedure was based on all subsets of this full model, we were confident that models that fit well overall would also fit well when reduced to a candidate set (Symonds and Moussalli 2011).

Data analysis: predatory hymenopterans and their relationship to successional age

To test hypotheses addressing predatory hymenopteran assemblage patterns among forest habitats in different successional stages, mean metrics of predatory hymenopteran assemblages were compared across predefined categories of successional age using two-sample t -tests. Sites were assigned by age as ‘early’ or ‘mid-late’ successional based on the time since the last burn. Sites that the BNZ LTER considers young (<15 years since fire) were categorized as ‘early-successional’ ($N = 13$). Because there were only four mature sites included in this study, all sites considered intermediate or mature (>40 years since fire) by the BNZ

LTER were categorized as ‘mid-late successional’ ($N = 16$). Two-sample t -tests were used to test for mean differences in ant, macropterous wasp, and micropterous wasp species (or morphospecies) richness and abundance between successional age categories (early vs. mid-late) ($\alpha = 0.05$). Predatory hymenopteran metrics were transformed in the same way as they were for the multimodel analysis prior to the two-sample t -test analysis to meet the assumptions of equal variance and normality. All two-sample t -tests were performed in JMP Pro version 11.2.1.

Data analysis: predatory hymenopteran assemblage composition

Relationships among particular ant species and forest categories were assessed using indicator species analysis (ISA), which assesses the specificity of a species to habitat types based on exclusivity, the degree to which a species is *only* found in that habitat type, and faithfulness, the degree to which it is *always* found in that habitat type. Indicator values (IV) range from 0 to 100, with 100 signifying perfect indication, meaning the species is only and always found in that habitat type (Dufrêne and Legendre 1997). Statistical significance of indicator values are assessed by comparing the observed IV with the mean IV from 4999 permutations of a Monte-Carlo random reassignment of species to habitat types. Here, the ISA assessed each species’ specificity to forest composition and successional age categories ($\alpha = 0.05$). The ISA was not performed for wasps because, lacking scientific names, identification of indicator taxa would be of little use to others. All non-parametric analyses were performed in PC-ORD version 6.21. (For assemblage composition comparisons of ants, macropterous wasps, and micropterous wasps among successional habitats, see Supplemental material 3).

Data analysis: predatory hymenopterans and their relationships with environmental variables

To explore the relationships between local environmental variability and predatory hymenopteran assemblages, we examined correlations between predatory hymenopteran assemblage metrics and key environmental variables. Predatory hymenopteran assemblage metrics include ant, macropterous wasp, and micropterous wasp richness and abundance. To address the influence of soil microclimate on predatory hymenopteran assemblages, we used three variables: soil moisture potential, mean soil temperature, and minimum soil temperature. Both mean and minimum soil temperatures were explored because in some areas of boreal Alaska, temperatures may

reach critical minimums for thermophilic species, such as ants (Higgins 2010). We also included site slope and percent canopy cover variables, due to their indirect influences on temperature and leaf litter deposition. To explore whether predatory hymenopterans may associate with aspen on the basis of shared environmental preferences, soil moisture and temperature were correlated to the relative basal area of aspen (Pearson’s r). Strengths of correlations (Pearson’s r) were assigned using the guidelines outlined by Cohen (1992), where strong, moderate, and weak correlations correspond to magnitudes of Pearson’s $r \geq 0.5$, $0.5 > r \geq 0.3$, and $0.3 > r \geq 0.1$, respectively. Magnitudes of $r < 0.1$ are considered non-correlated. All correlations were performed in JMP Pro version 11.2.1.

Results

Predatory hymenopteran richness and abundance

Pitfall trapping and sweep netting collected a total of 2659 ant individuals (1043 discrete occurrences) of seven species: *Camponotus herculeanus* (Linnaeus), *Myrmica alaskensis* (Wheeler), *Leptothorax muscorum* (Nylander), *Formica neorufibarbis* (Emery), *F. subaenescens* (Emery), *F. aserva* (Forel), and *F. podzolica* (Francoeur). Most ant captures occurred in pitfall traps (Table 1). All species of ant were captured from both collection methods except *Formica aserva*, which was absent from sweep net samples.

