HABITAT HETEROGENEITY, TROPHIC LINKS, AND LICHEN ASSEMBLAGES: MULTISCALE PREDICTORS OF ARTHROPOD COMMUNITIES IN NEWFOUNDLAND FORESTS

By

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A thesis submitted to the school of Graduate Studies in partial fulfilment of the requirements for the degree of

Master of Science

Department of Biology

Memorial University of Newfoundland

November 2023

St. John's, Newfoundland and Labrador

Abstract

Arthropods, a highly diverse and abundant groups of animals, are integral to ecosystem functioning worldwide. In forest environments, they act as pollinators, decomposers, nutrient cyclers, and more. However, these arthropod populations are susceptible to environmental changes, which are intensifying due to anthropogenic disturbances. Therefore, it is imperative to understand the dynamics of these communities in response to their surroundings. The aim of this thesis is to understand the variables that affect arthropod community structure in the forest, on trees and in soil. We hypothesized that habitat heterogeneity plays an important role in influencing arthropod diversity and abundance. This study was conducted in Newfoundland during the summer of 2022. We collected monthly arthropod samples from trees and soil in 45 replicate units distributed across three landscapes settings: Salmonier Nature Reserve, Pippy Park, and Outer Cove. Our findings underscore the significance of microhabitat variability, driven by differences in lichen communities, tree characteristics, and soil attributes, in shaping arthropod communities. Furthermore, our study found trophic correlations within and between habitat types, highlighting the importance of inter-group interactions. Finally, site variation underscores how landscape-level features influence arthropod abundance and diversity. Understanding the factors that influence arthropod assemblages can help develop proxy measurements for efficient monitoring of Newfoundland arthropod populations, while providing baseline measurements for future manipulative studies.

Acknowledgements

I would like to express my gratitude to my supervisors, Dr. Yolanda Wiersma and Dr. Troy McMullin, whose support and guidance have been instrumental throughout my thesis. Thank you for your mentorship, near and far away. I would also like to thank my third committee member, Dr. Tom Chapman, for his entomology knowledge and encouragement in sorting through thousands of samples. I am fortunate to have had great lab mates; a shout out to Hayley Paquette for taking me out into the field and inspiring me with her lichen enthusiasm. A special thank you to Dr. Paul Marino for giving me access to his backyard and guide dogs, and Dr. Ian Fleming for providing his truck for my fieldwork. I am immensely grateful to Annika Lindstrom, who was both an exceptional technician and friend in the field. My time in Newfoundland would not have been the same without my close friends and roommates, Coral San Roman and Rachael Moran. Similarly, I would not have gotten through this degree without the support of my family. Thank you to my partner, Shreyas Shah, for trekking into the field with me and providing constant encouragement. I want to acknowledge the funding I received from NSERC and the scholarship from the Entomological Society of Canada, which made this research possible. In addition, I am thankful for the Teaching Assistantships at Memorial University, which enriched my experience as a grad student. I am also thankful to Salmonier Nature Park for granting permission to conduct research within their nature reserve. Lastly, I am very grateful to have had the opportunity to do research on the ancestral homelands of the Beothuk and Mi'kmaq; I strive to be a responsible steward of the land as First Peoples have done since time immemorial.

| Abstract | i |
|---|-----|
| Acknowledgements | ii |
| Table of Contents | iii |
| List of Figures | vi |
| List of Tables | vii |
| Chapter 1: Introduction | 1 |
| 1.1 Background | 1 |
| 1.1 Ecological Theory | 2 |
| 1.2 Research Overview | 3 |
| 1.3 Co-Authorship Statement | 6 |
| 1.4 References | 7 |
| Chapter 2: Lichen 'neighbourhoods' and their arthropod 'residents': How does microhabit | tat |
| structure on balsam fir (Abies balsamea) influence arthropod community structure on the | |
| Avalon Peninsula, Newfoundland? | 11 |
| 2.1 Abstract | 11 |
| 2.2 Introduction | 11 |
| 2.3 Methods | 15 |
| 2.3.1 Sample Sites | 15 |
| 2.3.2 Lichen Surveys | 16 |
| 2.3.3 Arthropod Sampling | 17 |
| 2.3.4 Other Environmental Measurements | 17 |
| 2.3.5 Arthropod Sorting | 18 |
| 2.3.6 Statistical Analysis | 18 |
| 2.4 Results | 20 |
| 2.4.1 General Results | 20 |
| 2.4.2 Arthropod Abundance | 20 |
| 2.4.3 Arthropod Diversity | 21 |
| 2.4.4 Order Abundances | 21 |

| 2.4.5 Correlations between Arthropod Community Traits | 22 |
|---|---------------|
| 2.5 Discussion | 23 |
| 2.5.1 Lichen Community Traits | 23 |
| 2.5.2 Bark Texture | 25 |
| 2.5.3 Canopy Cover | 25 |
| 2.5.4 Correlations | 26 |
| 2.5.5 Site Effects | 27 |
| 2.5.6 Limitations and Conclusion | 28 |
| 2.6 References | 29 |
| Chapter 3: Down in the dirt: Unearthing the complex structure of arthropod co | ommunities in |
| soil ecosystems | 47 |
| 3.1 Abstract | 47 |
| 3.2 Introduction | 47 |
| 3.3 Methods | 51 |
| 3.3.1 Sample Sites | 51 |
| 3.3.2 Arthropod Sampling | 51 |
| 3.3.3 Other Environmental Measurements | 52 |
| 3.3.4 Arthropod Sorting | 53 |
| 3.3.5 Statistical Analyses | 53 |
| 3.4 Results | 55 |
| 3.4.1 General Results | 55 |
| 3.4.2 Total Arthropod Abundance | 55 |
| 3.4.3 Total Arthropod Diversity | 56 |
| 3.4.4 Order Abundances | 56 |
| 3.4.5 Site Effects | 57 |
| 3.4.6 Correlations between Arthropod Community Traits | 58 |
| 3.5 Discussion | 59 |
| 3.5.1 Soil pH | 59 |
| 3.5.2 Canopy Cover | 60 |
| 3.5.3 Ground Cover | 60 |
| 3.5.4 Tree Height | 61 |
| | |

| 3.5.5 Arthropod Community Traits without Significant Predictors | 62 |
|---|----|
| 3.5.6 Site Effects | 62 |
| 3.5.7 Correlations | 63 |
| 3.5.8 Limitations and Conclusion | 63 |
| 3.6 References | 65 |
| Chapter 4: Summary | 88 |
| 4.1 Summary of Results | 89 |
| 4.2 Limitations and Future Research | 93 |
| 4.3 Conclusion | 95 |
| 4.4 References | 96 |

List of Figures

| Figure 2-1. Map of the Avalon Peninsula, Newfoundland, Canada | 35 |
|--|----|
| Figure 2-2. Overall results of statistical models investigating environmental predictors of | |
| arthropod community traits in tree habitats | 36 |
| Figure 3-1. Map of the Avalon Peninsula, Newfoundland, Canada | 73 |
| Figure 3-2. Diagram of the pitfall trap used in this study | 74 |
| Figure 3-3. Correlation plot between the diversity and abundance of soil arthropods and tree | |
| arthropods | 75 |
| Figure 3-4. Overall results of statistical models investigating environmental predictors of | |
| arthropod community traits in soil habitats | 76 |

List of Tables

| Table 2-1. Competing models that were used to predict different arthropod community traits 37 |
|--|
| Table 2-2. List of arthropod orders collected on balsam fir trees by vacuuming between 0.5 and1.5 m above the ground for 5 minutes around the whole bole |
| Table 2-3. List of epiphytes found on balsam fir (<i>Abies balsamea</i>) trees between 0.5 m and 1.5 mabove the ground around the whole bole |
| Table 2-4. AICc of competing models that predict total arthropod abundance |
| Table 2-5. Analysis of best models predicting total arthropod abundance |
| Table 2-6. AICc of competing models that predict total arthropod diversity. 41 |
| Table 2-7. Analysis of the best model that predicts total arthropod diversity. 41 |
| Table 2-8. AICc of competing models that predict Acari (mite) abundance. 42 |
| Table 2-9. Analysis of the best models predicting Acari abundance |
| Table 2-10. AICc of competing models that predict Araneae (spider) abundance |
| Table 2-11. Analysis of the best models predicting Araneae abundance. 43 |
| Table 2-12. AICc of competing models that predict Collembola (springtail) abundance |
| Table 2-13. Analysis of the best model that predicts Collembola abundance. 44 |
| Table 2-14. AICc of competing models that predict Diptera (fly) abundance. 45 |
| Table 2-15. Analysis of the best models predicting Diptera abundance |
| Table 2-16. AICc of competing models that predict Opiliones (harvestmen) abundance |
| Table 2-17. Analysis of the best models predicting Opiliones abundance. 46 |
| Table 3-1. Loadings of the first four principal components from a PCA of ground cover variables. 77 |
| Table 3-2. Competing models used to predict different arthropod community traits |
| Table 3-3. List of arthropod groups collected from pitfall traps on the Avalon Peninsula fromJune through August 2023.79 |

| Table 3-4. AICc of competing models that predict total arthropod abundance. | . 80 |
|---|------|
| Table 3-5. Analysis of the best models predicting total arthropod abundance | . 80 |
| Table 3-6. AICc of competing models that predict total arthropod diversity. | . 81 |
| Table 3-7. Analysis of the best model predicting total arthropod diversity | . 81 |
| Table 3-8. AICc of competing models that predict Acari (mite) abundance. | . 82 |
| Table 3-9. Analysis of the best models predicting Acari abundance. | . 82 |
| Table 3-10. AICc of competing models that predict Araneae (spider) abundance | . 83 |
| Table 3-11. Analysis of the best models predicting Araneae abundance. | . 83 |
| Table 3-12. AICc of competing models that predict Collembola (springtail) abundance | . 84 |
| Table 3-13. Analysis of the best models predicting Collembola abundance. | . 84 |
| Table 3-14. AICc of competing models that predict Diptera (fly) abundance. | . 85 |
| Table 3-15. Analysis of the best models predicting Diptera abundance. | . 85 |
| Table 3-16. AICc of competing models that predict Hymenoptera (bees, wasps, ants) abundan | ce. |
| | . 86 |
| Table 3-17. Analysis of the best models predicting Hymenoptera abundance. | . 86 |
| Table 3-18. AICc of competing models that predict Opiliones (harvestman) abundance | . 87 |
| Table 3-19. Analysis of the best models predicting Opiliones abundance. | . 87 |

Chapter 1: Introduction

1.1 Background

The Earth's ecosystems are undergoing drastic changes due to the combined impacts of climate change and other anthropogenic disturbances. Deforestation, intensive agriculture, invasive species, pollution, extreme weather events, and urbanization are just some of the factors contributing to the devastation of the natural world. While the human population grows exponentially, most animals are facing widespread declines, leading biologists to declare a sixth mass extinction event (Wagner et al. 2021). Arthropods are not immune to these changes, despite their inconspicuous nature to humans. Recent reports have highlighted their alarming decline, with global estimates suggesting a decrease in arthropod abundance at a rate of 1 to 2% per year, with variations among different regions (Wagner et al. 2021).

Terrestrial arthropods, which include insects, arachnids, mites, centipedes, millipedes, and related taxa, are the planet's most diverse and vital group of organisms. They account for 80% of all animal diversity, with an estimated 7 million species (Stork 2018). Their roles as pollinators, decomposers, nutrient cyclers, soil aerators, and others, position them at the core of ecosystem functioning, while also providing invaluable economic benefits for humans (Losey and Vaughan 2006, McGeoch et al. 2011). It has been argued that the absence of arthropods would lead to worldwide collapse of ecosystems, having catastrophic impacts on the human population (Cardoso et al. 2020).

Despite their significant diversity and ecological importance, arthropods remain understudied. A recent review revealed they were the subject of less than a quarter of research papers on biodiversity, although they constitute over half of all animal species (Titley et al. 2017). Moreover, arthropods are often overlooked in wildlife conservation efforts. For example,

a somewhat amusing yet revealing decision by the California Supreme Court in 2022 ruled that insects can be classified and protected as "fish" (Sanders 2022). Given the research gap and the urgent crisis in the natural world, it is imperative to better understand the factors that influence arthropod distribution, abundance, diversity, and community structures.

Although not as diverse as in the southern regions of North America, arthropod diversity in Canada is still impressive. At least 44,000 species have been described in the country, which represent over half of its fauna (Langor 2019). Diptera, Hymenoptera, Coleoptera, Acari, and Thysanoptera make up the most speciose groups, with the latter two especially understudied (Langor 2019). Research on the island of Newfoundland in eastern Canada is particularly limited, with the majority of studies focusing on taxonomic aspects rather than from a community ecology perspective. The present study offers a valuable opportunity to examine some of the arthropod communities in Newfoundland.

1.1 Ecological Theory

One prominent hypothesis explaining the proliferation of arthropods is their small size, which enables them to occupy countless small-scale environmental niches (Lawton and Strong 1981, Wilson 1987, Nielsen et al. 2010). As ecosystems become more complex, the availability of unique niches increases, allowing ecological specialization and diversification (Nittérus and Gunnarsson 2006, Nielsen et al. 2010, Wehner et al. 2016). Habitat heterogeneity can affect biota phenology and physiology, as well as their interactions, which ultimately shapes arthropod assemblages (Adams et al. 2020). Therefore, the central hypothesis of this thesis is that habitat heterogeneity at various scales has an effect on arthropod diversity and abundance. It is widely recognized that arthropods are sensitive to microenvironmental factors, such as temperature fluctuations, physical structures, and interactions with other organisms (Kremen et al. 1993, Langor and Spence 2006, Santorufo et al. 2012). Due to their ability to respond and adapt to environmental gradients, arthropods are effective indicators of environmental conditions (Kremen et al. 1993, Nilsson et al. 1995, McGeogh 1998, Orabi 2012, Menta and Remelli 2020). Many studies have investigated the use of terrestrial invertebrates to monitor restoration progress, detect environmental change, and measure ecosystem functioning (Langor and Spence 2006, McGeoch et al. 2011). The presence of certain taxonomic groups, such as mites, springtails, and beetles, or overall diversity in an area has been proposed as evidence of healthy and thriving environments (McGeogh 1998, Langor and Spence 2006).

Other measurable conditions, such as environment structures like canopy cover, may serve as evidence for diverse or abundant arthropod communities, which are referred to as biodiversity indicators (Kerr et al. 2000, Rodrigues and Brooks 2007, Orabi 2012). A key step in preservation and conservation is systematic and long-term monitoring (Kremen et al. 1993, McGeoch et al. 2011, Duchenne et al. 2022). Investigating the correlations between arthropod abundance and diversity with environmental variables will not only shed light on the formation of arthropod communities, but also provide tools for monitoring their populations across different spatial and temporal scales.

1.2 Research Overview

Communities within an environment are influenced by their surroundings, which in turn influences ecosystem functioning. Understanding these interactions, at both small and large scales, is important for monitoring populations long-term. However, the challenge of replicating complex landscapes imposes limitations on the use of manipulative experiments in landscape ecology (Jenerette and Shen 2012). For example, attempting to replicate at a large scale when investigating the communities of larger-bodied organisms, such as birds or mammals, is difficult due to the size and complexity of the landscapes they live in (Filazzola and Cahill 2021). The use of microlandscapes, which serve as model systems, can enhance statistical significance by providing replicate units (Srivastava et al. 2004). In this study, I used trees as replicate 'microlandscapes'. In addition, lichen patterns on tree trunks have been proposed as micro-scale replicate units, and therefore serve as landscape 'patches' on the trees (Wiersma and McMullin 2018).

