PATTERNS AND IMPACTS OF ARBOREAL SPIDERS IN A BOREAL ECOSYSTEM, WESTERN NEWFOUNDLAND, CANADA

By

Megan L. Doyle

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Boreal Ecosystems and Agricultural Science Unit

The undersigned certify that they have read and recommend to the Boreal Ecosystems and Agricultural Science Unit (School of Graduate Studies) for acceptance, a thesis entitled "patterns and impacts of arboreal spiders in a boreal ecosystem, western Newfoundland, Canada" submitted by Megan L. Doyle in partial fulfillment of the requirements for the degree of Master of Science.

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Dr. Julie Sircom (thesis supervisor)

_____

Dr. Joe Bowden (thesis supervisor)

_____

Dr. Eric Moise (thesis supervisor)

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Abstract

Spiders are known for their direct (consumptive) and indirect (non-consumptive) impacts on herbivorous insects. It is unclear to what degree these effects occur in structurally complex habitats like boreal forest canopies. It is reasonable to expect that the relationship between vegetative structure and spider populations would manifest at the stand level; however, few studies have explored these relationships at this scale. I conducted two studies to examine the direct and indirect effects of spiders on a common forest insect pest and to compare the spider community in differing forest stands in the boreal forest.

Using a microcosm experiment, I established a study to determine both the consumptive and non-consumptive effects of spiders on spruce budworm. I found that spiders did not significantly affect the survival, mass or defoliation caused by spruce budworm. Instead, bottom-up control from the number of available shoots appeared to be a more important factor. Even though this study suggests spiders are less effective as natural enemies in controlling spruce budworm populations than predicted, much remains to be learned about their role in forest pest control. I also examined spider community assemblages in three different forest stands. Deciduous stands had greater spider abundance and species richness than coniferous and mixedwood stands, but diversity indices were similar among the three stand types.

My studies provide insights into the relationship between spiders and forest ecosystems and spiders as natural enemies of a common forest pest. These findings highlight the importance of considering diversity and complexity in biodiversity management and contribute to understanding how biodiversity responds to environmental conditions and forest management practices.

General Summary

Spiders represent an excellent model organism for investigating predator-prey interactions among boreal forest arboreal arthropods. I examined the arboreal spider community in western Newfoundland. I found that species abundance is significantly impacted by stand type. While the number of species differed slightly among stand types, how evenly those individuals were distributed among those species did not. I also investigated the potential direct (predation) and indirect (fear) effects of spiders on spruce budworm, a common boreal forest insect pest species. My results indicate that spider presence (both directly and indirectly) does not affect spruce budworm survival, mass, or herbivory rates. Overall, this study contributes to understanding the relationship between spider populations, forest structure, and their role in forest pest control, emphasizing the importance of considering the diversity and complexity of forest ecosystems in biodiversity management.

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1.0 Literature Review

Introduction

A diverse species assemblage is crucial for maintaining ecosystem health, structure, and functioning and serves as a benchmark for tracking changes over time. While research on biodiversity has predominantly focused on tropical forests or agricultural landscapes (Janz et al., 2006; Maynard et al., 2017), ecosystems at higher latitudes have received less attention. The boreal forest, which constitutes 75% of Canada's forests, harbours a significant proportion of the nation's biodiversity (Natural Resources Canada, 2009). Boreal forests are characterized by cold-tolerant tree species that form relatively even-aged stands due to their shade-intolerance and the natural disturbance regimes of the region (Brandt, 2009).

With 9% of the world's forested land cover (Natural Resources Canada, 2009), the Canadian boreal forest is home to an extensive diversity of arthropods that play various roles in the ecosystem. Given that arthropods, including insects, are one of the most abundant and diverse groups of organisms on earth (Schowalter, 2012; Sharkey, 2001), it's not surprising that insect outbreaks are the primary natural disturbance agent for eastern Canadian boreal forests (Brandt et al., 2013). Four main native insect defoliators; forest tent caterpillar (*Malacosoma disstria*) (Hubner) (Volney & Fleming, 2000), large aspen tortrix (*Choristoneura conflictana*) (Walker), jack pine budworm (*Choristoneura pinus pinus*) (Freeman) and eastern spruce budworm (*Choristoneura fumiferana*) (Clemens), periodically reach damaging population levels in the Canadian boreal forest, causing growth suppression and tree mortality if the outbreak persists for several years. The spruce budworm is the most destructive of these pests, causing severe defoliation, growth loss, and tree mortality (Pureswaran et al., 2016).

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Monitoring arthropod populations can increase our collective understanding of how their relationship with the environment influences biodiversity and ecosystem functioning. In particular, understanding the roles that arthropod predators play in forested ecosystems, either through direct (consumptive) or indirect (non-consumptive) interactions with prey, is not only valuable from an ecological perspective but also in situations that involve irruptive herbivorous forest pests (Johns et al., 2019). While traditional approaches to biocontrol have focused on native and introduced specialist predators and parasitoids (MacQuarrie et al., 2016), there is a growing appreciation for the role of other natural enemies in biological systems. Natural enemies play an essential role in regulating insect populations (Johns et al., 2019). The abundance and diversity of natural enemies may be related to habitat variability and the density of food resources (Boyd et al., 2013). For example, forest stands with multiple tree species may support more predators and parasitoids because they provide an alternative prey or food source and enhance structural complexity for natural enemies. There is limited information regarding the natural predators of spruce budworm, with spiders being particularly understudied. Maintaining balanced insect populations is crucial to forest ecosystem preservation by mitigating the destructive effects of irruptive insects. The few studies conducted on predation on spruce budworm by spiders make it challenging to determine whether spiders can exert enough mortality to influence spruce budworm populations (but see: (Bowden et al., 2022; Jennings, Dimond, et al., 1990; Jennings & Houseweart, 1989; Loughton et al., 1963; Mason et al., 1997).

Spiders are an ideal model taxon to study these interactions as they are present in all terrestrial ecosystems. They are relatively abundant, have high functional diversity, and have relatively stable and accessible taxonomy (Coddington & Levi, 1991). Studies have emphasized the significance of habitat structure in determining spider diversity and distribution, with several

researchers examining this relationship (Halaj et al., 1998, 2000; Jennings, Dimond, et al., 1990; Jennings et al., 1988; Pettersson, 1996; Sundberg & Gunnarsson, 1994). Among the factors influencing spider abundance and richness are the density, arrangement, and complexity of branches and twigs and the heterogeneity of the canopy (Corcuera et al., 2008; de Souza & Martins, 2005; Greenstone, 1984; Halaj et al., 2000; Hatley & MacMahon, 1980). Compared to coniferous forest stands, mixedwood and deciduous stands display greater structural diversity, possibly supporting a greater variety of prey for spiders and, thus, a more diverse spider population (Pinzon et al., 2011).

Habitat heterogeneity promotes increased abundance and diversity of natural enemies, which has been shown in agricultural ecosystems (Janz et al., 2006; Maynard et al., 2017; Palmer & Maurer, 1997; San Roman & Wagner, 2021). In contrast to monocultures, stand mixtures of tree species may support a greater abundance and diversity of natural enemies in boreal forests, which could increase predation on herbivorous insects and reduce herbivory. Specifically, in situations that involve irruptive insect pests, generalist natural enemies may also contribute to additive mortality, where management goals may seek to maintain pest populations at endemic levels. Thus, spiders can have important impacts on plant health, ecosystem processes, and biodiversity in an ecosystem. Understanding their role in regulating insect populations may be fundamental for effective pest management strategies that aim to promote healthy ecosystems and preserve biodiversity.

Despite some interest in spider community structure in the boreal forest (Halaj et al., 1998, 2000; Lawton, 1983; Southwood et al., 2005; Thunes et al., 2003), there has been substantially less focus relative to predator-prey interactions involving other taxa. As generalist predators, spiders can control insect herbivores from the top down, limiting their abundance and

activities (Bowden et al., 2022; Nyffeler & Benz, 1987; Nyffeler & Birkhofer, 2017). In fact, spiders have been shown to serve as important natural enemies in agricultural systems (Kahl et al., 2021), in the high Arctic (Roslin et al., 2013) and in forests (Bowden et al., 2022). They can have direct (consumptive) or indirect (non-consumptive) effects on prey populations. In addition to direct predation, many spider species exhibit a behaviour known as superfluous (wasteful) killing, which appears to be a density-dependent behaviour and particularly fitting for controlling irruptive insects (Maupin & Riechert, 2001). In addition to reducing herbivory by directly preying on herbivorous insects, they also influence herbivory indirectly by influencing their behaviour. This response is believed to be an evolutionary adaptation, as animals have developed the ability to detect chemical cues and respond to them to reduce their risk of predation (Beckerman et al., 1997; Schmitz et al., 1997). Indirect effects are caused by the prey species' fear of spiders, for example herbivorous insects may change their feeding behaviour, avoid certain parts of plants, or consume less overall, resulting in reduced plant damage (Beckerman et al., 1997; Kahl et al., 2021).

Biodiversity

Biodiversity is among the most significant components of ecosystem health, structure, and function. It supports many ecosystem services while allowing these systems to respond to environmental change and provides a baseline for measuring these changes in time (Thompson et al., 2009). A more diverse ecosystem (i.e., structural diversity and plant diversity) leads to a greater diversity of organisms (Hector & Bagchi, 2007).

Approximately 75% of Canada's forests are in the boreal zone, contributing significantly to the country's environment, culture, and economy (Brandt et al., 2013). In addition to

supporting most of Canada's rural and remote forest-dependent communities, the boreal forest

also hosts a significant portion of the country's biodiversity (Brant, 2009). The uniqueness of

boreal forests stems from their harsh environmental conditions, which include large annual

temperature ranges, cool brief summers, long cold winters, and moderate amounts of

precipitation concentrated in summer. The boreal forest is characterized by cold-tolerant tree

species such as fir, larch, spruce, pine, poplar, and birch that form relatively even-aged stands

due to the species' shade-intolerance and the natural disturbance regimes of the region. Most

diversity studies have been conducted in tropical forests or agricultural systems (Janz et al.,

2006; Maynard et al., 2017; Palmer & Maurer, 1997; San Roman & Wagner, 2021), while fewer

studies have assessed the diversity of the boreal forest (Angelstam, 1998; Venier et al., 2014).

Insect Outbreaks

Among the most important drivers of boreal ecosystem dynamics are natural disturbances

such as fires, insects, diseases, and climate-related disturbances (Brandt, 2009). Semi-continental

disturbances such as wildfires and insect outbreaks are characteristic of boreal forests (Brandt et

al., 2013; Waide et al., 1999). In western and central boreal forests, fire is the dominant driver of

forest turnover (Brandt et al., 2013). Eastern Canadian boreal forests, however, are more humid

and have a prolonged fire cycle (McCarthy & Weetman, 2006). In this region, insect outbreaks

are the primary natural disturbance agent for coniferous, and mixedwood stands (Brandt, 2009).

Four native insect defoliators in the Canadian boreal forest periodically reach damaging

population levels. They can defoliate millions of hectares of susceptible host species, causing

growth suppression and tree mortality if the outbreak persists for several years (Maclean, 2004).

Boreal deciduous trees are primarily defoliated by the forest tent caterpillar (Volney & Fleming,

2000) and large aspen tortrix. The primary defoliators of boreal conifers are jack pine budworm and spruce budworm (Ives & Wong, 1988; Rose et al., 1999; Rose & Lindquist, 1997; Rose & Linquist, 1994; Volney & Fleming, 2000). The shared hosts of these insects, spruce, fir, jack pine and poplar make up approximately 87% of the species composition of the boreal forest and over 90% of the timber volume (NFI (National Forest Inventory), 2017).

Of the North American native forest pests, the spruce budworm is the most destructive. A distinct characteristic of the spruce budworm is the sheer magnitude and longevity of outbreaks. In their endemic phase, populations are virtually undetectable but can erupt suddenly, causing severe defoliation, growth loss, and tree mortality. In Canada and the United States, outbreaks occur every 30-40 years, lasting up to 20 years, destroying millions of hectares of spruce-fir forests (Pureswaran et al., 2016).