A total of 1176 wasp individuals were collected, 1092 of which were grouped into 363 morphospecies belonging to nine superfamilies: Cerphronoidea, Chalcidoidea, Chrysidoidea, Cynipoidea, Diaprioidea, Ichneumonoidea, Platygastroidea, Proctotrupoidea, and Vespoidea. Of the wasps categorized to morphospecies, 853 individuals (326 morphospecies) were characterized macropterous and 239 individuals (37 morphospecies) were characterized micropterous. Macropterous wasps were abundant and morphospecies rich across both sweep and pitfall collection methods, but micropterous wasps were almost exclusively captured in pitfall traps (Table 1).

Predatory hymenopterans and tree composition

Both ant species richness and abundance were negatively related to the basal area of overstory aspen, birch, and black spruce. The magnitude of these relationships was qualitatively weaker for aspen overstory than for the other tree species. Ant species richness was positively, though weakly, related to the basal area of

Table 1. Species or morphospecies richness and abundance of ants, macropterous wasps, and micropterous wasps collected from sweep netting and pitfall trapping. Sample-based abundance values are noted parenthetically for ants.

Predatory hymenopteran assemblage metric	Pitfall collections	Sweep collections
Ant richness	7	6
Ant abundance	2555 (939)	104 (104)
Macropterous wasp richness	146	199
Macropterous wasp abundance	496	357
Micropterous wasp richness	37	2
Micropterous wasp abundance	237	2

understory aspen, and unrelated to birch or spruce understory (Table 2(a)). In all cases, ant metrics were most strongly negatively associated with birch overstory.

Macropterous wasp morphospecies richness and abundance were positively associated with both aspen understory and birch overstory (Table 2(b)). Based on the magnitude of the coefficients, the association of macropterous wasp abundance and morphospecies richness with aspen understory was stronger than the association with birch overstory. Macropterous wasp abundance was also negatively associated with birch understory.

Like macropterous wasps, micropterous wasp abundance was positively associated with aspen understory and birch overstory, though again the positive relationship with aspen understory was stronger than the relationship with birch overstory (Table 2(c)). Micropterous wasp abundance was also negatively associated with black spruce understory, black spruce overstory, and birch understory

(Table 2(c)). Micropterous wasp morphospecies richness was negatively associated with black spruce overstory (Table 2(c)), but as mentioned previously the modeling procedure overall was weak at explaining relationships of micropterous wasp morphospecies richness.

Predatory hymenopterans and successional age

Ant assemblages were more speciose and abundant in early relative to later succession habitats. Significantly more ant species were collected from early-successional sites than from mid-late successional sites ($t_{27} = -2.61$, $p = 0.015$). On average, there were two more ant species collected from early-successional sites than mid-late successional sites (early-successional: mean = 5 species, SE = 0; mid-late successional: mean = 3 species, SE = 0) (Figure 2(a)). Additionally, significantly more ant occurrences were collected from early successional sites than from mid-late successional sites ($t_{27} = -2.82$, $p = 0.009$). On average, there were 140% more ant occurrences in early-successional sites than in mid-late successional sites (early-successional: mean = 53 ant occurrences, SE = 9; mid-late successional: mean = 22 ant occurrences, SE = 5) (Figure 2(b)).

In contrast, neither macropterous nor micropterous wasp assemblages varied by successional age (Figure 2(c–f)). There were no significant differences in macropterous or micropterous wasp morphospecies richness or abundance between early and mid-late successional sites (Macropterous wasp

Table 2. Conditional model-averaged parameter coefficients with adjusted standard errors and 85% confidence intervals for all ant (a), macropterous wasp (b), and micropterous wasp (c) response variables. Parameters with coefficient 85% confidence intervals that do not overlap zero are denoted in bold.