In the summer of 2022, I conducted a study focusing on arthropod diversity and abundance in three forest stands on the Avalon Peninsula, Newfoundland, the easternmost region of Canada. The study sites are within the Maritime Barrens, an ecoregion characterized by cool summers, moderate winters, and significant precipitation and fog (Damman 1983). Our sampling areas consisted of balsam fir dominated stands within Pippy Park, Salmonier Nature Reserve, and Outer Cove. The collection period was from June to August.

Our research concentrated on studying communities in two distinct, yet interconnected forest habitats: trees and soil. In chapter two, I examine the relationship between arthropods and the lichen communities that are found on tree bark, as well as additional microhabitat variables. I hypothesized that arthropod communities respond to habitat heterogeneity both at the tree and landscape level. Arthropods make up 65–70% of the species in forests but are poorly studied (Langor and Spence 2006). Lichens are composite organisms comprising a symbiotic relationship between a fungus and an alga or cyanobacteria and are notable bioindicators of air quality (Conti and Cecchetti 2001). However, they may also provide important habitat for

arthropods, but this relationship is understudied. On trees, lichens create a microhabitat within the larger tree habitat, which I refer to as lichen 'neighbourhoods'. Newfoundland is a hotspot for lichen (Ahti 1983), and the interactions between lichens and arthropods may have broader implications for ecosystem functioning. I collected tree arthropods using a handheld vacuum and measured lichen community traits and other tree characteristics.

Soil is widely recognized as one of the most complex and heterogenous ecosystems in the world, accommodating a significant portion of the Earth's biodiversity (Kopittke et al. 2019, Ghiglieno et al. 2020). Chapter three of my thesis has a strong focus on the influence of abiotic factors such as soil pH, as well as surrounding vegetation, on arthropod community structure. I hypothesized that environment traits directly and indirectly shape microhabitats, which in turn influence the assemblages within them. Moreover, this chapter explores trophic relationships within the soil community and between soil and tree habitats, which I predicted to influence arthropod communities. To sample soil arthropods, I placed pitfall traps near the trees examined in chapter two.

In both chapters, I use statistical models to analyze the intricate and multifaceted interactions between the environment and arthropod community structure. These models allow for a comprehensive analysis of the complex relationships at play. In the concluding chapter, I provide a summary of our research findings on forest arthropod communities. Furthermore, I discuss how this research contributes to the broader ecological conversation on arthropod conversation, limitations of the study, and possibilities for future research.

The investigation of how arthropod communities are influenced by their habitats and interactions with each other aims to identify potential biodiversity indicators. Addressing the widespread declines in arthropod biodiversity is a highly urgent, complex, and expensive

undertaking. Therefore, proxies such as ecological indicators are appealing in working towards this goal. This study will hopefully promote further research on arthropod community ecology in the province, ultimately helping to monitor the hidden diversity that exists on trees and within soil. Furthermore, this research aims to inform effective conservation strategies, ensuring that arthropods are recognized and protected appropriately, rather than being lumped together as "fish".

1.3 Co-Authorship Statement

This research was co-supervised by Dr. Yolanda Wiersma of Memorial University in St. John's, Newfoundland and Dr. Troy McMullin of the Canadian Museum of Nature in Ottawa, Ontario. As primary author, I led the study design, field work, data collection and analysis, and writing of the four following chapters. This work was greatly assisted by the support, editing, and feedback from my committee members, Drs. Yolanda Wiersma, Troy McMullin, and Tom Chapman. Dr. Wiersma provided critical guidance on research design, field preparation, data analysis, and writing. Dr. McMullin particularly assisted with lichen identification and Dr. Chapman provided guidance on arthropod identification. I completed field work with my field assistant, Annika Lindstrom, and all laboratory work was completed by myself. All committee members helped with manuscript revision before final thesis submission. Since chapters 2 and 3 are written as stand-alone manuscripts (which I plan to submit to peer-reviewed journals in the coming months), there is necessarily some repetition in description of study site and duplication of one figure (Figures 2-1 and 3-1).

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Chapter 2: Lichen 'neighbourhoods' and their arthropod 'residents': How does microhabitat structure on balsam fir (*Abies balsamea*) influence arthropod community structure on the Avalon Peninsula, Newfoundland?

2.1 Abstract

Arthropods play crucial roles within forest ecosystems, an area that remains understudied in Newfoundland forests. As a region that is known for its ubiquitous and abundant lichen populations, we were interested in investigating the relationship between arthropod and lichen communities. We used a handheld vacuum to sample arthropods on balsam fir (*Abies balsamea*) trees on the Avalon Peninsula, Newfoundland, from June to August 2022. This study aimed to assess the impact of lichen communities, tree-level characteristics, and stand-level variation in shaping arthropod communities. Our findings indicate that both arthropod abundance and diversity are affected by variation in these three categories. In particular, lichen cover, canopy cover, and bark texture are important environmental factors that may in turn be used as proxy measurements for monitoring arthropod populations. This research provides a foundation of understanding arthropod dynamics in forest ecosystems on the Avalon.

2.2 Introduction

Arthropoda, the phylum that includes arachnids, myriapods, crustaceans, and insects, constitutes the most diverse group of organisms in the world (Zhang 2011). In terrestrial ecosystems, arthropods dominate in both number of species and biomass (Kremen et al. 1993). It is approximated that upwards of 7 million species of terrestrial arthropods exist, 1.3 million of which are currently described, and over 80% of which are insects (Zhang 2011, Stork 2018). Arthropods play critical roles in ecosystem functioning; they are pollinators, decomposers, nutrient cyclers, and food sources for higher trophic levels (Losey and Vaughan 2006).

Arthropods are highly responsive to environmental heterogeneity both at small and large scales. At the landscape scale, arthropod communities are affected by disturbances such as habitat loss, as well as changes to climate, which can alter their distribution, behaviour, and life cycles (Schowalter 2012, Egerer et al. 2017, Perry and Herms 2019). Several studies have demonstrated the impact of landscape complexity, characterized by composition, configuration, and connectivity, on arthropod abundance and richness (Jeanneret et al. 2003, Ali et al. 2022, Gallé et al. 2022). More diverse landscapes, for example, typically have higher arthropod species richness (Steiner and Kohler 2003, Wang et al. 2019, Marja et al. 2022). The spatial arrangement and heterogeneity of landscapes are identified as major drivers, affecting species ecology, dispersal abilities, population persistence, species interactions, and ecosystem function (Jeanneret et al. 2003, Fahrig et al. 2011, Egerer et al. 2017). At a smaller scale, arthropods may also respond to small-scale changes, due to preferences of niches within specific microhabitats (Nielsen et al. 2010, Buchholz et al. 2013). Their short generation times make it easier to study their responses to habitat change and fine environmental conditions (Langor and Spence 2006, Adams et al. 2020). For these minute organisms, the matter of scale is different than for birds or for mammals.

In many forest ecosystems, arthropods depend on lichens for habitat (Gerson 1973). Lichens are complex organisms formed by the intimate symbiosis of a fungus with an alga and/or cyanobacterium (Brodo et al. 2001). Over 19,000 lichen species are known today, and it is estimated that lichen cover 8% of terrestrial surfaces (Lücking et al. 2016). There is considerable inter- and intra-specific variation in physiological and morphological traits among lichen species, which help determine their functional roles (Asplund and Wardle 2014, Ellis et al. 2021).

Lichens often grow in multispecies assemblages with varying amounts of species diversity and trait variation, forming unique and elaborate lichen communities (Asplund and Wardle 2014, 2017). These communities are part of forest biogeochemistry processes due to their role in water and nutrient cycling (Knops et al. 1996, Ellis et al. 2021). In addition, their interactions with macrofauna, such as caribou, and microfauna, such as arthropods, frequently place lichens as focal points in forest food webs (Ellis 2012, Asplund and Wardle 2017). The resulting network of physical and biotic interactions can be considered a microhabitat, or a lichen 'neighbourhood'.

Arthropods 'reside' in and use these 'neighbourhoods' for food, oviposition sites, protection against abiotic environmental conditions, camouflage for predators or prey, and structures for spiderwebs (Lalley et al. 2006, Martinez et al. 2014). Arthropods potentially reciprocate these services by dispersing lichen reproductive structures (Gerson 1973). Despite these co-dependencies, lichen-arthropod interactions in forest ecosystems have attracted relatively little research attention.

At the scale of a single tree, lichen community patterns are consistent across trees within a single stand, and therefore can serve as replicate patches within the forest "landscape" (Wiersma and McMullin 2018). The variation of these patches, due to factors such as local weather, tree characteristics, and proximal biota, may correspond to the heterogeneity of arthropod communities within them. Wilkerson (2008) proposed that epiphytic lichens, such as those that grow on trees, may serve as surrogate organisms of microfauna assessments. For example, lichen biomass and abundance has been found to positively impact arthropod abundance and density (Stubbs 1989, Pettersson et al. 1995, Ellis 2012, Rich et al. 2013, Asplund and Wardle 2017). In addition, lichen physiological traits, such as nitrogen-fixing

ability, drive arthropod community composition and may explain over a third of variation in abundances of major invertebrate groups (Bokhorst et al. 2015). Various studies have shown the positive correlation between lichen species richness and spiders (Gunnarsson et al. 2004, Ellis 2012), a relationship that is also exhibited between lichens and beetles (Nilsson et al. 1995). On biological crusts, the complex collection of living organisms at the surface of soils, lichen species richness and morphological groups are positively correlated with arthropod species richness (Brantley and Shepherd 2004, Lalley et al. 2006).

The complexity of habitat may also determine the number of species a community can support (Lawton and Strong 1981). Lichens are commonly grouped into three growth forms: foliose (leaf-like), fruticose (bushy or hair-like), and crustose (crust-like), with the former two known together as 'macrolichens'. The morphological complexity of each growth form may dictate abundance, richness, and composition of arthropods (Andre 1985, Stubbs 1989, Lalley et al. 2006), and they have been shown to influence the numbers of Collembola, Psocodea and Acari found on tree trunks (Gunnarsson et al. 2004).

Newfoundland is globally recognized for its rich and interesting lichen biota, which has prompted multiple studies and surveys on lichens (Ahti 1983). However, there have been few studies on arthropods in Newfoundland, and no studies have investigated arthropod-lichen relationships in the province. To address this knowledge gap, we investigated the patterns of covariation between lichen 'neighbourhoods' and arthropod communities in balsam fir (*Abies balsamea*) stands on the Avalon Peninsula in Newfoundland. While lichen 'neighbourhoods' may play a significant role in determining arthropod communities, it is also important to consider other environmental factors, from the tree- to landscape-scale, to gain a more comprehensive understanding of the overall habitat structures that influence arthropod abundance and diversity.

Our objectives were to answer the following exploratory questions: 1) Does lichen community structure influence arthropod abundance and diversity, and if so, which community traits are most important? We hypothesized that lichen assemblages play an important role in shaping arthropod communities due to the degree of habitat complexity they provide. In particular, more complex lichen patches, through increased richness or coverage, will have a positive impact on arthropod abundance and diversity. 2) What microhabitat variables, other than lichen community, are important for predicting arthropod abundance and diversity? We hypothesized that habitat structures, such as bark texture, predict arthropod abundance and diversity in conjunction with lichen communities. Finally, 3) Do arthropod communities respond to habitat heterogeneity differently among sites (i.e., at the landscape scale)? We hypothesized that there will be similar trends in arthropod community response to habitat heterogeneity, but the strengths of response will differ among sites due to varying levels of landscape complexity at each site. This research aims to prompt further research on Newfoundland arthropods in general, as well as specifically investigating interactions between arthropods and lichens.

2.3 Methods

2.3.1 Sample Sites

The study was conducted on the Avalon Peninsula (The Avalon), Newfoundland, Canada. The Avalon is comprised of three broad ecoregions: Maritime Barrens, Avalon Forest, and South Avalon-Burin Oceanic Barrens (Bell 2002). All sampling was done in the Maritime Barrens, an area characterized by cool summers, moderate winters, and long periods of fog (Bell 2002). Mean temperatures range from 11.5°C in the summer down to -1°C in the winter. The average yearly precipitation is between 1200 mm and 1600 mm (Bell 2002). The region is dominated by balsam fir stands; although sparse stands of tamarack, black spruce, and shrubs are also present (Bell 2002).

We selected three large sampling areas (referred to as "sites"): Pippy Park, Salmonier Nature Reserve, and Outer Cove (Fig. 2-1). Pippy Park is a 13.75 km² urban park at the northern boundary of St. John's, a few minutes' drive from the downtown core. Salmonier Nature Park is a wildlife rehabilitation and education center with 14 km² of undeveloped land, 60 km southeast of the city. The Outer Cove site is a large piece of privately-owned land adjacent to the East Coast Trail and 10 km from downtown St. John's. Within each site, areas with homogenous balsam fir stands that were within ~ 1 km of each other were labelled as "plots". There were three plots selected per site.

Within each plot, five balsam fir trees were selected that were at least 5 m apart from each other and of similar diameter. Trees were not selected if they were in poor condition (dead, noticeable damage, or decaying) or if they had no lichen coverage.

We established sites (n = 3), plots (n = 9), and trees (n = 45) in May 2022 and recorded the geographic coordinates of each tree using a GPS.

2.3.2 Lichen Surveys

Lichen surveys were completed throughout the summer. We surveyed the entire bole surface of each tree between 0.5 m and 1.5 m above ground. We identified macrolichens (foliose and fruticose species) to genus, or species when possible, using a hand lens and identification guides, and crustose lichens were not identified. If identification was not possible in the field, samples were taken back to the lab for microscope examination. We visually estimated percent coverage of each lichen morphological group individually (foliose, fruticose, crustose), as well as percent coverage of the moss and liverworts growing on the tree, in the same area that lichens were surveyed.

2.3.3 Arthropod Sampling

Arthropod sampling occurred between June 1 and August 30, 2022, using a battery powered handheld vacuum (InsectaVac Aspirator, BioQuip). We vacuumed each tree for 5 minutes, covering the entire bole in the same area sampled for lichen (0.5 - 1.5 m above ground). Each tree was vacuumed once a month (approximately 30 days apart) in June, July, and August, for a total of 135 samples. We tried to sample trees in the same order each month, so that it was approximately one month between repeated vacuums. We did not sample on rainy days, and always sampled between 9 am and 4 pm.

We vacuumed the arthropods into a small container. The contents of the container were emptied into labelled plastic vials which we then filled with propylene glycol to kill and preserve the specimens. We kept the vials in a cooler until they could be refrigerated.

2.3.4 Other Environmental Measurements

Overhead canopy cover, a proxy for humidity and light availability, was measured using a convex spherical densiometer, averaged from readings at the North, East, South, and West points of the tree. Tree height was measured using a Suunto clinometer and tape measure. Diameter at breast height (DBH) was measured using the diameter side of a ProTape measurer. Bark texture was measured using a scale used by Wigle et al. (2021) that has been adapted for this geographic area. A rank of 1 is relatively smooth, 2 is moderately ridged, and 3 is deeply and heavily ridged. Bark pH, a proxy for substratum quality, was measured by taking thin samples of bark back to

the lab to dry for two weeks. After two weeks, lichen and other debris was removed from the bark using a razor blade, and samples were ground using a coffee grinder. Ground bark was transferred to a vial with 10 mL of distilled water and let to sit for two hours. A pH meter was calibrated and used to record pH.