Natural Enemies

Both predator and prey insects inhabit the boreal forest and play an important role in regulating populations of other insect species and their own. Understanding the population dynamics of forest pests, such as the factors contributing to outbreaks and the natural enemies associated with them, is crucial to developing successful management strategies (Duan et al., 2015). Various natural enemies exert top-down pressure on herbivorous insects, which can vary between habitats. A long-standing hypothesis, the 'enemies hypothesis' (Root, 1973), suggests that heterogeneous habitats may promote increased abundance and diversity of natural enemies, and their actions will result in lower herbivore population densities. Generalist natural enemies should be more abundant in complex systems since they can capitalize on a greater variety of

prey or hosts. As the seasons change, different prey species become available, allowing predators to access a greater variety of hosts or prey (Letourneau, 1987).

Many environmental variables, such as temperature and humidity, influence predator and prey populations. Moreover, differences in enemy pressure may be more closely related to habitat variability and the density of food resources (Schowalter, 2012). Several studies show positive effects of habitat heterogeneity on the abundance and diversity of natural enemies in agricultural ecosystems (Kelly et al., 2016; Landis et al., 2000; Langellotto & Denno, 2004; Prieto-Benítez & Méndez, 2011; Veres et al., 2013; Woltz et al., 2012). In contrast to monocultures, stand mixtures of tree species may support more predators and parasitoids by providing an alternative prey or food source. Forest stands with multiple tree species can also enhance structural complexity for natural enemies and provide microhabitats to reduce negative interactions and intraguild predation. A higher structural complexity can also lead to more branch connectivity, allowing natural enemies (which tend to be more mobile than their prey) to move between trees more easily (Korenko et al., 2011).

Keeping insect populations in check is critical for preventing damage caused to forest ecosystems by irruptive insects. Spruce budworm is an irruptive species and North America's most destructive forest pest (Pureswaran et al., 2016, making it an ideal model prey species to investigate natural enemy relationships in the boreal forest. While there is an abundance of studies focused on parasitoids (wasps and flies) (Blais, 1960; Cappuccino et al., 1998; Royama et al., 2017; Seehausen et al., 2016; Smith et al., 1990) and birds (Bolgiano, 2004; Crawford et al., 1983; Holmes et al., 2009; Morse, 1978; Venier et al., 2009; Venier & Holmes, 2010) that serve as natural enemies of spruce budworm, there is relatively little information available on other natural enemy groups, particularly spiders.

Spiders are among the most abundant and diverse taxa in the forest canopy (Langor, 2019; Michalko et al., 2019; Nyffeler & Birkhofer, 2017). As generalist predators, they play a significant role in structuring canopy food webs by preying on a vast number of insects (Nyffeler, 2000; Nyffeler & Benz, 1987), as well as serving as prey for other arthropods (Halaj et al., 1997), birds (Gunnarsson, 1996), and bats (Krull et al., 1991). Similarly, their role as predators means that they may exert top-down control and influence herbivory (Nyffeler & Birkhofer, 2017). There have been good descriptions of some arboreal spiders inhabiting northern coniferous forests, particularly in the United States (Jennings & Collins, 1986a; Mallis & Rieske, 2011; Mason et al., 1997). Nevertheless, limited knowledge is available regarding the spider communities inhabiting the boreal forest and their role as predators of spruce budworm (but see: (Bowden et al., 2022; Michalko et al., 2019)).

Non-Consumptive Effects

In agricultural systems, spiders have been shown to have significant non-consumptive impacts on herbivorous insects (e.g., Beckerman et al., 1997; Rypstra & Buddle, 2013). In response to new chemotactile cues such as spider excreta and silk, prey may move more or less, emigrate less, or consume less food (Barnes et al., 2002; Williams & Wise, 2003). This response is believed to be an evolutionary adaptation, as animals have developed the ability to detect chemical cues and respond to them to reduce their risk of predation (Beckerman et al., 1997; Schmitz et al., 1997). Several studies have focused on spiders influencing herbivory via indirect interactions in Coleoptera (Hermann & Landis, 2017; Kahl et al., 2021; Rypstra & Buddle, 2013; Schmitz et al., 1997) or Orthoptera (Beckerman et al., 1997; J. R. B. Miller et al., 2014; Wineland et al., 2015) but few on Lepidoptera (Rendon et al., 2016). Studying spiders in a

complex habitat like the boreal forest captures the intricate web of interactions between predators and their prey and how they interact to maintain balance in the environment. It also allows us to assess the role of spiders in controlling irruptive pest populations and represents a sustainable and cost-effective addition to current strategies that recognize the importance of natural enemies (e.g., Johns et al., 2019).

Considering the few studies conducted on the predation of spruce budworm by spiders (but see: (Bowden et al., 2022; Jennings, Dimond, et al., 1990; Jennings & Houseweart, 1989; Loughton et al., 1963; Mason et al., 1997)., it is difficult to determine whether spiders can exert enough mortality to influence spruce budworm populations. Thus, it is unclear whether spiders play a top-down role in the dynamics of spruce budworm populations. My research aims to fill these knowledge gaps by describing the community assemblage of spiders inhabiting the forest canopies of different stand types in the boreal forest and by investigating whether spiders can directly or indirectly influence herbivory by spruce budworm.

2.0 Forest Stand Type and Spider Community Composition

The Canadian boreal forest is defined by long, cold winters and short, cool summers. Though dominated by coniferous trees, deciduous species are not uncommon in the region. The boreal forest has three typical stand types: coniferous (> 70% conifer), mixedwood (30-60% conifer), and the less common deciduous stands (< 30% conifer) (Brandt, 2009). In eastern Canadian boreal forests, the most common coniferous trees are balsam fir (*Abies balsamea*) and black (*Picea mariana*), and white (*Picea glauca*) spruce. Deciduous trees primarily include white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*).

Tree structural diversity and species composition play a significant role in the diversity of arboreal arthropod communities (Gunnarsson, 1990; Halaj et al., 2000; Kennedy & Southwood, 1984; Summerville & Crist, 2004). Arthropod assemblages of a forest stand can be attributed to variations in tree structural diversity (Halaj et al., 2000) but also to the ability of trees to modify the thermal environment for arboreal invertebrates (Riechert & Tracy, 1975). Coniferous trees offer distinct microhabitats and resources compared to deciduous trees, and thus each supports different biological communities (Ampoorter et al., 2015; Pearce et al., 2004; Ziesche & Roth, 2008). For example, conifer needles offer greater protection from vertebrate predators than deciduous branches and leaves. In a Norway spruce (*Picea abies*) forest in Sweden, Gunnarsson et al. (2004) found that spider diversity increased with increasing amounts of arboreal lichen in the forest.

In contrast, deciduous trees often support a greater diversity of prey species than coniferous trees and may therefore support a larger predator community (Pinzon et al., 2011). The level of branch connectivity in a forest stand allows predatory arthropods (often more

mobile than their prey) to move between trees more easily (Korenko et al., 2011). Schowalter (1995) discovered that the number of snags increased arthropod diversity and the proportions of predatory invertebrates. These studies suggest that tree structural diversity and thereby, stand composition and stand type are key factors in shaping arthropod diversity in various habitats.

Beyond its influence on arthropod community structure and insect-tree interactions, forest composition can also mediate predator-prey interactions, which help shape ecological communities. Spiders are key predators in most terrestrial ecosystems, and they have the capacity to influence the dynamics of their prey with implications for trophic cascades, impacting productivity, biodiversity, nutrient cycling, disease dynamics, and carbon storage (Lawrence & Wise, 2000; Wise, 2004). They are among the most abundant and diverse arthropod species in the forest canopy (Langor, 2019; Nyffeler & Birkhofer, 2017). are the seventh most diverse order of organisms in terrestrial ecosystems and are key predators of invertebrates (Cardoso et al., 2011; Coddington & Levi, 1991; Jennings & Houseweart, 1989; Mallis & Rieske, 2011; Michalko et al., 2019; Symondson et al., 2002), particularly in forest canopies (Lowman & Wittman, 1996). In addition to preying on numerous insect species, spiders also serve as prey for ants (Halaj et al., 1997), birds (Gunnarsson, 1996), bats (Krull et al., 1991), and other arthropods (Cappuccino et al., 1998; Petráková et al., 2016; Royama et al., 2017). Spiders are ideal model organisms for studying biodiversity patterns in forests. Their taxonomy is relatively stable and accessible (Coddington & Levi, 1991), they perform critical ecological functions and can serve as bioindicators (Pearce & Venier, 2006).

Few have investigated the spider community associated with boreal trees despite the numerous studies on habitat associations of arboreal arthropods (Bowden et al., 2022; Gunnarsson, 1990; Jennings & Collins, 1986a; Jennings & Dimond, 1988; Mallis & Rieske,

2011; Thunes et al., 2003). Several studies indicate that at the tree level, spider abundance, richness and community structure are related to their variety of ecological roles, dependence on specific habitat features, construction of webs and retreats, use of vibratory signals (Bell et al., 2001) and their need for vegetation structural complexity (Gunnarsson, 1990; Halaj et al., 1998; Jennings & Collins, 1986b; Mallis & Rieske, 2011).

Describing the arboreal spider community in the boreal forest facilitates the study of spiders as indicator species and the investigation into their predatory role regarding pest populations, such as the destructive spruce budworm (Pureswaran et al., 2016). To determine how spider community structure differs among forest stands, I established nine field sites in the eastern boreal forest (Newfoundland and Labrador, Canada) and collected spiders from three different stand types (conifer-dominated, mixed, and deciduous-dominated). I posed the following question: Does the abundance, species richness, and diversity of the arboreal spider community differ among the three dominant stand types in the region? I predicted that the mixedwood stands would offer more structural diversity and, therefore, a more significant number of spider species. Samu et al. (2014) found a positive correlation between tree species richness and spider species richness. Furthermore, structural diversity leads to a greater diversity of associated taxa (Janz et al., 2006; Maynard et al., 2017; San Roman & Wagner, 2021).

2.1 Methods

Study Location

I conducted this study during the summers of 2021 and 2022 in an active commercial forestry area in insular western Newfoundland and Labrador (Figure 1). The forest in the region is dominated by two conifer species, balsam fir and black spruce, with limited deciduous stands

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dominated by white birch and trembling aspen. Only mature stands with a dominant tree height greater than five meters tall with an understory containing balsam fir regeneration were selected.