Model parameter	β	adj. SE	85% CI	β	adj. SE	85% CI
A) Ants						
Ant richness			Ant abundance			
intercept	1.53	0.15	1.31, 1.75	3.62	0.23	3.29, 3.95
Aspen understory	0.14	0.10	0.00, 0.28	0.20	0.15	-0.01, 0.42
Aspen overstory	-0.02	0.01	-0.04, -0.01	-0.04	0.02	-0.07, -0.01
Birch understory	0.07	0.12	-0.11, 0.25	0.03	0.18	-0.23, 0.29
Birch overstory	-0.08	0.04	-0.14, -0.03	-0.22	0.06	-0.31, -0.13
Black spruce understory	0.00	0.05	-0.06, 0.07	0.06	0.07	-0.04, 0.16
Black spruce overstory	-0.05	0.03	-0.08, -0.01	-0.07	0.04	-0.12, -0.12
B) Macropterous wasps			Macropterous abundance			
intercept	15.13	2.03	12.26, 18.00	4.66	0.39	4.09, 5.22
Aspen understory	4.12	1.43	2.10, 6.15	0.71	0.28	0.31, 1.11
Aspen overstory	0.13	0.20	-0.15, 0.40	0.04	0.04	-0.01, 0.09
Birch understory	-1.04	1.92	-3.76, 1.67	-0.47	0.33	-0.94, -0.01
Birch overstory	1.38	0.48	0.70, 2.07	0.20	0.09	0.07, 0.32
Black spruce understory	-0.19	0.66	-1.12, 0.74	-0.09	0.12	-0.25, 0.08
Black spruce overstory	0.03	0.37	-0.50, 0.55	-0.02	0.07	-0.12, 0.08
C) Micropterous wasps			Micropterous abundance			
intercept	4.06	0.58	3.23, 4.88	2.48	0.36	1.96, 2.99
Aspen understory	0.47	0.42	-0.12, 1.07	0.66	0.23	0.34, 0.99
Aspen overstory	0.00	0.06	-0.08, 0.08	-0.02	0.03	-0.06, 0.03
Birch understory	-0.36	0.51	-1.08, 0.36	-0.74	0.26	-1.11, -0.38
Birch overstory	0.18	0.15	-0.04, 0.39	0.23	0.08	0.12, 0.33
Black spruce understory	-0.22	0.17	-0.46, 0.03	-0.17	0.09	-0.29, -0.04
Black spruce overstory	-0.15	0.09	-0.29, -0.02	-0.08	0.05	-0.15, -0.01