2.3.5 Arthropod Sorting

We removed propylene glycol from each sample container using a filter cloth and discarded debris. We identified specimens to order by examining external morphological under a dissecting microscope. We recorded the number of individuals in each taxonomic group. We removed any specimens that were not arthropods (n = 2) prior to analysis. We poured the specimens back into the original vials, which were filled with ethanol. Samples are stored in a refrigerator in the Core Science Facility at Memorial University at approximately 4°C.

2.3.6 Statistical Analysis

All continuous explanatory variables (pH, macrolichen percent cover, total lichen percent cover, marcrolichen species richness, canopy cover) were tested for correlation, and all correlation coefficients fell below 0.6. These variables were then standardized by subtracting the mean from individual values of the variable and dividing by the standard deviation of the variable. Arthropod diversity was calculated using the Hill-Shannon index using the "rarity_plot" function from the MeanRarity package (Roswell and Dushoff 2022).

We investigated the effects of lichen and environmental factors on seven response variables: total arthropod abundance (TAA), total arthropod diversity (TAD) at the order level, as well as the abundance of the five most abundant arthropod orders: Araneae, Acari,

Collembola, Diptera, and Opiliones. Response variables were summed across months, to provide one measurement per tree (n = 45). For each of these seven response variables, we ran seven competing models (Table 2-1). We used a univariate approach to investigate the patterns between abiotic and biotic predictors in the environment and one arthropod community trait at a time. Using generalized linear mixed models using the "glmer" function from the lme4 package (Bates et al. 2015) allowed us to incorporate random effects to account for the nature of the hierarchical study design. Further studies can further expand on these relationships using multivariate statistics. All models used a Poisson error distribution with a log link function except for the TAD models, which used a Gaussian error distribution with an identity link. Each model included plot and sample number as a random effect, site as a fixed effect, and a combination of explanatory variables (Table 2-1). If the models were overfitted, we ran an ANOVA of plot and site effects on the response variable and removed plot as a random effect (Diptera abundance, Opiliones abundance, Araneae abundance, arthropod diversity) if plot was not significant. For each response variable, the seven competing models were compared using a corrected AIC due to the small sample size. AICc was calculated using the "aictab" function from the AIC moday package (Mazerolle 2020). The models within an Δ AIC c of two or less were then analyzed individually to determine which effects were significant by looking at beta estimates, confidence intervals, and p values. All analyses were conducted in R (R Core Team 2021).

TAA, TAD, and Araneae, Acari, Collembola, Diptera, and Opiliones abundances were tested for correlation to investigate trophic interactions. Correlations with a p-value < 0.05 were considered significant; those of which with an $r \ge 0.6$ were considered strong relationships, and with $0.6 > r \ge 0.35$ were considered moderate.

2.4 Results

2.4.1 General Results

A total of 3661 individual invertebrates from 16 major taxonomic groups (14 orders, 2 classes) were identified from 135 samples taken at 3 sites on the Avalon Peninsula from June through August 2022 (Table 2-2). All individuals are arthropods, other than two slugs, which were omitted from analysis. Most individuals are arachnids (58.9%), and at least one arachnid order appeared in 75-93% of all samples. Collembola are an abundant order, making up 23% of all individuals, and found in 90% of all samples. The five most abundant taxonomic orders, in descending order, were Acari, Collembola, Opiliones, Araneae, and Diptera, which all appeared in 65% or more of all samples.

We identified 14 lichen species or genera (Table 2-3). Crustose lichens typically covered more of the tree than any other type of lichen or bryophyte and were found on all trees. *Hypogymnia physodes, Parmelia squarrosa,* and *Platismatia glauca* were on every tree.

2.4.2 Arthropod Abundance

The model selection suggests that the Macro Cover, Total Cover, Canopy, and Bark Texture models are the best predictors of arthropod abundance, in that order (Table 2-4). All four of these models fell within a Δ AICc of 2.00 from the best model and have a combined weight of 0.94. After analyzing each model independently, the main effect was never found to be statistically significant. However, the effect of the Salmonier site is significant in each model, indicating that each model predicts arthropod abundance in Salmonier specifically (Table 2-5). Therefore, in Salmonier, arthropod abundance positively responds to the percent of macrolichen on a tree, the amount of total lichen coverage, an increase in canopy cover, and rougher bark textures.

2.4.3 Arthropod Diversity

The model selection suggests that the Total Cover model is the best predictor of arthropod diversity (Table 2-6). No other models fell within a Δ AICc of 2.00 and therefore were not analysed. The weight of the Total Cover model is 0.99. Total lichen cover did not have a significant effect overall on arthropod diversity, although, as with arthropod abundance, the model responds significantly well in Salmonier (Table 2-7). Therefore, total lichen cover is an important predictor of arthropod diversity in Salmonier with a negative relationship.

2.4.4 Order Abundances

The model selection suggests that the Canopy, Macro Cover, Total Cover, and Bark Texture models are the best models of Acari abundance (Table 2-8). All four of these models fell within a Δ AICc of 2.00 from the best model and have a combined weight of 0.91. After analyzing the models further, the main effect was never found to be statistically significant. All models responded positively in Salmonier specifically (Table 2-9). Therefore, at that site, the abundance of Acari increases with an increase in canopy cover, macrolichen cover, total lichen cover, and bark texture.

The model selection suggests that Canopy Cover, Macro Cover, Total Cover, and Bark Texture models are the best predictors of Araneae abundance, in that order (Table 2-10). All four models fell within a Δ AICc of 2.00 from the best model and have a combined weight of 0.94. In Pippy Park, Araneae abundance is shown to respond negatively to canopy cover and macrolichen cover (Table 2-11). Araneae abundance is predicted by total cover in Salmonier, with a negative response as well. Although one of the best models, bark texture does not affect Araneae abundance at any site. The model selection suggests that the Macro Cover model is the best predictor of Collembola abundance (Table 2-12). No other models fell within a Δ AICc of 2.00 and therefore were not analyzed. The weight of the Macro Cover model is 0.61. Macro Cover was found to be a significant and positive main effect (Table 2-13). Therefore, Collembola abundance can be predicted by the amount of macrolichen that is found on a tree at each site.

The model selection suggests that the Total Cover, Macro Cover, Canopy, and Bark Texture models are the best predictors of Diptera abundance, in that order (Table 2-14). All four of these models fell within a Δ AICc of 2.00 from the best model and have a combined weight of 0.97. Each model shows a significant response in both Pippy Park and Salmonier, although the response is stronger in Pippy Park for each model (Table 2-15). Therefore, in these two sites, Diptera abundance is positively affected by total cover, macrolichen cover, canopy cover, and bark texture, particularly in Pippy Park.

The model selection suggests that the Canopy, Total Cover, and Macro Cover models are the best predictors of Opiliones abundance, in that order (Table 2-16). All three of these models fell within a Δ AICc of 2.00 from the best model and their combined weight is 0.83. Opiliones abundance responds negatively to canopy cover, total cover, and macrolichen cover at Salmonier specifically (Table 2-17).

2.4.5 Correlations between Arthropod Community Traits

Total abundance strongly and positively correlated with Acari (r(43) = 0.74, p < 0.01) and Collembola (r(43) = 0.66, p < 0.01) abundances. There were moderate negative correlations between Abundance and Diversity (r(43) = -0.48, p < 0.01) and Diversity and Acari (r(43) = - 0.58, p < 0.01). Opiliones positively correlated with Araneae (r(43) = 0.52, p < 0.01), and Collembola (r(43) = 0.37, p = 0.01) to a moderate degree.

2.5 Discussion

Both lichen community traits and tree-level characteristics are important predictors of total arthropod abundance (TAA) and diversity (TAD), as well as the abundance of Acari, Araneae, Collembola, Diptera, and Opiliones (Fig. 2-2). Macrolichen cover, total lichen cover, canopy cover, and bark texture alone or in combination predicted each response variable with varying degrees of strength and direction at the three sites.

2.5.1 Lichen Community Traits

Regarding lichen community traits, we hypothesized that more complex microhabitats would increase arthropod abundance. TAA, Acari, Collembola, and Diptera abundance responded as expected; they increased with macrolichen cover. However, in all groups except Collembola, total lichen cover also predicted abundance, indicating that the amount of crustose lichen on the tree is also important. Although macrolichens may offer three-dimensional complexity for habitat, crustose lichen can increase habitat texture, which in turn has been shown to affect arthropod communities (Lalley et al. 2006, Miller et al. 2008). Lalley et al. (2006) found that crustose lichen cover is the dominant environmental factor in determining variation in arthropod assemblages. Crustose lichens have also showed more positive correlations than foliose and fruticose lichens with abundance of Dipteran families on red maple trees (Miller et al. 2008). Thus, it appears that a lichen community that has relatively equal proportions of all

morphological groups provides the structural heterogeneity to promote higher arthropod abundance.

In contrast to Ferrenberg and Mitton (2014) which demonstrated that greater texture promoted a greater diversity and abundance of microanimals, we found a negative relationship between TAD and total lichen cover. Although it seems intuitive for abundance and diversity to follow similar patterns, the two do not necessarily respond in the same way to their environmental conditions. For example, many urban areas have higher arthropod abundance and lower diversity as there may be more concentrated resources to help generalist species thrive (Adams et al. 2020). In addition, because diversity in this study was measured at a high taxonomic resolution, other patterns may have been observed if we had been able to identify arthropods to species or genus level. This perhaps offers an explanation as to why total lichen cover was the only strong predictor of TAD in this study.

Similarly, both Araneae and Opiliones exhibited negative responses to total lichen and macrolichen cover. This is an unexpected result as previous studies have shown that spiders increase with lichen abundance as they offer more space to create webs for prey capture, protection from environmental conditions, and a food source (Gunnarsson et al. 2004, Lalley et al. 2006, Miller et al. 2008). Miller et al. (2007) proposed a trophic link between Araneae and Acari, as well as Araneae and Collembola, where the depletion or addition of one group leads to a decline or increase in the other, respectively. However, these correlations were not found in this study. This suggests that another mechanism may be influencing Araneae and Opiliones populations in this environment. Structurally complex habitats, for instance, may provide refuge for prey, subsequently limiting the predator's food source and prompting the arachnid predators to seek more accessible prey in nearby habitats (Finke and Denno 2006). In addition, Asplund

and Wardle (2017) suggested that as organisms get smaller, they increasingly rely on lichen as habitat, whereas larger organisms depend more on lichen as a food source. Different functional uses of lichen at different trophic levels could help explain some of these opposing responses.

2.5.2 Bark Texture

TAA and Acari, Araneae, and Diptera abundances showed positive responses to increasing bark texture. We predicted that bark texture would affect arthropod communities both by increasing the habitat complexity, like crustose lichens, and by providing more grip for the arthropods. For example, trees may use smooth bark as a protection mechanism against insect attacks as it reduces their ability to grip the tree (Ferrenberg and Mitton 2014). Miller et al. (2007; 2008) also observed an increase in arthropod count with increased thickness and flakiness, particularly for Acari, Collembola, and Diptera, although we found no relationship between bark texture and Collembola.

2.5.3 Canopy Cover

Canopy cover is a difficult factor to consider in that it is often used as a proxy for other measurements. A change in canopy cover affects light availability, temperature and moisture, and forest floor vegetation. Therefore, we hypothesized that canopy cover would be a tree-level characteristic that would impact arthropod community structure. As predicted, TAA, and Acari and Diptera abundance responded positively to an increase in canopy cover, which is consistent with other studies. For example, Miller et al. (2007; 2008) showed that a greater number of arthropods are found in closed canopy forests than in open canopies, with Araneae, Collembola,

and Diptera responding strongest to this condition. Similarly, Greenberg and Forrest (2003) showed that microarthropod abundance and biomass are greater in closed canopy forests.

Araneae and Opiliones demonstrated a negative response to canopy cover, contrary to findings by Richardson et al. (2010) that indicated a lower biomass of arthropod predators in forest with canopy gaps. The negative relationship could be due to the secondary positive effects of an open canopy on the microhabitat. For example, increased canopy openness can lead to the growth of understory or forest floor vegetation by allowing more light in, which may provide more niches for insects and other arthropods. Opiliones, while phylogenetically more closely related to Acari, are superficially similar to Araneae. It is possible that the similarity in their life histories explain their similar responses to some environmental variables.

2.5.4 Correlations

Although no strong relationships were observed between Araneae and Acari or Collembola, Acari and Collembola abundance both strongly correlated with TAA. This suggests that these two orders may serve as critical indicators of the number of arthropods in a given habitat. Interestingly, a negative relationship was shown between TAA and TAD, indicating that trees with a greater number of individuals had lower levels of diversity. Occupying lower levels of the forest food web, Collembola and Acari are known for their ability to occupy diverse ecological niches, which may give them a significant influence in certain habitats and enable them to outcompete other arthropod groups, in turn decreasing overall diversity. Araneae and Opiliones are positively correlated, which is unsurprising considering their similar responses to different predictors. Both Araneae and Opiliones are predatory invertebrates, placing them in a higher

trophic level than Collembola and Acari, which are common prey items for the two predatory orders. Opiliones abundance also moderately correlates to Collembola abundance.

2.5.5 Site Effects

It is noteworthy that most of the observed relationships showed a strong response in only one or two of the study sites. These relationships were mostly observed in Salmonier, occasionally in Pippy Park, and only once in Outer Cove. Although we expected that there would be variation in the responses at each site, it was unexpected that the relationships would only be observed predominantly in one site. Of the three sites, Salmonier, which is a nature reserve, may be the most accurate representation of the natural environment for these arthropods. In contrast, the coastal location of Outer Cove may have other mechanisms at play that decrease the influence of lichen and tree-level heterogeneity on arthropod communities. For example, wind may be a particularly influential factor near the ocean, and flying insects decrease with increasing wind speed (Møller 2013). In addition, sea spray aerosol particles acidify as they transfer from the ocean to the air, which may create adverse conditions for arthropod populations in Outer Cove (Angle et al. 2020). Urbanization and human interference may also contribute to confounding effects in Pippy Park, which is located within a city. The three sites were located at a gradient of proximities from the city centre, with Pippy Park being the closest and Salmonier being the furthest, and therefore affected by varying degrees of urban disturbances such as pollution, human traffic, and human-made structures. A review of urban biodiversity concluded that urbanization generally reduces diversity and increases abundance of groups such as arthropods (Faeth et al. 2011).
2.5.6 Limitations and Conclusion

With respect to diversity, the difficulty of identifying arthropods to a fine taxonomic resolution may have obscured diversity patterns and ecological relationships among the arthropods examined in this study. More precise identification might have provided finer resolution that could show additional patterns and relationships, as well as the opportunity to investigate the potential influence of trophic interactions on community structure. While it is challenging to generalize about the life histories of different arthropod orders at this scale, it may be possible at lower taxonomic levels. Unfortunately, arthropod species-level identification is notoriously difficult, highlighting the need for alternative methods to study this biodiversity, such as using surrogates and indicators.