Using a stand composition layer in ArcMap 10.8 and confirming suitability in the field, I selected and established nine sites southwest of Corner Brook, NL. Using a blocked design, I created three replications of each stand type, with a minimum distance of 500 meters between treatments and at least six kilometers between replicates.
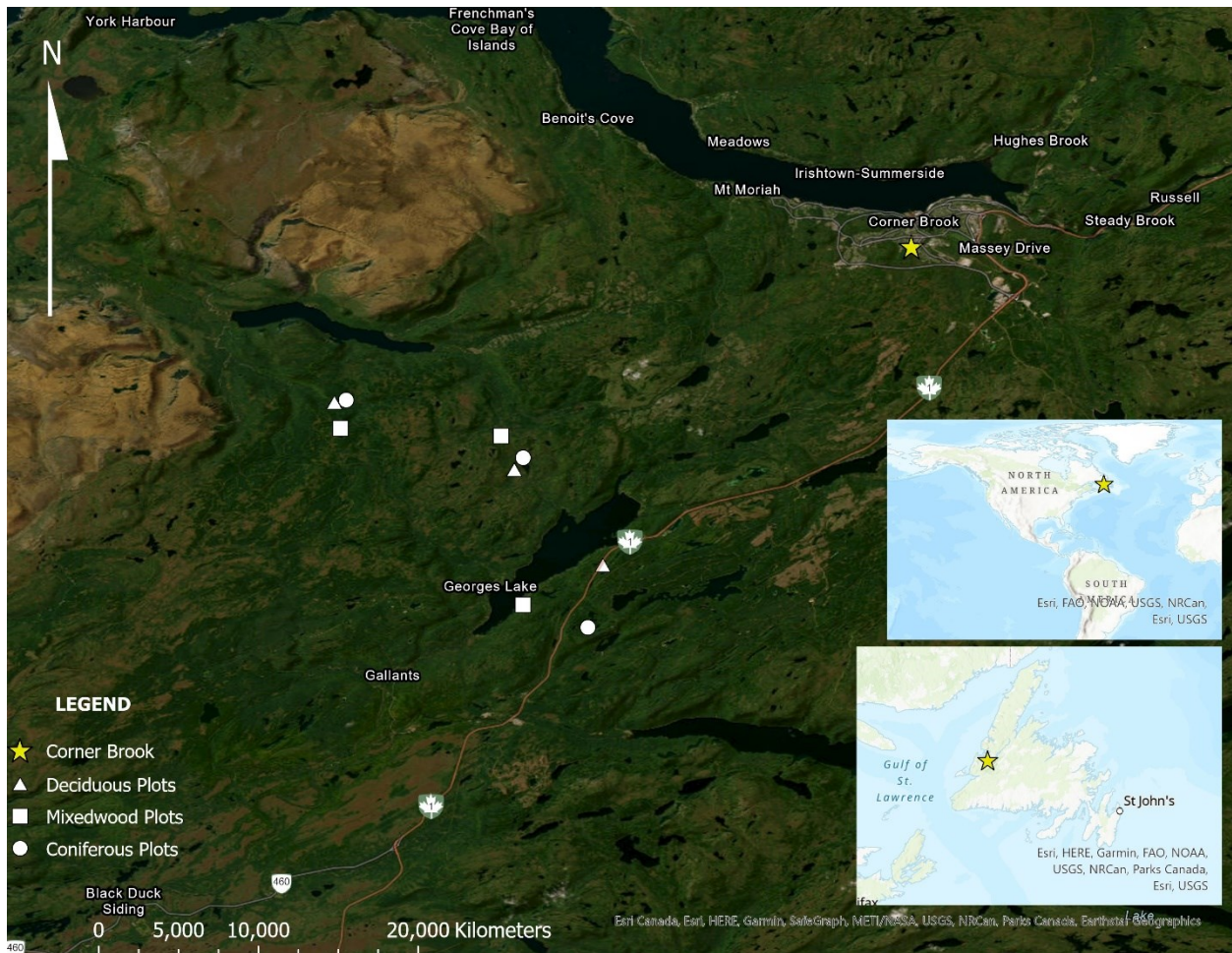
Figure 1. Spider community assemblage study plot locations near Corner Brook, Newfoundland and Labrador, Canada.

Sample Collection

I collected spiders using a modified beat sheet method at four time periods throughout the summer (June, July, August, and September) in 2021 and 2022. I sampled all sites each month

within two days to keep weather conditions consistent. My beat sheet method consisted of branches being beaten over a 1m-by-1m white cloth sheet held taut by a PVC frame. Balsam fir was selected as the experimental species due to its widespread ability to regenerate across different stand types, thus providing a standardized and consistent basis for the study. Any significant differences in spider assemblages would therefore reflect stand-level effects. Three balsam fir trees per site were haphazardly sampled for 40 seconds each for a total sampling effort of two minutes per site. My modified beat sheet had a hole cut in the center with a funnel glued to the sheet. The snap cap from a 16-dram vial with a hole in it was glued to the funnel spout to which a 16-dram vial was attached. The contents of the beat sheet were immediately deposited into the cup, which was then removed and quickly capped before the spiders could escape. After each site collection, 80% ethanol was added to the cup in the field to preserve the contents.

The samples were pooled together at the site level at the lab based on the collection date. The spiders were then sorted from the samples. I identified juveniles to the family level and adults to the species level using (*Bug Guide*, 2023; Murray & Lentz, 2023; Paquin & Dupérré, 2003; Pickavance & Dondale, 2005). Nomenclature followed the World Spider Catalogue 2022 (Natural History Museum Bern, 2022). I created a voucher collection of adults deposited at the Canadian Forest Service, Natural Resources Canada, Corner Brook, Newfoundland and Labrador. Juveniles were excluded from the analysis because they cannot be identified to the species level and do not impact the interpretation of diversity indices (Sackett et al., 2008).

Data Analysis

Abundance

  I compared spider communities among stand types. All analyses were performed in R version 4.2.2 (R Core Team, 2022) using R-studio GUI (RStudio Team, 2022). I used a fixed effects generalized linear model (GLM) using the 'glm' function from the base R package with a Poisson error family to test for the influence of stand type on overall spider abundance (excluding juveniles) (i.e., significance at $p < 0.05$). P-values were obtained using the Anova function of the 'car' package. This performs an analysis of variance (ANOVA) on a linear regression model. It provides an ANOVA table with type I, II, or III sums of squares. In this case, type II values were calculated. I used the function 'means' in the package 'emmeans' (Lenth, 2023) to perform a post hoc Tukey HSD test to examine pair-wise comparisons among stand types.

Diversity Indices

  I calculated diversity indices for each stand type using Hill numbers with the 'iNext' package (Chao et al., 2014; Hsieh et al., 2016), amalgamated by site, with the month as replicate and then averaged. I created diversity profiles with error bars using the 'ggiNEXT' function, using the extrapolated species diversity. Hill numbers are a family of diversity indices commonly used in ecology to quantify a biological community's species richness and evenness. For example, $q = 0$ represents species richness (the number of different species present in a community), while $q = 1$ represents the exponential of the Shannon entropy index (a measure of both species richness and evenness), and $q = 2$ represents the exponential of the Simpson index

(a measure of the dominance or concentration of species in a community). The higher the order of diversity captured by a Hill number, the more weight it places on rare or dominant species, and the more it reflects the overall distribution of abundance across species (Hill, 1973). Using the calculated Hill numbers, I employed a Poisson error family fixed effects generalized linear model (GLM) using the 'glm' function from the base R package to assess significant variations among stand types for each diversity index, with a significance threshold of $p < 0.05$. Additionally, I employed the 'means' function in the 'emmeans' package (Lenth, 2023) for conducting a post hoc Tukey HSD test to explore pairwise comparisons between stand types.

Indicator Species

I ran indicator species analysis for each habitat using the 'multipatt' function in the package 'indicspecies' (Dufrêne & Legendre, 1997). The 'multipatt' function calculates two values, specificity and sensitivity. Specificity (A) refers to the likelihood that a site belongs to a particular habitat based on the species collected. Sensitivity (B) refers to the number of sites harbouring the target species in that habitat. Based on running 999 random permutations, the resulting p-values represent how significantly a species is associated with a habitat.

Community Composition

To visualize the raw species richness in each stand type, I created a Venn diagram using the 'draw.triple.venn' function of the 'VennDiagram' package (Chen & Boutros, 2022). The Venn diagram displays the number of species unique to each stand type and the number shared among stand types. To visualize species composition, I used non-metric multidimensional scaling (NMDS) ordination (Legendre & Legendre, 2012) with the function 'metaMDS' in the

'vegan' package (Oksanen et al., 2015). The approach uses Bray-Curtis dissimilarity scores, allowing the visualization of the similarity among spiders collected among stand types. I used the function 'ggplot' in the package 'ggplot2' (Wickham, 2016) to create the NMDS plot, excluding singletons. To make statistical conclusions from the NMDS, I performed a PERMANOVA using the Bray-Curtis dissimilarity measure, as implemented in the 'adonis2' function from the 'vegan' R package (Oksanen et al., 2015).

2.2 Results

I collected 3395 spiders over the two field seasons (Appendix 1). Due to the large proportion of juveniles (n = 2636), only 760 adult spiders could be identified to 41 species (Appendix 2), representing 13 families. Linyphiidae constituted the largest proportion of total individual adult spiders collected (71%), followed by Dictynidae (12%), Theridiidae (8%), Clubionidae (3%), and Philodomidae (2%). Linyphiidae had the highest number of species (n = 16), followed by Theridiidae (n = 8), Clubionidae (n = 3), and Araneidae (n = 3). The most abundant species was *Ceraticelus atriceps* (n = 214, 28%). The second most abundant species was *Ceraticelus fissiceps* (n = 178, 23%), followed by *Grammonota angusta* (n = 107, 14%), *Dictyna brevitarsa* (n = 88, 12%), *Theridion varians* (n =42, 6%), and *Clubiona trivialis* (n = 16, 2%). The ten most abundant species comprised 90% of the collection and belonged to the families Clubionidae, Dictynidae, Linyphiidae, Philodomidae, Salticidae, and Theridiidae (Figure 2). Only the top three most abundant species were each represented by >100 individuals. Of the 760 spiders identified, three species were new records for the island of Newfoundland. Of the 760 adult spiders identified, three were new records for the island of Newfoundland:

Islandiana longisetosa (Linyphiidae, n=1), *Ohlertidion ohlerti* (Theridiidae, n=4), and *Pelgrina flaviceps* (Salticidae, n=11) (Pickavance & Dondale, 2005).
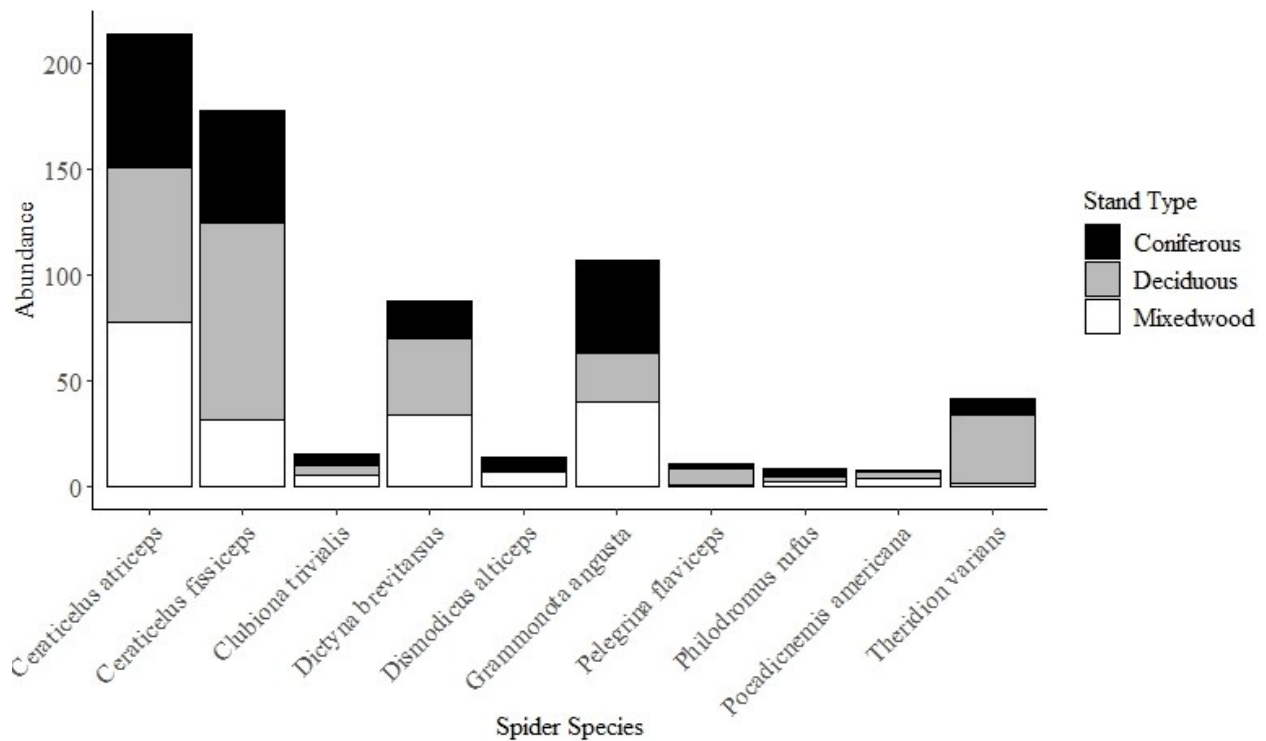
Figure 2. Raw abundance of the ten most abundant spider species collected by stand type. Data was pooled by stand type from three sites of each stand type in the boreal forest of western Newfoundland, Canada.