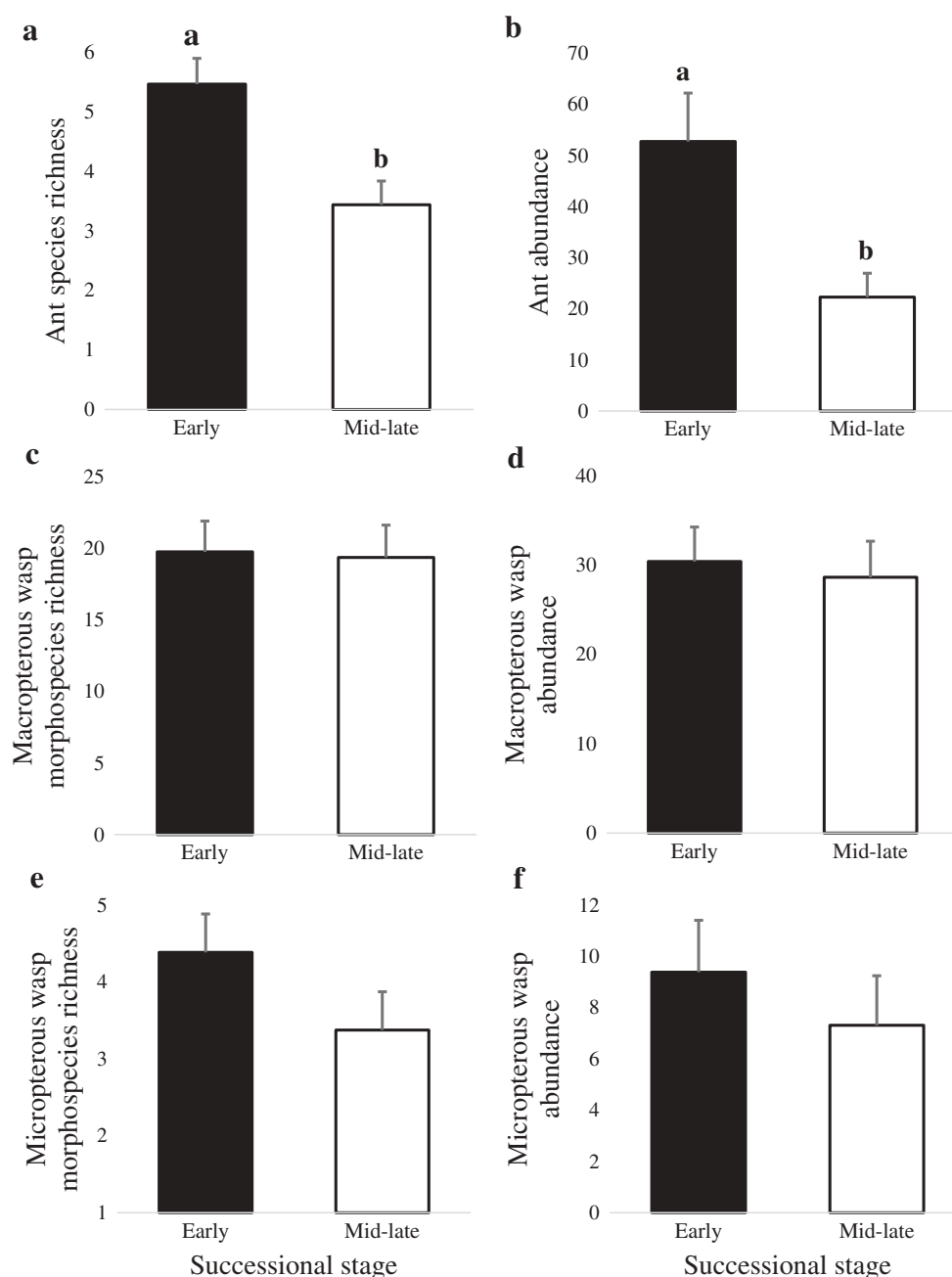


Figure 2. Mean richness and abundance of ants, macropterous wasps, and micropterous wasps by successional age (early/mid-late) categories. Error bars represent standard errors. Lower case letters above bars indicate statistically significant differences between the means (two-sample t-test).

morphospecies richness: $t_{27} = -0.12$, $p = 0.902$, macropterous wasp abundance: $t_{27} = -0.39$, $p = 0.703$, micropterous wasp morphospecies richness: $t_{27} = -1.41$, $p = 0.169$, micropterous wasp abundance: $t_{27} = -1.19$, $p = 0.245$).

Ant assemblage composition

The frequency with which ants were collected from the four habitat types varied by species (Figure 3).

Five of the seven species of ants were collected predominantly from early-successional sites, whereas two species of ants were not collected in greater proportions from any one age class. The indicator species analysis of the associations of each ant species with forest categories showed that four species of ants, *Leptothorax muscorum*, *Formica aserva*, *F. subaenescens*, and *F. podzolica*, were strongly associated with early-successional aspen stands (Table 3).