In conclusion, we have identified four environmental variables, macrolichen cover, total lichen cover, canopy cover, and bark texture that may serve as valuable indicators of arthropod community structure. Our results demonstrate that local factors influence arthropod communities, with varying strengths of lichen community and tree-level effects at different sites on the Avalon Peninsula. Notably, all groups exhibit a response to at least one lichen community trait, highlighting the importance of lichen 'neighbourhoods' in predicting arthropod abundance and diversity. The ecological significance and prevalence of Acari, Diptera, Araneae, Collembola, and Opiliones, and general arthropod survival, underscores the importance of further research on their relationships to their environments. Although Newfoundland is appreciated for its lichen hotspots, there is still a significant research gap on their relationship with arthropods in the province. Therefore, future research could build on these findings with increased replicates at Salmonier and Pippy Park.

2.6 References

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Figure 2-1. Map of the Avalon Peninsula, Newfoundland, Canada. Study sites represented by a star (red: Salmonier Nature Reserve, blue: Pippy Park, yellow: Outer Cove).



Figure 2-2. Overall results of the statistical models investigating environmental predictors of arthropod community traits in tree habitats. Arthropod symbols represent the abundance of individuals in a specific order (Acari, Araneae, Collembola, Diptera, and Opiliones), total arthropod abundance, or total arthropod diversity. Arthropod traits under "Positive Effect" had a significant positive relationship with the explanatory variable in the left column. Arthropod traits under "Negative Effect" had a significant negative relationship with the explanatory variable in the left column.

Table 2-1. Competing models that were used to predict different arthropod community traits. All models (A-G) were run with each of the seven response variables. An 'x' indicates which variables were included in each model. Plot and Sample were random effects.

| Model | Description | Macro | Macro | Total | Bark | Bark | Canopy | Site | Plot | Sample |
|-------|--------------|----------|-------|-------|---------|------|--------|------|------|--------|
| | | Richness | Cover | Cover | Texture | pН | Cover | | | |
| А | Global | | Х | | Х | х | Х | Х | Х | Х |
| В | Lichen | Х | Х | Х | | | | х | х | Х |
| С | Macro cover | | Х | | | | | х | х | Х |
| D | Total cover | | | Х | | | | х | х | Х |
| Е | Tree | | | | Х | х | Х | х | х | Х |
| F | Bark texture | | | | Х | | | х | х | х |
| G | Canopy | | | | | | Х | Х | Х | Х |

| Class | Order | Common name | Total count | Mean count | Frequency (%) |
|---------------------|--------------|--------------------|-------------|------------|------------------|
| Arachnids | | | | | , <i>i</i> |
| Arachnida | Acari | Mites | 1404 | 10.4 | 92.59 |
| Arachnida | Araneae | Spiders | 299 | 2.21 | 79.26 |
| Arachnida | Opiliones | Harvestmen | 452 | 3.35 | 75.56 |
| Insects | | | | | |
| Insecta | Coleoptera | Beetles | 17 | 0.13 | 11.85 |
| Insecta | Diptera | Flies | 284 | 2.10 | 65.19 |
| Insecta | Hemiptera | True Bugs | 194 | 1.44 | 32.59 |
| Insecta | Hymenoptera | Bees, wasps, ants | 40 | 0.30 | 20.74 |
| Insecta | Lepidoptera | Butterflies, moths | 44 | 0.33 | 20.74 |
| Insecta | Odonata | Dragonflies | 1 | 0.01 | 0.74 |
| Insecta | Psocodea | Bark lice | 51 | 0.38 | 25.19 |
| Insecta | Thysanoptera | Thrips | 1 | 0.01 | 0.74 |
| Other arthropods | | | | | |
| Diplopoda* | | Millipedes | 15 | 0.11 | 5.93 |
| Entognatha | Collembola | Springtails | 845 | 6.26 | 90.37 |
| Malacostraca | Isopoda | Woodlice | 12 | 0.09 | 6.67 |
| Other invertebrates | | | | | |
| Gastropods*† | | Snails and slugs | 2 | 0.01 | 0.74 |

Table 2-2. List of arthropod orders collected on balsam fir trees by vacuuming between 0.5 and 1.5 m above the ground for 5 minutes around the whole bole. Total count is the number of individuals throughout all samples. Mean count is the average count per sample (total count/135). Frequency is the percent of total samples that the group was found in.

Note: Groups denoted with * were identified to class level. Groups with † were omitted from analyses.

| Species | Mean % Cover | Frequency (%) |
|------------------------|--------------|---------------|
| Bryophyte | | |
| Liverworts* | 8.01 | 51.11 |
| Moss* | 1.08 | 66.67 |
| Crustose* | 42.19 | 100 |
| Foliose | 25.9 | |
| Coccocarpia palmicola | | 2.22 |
| Hypogymnia incurvoides | | 75.56 |
| Hypogymnia physodes | | 100 |
| Hypogymnia tubulosa | | 42.22 |
| Hypogymnia vittata | | 73.33 |
| Parmelia squarrosa | | 100 |
| Platismatia glauca | | 100 |
| Platismatia norvegica | | 46.67 |
| Fruticose | 6.17 | |
| Alectoria sarmentosa | | 42.22 |
| Bryoria spp. | | 95.56 |
| Cladonia spp. | | 55.56 |
| Ramalina roesleri | | 4.44 |
| Sphaerophorus globosus | | 20 |
| Usnea spp. | | 82.22 |

Table 2-3. List of epiphytes found on balsam fir (*Abies balsamea*) trees between 0.5 m and 1.5 m above the ground around the whole bole. Lichen percent cover was observed for each morphological group as a total. Frequency is the percent of total trees that epiphyte was found on.

Note: Groups denoted with * were identified to specified level in the field.

| Model | Κ | LogLik | AICc | ΔAICc | Cum. Wt. |
|-----------------|---|---------|--------|-------|----------|
| C: Macro Cover | 6 | -219.76 | 453.73 | 0.00 | 0.32 |
| D: Total Cover | 6 | -219.79 | 453.78 | 0.05 | 0.63 |
| G: Canopy Cover | 6 | -220.25 | 454.70 | 0.97 | 0.83 |
| F: Bark Texture | 7 | -219.35 | 455.72 | 1.99 | 0.95 |
| B: Lichen | 8 | -218.87 | 457.73 | 4.00 | 0.99 |
| A: Global | 8 | -219.53 | 461.09 | 7.36 | 1.00 |
| E: Tree | 9 | -218.97 | 463.24 | 9.50 | 1.00 |

Table 2-4. AICc of competing models that predict total arthropod abundance. Models C, D, G, and F all had a \triangle AICc within 2.00 and were analysed further.

| Model | β | 95% CI | р | SE |
|--------------|--------|-------------|---------|------|
| Macro Cover | | | | |
| Intercept | 3.95 | 3.52, 4.38 | < 0.001 | 0.22 |
| Salmonier | 0.52 | 0.14, 0.90 | 0.007 | 0.19 |
| Macro Cover | 0.32 | -0.30, 0.94 | 0.318 | 0.32 |
| Total Cover | | | | |
| Intercept | 3.97 | 3.58, 4.37 | < 0.001 | 0.20 |
| Salmonier | 0.44 | 0.12, 0.75 | 0.007 | 0.16 |
| Total Cover | 0.30 | -0.31, 0.91 | 0.34 | 0.31 |
| Canopy Cover | | | | |
| Intercept | 4.09 | 3.37, 4.81 | < 0.001 | 0.37 |
| Salmonier | 0.42 | 0.04, 0.80 | 0.032 | 0.20 |
| Canopy | 0.034 | -0.73, 0.80 | 0.93 | 0.39 |
| Bark Texture | | | | |
| Intercept | 4.10 | 3.81, 4.39 | < 0.001 | 0.15 |
| Salmonier | 0.40 | 0.10, 0.71 | 0.010 | 0.16 |
| Texture 2 | -0.082 | -0.40, 0.23 | 0.61 | 0.32 |
| Texture 3 | 0.19 | -0.16, 0.54 | 0.29 | 0.18 |

Table 2-5. Analysis of best models predicting total arthropod abundance.

| Model | Κ | LogLik | AICc | ΔAICc | Cum. Wt. |
|-----------------|---|--------|---------|-------|----------|
| D: Total Cover | 6 | 319.04 | -623.88 | 0.00 | 0.99 |
| B: Lichen | 8 | 317.60 | -615.19 | 8.69 | 1 |
| F: Bark Texture | 7 | 313.49 | -609.96 | 13.92 | 1 |
| C: Macro Cover | 6 | 311.28 | -608.34 | 15.54 | 1 |
| G: Canopy | 6 | 298.71 | -583.21 | 40.66 | 1 |
| A: Global | 9 | 301.27 | -579.39 | 44.49 | 1 |
| E: Tree | 9 | 299.88 | -576.62 | 47.26 | 1 |

Table 2-6. AICc of competing models that predict total arthropod diversity. No models fell within a \triangle AICc of 2.00, therefore only the best model was analysed further.

Table 2-7. Analysis of the best model that predicts total arthropod diversity.

| Model | β | 95% CI | р | SE |
|-------------|--------|--------------|---------|------|
| Total Cover | | | | |
| Intercept | 11.29 | 9.54, 13.04 | < 0.001 | 0.87 |
| Salmonier | -3.064 | -4.61, -1.51 | < 0.001 | 0.76 |
| Total Cover | 0.94 | -1.87, 3.75 | 0.50 | 1.39 |

| Model | Κ | LogLik | AICc | ΔAICc | Cum. Wt. |
|-----------------|---|---------|--------|-------|----------|
| G: Canopy | 6 | -180.61 | 375.42 | 0.00 | 0.32 |
| C: Macro Cover | 6 | -180.99 | 376.19 | 0.77 | 0.53 |
| D: Total Cover | 6 | -181.00 | 376.20 | 0.78 | 0.75 |
| F: Bark Texture | 7 | -180.01 | 377.04 | 1.62 | 0.89 |
| E: Tree | 9 | -178.04 | 379.22 | 3.80 | 0.94 |
| A: Global | 8 | -179.81 | 279.62 | 4.20 | 0.98 |
| B: Lichen | 8 | -180.32 | 380.65 | 5.23 | 1.00 |

Table 2-8. AICc of competing models that predict Acari (mite) abundance. Models G, C, D, andF all had a \triangle AICc within 2.00 and were analysed further.

| Model | β | 95% CI | р | SE |
|--------------|-------|-------------|---------|------|
| Canopy | | | | |
| Intercept | 2.35 | 1.32, 3.39 | < 0.001 | 0.53 |
| Salmonier | 1.22 | 0.71, 1.73 | < 0.001 | 0.26 |
| Canopy | 0.53 | -0.49, 1.56 | 0.31 | 0.52 |
| Macro Cover | | | | |
| Intercept | 2.70 | 2.00, 3.40 | < 0.001 | 0.36 |
| Salmonier | 1.14 | 0.63, 1.66 | < 0.001 | 0.26 |
| Macro Cover | 0.23 | -0.65, 1.11 | 0.61 | 0.45 |
| Total Cover | | | | |
| Intercept | 2.72 | 2.08, 3.36 | < 0.001 | 0.33 |
| Salmonier | 1.08 | 0.66, 1.51 | < 0.001 | 0.22 |
| Total Cover | 0.21 | -0.62, 1.03 | 0.62 | 0.42 |
| Bark Texture | | | | |
| Intercept | 2.76 | 2.23, 3.28 | < 0.001 | 0.27 |
| Salmonier | 1.04 | 0.63, 1.45 | < 0.001 | 0.21 |
| Texture 3 | 0.35 | -0.13, 0.82 | 0.15 | 0.15 |
| Texture 2 | -0.01 | -0.44, 0.41 | 0.95 | 0.95 |

Table 2-9. Analysis of the best models predicting Acari abundance.

Table 2-10. AICc of competing models that predict Araneae (spider) abundance. Models G, C, D, and F all had a Δ AICc within 2.00 and were analysed further.

| Model | Κ | LogLik | AICc | ΔAICc | Cum. Wt. |
|-----------------|---|---------|--------|-------|----------|
| G: Canopy | 5 | -115.53 | 242.60 | 0.00 | 0.27 |
| C: Macro Cover | 5 | -115.57 | 242.68 | 0.08 | 0.53 |
| D: Total Cover | 5 | -115.58 | 242.69 | 0.09 | 0.79 |
| F: Bark Texture | 6 | -114.81 | 243.83 | 1.24 | 0.94 |
| Tree | 8 | -113.31 | 246.61 | 4.01 | 0.97 |
| Lichen | 7 | -115.57 | 248.17 | 5.57 | 0.99 |
| Global | 8 | -114.57 | 249.14 | 6.54 | 1.00 |

Table 2-11. Analysis of the best models predicting Araneae abundance.

| Model | β | 95% CI | р | SE |
|--------------|-------|-----------------|---------|------|
| Canopy | | | | |
| Intercept | 1.96 | 1.19, 2.72 | < 0.001 | 0.39 |
| Pippy Park | -0.35 | -0.70, -0.31e-4 | 0.05 | 0.18 |
| Canopy | 0.14 | -0.69, 0.96 | 0.75 | 0.42 |
| Macro Cover | | | | |
| Intercept | 2.05 | 1.62, 2.48 | < 0.001 | 0.22 |
| Pippy Park | -0.36 | -0.70, -9.9e-3 | 0.044 | 0.18 |
| Macro Cover | 0.05 | -0.62, 0.72 | 0.89 | 0.34 |
| Total Cover | | | | |
| Intercept | 2.06 | 1.67, 2.45 | < 0.001 | 0.20 |
| Salmonier | -0.35 | -0.70, -2.03e-3 | 0.049 | 0.18 |
| Total Cover | 0.03 | -0.61, 0.68 | 0.92 | 0.33 |
| Bark Texture | | | | |
| Intercept | 2.14 | 1.89, 2.39 | < 0.001 | 0.13 |
| Texture 3 | -0.12 | -0.51, 0.27 | 0.55 | 0.55 |
| Texture 2 | -0.21 | -0.54, 0.13 | 0.22 | 0.22 |

| Model | Κ | LogLik | AICc | ΔAICc | Cum. Wt. |
|-----------------|---|---------|--------|-------|----------|
| C: Macro Cover | 6 | -161.52 | 337.24 | 0.00 | 0.61 |
| F: Bark Texture | 7 | -161.19 | 339.40 | 2.16 | 0.81 |
| B: Lichen | 8 | -160.91 | 341.81 | 4.57 | 0.87 |
| A: Global | 8 | -161.17 | 342.34 | 5.10 | 0.92 |
| D: Total Cover | 6 | -164.46 | 343.13 | 5.89 | 0.95 |
| G: Canopy | 6 | -164.50 | 343.20 | 5.96 | 0.98 |
| E: Tree | 9 | -160.70 | 344.54 | 7.30 | 1.00 |

Table 2-12. AICc of competing models that predict Collembola (springtail) abundance. No models fell within a \triangle AICc of 2.00, therefore only the best model was analysed further.