Spider Abundance

Stand type significantly affected total spider abundance (Chi-Squared = 14.983, p = 0.001), ranging from 219 individuals in conifer stands to 303 individuals in deciduous stands (Figure 3). The post hoc analysis revealed that spider abundance significantly differed between conifer stands and deciduous stands (p = 0.001) and between deciduous stands and mixedwood stands (p = 0.015). However, spider abundance did not significantly differ between coniferous and mixedwood stands (p = 0.648).
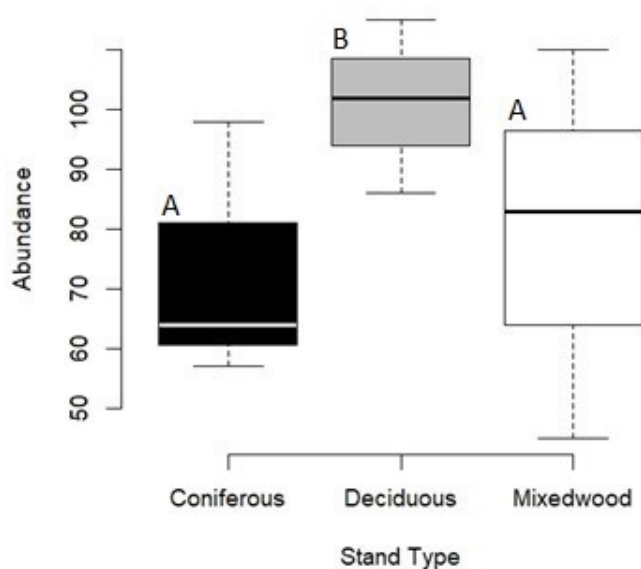
Figure 3. The effect of stand type (coniferous, deciduous, mixedwood) on overall spider abundance. The boxes represent the data's interquartile range (IQR), with the median line inside each box. The whiskers extend to the minimum and maximum values within 1.5 times the IQR. Data was pooled by stand type from three sites of each stand type in the boreal forest of western Newfoundland, Canada.

Species Diversity

Species richness (Hill number, $q = 0$; Figure 4) displayed a marginally significant difference among stand types (Chi-Squared = 13.377, $p = 0.099$). There was not a significant difference among stand types for Shannon diversity ($q = 1$) (Chi-Squared = 5.915, $p = 0.656$) or Simpson diversity ($q = 2$) (Chi-Squared = 3.404, $p = 0.907$). The deciduous stands yielded 11% more spider species than the coniferous forest stands and 1% more than mixedwood stands. Both diversity measures indicate that mixedwood stands represent an intermediate stand type for spider communities. Similarly, coniferous and deciduous stands differ most from each other. Indicator species analysis did not identify any spider species as a significant indicator of the three stand types.
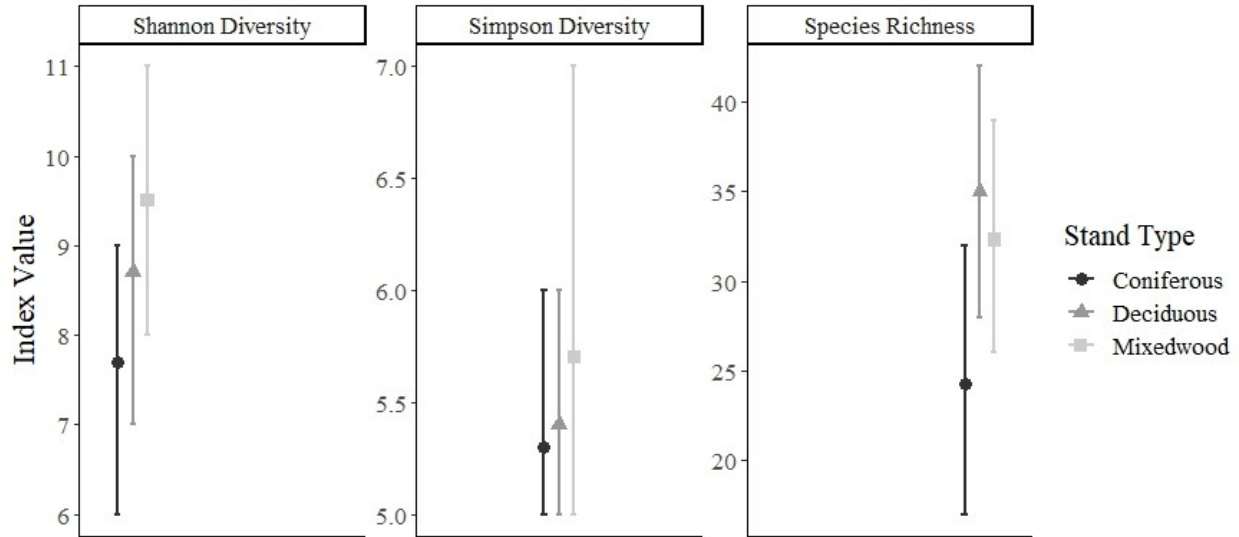
Figure 4. Spider community assemblage diversity profiles, characterized by an adequate number of species (± 95% confidence intervals) for Hill number order q = 0 (species richness), q = 1 (Shannon diversity), and q = 2 (Simpson diversity), at each stand type. Data was pooled by stand type from three sites of each stand type in the boreal forest of western Newfoundland, Canada.

Species Composition

In total, 41 species were collected across all nine field sites, 12 of which (29%) were collected in all three stand types (Figure 5). In total, five species (12% of the total) were exclusive to coniferous stands, nine species (22% of the total) to deciduous stands, and six species (15% of the total) to mixedwood stands. Conifer stands shared two species with deciduous stands. There were no species shared only between conifers and mixedwood stands. There were seven species shared among deciduous and mixedwood stands.
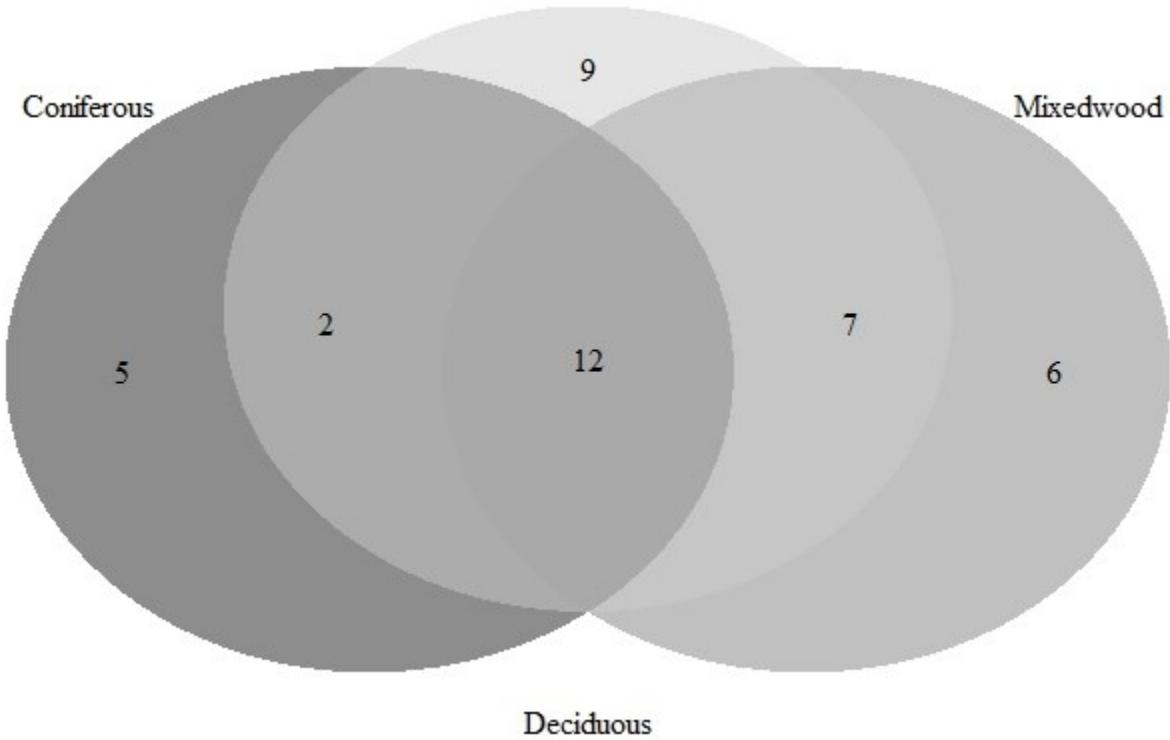
Figure 5. Raw species richness by stand type, with the number of unique and shared species of arboreal spiders within coniferous, deciduous, and mixedwood stands. Data was pooled by stand type from three sites of each stand type in the boreal forest of western Newfoundland, Canada.

Distinct spider assemblages were not observed among stand types in the NMDS ordination (method = 'Bray-Curtis,' stress = 0.18) (Figure 6 A, B, C). The 95% confidence ellipses indicate that all stand types overlap in the ordination. I confirmed through the PERMANOVA analysis that spider communities did not differ significantly by stand type (F = 1.354, p = 0.140).