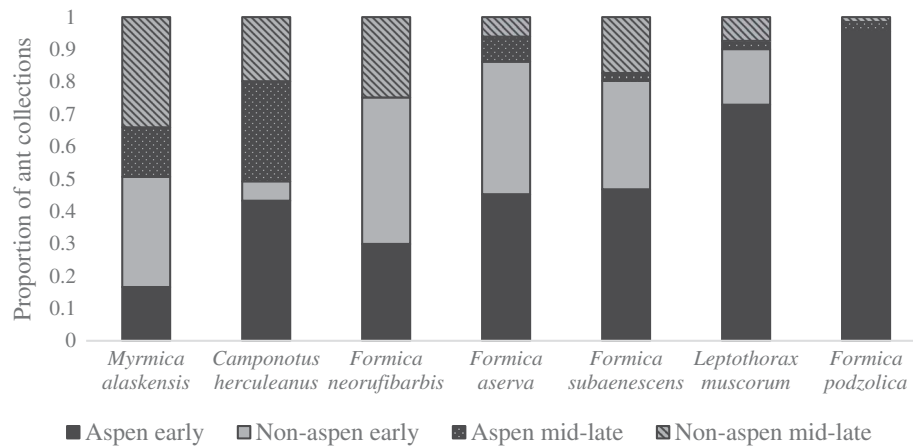


Figure 3. Proportion of ant species collected by forest composition (aspen/non-aspen) and successional age (early/mid-late) categories. Proportions were standardized by the number of sites that constituted each forest category.

Table 3. Observed versus simulated indicator values (IV) for ant species. Displayed forest category represents the group that ant species is most indicative of (degree to which they are always and only found in that habitat type). Bold *p* denotes statistical significance ($\alpha = 0.05$).

Ant species	Forest category	Observ. IV	Randomized IV		<i>p</i>
			Mean	St. dev	
<i>Myrmica alaskensis</i>	Early non-aspen	34.0	34.1	5.2	0.447
<i>Leptothorax muscorum</i>	Early aspen	72.9	36.2	10.8	0.002
<i>Camponotus herculeanus</i>	Early aspen	43.3	34.4	5.9	0.082
<i>Formica aserva</i>	Early aspen	45.3	25.9	9.0	0.037
<i>Formica neorufibarbis</i>	Early non-aspen	35.2	28.6	8.7	0.201
<i>Formica subaenescens</i>	Early aspen	46.8	31.2	7.0	0.033
<i>Formica podzolica</i>	Early aspen	47.8	20.2	10.4	0.018

Predatory hymenopterans and their relationships with environmental variables

In general, ant species richness was poorly related to soil microclimate. Ant species richness was weakly positively correlated with mean soil temperature, but no correlation was detected between ant species richness and soil moisture potential or minimum soil temperature (Table 4). However, ant abundance was somewhat more related to soil microclimate (Table 4). Ant species richness and abundance were both strongly and negatively related to canopy cover (Table 4).

Macropterous wasp abundance was moderately and positively correlated to mean and minimum soil temperatures, whereas macropterous wasp morphospecies

richness was only weakly correlated to soil temperature (Table 4). Both macropterous wasp morphospecies richness and abundance had moderate negative relationships with soil moisture potential.

Micropterous wasp morphospecies richness and abundance were unrelated to soil moisture and somewhat positively correlated to both mean and minimum soil temperatures; relationships were wholly positive but ranged from weak to moderate for soil temperatures (Table 4). Both micropterous wasp morphospecies richness and abundance were negatively correlated to slope (Table 4). Neither morphospecies richness nor abundance of micropterous wasps were correlated to percent canopy cover.

Table 4. Pearson's correlations (*r*) of predatory hymenopteran assemblage metrics and environmental variables of sites. Bold denotes 'moderate' correlation ($r \geq 0.30$), bold and underline denotes 'strong' correlation ($r \geq 0.50$).

Predatory hymenopteran assemblage metrics	Environmental variables				
	Soil moisture	Soil temp. (mean)	Soil temp. (min.)	Slope	Canopy cover
Ant richness	-0.04	0.27	0.06	0.11	-0.62
Ant abundance	0.13	0.30	-0.04	0.01	-0.75
Ant biomass	0.01	0.27	-0.01	0.03	-0.62
Macropterous wasp richness	-0.34	0.22	0.26	-0.12	0.26
Macropterous wasp abundance	-0.42	0.36	0.46	-0.18	0.22
Micropterous wasp richness	0.02	0.33	0.32	-0.50	-0.10
Micropterous wasp abundance	-0.03	0.18	0.28	-0.44	0.02

As expected, aspen was associated with warm, well-drained soil conditions. Soil moisture was strongly negatively related to the percent of aspen at a site (Pearson's $r = -0.55$). Mean and minimum soil temperatures were strongly positively related to percent aspen (Pearson's $r = 0.66$, $r = 0.79$, respectively).