Table 2-13. Analysis of the best model that predicts Collembola abundance.

| Model | β | 95% CI | р | SE |
|-------------|-------|------------|---------|------|
| Macro Cover | | | | |
| Intercept | 2.02 | 1.40, 2.65 | < 0.001 | 0.32 |
| Macro Cover | 1.037 | 0.25, 1.82 | 0.010 | 0.40 |

Table 2-14. AICc of competing models that predict Diptera (fly) abundance. Models D, C, G, and F all had a Δ AICc within 2.00 and were analysed further.

| Model | Κ | LogLik | AICc | ΔAICc | Cum. Wt. |
|-----------------|---|---------|--------|-------|----------|
| D: Total Cover | 6 | -115.25 | 244.70 | 0.00 | 0.29 |
| C: Macro Cover | 6 | -115.30 | 244.80 | 0.10 | 0.56 |
| G: Canopy | 6 | -115.30 | 244.82 | 0.11 | 0.83 |
| F: Bark Texture | 7 | -114.67 | 246.37 | 1.67 | 0.95 |
| A: Global | 8 | -114.88 | 249.76 | 5.06 | 0.98 |
| B: Lichen | 8 | -115.19 | 250.38 | 5.67 | 0.99 |
| E: Tree | 9 | -114.36 | 251.86 | 7.15 | 1.00 |

Table 2-15. Analysis of the best models predicting Diptera abundance.

| Model | β | 95% CI | р | SE |
|--------------|-------|-------------|---------|-------|
| Total Cover | - | | | |
| Intercept | 1.06 | 0.47, 1.65 | < 0.001 | 0.30 |
| Pippy Park | 1.25 | 0.77, 1.72 | < 0.001 | 0.24 |
| Salmonier | 0.70 | 0.24, 1.15 | 0.003 | 0.23 |
| Total Cover | -0.14 | -0.94, 0.66 | 0.73 | 0.41 |
| Macro Cover | | | | |
| Intercept | 1.06 | 0.47, 1.65 | < 0.001 | 0.32 |
| Pippy Park | 1.25 | 0.77, 1.72 | < 0.001 | 0.22 |
| Salmonier | 0.70 | 0.24, 1.15 | 0.003 | 0.69 |
| Macro Cover | 0.23 | -0.65, 1.11 | 0.61 | 0.40 |
| Canopy | | | | |
| Intercept | 1.00 | 0.04, 1.97 | < 0.001 | 0.042 |
| Pippy Park | 1.21 | 0.77, 1.65 | < 0.001 | 0.22 |
| Salmonier | 0.70 | 0.16, 1.24 | 0.011 | 0.28 |
| Canopy | -0.02 | -0.99, 0.96 | 0.97 | 0.50 |
| Bark Texture | | | | |
| Intercept | 0.95 | 0.51, 1.40 | < 0.001 | 0.23 |
| Pippy Park | 1.26 | 0.82, 1.70 | < 0.001 | 0.23 |
| Salmonier | 0.69 | 0.24, 1.14 | 0.003 | 0.23 |
| Texture 3 | 0.23 | -0.22, 0.69 | 0.32 | 0.23 |
| Texture 2 | -0.06 | -0.46, 0.35 | 0.79 | 0.21 |

Table 2-16. AICc of competing models that predict Opiliones (harvestmen) abundance. Models G, D, and C all had a Δ AICc within 2.00 and were analysed further.

| Model | Κ | LogLik | AICc | ΔAICc | Cum. Wt. |
|----------------|---|---------|--------|-------|----------|
| G: Canopy | 5 | -137.26 | 286.06 | 0.00 | 0.35 |
| D: Total Cover | 5 | -137.61 | 286.77 | 0.71 | 0.59 |
| C: Macro Cover | 5 | -137.73 | 287.01 | 0.95 | 0.80 |
| Bark Texture | 6 | -136.99 | 288.18 | 2.12 | 0.93 |
| Global | 7 | -136.65 | 290.33 | 4.28 | 0.96 |
| Lichen | 7 | -137.26 | 291.54 | 5.48 | 0.98 |
| Tree | 8 | -136.10 | 292.20 | 6.15 | 1.00 |

Table 2-17. Analysis of the best models predicting Opiliones abundance.

| Model | β | 95% CI | р | SE |
|-------------|-------|--------------|---------|------|
| Canopy | | | | |
| Intercept | 1.89 | 0.79, 2.99 | < 0.001 | 0.56 |
| Salmonier | -0.91 | -1.52, -0.30 | 0.003 | 0.31 |
| Canopy | 0.63 | -0.56, 1.83 | 0.30 | 0.61 |
| Total Cover | | | | |
| Intercept | 2.31 | 1.74, 2.87 | < 0.001 | 0.29 |
| Salmonier | -1.07 | -1.59, -0.55 | < 0.001 | 0.26 |
| Total Cover | 0.29 | -0.64, 1.22 | 0.54 | 0.47 |
| Macro Cover | | | | |
| Intercept | 2.35 | 1.74, 2.97 | < 0.001 | 0.31 |
| Salmonier | -1.04 | -1.64, -0.43 | < 0.001 | 0.31 |
| Macro Cover | 0.17 | -0.76, 1.11 | 0.72 | 0.48 |

Chapter 3: Down in the dirt: Unearthing the complex structure of arthropod communities in soil ecosystems

3.1 Abstract

Soil ecosystems stand out as one of the world's most diverse terrestrial habitats. Arthropods contribute to making soil a fundamental resource for other living organisms by providing pivotal ecosystem services. This study aimed to investigate the factors that influence soil arthropod community structure. We used pitfall traps to sample soil arthropods from three sites across the Avalon Peninsula, Newfoundland, from June to August 2023. Our findings underscore the importance that environmental structures, notably canopy cover and soil pH, have in influencing overall and taxon-specific arthropod abundance. Conversely, arthropod diversity displayed no significant correlation with any environment factors. Furthermore, this investigation emphasizes the intricate connection between above and below ground biota. Trophic correlations were identified both within the soil community, and between soil and tree communities. These results provide a baseline understanding of the complexity of soil arthropod communities in Newfoundland forests, thereby establishing a foundational framework for future research to expand on.

3.2 Introduction

Arthropods play important roles in all forest ecosystems, which make up almost a third of total global land area (Ritchie and Roser 2021). In these environments, arthropods comprise 70% - 90% of biomass and taxa, heavily outnumbering plant and vertebrate species (Langor and Spence 2006, McGeoch et al. 2011, Schowalter 2017). They provide essential ecosystem services, allow communities to be more adaptive, and play vital roles in forest food webs that maintain the

success of charismatic species (Langor and Spence 2006, Cosović et al. 2020). Preserving arthropod diversity is critical for forest resilience.

One of the most diverse and intricate communities in forest ecosystems is in the soil. Soil plays a vital role in sustaining the human population through food production, carbon storage, greenhouse gas regulation, and infrastructure support (Kopittke et al. 2019). Ecologically, soil ecosystems are biodiversity hotspots, accommodating a quarter of all living species (Ghiglieno et al. 2020). Soil arthropods are the main drivers of soil ecosystem functioning, contributing to essential processes such as decomposition, plant growth, soil respiration, and nutrient recycling (Menta and Remelli 2020). Simultaneously, soil conditions – including abiotic factors such as pH, temperature, and humidity, and biotic factors such as vegetation, bacterial communities, and other invertebrates – shape and regulate soil arthropod communities.

Both global soil integrity and arthropod communities are facing widespread degradation and declines due to human modifications of terrestrial ecosystems and the impacts of climate change. Anthropogenic land use has weakened ecosystem functioning, and the specific effects on soil organisms is poorly understood (George et al. 2017, Kopittke et al. 2019). The deterioration and reduced quality of soils result in increased erosion and acidification, the release of greenhouse gases, and the loss of organic matter and biodiversity (Kopittke et al. 2019). Consequently, it is imperative to monitor and conserve both soil ecosystems and the intricate biotic systems they support.

Because of their immense contributions to soil ecosystems and their sensitivity to environmental factors such as microhabitat and microclimate conditions, arthropods have been proposed as ecological indicators of soil quality and ecosystem health (Gerlach et al. 2013). Soils that host a diverse invertebrate community are generally considered to be of good quality (Menta

and Remelli 2020). Among the arthropod groups, mites, springtails, and spiders are often recommended as indicators because they are easy to sample, well-studied, widespread, and responsive to environmental changes (Ghiglieno et al. 2020)

Ecological indication is defined as the "application of scientific knowledge to the management of ecological relationships" (McGeogh 1998, p. 182). Although the selection and application of ecological indicators remains an open discussion, it is widely agreed that indicators should be inexpensive, time-effective, and easy to measure (Cosović et al. 2020), and should strongly correlate with the ecological parameters they represent (Gaston and Blackburn 1995). Biodiversity indicators, a specific type of ecological indicator, reflect the abundance or diversity of taxonomic groups. Other taxa can be applied as bioindicators and are called surrogate groups, as can environment structures, which are known as structural indicators (Gaston and Blackburn 1995).

Structural indicators, such as canopy cover and ground cover composition, are often easy to observe and measure by non-professionals, and therefore may provide an efficient method to investigate arthropod communities (Cosović et al. 2020). Generally, high structural complexity positively corresponds with arthropod abundance and/or diversity, as small-scale heterogeneity allows for great diversity and coexistence (Lawton and Strong 1981, Nittérus and Gunnarsson 2006, Wehner et al. 2016). In addition, vegetation, including canopy and ground cover, is important in influencing arthropod community structure (Natuhara et al. 1994, Ali et al. 2022). Terrestrial arthropods are also sensitive to microclimate gradients, such as temperature, humidity, rainfall, and wind (Kremen et al. 1993, Adams et al. 2020).

Trophic interactions also play an important role in shaping arthropod assemblages. The relative presence of functional groups influences the amount of competition and predation that

occurs in the community. Direct effects of predation can exert cascading effects on herbivore populations and primary producers, while intraguild competition may reduce the effects of trophic cascades (Halaj and Wise 2001, Gagnon et al. 2011). For example, Dominik et al. (2018) determined that the abundance of prey has a higher impact on arthropod populations than landscape heterogeneity. In turn, belowground interactions play a role in shaping soil structure through the movement of mineral and organic compounds (Erktan et al. 2020). By exploring habitat structures and investigating trophic correlations, potential bioindicators can be identified that would provide valuable insights into the status of arthropod communities, consequently shedding light on the overall health of soil ecosystems.

Taking a broader perspective, landscape structure is also a major driver of arthropod communities as it defines the composition, arrangement, size, heterogeneity, and location of available habitats, thus affecting ecological processes (Jeanneret et al. 2003, Gallé et al. 2022, Marja et al. 2022). Landscape diversity is found to influence arthropod abundance and richness, with different taxonomic groups responding variably based on their mobility (Fahrig et al. 2011, Egerer et al. 2017). Therefore, it has been proposed that landscape components should be included as relevant explanatory variables in biodiversity models (Jeanneret et al. 2003).

The objective of this study is to investigate multiscale interactions between soil arthropod communities and their environment. We conducted our investigation in three forest stands on the Avalon Peninsula in Newfoundland, Canada, with the goal of identifying the key factors that best explain variation in arthropod abundance and diversity. We hypothesized that environment traits, such as ground cover and soil pH, influence the abundance and diversity of arthropod communities due to their direct and indirect impacts on microhabitat variation. Therefore, these effects may serve as structural bioindicators. We also hypothesized that there may be trophic correlations among total abundance, total diversity, and the abundances of different orders, as interdependencies and functional roles of different arthropod groups help shape arthropod communities. These correlations could then potentially serve as surrogate bioindicators. Finally, we hypothesized that there will be significant differences in arthropod community responses between sites, as landscape complexity can play a role in arthropod ecology.

3.3 Methods

3.3.1 Sample Sites

The present study was conducted at three sites on the Avalon Peninsula in Newfoundland, Canada (Fig. 3-1). Our sites were all located in the Maritime Barrens, an ecoregion with cool summers, moderate winters, and significant fog, and dominated by balsam fir stands (Bell 2002). At each site, Pippy Park, Salmonier Nature Reserve, and Outer Cove, three areas with homogenous balsam fir stands were chosen and are hereafter referred to as "plots" (n = 9). Pippy Park is a 13.75 km² urban park only a few kilometers from downtown St. John's. Salmonier Nature Reserve includes 14 km² of undeveloped land and is situated 60 km from the city. The Outer Cove site is a large piece of privately-owned land 10 km from downtown and the only site that is directly on the Atlantic Ocean coast. Five balsam fir trees in each plot (n = 45) at least 5 m apart were selected and flagged.

3.3.2 Arthropod Sampling

Pitfall trapping is a relatively non-invasive, simple, and cost-effective method of taking a sample of ground-dwelling arthropods over time (Boetzl et al. 2018). Hohbein and Conway (2018) proposed a standard pitfall trapping method, and we considered many of their recommendations

when creating our traps. Traps were placed 1 m from the base of each tree. They were made from plastic containers and were approximately 10 cm deep with a 10 cm diameter. Each trap was filled with water and a pinch of salt plus dish soap to break the surface tension. Leaving the traps outside for several days leaves them vulnerable to environmental conditions, therefore we covered the traps with roofs made of corrugated plastic that were secured in place using garden staples (Fig. 3-2). The traps were left, and contents were collected after 10 days. To collect the specimens, the trap contents were poured into a labelled Nalgene bottle using a funnel, making sure all trap contents were transferred into the bottle. In the lab, Nalgene bottles were filled with propylene glycol for preservation. This protocol was repeated once a month in June, July, and August for each tree, resulting in a total of 135 samples.

In addition, arthropod samples were taken from each tree using a handheld vacuum once a month in June, July, and August, leading to 135 more samples. The dates of tree sampling from each tree correspond when the pitfall traps were deployed. The contents from the vacuum were emptied into labelled plastic vials which we then filled with propylene glycol to kill and preserve the specimens. We kept the vials in a cooler until they could be refrigerated. These specimens were used for the chapter two analysis but were included in this chapter to investigate correlations between tree and soil samples.

3.3.3 Other Environmental Measurements

We measured canopy cover at the north, east, south, and west points of the tree using a convex spherical densiometer. The canopy cover of each tree was averaged across the four directional points and serves as a proxy for light and humidity. We measured tree height using a Suunto clinometer and tape measure. Soil samples were collected near the pitfall trap and added to a vial

of water. Soil was taken from the topmost layer of soil, under the moss layer. The pH of the soil solution was measured in the field using a waterproof pH meter, which was calibrated prior to measurements. We took ground cover measurements once a month in June, July, and August to account for seasonal variation in vegetation. At each tree, four 1 m by 1 m quadrats were placed 2 m from the base in each of the cardinal directions. We recorded the general percent cover of lichen, moss, fungi, deadwood, leafy plants, woody plants, bare ground, rock, leaf litter and needle duff, and lichen debris. Percent estimates in each category are an average of the four directions per tree.

3.3.4 Arthropod Sorting

Using a filter cloth, we removed the water and propylene glycol from each Nalgene bottle or vial. We dumped the remaining contents of the bottle or vial into a medium sized petri dish, using propylene glycol to completely empty them. We placed specimens under a dissecting microscope, identified them to order level by morphological examination, and placed them into smaller petri dishes by order. We counted and recorded the number of individuals in each taxonomic order. We placed these specimens back into the original container and filled with ethanol. Samples are stored in a refrigerator at approximately 4.5°C in the Core Science Facility at Memorial University of Newfoundland.