Stress = 0.18
NMDS Dimension 3
NMDS Dimension 2

Stand Type
● Coniferous
▲ Deciduous
■ Mixedwood

Stress = 0.18
NMDS Dimension 3
NMDS Dimension 1

Stand Type
● Coniferous
▲ Deciduous
■ Mixedwood
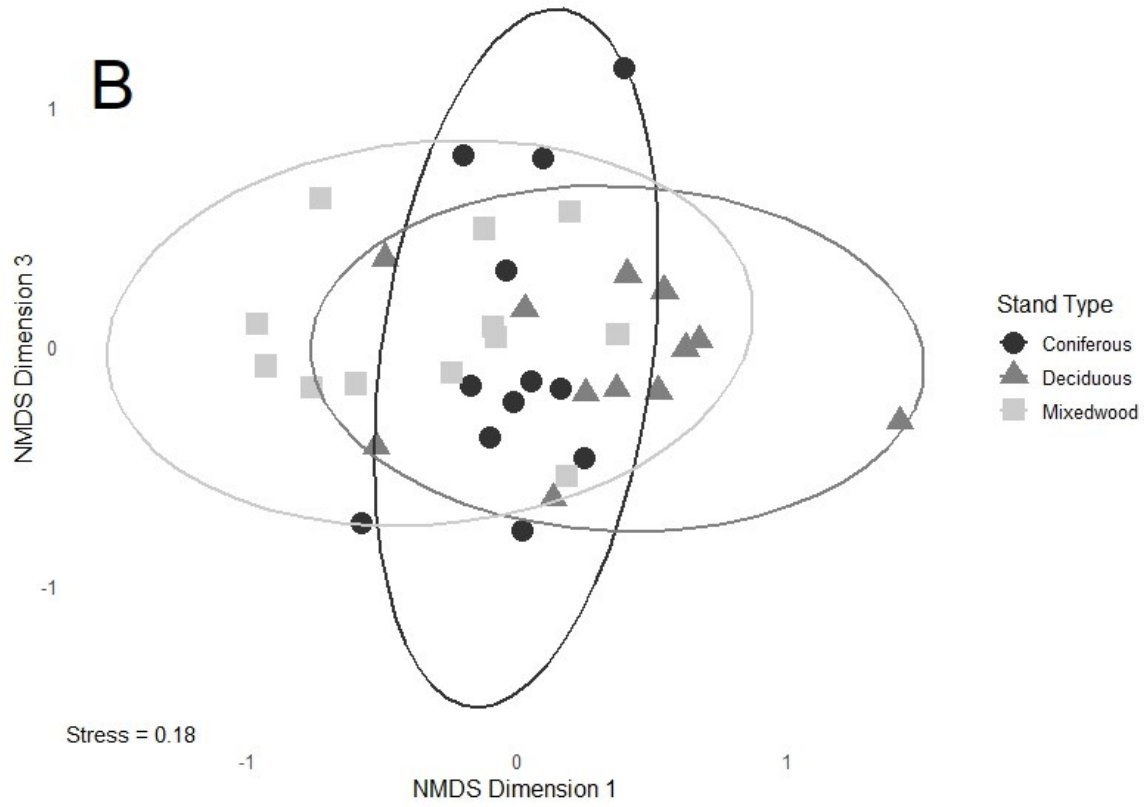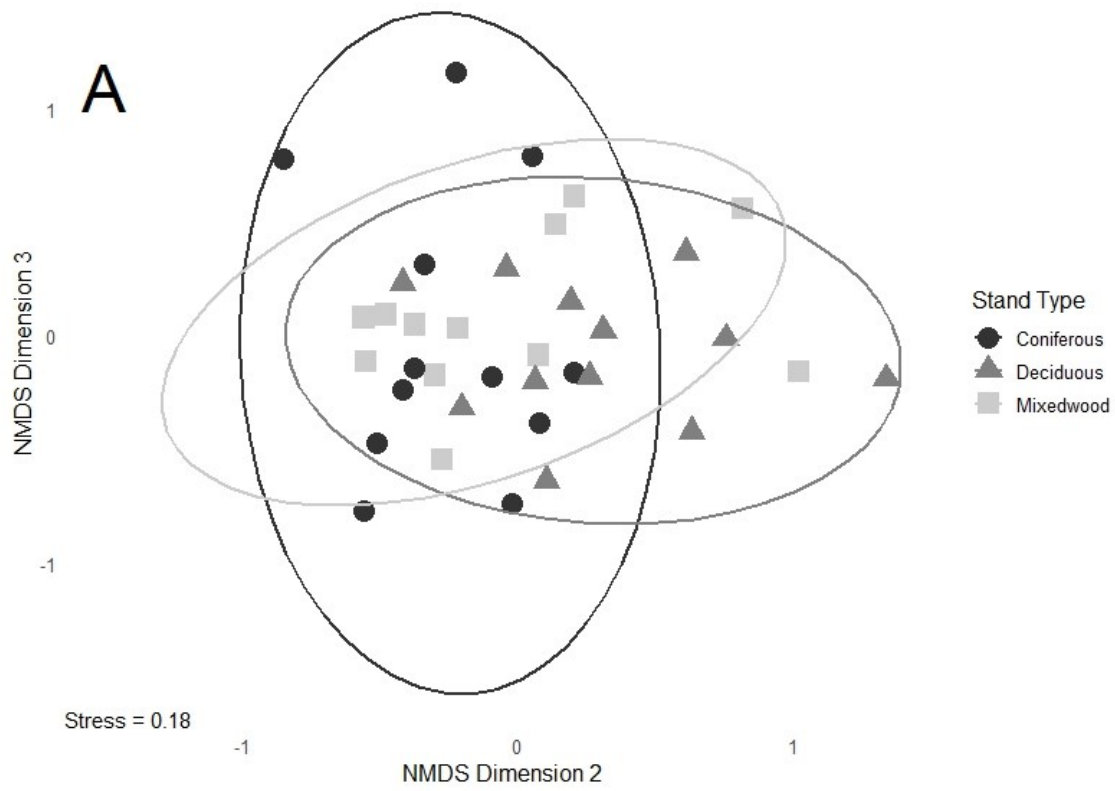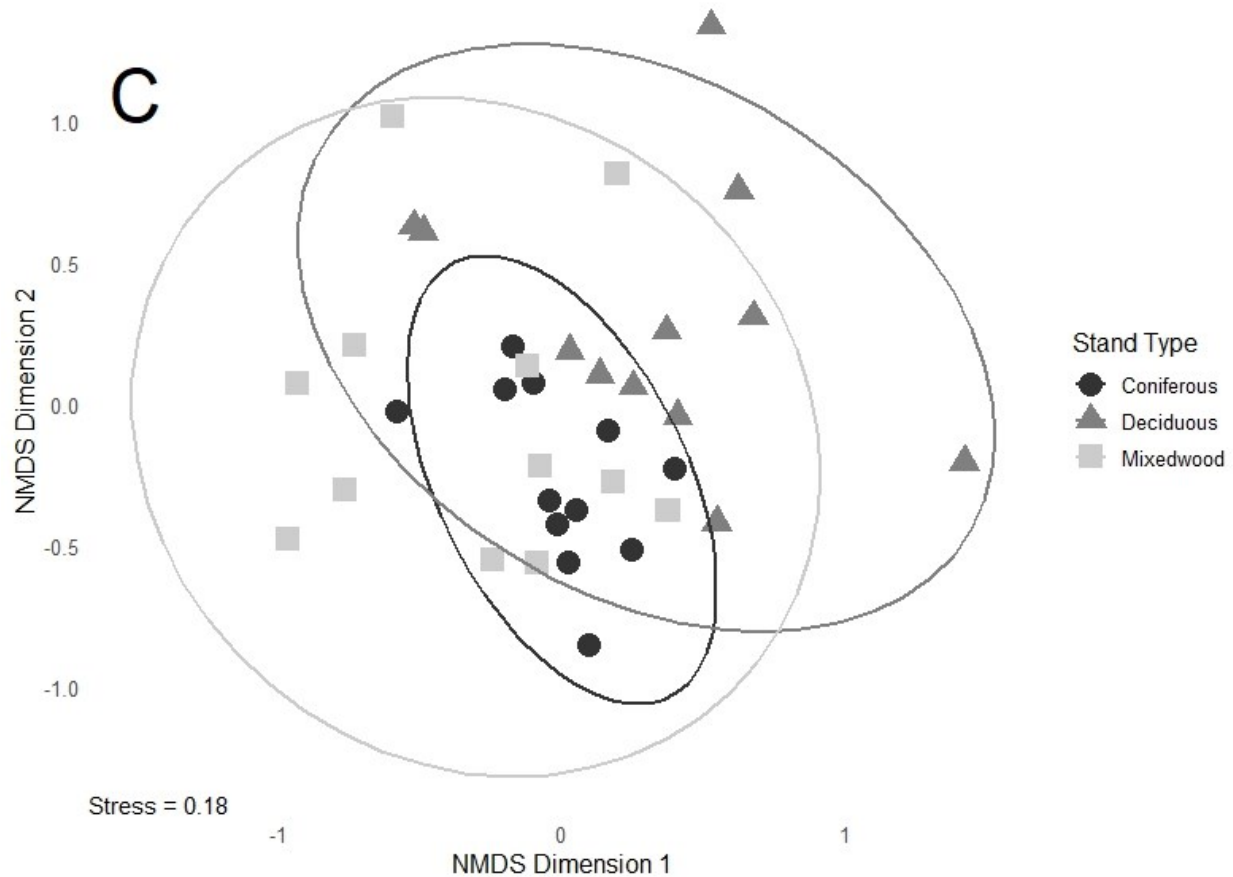
Figure 6. Nonmetric multidimensional scaling of species abundances pooled across all dates using the Bray-Curtis dissimilarity method with 95% confidence ellipses. A) ellipses on axis 2 and 3, B) ellipses on axis 1 and 3, and C) ellipses on axis 2 and 3. Each point represents spider abundance each month by stand type. Data was pooled by stand type from three sites of each stand type in the boreal forest of western Newfoundland, Canada.

2.3 Discussion

Spider Abundance

Spider abundance was lowest in coniferous stands. The highest abundances were in deciduous stands and significantly differed from those of mixedwood and coniferous stands. These findings suggest that the type of vegetation cover can play a crucial role in determining the size of the spider population in a given area. Though the original objective was not focused on plant composition and time did not allow for plant surveys, I expected the mixedwood stands to yield greater diversity and an abundant spider community. This hypothesis was based on the

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overabundance of data indicating that greater plant diversity leads to greater species abundance at higher taxon levels (Maynard et al., 2017; San Roman & Wagner, 2021; Schuldt et al., 2019; Staab et al., 2016; Zhang et al., 2016). Although much of this work has focused on temperate or tropical latitudes (Janz et al., 2006; Maynard et al., 2017), results from the boreal region also suggest that deciduous stands can support higher spider abundance (Staab & Schuldt, 2020; Stemmelen et al., 2022). While assessing bark-dwelling spider assemblages, Pinzón & Spence (2010) observed greater spider abundance in deciduous stands compared to conifer stands. Spider abundances have also been found to be greater in deciduous stands while examining the spider assemblages at different forest strata (Pinzon et al., 2011). This is consistent with my findings and provides further evidence of the importance of stand type in shaping spider populations.

Many factors associated with stand composition may influence spider abundance. For instance, prey availability can be a significant factor, as spiders are carnivores that feed on insects. The presence or absence of vegetation cover can also affect prey availability (Halaj et al., 1998, 2000), significantly impacting spider abundance. In more diverse stands, prey are provided with greater quantity and better-quality food (Haddad et al., 2009). In areas with dense vegetation cover, there may be a higher abundance of prey, which can support a greater number of spiders.

Different stand compositions offer unique vegetation structures, which can modify environmental conditions (Chen et al., 1995). Vegetation structure can provide hiding places for spiders, which can help protect them from predators and adverse weather conditions (Halaj et al., 1998, 2000; Jennings, Dimond, et al., 1990; Jennings & Dimond, 1988). Vegetation cover can also provide a suitable microclimate for spiders to thrive, particularly in areas with high humidity

(Agnew & Smith, 1989; Gunnarsson, 1990; Rypstra et al., 1999). Therefore, the availability and distribution of hiding places in different stand types can influence spider abundance.

Moreover, the 'enemies hypothesis' (Root, 1973) is another mechanism that may drive spider abundance in different stand types. This hypothesis predicts that generalist natural enemies may benefit more from increased tree diversity than specialists. Generalists would be more proficient in utilizing the greater variety of alternative prey and host species found in mixed habitats. As generalist predators, spiders do not differentiate between specific prey species. In terms of natural enemies of spiders, however, in areas where the density of natural enemies is high, spiders may experience higher mortality rates, leading to lower spider abundance (Halaj et al., 1997; Petráková et al., 2016). Conversely, spiders may be more abundant in areas with lower predator density. Therefore, the presence of natural enemies of spiders may vary across different stand types, which can affect spider abundance.

Species Diversity

While I found significant differences in spider abundance and marginally significant differences in spider species richness among stand types, I did not detect a difference among stand types for Shannon or Simpson diversity indices. Given that species richness is determined by the number of species per stand type (Magurran, 2005), and 22% of the total number of species collected were exclusively found in deciduous stands, it is reasonable to conclude that there would be a marginally significant difference in species richness between stand types. In contrast, while Shannon and Simpson both consider species richness and their evenness in a community, Simpson gives more weight to rare species and Simpson more weight to dominant species (Magurran, 2005). The spider community of insular western Newfoundland had very few

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dominant species and many singletons and doubletons, with one-third of species collected in all stand types. Further, the number of species found exclusively in one stand type was relatively similar among the three stand types. Thus, the abundance and richness of spiders differ among the stand types, but the evenness of the community is similar, resulting in similar Shannon or Simpson diversity indices.

Species Composition

Spider assemblages did not differ significantly among stand types (Figure 5). Similarly, Pearce et al. (2004) found similar species composition between deciduous and mixedwood stands. The presence of similar environmental conditions across stand types could be a factor. Turnbull (1973) suggested that several factors could influence spider communities, such as the architectural characteristics of the plants themselves or the mediation of microclimatic conditions by the plants. Similarly, temperate deciduous and mixedwood stands have shown little differences in species richness and diversity at the stand level. Still, they are more evident at the individual tree level, which is a general trend observed in other studies (Mupepele et al., 2014). At the individual tree level, microhabitats and tree architecture differences may explain differences in spider communities. The similarity in spider assemblages between deciduous and mixedwood stands may be due to similar environmental conditions. However, differences in microhabitats and tree architecture may still shape spider communities at the individual tree level.