Discussion

Predatory hymenopteran assemblages varied considerably among forests composed of different tree species and stand structures. Macropterous wasps, and to a lesser extent ants, were most species-rich in forest stands composed of aspen seedlings and saplings relative to birch and black spruce. Both macropterous and micropterous wasps were most abundant in stands composed of aspen seedlings and saplings. There was little evidence that macropterous or micropterous wasps were influenced by successional time, however, the strong negative associations between ants and mid-late successional forests suggest that ants decline in abundance and species richness as post-fire succession proceeds. These changes in ant assemblages are consistent with differences in soil microclimate.

Predatory hymenopterans and their relationship to tree composition

Ants and wasp assemblages differed in their response to variation in boreal forest composition and structure. The results of this study suggest that ant assemblages are not strongly influenced by dominant tree composition in boreal Alaska, which is contrary to our initial prediction. We predicted that ant richness and abundance would be positively influenced by aspen, particularly when it occurred in the understory. We found a weak association between ant richness and aspen basal area in the understory, and a stronger negative association between both richness and abundance and aspen basal area in the overstory. This provides little evidence for the hypothesis that aspen, through the provisioning of extrafloral nectar and increased palatability, supports more abundant and species-rich ant assemblages; a surprising result given that ants are the predominant visitors of extrafloral nectaries (Heil 2015). However, in this study we characterized the ant assemblage as a whole, not just those ant species that commonly use foliar resources. Our results indicate that the magnitude of the aspen understory coefficient was relatively large for all ant assemblage metrics, but the variability around that coefficient was also high. Ants are opportunistic foragers, and this result suggests that some species of ants may be influenced by tree composition in some successional contexts. The

indicator-species analysis shows that four of the seven species of ants were associated specifically with early-successional aspen sites. This suggests that for some ant species in interior Alaska, early-successional aspen stands may provide critical resources such as extrafloral nectar or prey availability.

In contrast to ants, macropterous and micropterous wasps showed clear preferences with respect to tree composition. While parasitoid wasps are important consumers of extrafloral nectar, the contribution of extrafloral nectar resources in shaping wasp communities is poorly understood (Heil 2015). Our results are consistent with a combination of extrafloral nectar and foliage palatability as drivers of the relationship between tree composition and wasp assemblages, as we observed a positive relationship between macropterous wasp abundance and morphospecies richness and the basal area of aspen seedlings and saplings. As expected, macropterous wasps had stronger relationships with aspen seedlings and saplings than with mature aspen trees, consistent with evidence that extrafloral nectary expression is more frequent on smaller aspen than on larger-sized aspen (Doak et al. 2007). While overstory trees produce more leaves than small trees, extrafloral nectar may be more efficiently located in early-successional stands, which would explain why macropterous wasps were most abundant and morphospecies rich in early-successional aspen stands. However, because micropterous wasps, by virtue of tiny size and limited mobility, are unlikely to access foliar resources such as extrafloral nectar, a more parsimonious explanation is that both micropterous and macropterous wasp abundances were positively associated with aspen seedlings and saplings for reasons other than extrafloral nectar.

The positive relationships that macropterous wasp assemblages had with young aspen and mature birch are also consistent with the idea that foliage palatability, acting through its effects on the prey base, may influence these assemblages. The evidence for prey availability as an influential factor stems from the observations that both macropterous and micropterous wasp abundances were negatively associated with birch seedlings and saplings, but positively associated with mature birch trees. Younger hardwood trees tend to invest more energy into defense than more mature trees (Bryant et al. 1983; Bryant and Julkunen-Tiitto 1995; Boege and Marquis 2005; Donaldson et al. 2006), therefore mature trees may support more abundant, diverse, and palatable herbivores as prey for predators (Price et al. 1980). Additionally, overstory trees offer more structural niches than understory vegetation, and typically are associated with increased herbivore