3.3.5 Statistical Analyses

We used univariate models to explore arthropod community patterns one trait at a time. This allowed us to connect abiotic and biotic environmental drivers to the response of specific arthropod community traits. To investigate other community patters, we looked at inter-

taxonomic associations through correlation analyses. Specimens that are not arthropods, such as snails and slugs, were removed prior to analysis. Arthropod diversity was calculated to order level using the Hill-Shannon index using the "rarity plot" function from the MeanRarity package (Roswell and Dushoff 2022). To summarize the ten ground cover categories into fewer variables, we conducted a principal components analysis (PCA). We used the first four axes (PC1, PC2, PC3, and PC4) for further analyses, as together they explained over 60% of the total variation (Table 3-1). We used generalized linear mixed effects models using the "glmer" function from the lme4 package to investigate the effects of environmental variables on the response variables (Bates et al. 2015). The response variables we were interested in were total arthropod abundance (i.e., the total number of individuals) and total ordinal diversity, and the abundance of the six most frequent arthropod orders: Acari, Araneae, Collembola, Diptera, Hymenoptera, and Opiliones. For each abundance response variable, we ran eight competing generalized linear models (Table 3-2) with a Poisson error distribution and a log link function. The arthropod diversity model used a Gaussian error distribution with an identity link. "Site" was included in all models, as well as "Sample" as a random effect. As a categorical variable, site categories were reordered to investigate if all sites were significant. Continuous explanatory variables were centered prior to model analysis.

The models were compared for each response variable with a corrected AIC using the "aictab" function from the AICmodavg package (Mazerolle 2020). If a model was within a Δ AICc of two or less, the model was analyzed further. We ran separate additional models that included all combinations of the principal component axes. If a PCA model was within a Δ AICc of two or less, the model was analyzed further. None of the axes were ever found to be

significant, except for one model predicting Araneae. We then included this model into the AICc of the original eight models predicting Araneae.

We conducted a correlation analysis between all the response variables. In addition, we included the diversity and abundance of the arthropods collected from the tree 1 m from each pitfall trap in the correlations, to investigate patterns between soil and tree arthropod communities. Correlations with a p-value < 0.05 were considered significant; those of which with an $r \ge 0.6$ were considered strong relationships, and with $0.6 > r \ge 0.35$ were considered moderate. Statistical analysis was conducted in R (R Core Team 2021).

3.4 Results

3.4.1 General Results

A total of 38,500 individual invertebrates from 22 taxonomic groups (19 orders, 3 classes) were identified from 135 samples obtained between June and August 2022 (Table 3-3). Of these individuals, 38,218 were arthropods. Snails, slugs, and earthworms (n = 282) were omitted from the data before analysis. Collembola were found in all samples and account for about half of all individuals (50.8%). Hymenoptera, Diptera, Acari, and Araneae were present in almost every sample. These orders, alongside Opiliones and Coleoptera, were also the most abundant orders. Arachnids made up about a quarter of all individuals (25.7%), and insects counted for one fifth (20.9%).

3.4.2 Total Arthropod Abundance

The model selection suggested that models including canopy cover, or canopy cover and soil pH were the best fit for predicting total arthropod abundance (TAA) (Table 3-4). In both models,

canopy cover had a significant and positive main effect (soil pH and canopy: beta = 0.016, 95% CI [3.85e-03, 0.03], p = 0.0099, canopy: beta = 0.016, 95% CI [2.84e-03, 0.03], p = 0.017; Table 3-5) and in the combined model, soil pH also had a very significant positive effect (beta = 0.25, 95% CI [1.91e-03, 0.50], p = 0.048; Table 3-5).

3.4.3 Total Arthropod Diversity

For the model selection of total arthropod diversity (TAD), the only model that was analyzed further was the one that included soil pH and ground cover principal components, as no other models fell within a Δ AICc of two or less (Table 3-6). No main effects were found to be significant predictors of arthropod diversity (Table 3-7).

3.4.4 Order Abundances

The tree model was the only model that was analyzed further for Acari abundance (Table 3-8). Tree height was the only significant main effect and was found to be a positive predictor of Acari abundance (beta = 0.18, 95% CI [0.05, 0.30], p = 0.0047; Table 3-9).

The model selection suggested that models that included PC 2, soil, or soil and canopy were fit for further analysis when considering Araneae abundance (Table 3-10). The second principal component had a significant effect in the top model (beta = -0.086, 95% CI [-0.17, -1.88e-03], p = 0.045). The strongest loadings for PC 2 (Table 3-1) include leafy plants (0.60), woody plants (0.41), and moss (-0.37), indicating a negative relationship with the former two, and a positive one with moss. In the combined soil and canopy model, soil pH had a significant negative effect on predicting Araneae abundance (beta = -0.44, 95% CI [-0.87, -8.21e-03], p = 0.046; Table 3-11).

In the model selection for Collembola abundance, the model that included soil pH and canopy, as well as the model with only soil pH, performed best (Table 3-12). In both models, soil pH was found to have a positive and significant effect on Collembola abundance (soil pH: beta = 0.46, 95% CI [0.06, 0.85], p = 0.025; soil pH and canopy: beta = 0.47, 95% CI [0.08, 0.86], p = 0.019; Table 3-13).

The top models for Diptera abundance were the model that includes canopy cover, as well as the model that includes soil pH and canopy cover (Table 3-14). In both models, canopy cover had a significant positive effect for predicting Diptera abundance (soil and canopy: beta = 0.036, 95% CI [0.01, 0.06], p = 0.0041; canopy: beta = 0.035, 95% CI [9.80e-03, 0.06], p = 0.0065; Table 3-15).

The two models that performed the best for Hymenoptera abundance were soil pH and canopy cover, individually (Table 3-16). In both models, the main effects were not found to be significant (Table 3-17).

The top models for Opiliones abundance were 1. canopy cover and 2. soil pH and canopy cover (Table 3-18). After further analysis, both models showed that canopy cover is a significant positive predictor of Opiliones abundance (canopy: beta = 0.034, 95% CI [8.25e-05, 0.07], p = 0.049; soil and canopy: beta = 0.035, 95% CI [1.39e-03, 0.07], p = 0.041; Table 3-19).

3.4.5 Site Effects

All models that were analyzed after original model selections were shown to have Pippy Park as a significant effect on the response variable (Tables 3-4 - 3-19). After reordering which site was pulled out of the intercept, it was confirmed that the other two sites were also significant as well.

Therefore, there is a significant difference in arthropod diversity and abundances between the three sites.

3.4.6 Correlations between Arthropod Community Traits

Correlations are shown in Fig. 3-3. There were strong negative correlations between TAA and TAD (r(34) = -0.71, p < 0.001) and TAD and Collembola abundance (r(34) = -0.79, p < 0.001). There was a strong positive correlation between TAA and Collembola abundance (r(34) = 0.9, p < 0.001). In the soil, there were moderate positive correlations between TAA and Diptera (r(34) = 0.9, p < 0.001). In the soil, there were moderate positive correlations between TAA and Diptera (r(34) = 0.48, p < 0.001), Opiliones (r(34) = 0.39, p < 0.01), and Hymenoptera (r(34) = 0.44, p < 0.01) abundances, as well as between Collembola abundance and Hymenoptera abundance (r(34) = 0.41, p < 0.01). There were moderate negative correlations between TAD and Hymenoptera abundance (r(34) = -0.36, p = 0.014), Acari abundance and Araneae abundance (r(34) = -0.37, p = 0.012), and Acari abundance and Diptera abundance (r(34) = -0.38, p < 0.01).

When looking at interactions between tree and soil arthropods, there were moderate positive correlations between soil TAA and tree Opiliones abundance (r(34) = 0.58, p < 0.001), soil Collembola abundance and tree Opiliones abundance (r(34) = 0.53, p < 0.001), soil Diptera abundance and tree Diptera abundance (r(34) = 0.53, p < 0.001), soil Opiliones abundance and tree Opiliones abundance (r(34) = 0.53, p < 0.001), soil Opiliones abundance and tree TAD (r(34) = 0.44, p < 0.01), and tree TAD and soil Collembola abundance (r(34) = 0.35, p = 0.019). There were moderate negative correlations between soil Opiliones abundance and tree Acari abundance (r(34) = -0.43, p < 0.01), and soil Hymenoptera abundance and tree Acari abundance (r(34) = -0.35, p = 0.017).

3.5 Discussion

Consistently emerging in the top models, soil pH and canopy cover were key factors influencing overall arthropod abundance and the abundance of various taxonomic groups, as predicted, alongside other environmental variables (Fig. 3-4). Interestingly, models predicting total diversity did not reveal any significant main effects. Site was a significant effect for all response variables, suggesting variations in total abundance and diversity and order abundances across sites.

3.5.1 Soil pH

Soil properties directly influence the functioning and survival of arthropods, with soil pH being a significant driver of distributions (Ghiglieno et al. 2020). Soil pH can affect an organism's physiological functioning, the availability of nutrients in a habitat, and the microbial communities that the arthropods rely on for food or symbiotic relationships (Menta and Remelli 2020). A positive relationship between total arthropod abundance and soil pH suggests that there is a general increase in arthropods in less acidic habitats. This result is consistent with other studies highlighting the preference of arthropod communities for more alkaline soil (Santorufo et al. 2012, Mo et al. 2021). This relationship is also seen with Collembola abundance, a group that is highly sensitive to soil properties and prefers less acidic environments (Mo et al. 2021).

Conversely, Araneae abundance demonstrated the opposite relationship, with higher numbers observed in more acidic environments. Different arthropod groups exhibit diverse pH preferences and Araneae may favour lower pH levels (Van Straalen 1998). Coexistence through resource partitioning in Araneae can be generally categorized by variation in prey type, daily and seasonal activity time, and use of different microhabitats (Villanueva-Bonilla et al. 2019).

Therefore, as a prominent but generalist macroinvertebrate predator, Araneae may occupy habitats that are unfavourable to other top predators with higher niche specialization, such as Opiliones, to avoid resource competition (Menta and Remelli 2020).

3.5.2 Canopy Cover

Canopy cover can alter abiotic characteristics of the ecosystem, such as light availability, soil moisture, temperature, and pH, which are key factors in regulating arthropod composition (Deng et al. 2022). These abiotic changes affect biotic elements like vegetation growth or insectivore populations, shaping arthropod habitats and interspecific interactions. Total arthropod abundance and Diptera and Opiliones abundances were all positively affected by canopy cover, indicating that a denser canopy contributes to favourable habitat conditions for these populations. Canopy effects are indirect, which makes investigating canopy cover complex and can yield contradictory results. In contrast to our findings, Damptey et al. (2023) reported a positive association between canopy openness and arthropod communities, attributing it to increased light availability that creates advantageous conditions for arthropod activity. However, Miller et al. (2007) demonstrated that trees under covered canopies host more arthropods. Our study found correlations between the abundance of Diptera and Opiliones in the soil to the abundances of Diptera and Opiliones, respectively, in the tree. Thus, tree and soil communities alike may be influenced by canopy cover.

3.5.3 Ground Cover

Numerous studies emphasize the strong link between aboveground vegetation and soil food webs (Adeduntan 2010, Nielsen et al. 2010, Ali et al. 2022). We hypothesized that ground cover would

play an important role in the structure of arthropod communities by contributing to habitat heterogeneity, soil quality, and food availability. Changes in plant energy pathways also have significant effects on soil arthropods (Deng et al. 2022), and vegetation cover typically has a positive effect on arthropod abundance (Silva et al. 2010, Blaise et al. 2022). However, among all response groups, only Araneae displayed a significant relationship with ground cover. Specifically, a negative association was observed between Araneae and woody and leafy plant cover, while moss cover had a positive association. This finding is consistent with the high sensitivity of Araneae to microhabitat changes, including variations in vegetation (Menta and Remelli 2020). Because we analyzed arthropod communities to the average ground cover over the season, we may have overlooked the temporal variation in vegetation, which could have a considerable impact on community structure.

3.5.4 Tree Height

Soil Acari are widely studied and often proposed as bioindicators due to their sensitivity to environmental gradients (George et al. 2017, Nsengimana et al. 2021). Curiously, in our study Acari abundance had a positive relationship with tree height but was unaffected by other variables. While tree height itself may not directly influence the abundance of Acari in the soil, it is established as a strong indicator of other forest characteristics, such as habitat complexity, above-ground biomass, canopy structure, and site productivity (Campos et al. 2006, De Petris et al. 2022). Campos et al. (2006) demonstrated that taller trees have a larger abundance and species richness of insect herbivores. Given the moderate correlation between soil and tree Acari abundances, tree height may impact Acari populations on trees, which in turn may influence Acari populations in the soil.

3.5.5 Arthropod Community Traits without Significant Predictors

Notably, total arthropod diversity was not predicted by any of the variables measured. Determining the most accurate method for calculating diversity and at which taxonomic level remains uncertain (Timms et al. 2013). It is generally acknowledged that finer taxonomic resolutions, such as species level assessments, tend to yield stronger relationships with environmental factors (de Oliveira et al. 2020). Calculating diversity at the order level might not capture enough variation to identify clear relationships with the environment.

Hymenoptera abundance also did not show significant relationships with any of the measured variables. Formicidae (ants) are a dominate Hymenoptera family in soil ecosystems both in species richness and biomass (Menta and Remelli 2020). Due to their ubiquity, ants are widely studied and have been proposed as indicators for taxonomic richness in soil studies (Leal et al. 2010). We predicted that soil pH would be a predictor of Formicidae abundance, as several studies have shown strong correlations between Formicidae and soil pH (Nsengimana et al. 2021). However, Frouz and Jilková (2008) found that ants can alter soil pH, either by raising it in acidic soils or by lowering it in alkaline soils, ultimately shifting it towards a neutral pH. Their functions as ecosystem engineers may allow them to occupy environments with a range of pH values, and potentially other challenging environmental conditions, therefore lessening the strength of any specific environment predictor (Luke et al. 2014).

3.5.6 Site Effects

Site was a strong predictor of all arthropod community traits, which indicates that arthropods respond to variations at the landscape scale. Diverse environmental pressures, such as changes in local climate or landscape complexity, may result in distinct assemblages of arthropod

communities in different forests. For example, the landscape of Outer Cove is highly influenced by the presence of the ocean and the sea spray, fog, and wind that accompanies coastal sites (Angle et al. 2020), whereas the urban location of Pippy Park leaves it more exposed to anthropogenic disturbances. In addition, Salmonier may have a more complex landscape because it is a managed nature reserve (Marja et al. 2022). Landscape-level characteristics can affect arthropod communities because they determine ecosystem arrangement and interactions, thus influencing species ecology, distribution, and movement (Jeanneret et al. 2003). Future studies should consider characterizing landscape and habitat types, including size, composition, configuration, and connectivity, to unravel landscape-level mechanisms on arthropod community structure on the Avalon.

3.5.7 Correlations

Within the soil arthropod community, we observed three notable relationships: a strong positive correlation between total abundance and Collembola abundance, and significant negative correlations between both of these abundance measures and overall diversity. The positive correlation between total abundance and Collembola abundance is similarly observed in tree habitats, suggesting this relationship may be observed across different habitat types. Considering their shared sensitivity to soil properties, we propose that Collembola abundance can serve as a surrogate taxon for overall arthropod abundance.

3.5.8 Limitations and Conclusion

As previously mentioned, the resolution to which community diversity is measured can have implications in the observed statistical relationships (Timms et al. 2013; de Oliveira et al. 2020).
However, when dealing with diverse groups that are taxonomically challenging, it can be difficult to identify at a finer level (e.g., genus or species) and using higher taxonomic resolutions may be a more viable option. Alternatively, it has been suggested that an equally, if not more, important community trait to measure is functional diversity, because individuals belonging to the same functional group exhibit similar and predictable interactions with their environments (Nielsen et al. 2010). Investigating differences in arthropod community structure based on their ecological roles could improve the potential specificity and efficacy of bioindicators (Van Straalen 1998, McIntyre et al. 2001).