The tree structure may influence several microclimatic variables humidity affecting spider species composition such as wind speed and air temperature. The high dispersal capacity of juvenile spiders allows them to quickly move from one stand type to another in search of

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(lower competition) food and avoid intraguild predation (Pinzon et al., 2011). Also, as generalist predators, spider diversity is primarily affected by local conditions and food availability rather than stand type (Pinzon et al., 2011). As a result, spider populations can quickly respond to seasonal variations in environmental conditions by changing their behaviour, diet, and habitat selection. Understanding these mechanisms can help develop better management strategies for biodiversity and ecosystem health.

Overall, my findings suggest that, similar to tree-level analysis, community assemblage metrics such as abundance and richness vary among stand types. However, I did not find differences among stand types for species evenness or diversity. The mechanisms that drive spider communities are complex and multifaceted. Evidently, vegetation structure, which is affected by stand composition, plays a critical role in determining spider populations. The availability of prey, hiding places, and the presence of natural enemies are all factors that can influence spider abundance and diversity in different stand types.

It is worth noting that the analyses for this study were conducted at the stand level, which differs from most of the literature on spider abundance conducted at the tree level. This study provides insight into spider abundance patterns in boreal forest stands, which are poorly represented in the literature. Future studies could compare the species assemblages at a multi-spatial scale rather than only at the stand level to help deduce at what level assemblages can be differentiated. Looking at spider community assemblages across a range of spatial scales, from the individual tree level to the entire forest landscape, could help to identify whether spider community assemblages differ depending on the spatial scale of analysis and whether certain environmental factors are more important at different spatial scales. Finally, it would also

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provide more detailed information about the community structure, which can be used to identify

the underlying mechanisms driving change.

3.0 Consumptive and Non-Consumptive Effects of Spiders on Spruce Budworm

Pest control is an essential function of the arthropod predator community and relies heavily on a diverse predator assemblage (Jonsson et al., 2017). Various natural enemies exert top-down pressure on herbivorous insects, which can vary between habitats. In forests of Eastern Canada, natural enemies contribute to the regulation of irruptive pest insect species and thereby help maintain the health and productivity of forest ecosystems (Johns et al., 2019). Natural enemies can include a range of predators, parasitoids, and pathogens that target specific pest species, and their interactions can have complex effects on pest populations. By reducing pest abundance and controlling their behaviour, natural enemies help prevent outbreaks and minimize damage to forest trees, which can have significant ecological and economic benefits (Johns et al., 2019). Additionally, natural enemies can help maintain biodiversity by preventing the dominance of particular pest species, allowing other species to thrive (Johns et al., 2019).

For centuries, the boreal forest has been subject to periodic insect outbreaks. Though there have been many native and non-native insect pests, none have been more destructive than the spruce budworm (*Choristoneura fumiferana*, Clem.) (Johns et al., 2019). The sheer magnitude and longevity of outbreaks set spruce budworm apart from other insect defoliators. Populations are nearly undetectable at the endemic phase but can erupt, without warning, to several hundred larvae per branch, causing severe defoliation, growth loss, and tree mortality (Pureswaran et al., 2016). With outbreaks occurring every 30-40 years and each outbreak lasting up to 20 years, it is the most destructive native forest pest in North America. It has killed millions of hectares of spruce-fir forests in Canada and the United States (Pureswaran et al., 2016).

Spruce budworm prefers balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and red spruce (*Picea rubens*), in that order (MacLean & MacKinnon, 1997; Nealis & Régnière, 2004). Adult spruce budworm moths lay eggs in July on the needles of host trees. Larvae overwinter as a second instar, emerge in the spring, and develop into a sixth instar larva, feeding on the current year's foliage (Miller, 1975), after which they pupate and emerge as moths. After five years of spruce budworm larvae consuming the current year's foliage, the affected tree will die. Tree mortality following an outbreak and subsequent forest regeneration can therefore be observed in localized patches or across entire landscapes (Miller, 1975).

Spiders are important natural enemies of many arthropod pest species (Jennings & Houseweart, 1989; Mallis & Rieske, 2011; Michalko et al., 2019). They are an ideal model taxon to study arthropod predator-prey interactions because they are present in all terrestrial ecosystems, are relatively abundant, and have high functional diversity. As generalist predators, they consume large numbers of invertebrate prey and play a crucial role in controlling insect herbivores within an ecosystem (Mallis & Rieske, 2011; Michalko et al., 2019; Nyffeler & Benz, 1987). Spiders have demonstrated their significance as natural enemies in various environments, including agricultural systems (Kahl et al., 2021), the high Arctic (Roslin et al., 2013), and forests (Bowden et al., 2022).

In addition to being influenced by habitat diversity, predator species richness and abundance is positively correlated with prey species richness and abundance (Halaj et al., 1998, 2000). Spiders exhibit within-habitat movement to areas of higher prey density (Riechert & Tracy, 1975). Spiders spend less time searching and handling at high densities, thus consuming more prey and reaching satiation levels faster than at low prey densities (Foelix, 2011; Jennings,

Diamond, et al., 1990; Riechert & Tracy, 1975). Spiders exert the greatest pressure at the beginning stages of a growing population of insect prey, suggesting that spiders may play a regulatory role in outbreaking species (Mallis & Rieske, 2011). Several studies have indicated that spiders may exert a stabilizing force on spruce budworm populations in spruce-fir forests in Eastern North America (Halaj et al., 1996; Jennings, Dimond, et al., 1990; Jennings & Houseweart, 1989; Loughton et al., 1963). Recently Bowden et al. (2022) confirmed through gut content analysis that spiders are common predators of spruce budworm in eastern boreal forests. This highlights the potential for spiders to impact plant health, ecosystem processes, and biodiversity within an ecosystem.

Superfluous killing, a behaviour exhibited by many spider species, is a density-dependent behaviour particularly suited for controlling irruptive insects. They accomplish this by limiting the abundance and activities of herbivorous insects through direct predation and indirect influences on their behaviour. In agricultural systems, spiders have been recognized to exert indirect effects on plants via direct predation on herbivores but also via trait-mediated indirect interactions with herbivores (spiders mediate herbivory by modifying the behaviour of herbivores (e.g., Beckerman et al., 1997)). The mere presence of spiders can indirectly affect herbivorous insects by instilling fear and causing them to alter their feeding behaviour. This can lead to prey avoidance of certain parts of plants or less consumption overall (Barnes et al., 2002; Williams & Wise, 2003), reducing foraging activity and, thus, less plant damage (Beckerman et al., 1997; Michalko et al., 2019; Rypstra & Buddle, 2013). For example, Beckerman et al. (1997) showed that herbivory by grasshoppers was reduced in the presence of spiders. Similar prey behavioural responses, such as avoidance behaviour, have also been recorded for the Colorado potato beetle (*Leptinotarsa decemlineata*) (Say) (Hermann & Thaler, 2014), striped cucumber

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beetles (*Acalymma vittatum*) (Fabricius) and spotted cucumber beetles (*Diabrotica unde-cimpunctata howardi*) (Barber) (Kahl et al., 2021), and cotton bollworms (*Helicoverpa armigera*) (Hübner) (Rendon et al., 2016). Thus, the role of spiders as natural enemies in ecosystems may depend as much on the abundance of silk and chemical or visual cues to herbivores as it does on direct predation by spiders.

Spiders have recently been confirmed as natural enemies of spruce budworm in the boreal forest (Bowden et al., 2022). Since spruce budworm is commonly reared for scientific research, it is an ideal study subject to test if spiders exert indirect or non-consumptive effects on herbivorous insects. With this study, I aimed to determine the mechanism by which spiders may influence herbivory by spruce budworm. I specifically asked whether spiders elicit both consumptive and non-consumptive behavioural responses in spruce budworm. I predicted that spiders would have a direct, consumptive effect on spruce budworm. I also predicted that spruce budworm would exhibit a behavioural response to the spider's non-consumptive behaviour, thus reducing foliar feeding.

3.1 Methods

Experimental Design

Balsam fir, the preferred host tree for spruce budworm, was unavailable from nursery stock in the required size and quantity, so I used white spruce, the second most common host for spruce budworm. The Canadian Forest Service of Natural Resources Canada (Atlantic Forestry Center - Fredericton, New Brunswick) provided 72 potted white spruce seedlings aged 3-4 years old. Seedlings were used in a growth chamber rather than a field study to control environmental conditions and minimize spruce budworm mortality due to environmental factors. The tree

seedlings were sprayed with dormant oil at a rate of 4ml per liter of water to kill any existing arthropods. The dormant oil was left on for 24 hours. The trees were then thoroughly rinsed with warm water. The trees were placed in a walk-in growth chamber seven days before the experiment began to allow the buds time to begin swelling. Conditions in the growth chamber were maintained at 25°C, 70% RH and 16/8 photoperiod for the duration of the experiment. Fans were set up in two opposite corners of the growth chamber to ensure proper airflow and prevent mould growth.

Lab colony second instar spruce budworm larvae were obtained from the Insect Production and Quarantine Laboratories (IPQL, Roe et al., 2018), Great Lakes Forestry Center in Sault St. Marie, Ontario. The spruce budworm were removed from diapause three days before the experiment began, and ten spruce budworm were placed in each of 72 1oz cups and placed in the fridge. The day before the initiation of the experiment, spruce trees in a nearby forest were haphazardly beaten using the beat sheet method to collect spiders. A total of 144 spiders were collected. Half of the collected spiders were placed individually in 7.62cm by 10.16cm organza bags, and half in 2oz. Dixie® cups in groups of three spiders per cup. The spiders did not prey on each other overnight before the experiment was set up.

On day one of the experiment, all 72 trees were haphazardly assigned to 3 treatment groups (consumptive effects, non-consumptive effects, and predator-free control; n = 24 for each treatment), and newly flushing buds were measured for each individual. All trees had ten lab-reared spruce budworm placed on each tree by pinning the cup to a branch. Preliminary experiments showed that spiders could survive at least eight weeks without food (pers. obs.) but need constant access to water. So as not to disturb the spruce budworm or the spiders, the room was kept at 70% RH to minimize desiccation stress. After set up, all trees were covered in a

sleeve cage secured around the pot using an elastic band, containing test subjects and excluding outside interference. All 72 trees were placed in the walk-in growth chamber haphazardly so that no one treatment type was all in the same area of the room. This ensured that minute differences in temperature, humidity, light and proximity to the door and fans would not be conflated with treatment effects.

To assess indirect effects, 24 trees had three field-collected spiders placed on the branches in organza bags so they were present but could not feed. This allowed for the observation of reduced feeding without loss of spruce budworm due to predation. Another 24 trees were used to assess the direct predation of spruce budworm by spiders. For the direct treatment, however, three spiders in a Dixie® cup were released onto the foliage, free to roam and consume spruce budworm. Lastly, 24 trees were assigned as predator-free controls, each with a diet cup containing ten spruce budworm only. Since spiders can only be correctly identified using a microscope to the species level as adults and the family level (Appendix 3) as juveniles, spiders were placed on trees haphazardly so that no one particular feeding guild (Appendix 4) was assigned to one treatment over another.

Data Collection

Weekly, for four weeks (until the spruce budworm eclosed as moths), six trees each of the control and two treatments were selected haphazardly and destructively harvested and assessed for the direct and indirect effect of spiders on spruce budworm defoliation. The sleeve cage was first examined for spruce budworm or spiders on the sleeve cage. The sleeve cage was carefully removed, and anything found was carefully collected. The tree was assessed for the bud burst stage (Dhont et al., 2010) and then evaluated for defoliation. The tree was then cut at the

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soil level, shaken, and beaten with a stick over a white sheet. All spiders and spruce budworm were collected and counted. Adult spiders were identified to species and juveniles to family.