diversity (Lawton 1983). Because conifer species tend to invest more energy in defense than hardwood species (Loehle 1988), the strong negative relationships that micropterous wasp morphospecies richness and abundance have with black spruce were also consistent with the idea that prey may structure these wasp assemblages. However, distributional patterns of macropterous wasps differed from those of micropterous wasps in this regard and did not have strong negative relationships with black spruce, which suggests that macropterous and micropterous wasps are responding to different factors. Additionally, the relationships between wasps and aspen were inconsistent with what would be expected if prey availability alone were driving these assemblages. Macropterous wasp abundance and morphospecies richness, and micropterous wasp abundance, were positively influenced by aspen seedlings and saplings, but not by mature aspen. This contradicts the foliage palatability hypothesis because smaller aspen seedlings and saplings produce more phenolic glycosides and should be less palatable to generalist herbivores than larger, mature aspen (Donaldson et al. 2006; Young et al. 2010). While the relationships between wasp assemblages and tree composition were not wholly consistent with extrafloral nectar or plant palatability alone, some combination of these potential influences could explain the observed patterns in predatory hymenopteran assemblages.

It is also possible that microclimatic factors associated with aspen stands may contribute to the association between predatory hymenopteran assemblages and aspen. The relative abundance of aspen was negatively associated with soil moisture and positively associated with soil temperature. While macropterous wasps were the only predatory hymenopterans with moderate negative relationships to soil moisture, all predatory hymenopteran groups were positively associated with soil temperature. The correlations between soil temperature and the abundance and richness of ants, macropterous wasps, and micropterous wasps were consistently positive but ranged from weak to moderate, suggesting temperature is important for predatory hymenopterans, but is likely not solely responsible for the patterns seen in these assemblages. Unexpectedly, macropterous wasps were more strongly negatively associated with soil moisture than ants or micropterous wasps, and were similarly positively associated with soil temperature. This contradicts the prediction that ants and micropterous wasps would be more directly dependent upon, and thus related to, soil properties than macropterous wasps. Interestingly, micropterous wasp morphospecies richness and abundance were,

respectively, strongly and moderately negatively related to slope across sites (Table 4). Sites with steeper slopes may accumulate a shallower layer of leaf litter necessary to sustain micropterous wasp assemblages.

Predatory hymenopteran assemblages and post-fire successional stage

This study provides evidence that changes occur in ant assemblages during post-fire succession in the boreal forest. In contrast to wasp assemblages, which did not vary with successional age, ant assemblages were significantly more species-rich and abundant in early-successional forests compared to mid-late successional forests. Previous studies in eastern Nearctic boreal black-spruce forests (Quebec, Canada) found that, in general, abundance of ant nests increased throughout the first 30 years after fire, but ant nest abundance was strongly reduced by year 62 post-fire (Boucher et al. 2015). This general pattern holds true for our study as well; ant occurrences were most frequent in early-successional sites, burned in 2004. However, the patterns of species composition have not been consistent across studies. In the Quebec boreal forest, *C. herculeanus* and *F. neorufibarbis* were predominantly found in 60-year old burn sites, suggesting these species thrive late in post-fire succession (Boucher et al. 2015), whereas a study of post-logging succession in sub-boreal lodgepole pine forests (British Columbia, Canada) found that both *C. herculeanus* and *F. neorufibarbis* were found in regenerating forests up to 25 years post-harvest (early succession), but were not present in unharvested sites (late succession) (Higgins and Lindgren 2015). The assemblage composition results of our study were consistent with aspects of both previous studies, in that both *C. herculeanus* and *F. neorufibarbis* were represented in both early- and mid-late-successional forests. These species apparently arrive early in post-fire succession, and unlike many other Alaskan formicine species, they also persist into later successional stages (Figure 3).