Furthermore, soil ecosystems are incredibly complex, and different soil layers can contain distinct faunal communities (Deng et al. 2022). While pitfall trapping is one of the most common sampling methods in ecological field studies, it is important to note that the traps may bias towards certain taxa such as larger and faster organisms, and underrepresent other taxa, including deep soil groups (Work et al. 2002, Hohbein and Conway 2018). Future studies could differentiate microhabitats and incorporate other soil properties, such as temperature and moisture, to gain a more comprehensive understanding of the intricacies of soil biodiversity. Finally, there is a lack of studies investigating the relationships between arthropod abundance and their environments over time (Van Klink et al. 2022). To address this gap, future investigations should prioritize longitudinal surveys of previously studied sites to identify temporal trends and validate previously observed patterns.

To conclude, our study reveals the impacts of various factors on arthropod abundance in soil ecosystems, including environmental structures and interactions within arthropod communities. The results show that soil pH and canopy cover may function as structural indicators of overall abundance, although different orders exhibit distinct responses to different

habitat conditions, including soil pH, canopy cover, tree height, and ground cover. Furthermore, strong trophic relationships offer potential as bioindicators. Specifically, the positive correlation between Collembola and total arthropod abundance suggests that Collembola may be used as a proxy for overall abundance in these habitats. The tight relationship between Collembola abundance and soil pH further emphasizes the link between soil pH and site productivity. Conversely, calculating diversity at a low taxonomic resolution may have limited the observed environmental relationships within soil ecosystems. Exploring alternative methods of categorizing data, such as by functional diversity, may reveal meaningful patterns without the challenges of species identification. Future research should consider this and prioritize investigations of temporal dynamics, microhabitat differentiation, landscape characteristics, and incorporation of additional soil properties, for a more comprehensive understanding of soil biodiversity. By shedding light on the intricate connections between soil arthropods and their environments in Newfoundland forests, our study contributes to the development of effective bioindicators for assessing soil ecosystem health.

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Figure 3-1. Map of the Avalon Peninsula, Newfoundland, Canada. Study sites are represented by a star (red: Salmonier Nature Reserve, blue: Pippy Park; yellow: Outer Cove).



Figure 3-2. Diagram of the pitfall trap used in this study.



Figure 3-3. Correlation plot between the diversity and abundance of soil arthropods and tree arthropods. Titles without a prefix were sampled from the soil, those with a "Tree" suffix were sampled from a tree that was 1 m away from the soil samples. Blank squares indicate correlations that were not significant. Size of the circle, intensity of colour, and correlation coefficient indicate the strength of the relationship. Red indicates more negative relationships; blue indicates more positive relationships. Variables are ordered by hierarchical clustering.



Figure 3-4. Overall results of the statistical models investigating environmental predictors of arthropod community traits in soil habitats. Arthropod symbols represent the abundance of individuals in a specific order (Acari, Araneae, Collembola, Diptera, and Opiliones), or total arthropod abundance. Arthropod traits under "Positive Effect" had a significant positive relationship with the explanatory variable in the left column. Arthropod traits under "Negative Effect" had a significant negative relationship with the explanatory variable in the left column. Total arthropod diversity and Hymenoptera abundance were not included as they did not have any strong environmental predictors.

| Variable | PC1 | PC2 | PC3 | PC4 |
|-------------|-------|-------|-------|-------|
| Lichen | 0.12 | -0.28 | 0.46 | -0.08 |
| Moss | -0.52 | -0.37 | -0.16 | 0.12 |
| Fungi | -0.14 | -0.25 | -0.22 | -0.47 |
| Deadwood | 0.41 | -0.35 | 0.10 | -0.02 |
| Leafy | 0.03 | 0.60 | 0.12 | -0.26 |
| Woody | 0.08 | 0.13 | 0.64 | -0.11 |
| Bare ground | -0.15 | 0.41 | -0.21 | 0.40 |
| Rock | 0.10 | -0.14 | 0.20 | 0.72 |
| Debris | 0.48 | -0.14 | -0.32 | -0.01 |
| Needle | 0.51 | 0.13 | -0.32 | 0.04 |

Table 3-1. Loadings of the first four principal components from a PCA of ground cover variables.

Table 3-2. Competing models used to predict different arthropod community traits. All models were run with each of the 8 response variables (total arthropod abundance and diversity, Acari, Araneae, Collembola, Diptera, Hymenoptera, and Opiliones abundance). 'X' indicates which variables were included in the model. Site and Sample were included in every model, with Sample included as a random effect.

| Model | Description | PC1 | PC2 | PC3 | PC4 | Soil pH | Canopy Cover | Tree Height | Site | Sample |
|-------|-----------------|-----|-----|-----|-----|---------|-----------------|----------------|------|--------|
| ٨ | Global | v | v | v | v | v | v | v | v | v |
| A | Global | Λ | Λ | Λ | Λ | Λ | Λ | Λ | Λ | Λ |
| В | PC | Х | Х | Х | Х | | | | Х | Х |
| С | PC and Soil | Х | Х | Х | х | Х | | | Х | х |
| D | PC and Canopy | Х | Х | Х | х | | Х | | Х | х |
| E | Soil pH | | | | | Х | | | Х | х |
| F | Canopy | | | | | | Х | | Х | х |
| G | Soil and Canopy | | | | | Х | Х | | Х | х |
| Н | Tree | | | | | Х | Х | Х | Х | Х |

| Class Order | | Common name | Total count | Mean count | Frequency (%) |
|-------------------------|------------------|--------------------|-------------|------------|------------------|
| Arachnids | | | | | |
| Arachnida | Acari | Mites | 6936 | 51.38 | 98.52 |
| Arachnida | Araneae | Spiders | 988 | 7.32 | 98.52 |
| Arachnida | Opiliones | Harvestmen | 1969 | 14.59 | 89.93 |
| Arachnida | Pseudoscorpiones | Pseudoscorpions | 6 | 0.04 | 4.44 |
| Insects | | | | | |
| Insecta | Coleoptera | Beetles | 1165 | 8.63 | 85.93 |
| Insecta | Diptera | Flies | 5395 | 39.96 | 99.26 |
| Insecta | Hemiptera | True Bugs | 151 | 1.12 | 47.41 |
| Insecta | Hymenoptera | Bees, wasps, ants | 1154 | 11.51 | 99.26 |
| Insecta | Isoptera | Termites | 3 | 0.02 | 1.48 |
| Insecta | Lepidoptera | Butterflies, moths | 118 | 0.87 | 45.19 |
| Insecta | Neuroptera | Lacewings | 6 | 0.04 | 4.44 |
| Insecta | Odonata | Dragonflies | 1 | 0.01 | 0.74 |
| Insecta | Psocodea | Bark lice | 31 | 0.38 | 17.78 |
| Insecta | Siphonaptera | Fleas | 1 | 0.01 | 0.74 |
| Insecta | Thysanoptera | Thrips | 7 | 0.05 | 4.44 |
| Insecta | Trichoptera | Caddisflies | 3 | 0.02 | 1.48 |
| Other arthropods | | | | | |
| Chilopoda* | | Centipedes | 16 | 0.12 | 11.11 |
| Diplopoda* | | Millipedes | 376 | 2.79 | 71.85 |
| Entognatha | Collembola | Springtails | 19,573 | 144.99 | 100.00 |
| Malacostraca | Isopoda | Woodlice | 319 | 2.36 | 60.00 |
| Other invertebrates | | | | | |
| Gastropoda*† | | Snails and slugs | 281 | 2.08 | 60.74 |
| Clitellata [†] | Opisthopora | Earthworms | 1 | 0.01 | 0.74 |

Table 3-3. List of arthropod groups collected from pitfall traps on the Avalon Peninsula from June through August 2023. Total count: number of individuals in all samples. Mean count: count per sample (total count/135 samples). Frequency: percent of total samples that group was found in.

Note: Groups denoted with * were identified to class level. Groups with [†] were omitted from analyses.

| Model | Κ | AICc | ΔAICc | Cum. Wt | LL |
|-----------------|----|--------|-------|---------|---------|
| Soil and Canopy | 6 | 610.89 | 0.00 | 0.54 | -298.34 |
| Canopy | 5 | 611.96 | 1.07 | 0.86 | -300.21 |
| Soil | 5 | 614.43 | 3.54 | 0.96 | -301.45 |
| Tree | 6 | 616.17 | 5.27 | 0.99 | -300.98 |
| Canopy and PC | 9 | 622.10 | 11.21 | 1.00 | -299.48 |
| Global | 11 | 622.33 | 11.43 | 1.00 | -296.16 |
| Soil and PC | 9 | 622.68 | 11.79 | 1.00 | -299.77 |
| PC | 8 | 624.49 | 13.59 | 1.00 | -302.24 |

Table 3-4. AICc of competing models that predict total arthropod abundance. Soil and Canopy and Canopy models had a Δ AICc within 2.00 and were analysed further.

Table 3-5. Analysis of the best models predicting total arthropod abundance.

| Model | β | 95% CI | р | SE |
|-----------------|--------|-----------------|---------|--------|
| Soil and Canopy | | | | |
| Intercept | 6.66 | 6.53, 6.79 | < 0.001 | 0.066 |
| Soil pH | 0.25 | 1.91e-03, 0.50 | 0.048 | 0.13 |
| Canopy | 0.016 | 3.85e-03, 0.03 | 0.0099 | 0.0062 |
| Pippy Park | 0.21 | 0.05, 0.38 | 0.010 | 0.083 |
| Salmonier | -0.085 | -0.31, 0.14 | 0.46 | 0.11 |
| Canopy | | | | |
| Intercept | 6.70 | 6.57, 6.83 | < 0.001 | 0.065 |
| Canopy | 0.016 | 2.84e-03, 0.03 | 0.017 | 0.0065 |
| Pippy Park | 0.20 | 0.03, 0.37 | 0.020 | 0.087 |
| Salmonier | -0.20 | -0.40, 5.16e-03 | 0.056 | 0.10 |

| Model | Κ | AICc | ΔAICc | Cum.Wt | LL |
|-----------------|----|---------|-------|--------|--------|
| Soil and PC | 10 | -623.45 | 0.00 | 0.92 | 324.96 |
| PC | 9 | -618.02 | 5.43 | 0.98 | 320.58 |
| Tree | 7 | -615.27 | 8.18 | 1.00 | 316.15 |
| Soil and Canopy | 7 | -612.32 | 11.12 | 1.00 | 314.68 |
| Canopy and PC | 10 | -609.13 | 14.32 | 1.00 | 317.80 |
| Global | 12 | -588.13 | 35.32 | 1.00 | 310.94 |
| Soil | 6 | -576.45 | 46.99 | 1.00 | 295.33 |
| Canopy | 6 | -569.21 | 54.24 | 1.00 | 291.71 |

Table 3-6. AICc of competing models that predict total arthropod diversity. Only the top model, Soil and PC, had a \triangle AICc within 2.00 and was analysed further.

Table 3-7. Analysis of the best model predicting total arthropod diversity.

| Model | β | 95% CI | р | SE |
|-------------|-------|--------------|---------|------|
| Soil and PC | | | | |
| Intercept | 10.77 | 9.75, 11.80 | < 0.001 | 0.50 |
| PC1 | 0.21 | -0.35, 0.77 | 0.45 | 0.28 |
| PC2 | -0.15 | -0.82, 0.22 | 0.43 | 0.19 |
| PC3 | 0.12 | -0.37, 0.62 | 0.53 | 0.20 |
| PC4 | 0.16 | -0.43, 0.59 | 0.50 | 0.24 |
| Soil pH | -1.10 | -3.06, 0.85 | 0.25 | 0.96 |
| Pippy Park | -1.30 | -2.55, -0.06 | 0.034 | 0.61 |
| Salmonier | 0.79 | -1.28, 2.87 | 0.44 | 1.02 |

| Model | Κ | AICc | ΔAICc | Cum. Wt | LL |
|-----------------|----|--------|-------|---------|---------|
| Tree | 7 | 522.72 | 0.00 | 0.46 | -252.85 |
| Soil | 5 | 524.82 | 2.10 | 0.63 | -256.64 |
| Canopy | 5 | 524.83 | 2.11 | 0.79 | -256.65 |
| Global | 11 | 526.03 | 3.31 | 0.87 | -248.01 |
| Soil and Canopy | 6 | 527.31 | 4.59 | 0.92 | -256.55 |
| PC | 8 | 527.56 | 4.84 | 0.96 | -253.78 |
| Soil ad PC | 9 | 528.30 | 5.58 | 0.99 | -252.58 |
| Canopy and PC | 9 | 530.63 | 7.91 | 1.00 | -25.73 |
| | | | | | |

Table 3-8. AICc of competing models that predict Acari (mite) abundance. The Tree model was the top model and was analysed further. No other models fell within a \triangle AICc of 2.00.

Table 3-9. Analysis of the best models predicting Acari abundance.

| Model | β | 95% CI | р | SE |
|--------------|--------|--------------|---------|-------|
| Tree | | | | |
| Intercept | 4.99 | 4.66, 5.31 | < 0.001 | 0.17 |
| Tree Height | 0.18 | 0.05, 0.30 | 0.0047 | 0.063 |
| Soil pH | 0.23 | -0.37, 0.83 | 0.45 | 0.31 |
| Canopy Cover | 0.0020 | -0.02, 0.04 | 0.51 | 0.015 |
| Pippy Park | -0.82 | -1.24, -0.39 | < 0.001 | 0.22 |
| Salmonier | 0.29 | -0.27, 0.84 | 0.32 | 0.28 |

| Model | Κ | AICc | ΔAICc | Cum.Wt | LL |
|-----------------|----|--------|-------|--------|---------|
| PC 2 | 5 | 321.13 | 0.00 | 0.31 | -154.80 |
| Soil | 5 | 321.46 | 0.33 | 0.58 | -154.96 |
| Soil and Canopy | 6 | 321.95 | 0.82 | 0.79 | -153.87 |
| Canopy | 5 | 323.21 | 2.08 | 0.90 | -155.84 |
| Tree | 6 | 323.98 | 2.85 | 0.97 | -154.88 |
| PC | 8 | 327.66 | 6.53 | 0.98 | -153.83 |
| Canopy and PC | 9 | 328.32 | 7.19 | 0.99 | -152.59 |
| Soil and PC | 9 | 328.93 | 7.80 | 1.00 | -152.89 |
| Global | 11 | 333.14 | 12.01 | 1.00 | -151.57 |

Table 3-10. AICc of competing models that predict Araneae (spider) abundance. Soil, Soil and Canopy, and Canopy models all had a \triangle AICc within 2.00 and were analysed further.