When the sixth instar spruce budworm were found on the tree, they were individually weighed and left to pupate in a Dixie® cup. After eclosion, the moths were killed by placing them in the freezer overnight and then dried in a soil drying oven at 60℃ for 48 hours, after which moth dry mass was recorded. The experiment ended after four weeks when the majority of spruce budworm were found as pupae or moths. After a period of two weeks post-experiment, if a sixth instar spruce budworm failed to pupate or a pupa failed to eclose, it was recorded as dead.

Statistical Analysis

Data used for the analysis only included the last two sampling dates when sixth instar larvae were collected. The data was pooled for the last two collection periods as the spruce budworm had all reached the sixth instar stage. From a logistical perspective, finding second and fourth instar spruce budworm on foliage is challenging. Therefore, inferring mortality in the absence of individuals at the fourth instar or beyond is more feasible. In addition, investigating cumulative defoliation resulting from older larvae after inflicting substantial damage would be a more compelling approach instead of focusing on defoliation at earlier developmental stages such as the third or fourth instar.

I used a fixed effects generalized linear model (GLM) using the 'glm' function from the base R package with a Poisson error family to test for the effect of treatment and the number of shoots on spruce budworm defoliation (i.e., significance at $p < 0.05$) with the number of shoots as a random factor. I also analyzed the impact of treatment and the number of shoots separately on defoliation, spruce budworm mass, and survival at the sixth instar, pupa and moth stages. I

used the function 'means' in the package 'emmeans' (Lenth, 2023) to perform a post hoc Tukey HSD test to examine pair-wise comparisons among treatments. All analyses were performed in R version 4.2.2 (R Core Team, 2022) using R-studio GUI (RStudio Team, 2022).

3.2 Results

Shoot Availability

Trees were haphazardly selected for each treatment resulting in an average of 90 buds flushed per tree in the control treatment. In contrast, the direct treatment only had an average of 54 buds per tree, and the indirect treatment had an average of 71 buds per tree (Figure 7). Treatment did not significantly affect the number of shoots available (p =0.096).
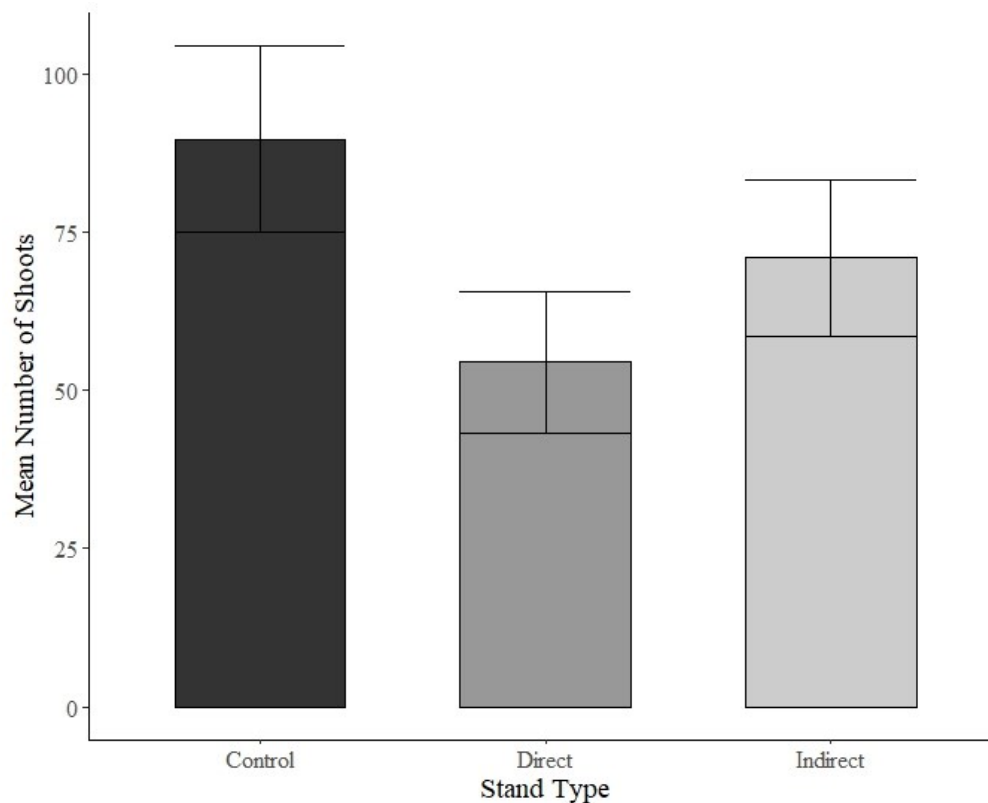
Figure 7. Mean number of white spruce shoots per treatment (± standard error) available for defoliation by spruce budworm in a microcosm experiment. Data was pooled for the last two collection dates of the experiment.

Survival

The control treatment had the highest number of pupae and moths collected, while the direct treatment had the greatest number of sixth instar collected (Figure 8). Treatment did not significantly impact spruce budworm survival (p = 0.791). The number of shoots, however, did significantly affect the survival of spruce budworm sixth instar (F = 7.672, p = 0.008) but not that of moths or pupae.
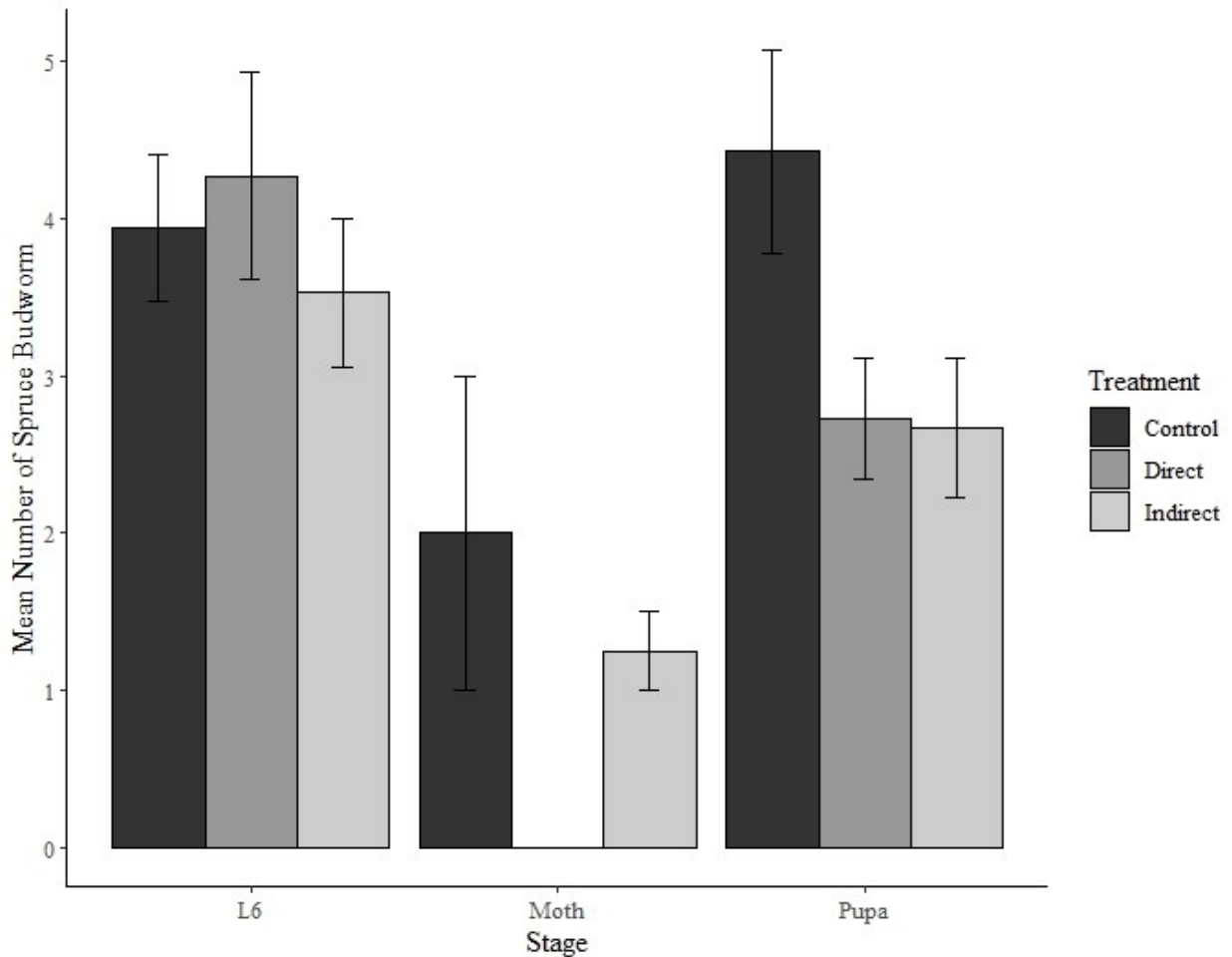
Figure 8. Mean number of spruce budworm (± standard error) collected per treatment by life stage in a microcosm experiment. Data was pooled for the last two collection dates of the experiment.

Mass

Treatment type did not significantly affect the mass (**Error! Reference source not found.**) of either spruce budworm sixth instar (p = 0.845), pupae (p = 0.923) or moths (p = 0.548). However, the mass of the sixth instar spruce budworm, pupae, and moths exhibited a significant negative relationship with the number of shoots (F = 5.03, p =0.031; F = 42.14, p = 7.838e-10; F = 21.99, p = 5.487e-06, respectively).

Table 1. Mean spruce budworm mass (mg) (± standard error (SE)) collected per treatment by life stage in a microcosm experiment. Data was pooled for the last two collection dates of the experiment.

Treatment	sixth instar		Moth		Pupa	
	Mean Mass (mg)	SE	Mean Mass (mg)	SE	Mean Mass (mg)	SE
Control	61.873	2.211	9.412	0.079	53.388	0.422
Direct	67.382	1.213	9.434	0.083	55.027	0.363
Indirect	63.864	1.200	9.840	0.065	54.401	0.334

Defoliation

Treatment type did not significantly affect the percent of defoliation (p = 0.905, **Error! Reference source not found.**). However, the percent of defoliation exhibited a significant negative relationship with the number of shoots available (F = 9.856, p = 0.003). As the number of shoots decreased, the percent of defoliation increased.

Table 2. Mean defoliation per treatment (± standard error (SE)) caused by spruce budworm in a microcosm experiment. Data was pooled for the last two collection dates of the experiment.

Treatment	Mean Defoliation (%)	SE
Control	0.525	0.099
Direct	0.586	0.076
Indirect	0.505	0.110

3.3 Discussion

I used a common boreal tree species (white spruce seedlings) to test whether spiders showed direct or indirect effects on herbivory by eastern spruce budworm. I predicted that in the presence of spiders, defoliation caused by spruce budworm would be reduced due to fear of consumption by spiders, thus resulting in lighter budworm larvae. In the direct experiment, I also predicted that when spiders were free to roam, spruce budworm survival would be significantly lower. I found that neither the indirect treatment in which spiders were present but not able to consume budworm, nor the direct treatment in which spiders were free to roam and able to consume budworm had an impact on the percent defoliation caused by spruce budworm, their mass, or their survival.

Although I did not detect the expected predator effects, I did find significant effects of shoot number (i.e., the amount of food available). The percentage of defoliation is positively correlated with the amount of food available. Despite the haphazard selection of trees for each treatment, the control trees produced more buds that flushed compared to the other two treatments. Having fewer shoots available resulted in lower food availability, meaning that spruce budworm could not accumulate as much mass, hindering their survival. This led to a decrease in the number of spruce budworm reaching adulthood, which ultimately reduced their population size regardless of predator presence.

The spruce budworm may not change its behaviour in response to cues from generalist arthropod predators like spiders and continue defoliating regardless of predation risk. After emerging from diapause in the spring, the second instar spruce budworm establishes feeding sites on the current year's shoots. Following their establishment in a feeding site, larvae undergo four additional instars before pupating (Régnière et al., 2012). These feeding sites provide them with

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protection from predators. Upon being disturbed, they will drop from the branch on silk threads and quickly retreat to the foliage along the silk (Régnière et al., 2012). These defence mechanisms suggest that spruce budworm are co-adapted to predation by spiders and are successful at evading their predators. It is also possible that due to space limitations and the proximity of treatments, the spruce budworm could detect chemotactile cues of the presence of spiders across all treatments equally. Future experiments could set up the treatments under the same conditions but further apart.