The facultative wood-nesting behavior of some ant species may facilitate their persistence into the later successional stages. Wood can provide a warmer nesting substrate than soil (Higgins and Lindgren 2012). In particular, *C. herculeanus*, *F. neorufibarbis*, and *M. alaskensis* have been frequently observed as wood nesters (Francoeur 1997), which is consistent with the frequencies of which these species have been observed in our study in early-successional forests relative to other, predominantly soil-nesting, species (Figure 3). Our results are similar to those from sub-boreal forests of British Columbia, Canada, which found that *M. alaskensis* persisted into later successional stages and was particularly cold-tolerant

(Higgins 2010). Results from sub-boreal studies of *F. aserva* and *L. muscorum* found that these species are sensitive to advances in succession, because the canopy shading in older successional forests prevents nest heat gain from insolation (Higgins 2010; Higgins and Lindgren 2012). Consistent with these results, we collected *F. aserva* and *L. muscorum* predominantly from early-successional aspen stands (Figure 3), where the warmest mean soil temperatures were observed (early-successional aspen: $10.5 \pm 0.98^\circ\text{C}$, mid-late successional aspen: $8.7 \pm 0.33^\circ\text{C}$, early-successional non-aspen: $7.9 \pm 0.40^\circ\text{C}$, mid-late successional non-aspen: $7.5 \pm 0.41^\circ\text{C}$).

Implications of a changing boreal forest on predatory hymenopteran assemblages

As climate-driven changes in the boreal fire regime increase in magnitude, the resulting changes in boreal vegetation communities (Hollingsworth et al. 2013) are likely to influence predatory hymenopteran assemblages. Because aspen persistence is favored by frequent and severe fires, aspen may become more widely distributed on the landscape (Johnstone and Kasischke 2005; Johnstone et al. 2010b). Based on our results, increased aspen prevalence on the landscape would increase the species richness of macropterous wasps, and to a lesser extent ants, as well as the abundance of macropterous and micropterous wasps. One potential implication of this is that the support of predatory hymenopterans by aspen could shift the ratio of predators to prey, which could reduce herbivore pressure across plants within the community.

An increase in forest fire frequency and extent will increase the proportion of forests in younger successional stages. Our results indicate that this will increase the species richness and abundance of ants on the landscape. Conversely, many species of parasitoid wasps, but especially the micropterous wasps, dwell within soil and leaf litter, and frequent, severe burns may reduce the available habitat for these species. Parasitoid wasps as a group are considered extinction-prone largely due to four characteristics: rarity, high trophic positioning, dependence on an unreliable resource, and poor dispersal capabilities (LaSalle and Gauld 1991, 1993; LaSalle 1993). Many parasitoids regulate their hosts at low-population levels, limiting their own abundance as well as the availability of the resources they depend on (LaSalle and Gauld 1991, 1993; LaSalle 1993). The dispersal limitations are especially acute for micropterous wasps, which lack flight capability. If fires increase in frequency to the point that these litter-dwelling wasps have little time to

establish, or fires expand in extent to the point of severely hindering their access to resources, then species diversity may decline throughout interior Alaska.

Northern high-latitude biomes, including the boreal forest, are warming at twice the average global rate (IPCC 2013). Climate change has altered forest and vegetation composition (Hollingsworth et al. 2013) in ways that will cascade to forest-associated animal communities. This study increases our baseline understanding of the assemblage composition and distribution of predatory hymenopterans, including litter and soil-dwelling Hymenoptera. Litter and soil-dwelling Hymenoptera are exceptionally diverse, and have been estimated to represent up to 30% of the soil-associated fauna in temperate beech forests (Ulrich 2004). Despite their numbers, micropterous Hymenoptera have been especially overlooked, not just in the boreal forest, but globally (Ulrich 2004; Silva and Feitosa 2017). To our knowledge, this study is the first to characterize the composition of micropterous wasp assemblages and their relationships with forest characteristics in the boreal forest. The wasp individuals captured in this study represented a wide diversity of taxa, and because the species accumulation curves were unsaturated and many of the morphospecies captures were singletons, the diversity of wasps detected in this study represents only a fraction of the total diversity in the boreal forest (See Supplemental material 4). Sampling methods specifically designed to target these organisms, such as via use of Winkler or Burlese funnels, may yield a more thorough representation of the soil and litter associated hymenopterans of boreal Alaska (Silva and Feitosa 2017).

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