Spiders are generalist predators that operate more on opportunity and chance rather than seeking specific prey. The environmental conditions strongly influence the prey spectrum of interception feeders. Consequently, it is predicted that the diet of generalist and opportunistic predators will reflect the diversity of species in the community of their prey (Schmidt et al., 2018). Spiders have been confirmed as predators of spruce budworm (Bowden et al., 2022; Symondson, 2002); however, they did not impact spruce budworm survival in the direct predation portion of this study. In an agricultural system, Beckerman et al. (1997) also found that neither predation nor predation risk significantly affected grasshopper densities relative to a control; still, they influenced herbivore feeding behaviour.

Focusing on the sixth instar to adult life stages may result in the inability to consider direct predation, which may be more prevalent in younger life stages. Due to a combination of logistical and biological considerations (older spruce budworm larvae are easier to retrieve and contribute significantly more to defoliation, respectively), it is possible that treatment effects present at earlier stages could have gone undetected. It is also possible that mortality caused by predation is compensated by natural mortality (Rosenzweig, 1977). As a result of the natural mortality resulting from density-dependent (e.g., intraspecific competition) and density-

independent (e.g., trait-mediated indirect interactions) factors within herbivore populations, predator mortality may be less or equal to natural mortality resulting from these factors.

Overall, these results suggest that the presence of spiders did not have a significant impact on herbivory by eastern spruce budworm. Contrary to the initial hypothesis, neither the indirect nor the direct treatment led to reduced defoliation, lighter budworm larvae, or lower survival rates, indicating that the presence of predators did not deter the herbivores. Instead, food availability was a more significant factor in limiting budworm population size, as evidenced by fewer larvae reaching adulthood in all treatments. Studying spiders in a complex habitat like the boreal forest represents the intricate web of interactions between predators and their prey and how they interact to maintain balance in the environment. It also allows us to assess the role of spiders in controlling irruptive pest populations and if they could be considered as a sustainable and cost-effective addition to current strategies that recognize the importance of natural enemies (e.g., Johns et al., 2019).

4.0 Conclusion

Spiders are abundant, generalist arthropod predators. Their abundance and diversity in the forest is influenced by prey distribution and abundance as well as structural features of their habitat that regulate environmental conditions and provide attachment sites for webs and shelters from predators. Understanding their role as regulators of herbivorous insects, particularly irruptive forest pests, is critical for effective biodiversity and pest control management. These two studies help fill knowledge gaps and provide new information regarding the interactions and biodiversity of arboreal spiders in eastern Canadian boreal forests. I have contributed valuable arboreal spider diversity data from the eastern boreal forest. I observed a higher abundance and richness of spiders in deciduous stands than coniferous stands. This study provides new insight into the relationships between spiders and their habitats, which can help inform ongoing biodiversity maintenance efforts.

Contrary to expectations, I found that budworm herbivory was unaffected by spiders, either through direct consumption or indirectly through behavioural changes. However, I did find that food availability had the most significant impact on spruce budworm survival and herbivory, suggesting that bottom-up factors may be more substantial in spruce budworm population dynamics. Further research is needed to better understand the relationship between spiders and their habitats, as well as the effects of spiders on other species in the ecosystem. I concluded that resource availability was a more important factor in spruce budworm control. While the greater abundance of spiders in deciduous stands may suggest their potential for insect pest control, my findings indicate their contribution may be weak. Future research could directly assay collected spiders for evidence of feeding to confirm their role in controlling spruce budworm populations. Although it falls outside the scope of the present study, it will be necessary to examine the

additive and interactive effects of climate change on boreal forest spiders and the ecosystems they inhabit (Boulanger et al., 2017; Price et al., 2013; Taylor & Chen, 2011).

Overall, my study highlights the need to consider multiple factors and take a holistic approach to pest management. Effective spruce budworm management needs to consider the interaction between the pest and its natural enemies and the environmental factors that influence both their populations. This approach can include cultural, biological, and chemical control methods used in an integrated pest management strategy. Insect predators such as spiders, parasites, and pathogens can help to keep spruce budworm populations in check. Still, their effectiveness can be influenced by factors such as weather, habitat fragmentation, and human disturbance. More work is required to develop a complete understanding of the diversity and composition of arboreal spider assemblages and their role in suppressing pest populations in boreal forests of North America.

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Appendices

Appendix 1. Raw spider abundance, alphabetically by family and life stage. Collection days amalgamated per month. Sites (C= coniferous, D= deciduous, M=mixedwood) amalgamated by stand type. Data was collected in western Newfoundland, Canada.

| Family	Life Stage	June C	D	M	July C	D	M	August C	D	M	September C	D	M
Araneidae	Juvenile	55	50	59	34	31	35	6	51	31	21	72	58
	Mature		1	7	1	1	1			1			
Clubionidae	Juvenile	5	5	7	8	3	16	5	11	8	3	1	6
	Mature	1	1	1				2	6	2	3		3
Cybaeidae	Juvenile												
	Mature	1											
Dictynidae	Juvenile	3	3	19	12	10	25	3	3	1	9	10	27
	Mature	3	4	3	7	6	13	4	21	8	5	5	10
Linyphiidae	Juvenile	101	41	51	51	41	67	113	221	196	90	117	93
	Mature	24	13	16	16	29	23	64	97	40	66	64	89
Lycosidae	Juvenile							1					
	Mature												
Mimetidae	Juvenile												
	Mature			1									
Philodromidae	Juvenile	13	2	19	29	11	27	18	5	12	24	35	35
	Mature	1	1	1	1		2	5	2	2			
Salticidae	Juvenile		20	3		2	2		5				
	Mature						1	1	7	1	1	3	
Tetragnathae	Juvenile				2	5	5						
	Mature					2							
Tetragnathidae	Juvenile		2	4	3	4	4	2	4		20	15	4
	Mature									1			1
Theridiidae	Juvenile	22	65	21	9	36	15	14	30	26	25	95	45
	Mature	3	5		4	14	7	4	11	2	2	8	2
Thomisidae	Juvenile							1		1			
	Mature					1							
Uloboridae	Juvenile				2	1						3	
	Mature									1			

Appendix 2. Raw adult spider species abundance, alphabetically by species. Collection days amalgamated per month. Sites (C= coniferous, D= deciduous, M=mixedwood) amalgamated by stand type. Data was collected in western Newfoundland, Canada.

Species	June C	June D	June M	July C	July D	July M	August C	August D	August M	September C	September D	September M
Agyneta fabra				1								
Araniella displicata		1	4						1			
Canalidion montanum				1							1	2
Centromeres denticulatus		1										
Ceraticelus atriceps	10	1	5	5	6	1	16	32	13	32	34	59
Ceraticelus fissiceps	3	1		2	18	6	28	58	9	20	16	17
Ceratinopsis nigriceps					1							1
Clubiona canadensis								1				
Clubiona kulczynskii								2				
Clubiona trivialis	1	1	1				2	3	2	3		3
Cryphoeca montana	1											
Cylcosa conica			3		1	1						
Dictyna brevitarsa	2	4	3	7	6	13	4	21	8	5	5	10
Dismodicus alticeps	4		5					1	2	1		
Enoplognatha ovata					1	2		1				
Ero canionis			1									
Estrandia grandeva	1					1						
Grammonota angusta	6	3	5	5	3	9	20	6	14	13	11	12
Hyptiotes gertschi									1			
Islandiana longisetosa		1										
Larinioides patagiatus					1							
Lepthyphantes leprosus									1			
Misumena vatia					1							
Neriene radiata		1										
Ohlertidion ohlerti						1		1	1		1	
Pelegrina flaviceps						1	1	5	1	1	2	
Pelegrina flavipes								2			1	
Philodromus imbecillus							3	1	2			
Philodromus rufus	1	1	1	1		2	2	1				
Pityohyphantes limitaneus		1										
Pityohyphantes subarcticus			1			2						
Pocadicnemis americana				1		3			1		3	
Poeciloneta bihamata		1			1	1						
Poeciloneta calcaratus				2								
Rugathodes aurantius		2					1					
Rugathodes sexpunctatus					1							
Tetragnatha versicolor					2	1						1
Theridion differens					1							

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Appendix 1 (Continued)

Species	June			July			August			September		
	C	D	M	C	D	M	C	D	M	C	D	M
Theridion varians	2	5		1	12	1	3	9	1	2	6	
Theridiosoma gemmosum					1	1						
Theridula emertoni	1			2								

Appendix 3. Proportion of spiders by family per treatment in a microcosm experiment. Data was pooled for the last two collection dates of the experiment.
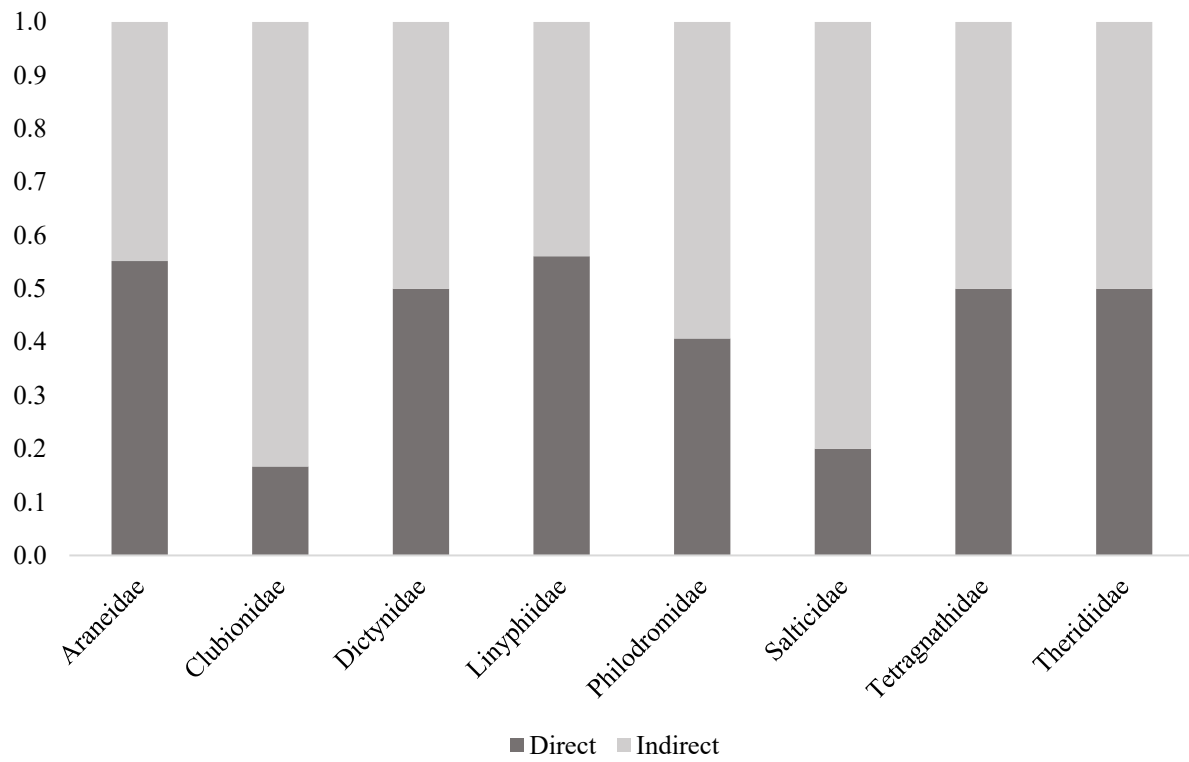
Appendix 4. Proportion of spiders by feeding guild per treatment in a microcosm experiment. Data was pooled for the last two collection dates of the experiment.