Table 3-11. Analysis of the best models predicting Araneae abundance.

| Model | β | 95% CI | р | SE |
|-----------------|--------|------------------|---------|-------|
| PC 2 | | | | |
| Intercept | 2.95 | 2.76, 3.15 | < 0.001 | 0.10 |
| PC 2 | -0.086 | -0.17, -1.88e-03 | 0.045 | 0.043 |
| Pippy Park | 0.47 | 0.20, 0.74 | < 0.001 | 0.138 |
| Salmonier | -0.38 | -0.67, -0.10 | 0.0089 | 0.15 |
| Soil | | | | |
| Intercept | 3.031 | 2.82, 3.24 | < 0.001 | 0.11 |
| Soil pH | -0.43 | -0.86, 0.01 | 0.057 | 0.22 |
| Pippy Park | 0.41 | 0.14, 0.68 | 0.0027 | 0.14 |
| Salmonier | -0.57 | -0.92, -0.22 | 0.0015 | 0.18 |
| Soil and Canopy | | | | |
| Intercept | 3.093 | 2.87, 3.31 | < 0.001 | 0.11 |
| Soil pH | -0.44 | -0.87, -8.21e-03 | 0.046 | 0.22 |
| Canopy Cover | -0.016 | -0.04, 4.82e-03 | 0.13 | 0.010 |
| Pippy Park | 0.38 | 0.11, 0.65 | 0.0054 | 0.14 |
| Salmonier | -0.72 | -1.12, -0.32 | < 0.001 | 0.20 |

| Model | K | AICc | ΔAICc | Cum. Wt | LL |
|-----------------|----|--------|-------|---------|---------|
| Soil | 5 | 582.17 | 0.00 | 0.44 | -285.31 |
| Soil and Canopy | 6 | 582.76 | 0.60 | 0.76 | -284.28 |
| Tree | 6 | 584.54 | 2.37 | 0.89 | -285.16 |
| Canopy | 5 | 585.29 | 3.12 | 0.98 | -286.87 |
| Soil and PC | 9 | 589.81 | 7.64 | 0.99 | -283.33 |
| PC | 8 | 591.59 | 9.42 | 1.00 | -285.79 |
| Canopy and PC | 9 | 592.39 | 10.22 | 1.00 | -284.62 |
| Global | 11 | 594.23 | 12.06 | 1.00 | -282.11 |

Table 3-12. AICc of competing models that predict Collembola (springtail) abundance. Soil and Soil & Canopy models had a \triangle AICc within 2.00 and were analysed further.

Table 3-13. Analysis of the best models predicting Collembola abundance.

| Model | β | 95% CI | р | SE |
|--------------------|-------|-----------------|---------|--------|
| Soil pH | | | | |
| Intercept | 5.88 | 5.68, 6.07 | < 0.001 | 0.099 |
| Soil pH | 0.46 | 0.06, 0.85 | 0.025 | 0.20 |
| Pippy Park | 0.45 | 0.19, 0.71 | < 0.001 | 0.13 |
| Salmonier | -0.28 | -0.59, 0.03 | 0.079 | 0.16 |
| | | | | |
| Soil pH and Canopy | | | | |
| Intercept | 5.82 | 5.62, 6.03 | < 0.001 | 0.10 |
| Soil pH | 0.47 | 0.08, 0.86 | 0.019 | 0.20 |
| Canopy Cover | 0.014 | -4.94e-03, 0.03 | 0.15 | 0.0098 |
| Pippy Park | 0.48 | 0.22, 0.73 | < 0.001 | 0.13 |
| Salmonier | -0.15 | -0.50, 0.21 | 0.42 | 0.18 |

| Model | K | AICc | ΔAICc | Cum. Wt | LL |
|-----------------|----|--------|-------|---------|---------|
| Soil and Canopy | 6 | 479.22 | 0.00 | 0.43 | -232.51 |
| Canopy | 5 | 479.23 | 0.00 | 0.85 | -233.84 |
| Tree | 7 | 481.98 | 2.76 | 0.96 | -232.48 |
| Soil | 5 | 484.18 | 4.95 | 0.99 | -236.23 |
| Canopy and PC | 9 | 488.69 | 9.47 | 1.00 | -232.77 |
| Soil and PC | 9 | 490.94 | 11.72 | 1.00 | -233.90 |
| PC | 8 | 491.08 | 11.86 | 1.00 | -235.54 |
| Global | 11 | 492.34 | 13.11 | 1.00 | -231.17 |

Table 3-14. AICc of competing models that predict Diptera (fly) abundance. Soil & Canopy and Canopy models had a Δ AICc within 2.00 and were analysed further.

Table 3-15. Analysis of the best models predicting Diptera abundance.

| Model | β | 95% CI | р | SE |
|-----------------|-------|----------------|---------|-------|
| Soil and Canopy | | | | |
| Intercept | 4.54 | 4.29, 4.79 | < 0.001 | 0.13 |
| Soil pH | 0.41 | -0.07, 0.90 | 0.095 | 0.25 |
| Canopy Cover | 0.036 | 0.01, 0.06 | 0.0041 | 0.012 |
| Pippy Park | 0.43 | 0.11, 0.75 | 0.0077 | 0.16 |
| Salmonier | -0.38 | -0.82, 0.06 | 0.094 | 0.23 |
| Canopy Cover | | | | |
| Intercept | 4.61 | 4.36, 4.86 | < 0.001 | 0.13 |
| Canopy Cover | 0.035 | 9.80e-03, 0.06 | 0.0065 | 0.013 |
| Pippy Park | 0.41 | 0.08, 0.74 | 0.014 | 0.17 |
| Salmonier | -0.57 | -0.97, -0.17 | 0.0050 | 0.20 |

| Model | K | AICc | ΔAICc | Cum. Wt | LL |
|-----------------|----|--------|-------|---------|---------|
| Soil | 5 | 350.83 | 0.00 | 0.41 | -169.65 |
| Canopy | 5 | 350.97 | 0.14 | 0.79 | -169.72 |
| Soil and Canopy | 6 | 353.43 | 2.60 | 0.90 | -169.61 |
| Tree | 7 | 355.15 | 4.32 | 0.95 | -169.06 |
| PC | 8 | 355.64 | 4.81 | 0.98 | -167.78 |
| Soil and PC | 9 | 358.70 | 7.87 | 0.99 | -167.78 |
| Canopy and PC | 9 | 358.75 | 7.92 | 1.00 | -167.81 |
| Global | 11 | 364.27 | 13.44 | 1.00 | -167.13 |

Table 3-16. AICc of competing models that predict Hymenoptera (bees, wasps, ants) abundance. Soil and Canopy models had a \triangle AICc within 2.00 and were analysed further.

Table 3-17. Analysis of the best models predicting Hymenoptera abundance.

| Model | β | 95% CI | р | SE |
|--------------|---------|-------------|---------|--------|
| Soil pH | | | | |
| Intercept | 3.36 | 3.18, 3.54 | < 0.001 | 0.091 |
| Soil pH | -0.084 | -0.44, 0.27 | 0.65 | 0.18 |
| Pippy Park | 0.47 | 0.24, 0.70 | < 0.001 | 0.12 |
| Salmonier | -0.15 | -0.44, 0.13 | 0.29 | 0.15 |
| Canopy Cover | | | | |
| Intercept | 3.36 | 3.18, 3.54 | < 0.001 | 0.093 |
| Canopy Cover | -0.0024 | -0.02, 0.02 | 0.80 | 0.0092 |
| Pippy Park | 0.47 | 0.24, 0.71 | < 0.001 | 0.12 |
| Salmonier | -0.14 | -0.43, 0.15 | 0.35 | 0.15 |

| Model | Κ | AICc | ΔAICc | Cum. Wt | LL |
|-----------------|----|------|-------|---------|--------|
| Canopy | 5 | 0.00 | 0.43 | -188.73 | 389.00 |
| Soil and Canopy | 6 | 1.92 | 0.59 | -188.36 | 390.93 |
| Canopy and PC | 9 | 2.43 | 0.72 | -184.15 | 391.44 |
| Soil | 5 | 3.21 | 0.80 | -190.34 | 392.22 |
| PC | 8 | 3.36 | 0.88 | -186.18 | 392.36 |
| Tree | 7 | 3.63 | 0.95 | -187.80 | 392.64 |
| Global | 11 | 5.68 | 0.98 | -182.34 | 394.68 |
| Soil and PC | 9 | 5.70 | 1.00 | -185.78 | 394.70 |

Table 3-18. AICc of competing models that predict Opiliones (harvestman) abundance. Canopy and Soil and Canopy models had a Δ AICc within 2.00 and were analysed further.

Table 3-19. Analysis of the best models predicting Opiliones abundance.

| Model | β | 95% CI | р | SE |
|-----------------|-------|----------------|---------|-------|
| Canopy | | | | |
| Intercept | 4.17 | 3.85, 4.48 | < 0.001 | 0.16 |
| Canopy Cover | 0.034 | 8.25e-05, 0.07 | 0.049 | 0.017 |
| Pippy Park | -0.73 | -1.15, -0.31 | < 0.001 | 0.21 |
| Salmonier | -1.98 | -2.51, -1.45 | < 0.001 | 0.27 |
| Soil and Canopy | | | | |
| Intercept | 4.12 | 3.79, 4.45 | < 0.001 | 0.17 |
| Soil pH | 0.29 | -0.37, 0.96 | 0.38 | 0.34 |
| Canopy Cover | 0.035 | 1.39e-03, 0.07 | 0.041 | 0.017 |
| Pippy Park | -0.71 | -1.13, -0.30 | < 0.001 | 0.21 |
| Salmonier | -1.84 | -2.45, -1.22 | < 0.001 | 0.31 |

Chapter 4: Summary

In a 1987 speech given in Washington D.C., prominent biologist and ecologist Edward O. Wilson stressed the importance of conserving invertebrates, deeming them "the little things that run the world" (Wilson 1987). In the decades since, these 'little things' have not evaded the impacts of climate change and other anthropogenic disturbances on the environment. It may seem like an impossible feat to study a group of organisms whose species number in the millions, many of which are barely observable by the naked eye. However, their importance in habitats everywhere cannot be overstated, which justifies continual research on invertebrate communities.

One of the central goals of ecology is to better understand the processes that drive biodiversity at various spatial and temporal scales (Levin 1992). However, due to the inherent complexity of ecosystems, it is intangible to measure their complete biodiversity. In addition, observational experiments are often limited to a single site, which limits the possibility of conducting follow-up manipulations (Jenerette and Shen 2012). Therefore, ecologists rely on extrapolations from field data and statistical models, and make use of microcosm model systems, to construct a comprehensive understanding of ecosystem structure and changes (Srivastava et al. 2004, Rodrigues and Brooks 2007). This is particularly applicable for biodiversity that is challenging to measure and, more importantly, facing widespread declines. In this master's research, I explored various microhabitat structures and inter-taxonomic correlations that influence arthropod diversity and abundance in two habitat types: trees and soil. By investigating observable and measurable parameters that covary with arthropod community patterns, the goal is to establish biodiversity indicators that could facilitate monitoring of arthropod communities. This is one of the first studies to investigate arthropod community patterns in tree and soil habitats on the island of Newfoundland.

4.1 Summary of Results

As predicted, habitat heterogeneity, stemming from variations in environment characteristics, significantly contributes to shaping arthropod community patterns. The results of this study underscore the impact of microhabitat traits on the structure of arthropod assemblages, particularly the total abundance of arthropods, as well as the number of individuals in specific taxonomic groups. In addition, the observed trophic correlations demonstrate the role of taxonomic interactions in forming communities. This yields insight into the complexity of community patterns that would be difficult to observe in systems with large-bodied animals, where experimental replication is difficult.

Chapter two of my thesis examines lichen community traits, specifically macrolichen richness, macrolichen cover, and total lichen cover, and tree characteristics such as bark texture, bark pH, and canopy cover, to assess their impact on arthropod community structure. Arachnids and Collembola emerged as the most abundant groups in this habitat, constituting more than three-quarters of all individuals. Apart from investigating total arthropod diversity and abundance, I also focused on the abundance of Acari (mites), Araneae (spiders), Collembola (springtails), Diptera (flies), and Opiliones (harvestmen), the five most abundant groups. Additionally, I identified 14 distinct lichen groups that are present in the habitat.

Lichen community traits were found to play a significant role in shaping arthropod communities. Total lichen coverage on the trees emerged as a strong predictor for almost all measured arthropod community traits, except for Collembola. The presence of macrolichen

proved to also be a predictor for overall abundance and the abundance of Acari, Collembola, and Diptera. This observation suggests that certain arthropod groups exhibit more sensitivity to the three-dimensional, large, and bushy lichens on trees, while other groups may be equally responsive to different lichen types, including the flat crustose lichens incorporated into the "total lichen" measurement. In general, arthropods displayed a positive response to the amount of lichen present on trees. Intriguingly, two groups showed an opposite response: Araneae and Opiliones. This divergence might stem from different requirements from lichen communities or cascading effects as prey are able to hide in the lichen. Hence, the relationship between arthropod and lichen communities is not straightforward and varies across different groups.

The investigation of tree characteristics revealed that bark texture and canopy cover also influence arthropod assemblages. Bark texture is an important predictor for total abundance, as well as Acari, Araneae, Diptera, and Opiliones abundances. Similar to the findings of lichen effects, Araneae and Opiliones exhibited opposite responses to bark texture. The influence of bark texture on arthropods can be attributed to habitat heterogeneity. Bark texture increases the surface area of the tree, creating crevices that serve as protective niches and microhabitats for arthropods (Lamit et al. 2015).

Canopy cover also has a positive significant effect on total abundance and the abundance of Acari and Diptera. Canopy cover likely alters arthropod habitats by influencing the amount of sunlight, precipitation, and humidity in the environment (Deng et al. 2022). Such environmental factors influence the availability of resources and microclimatic conditions that can support arthropod populations.

Understanding the interactions between arthropods and their environment naturally raises questions about potential interactions among arthropod groups themselves. Acari and

Collembola, the two most abundant groups, exhibited a strong positive correlation with overall arthropod abundance. Unsurprisingly, considering their similar responses to environmental variables, Araneae and Opiliones also showed a positive correlation, indicating a trophic link between these two morphologically similar groups, suggesting that these two groups are not in competition in the tree habitat.

Chapter three is an examination of the influence of environmental structures, such as ground cover, soil pH, canopy cover, and tree height, on arthropod diversity and abundance. Although the number of individuals collected from the soil was several times greater than those on trees, the relative abundances of each group were similar. Again, arachnids and Collembola constituted three-quarters of all individuals, although Collembola abundance was notably higher in comparison. I investigated the total arthropod abundance and diversity once more, as well as the same five arthropod groups in chapter two: Acari, Araneae, Collembola, Diptera, and Opiliones, with the addition of Hymenoptera (wasps, bees, ants).

All arthropod community traits in chapter three exhibited associations with at least one environmental factor, excluding total arthropod diversity and Hymenoptera abundance. Unlike the patterns observed in chapter two, the relationships in chapter three were less consistent and straightforward across arthropod groups. For example, total abundance and Collembola abundance demonstrated a positive correlation with soil pH, while Araneae showed a preference for more acidic soils. Previous research has highlighted arthropod preference for alkaline soils (Santorufo et al. 2012, Mo et al. 2021), and this finding highlights the complexity of how different arthropod groups respond to soil pH variations.

Diptera, Opiliones, and total abundance displayed a positive response to a more closed canopy. This indicates that factors with more indirect and larger-scale effects can also play a role

in shaping the communities of these tiny organisms. This underscores the importance of including broader environmental influences when investigating arthropod assemblages.

Interestingly, the only group influenced by ground cover was Araneae. Ground cover was predicted to influence arthropod abundance and diversity as it can affect habitat heterogeneity, soil quality, and food availability (Silva et al. 2010, Blaise et al. 2022, Deng et al. 2022); although, not incorporating seasonal variation may have influenced these relationships. Additionally, Acari abundance was solely predicted by tree height, which serves as a proxy measure for other environment features, similar to canopy cover. It is worth noting that neither total diversity nor Hymenoptera abundance were predicted by any of the measured environmental measures. This perhaps suggests that other factors not included in this study could be influencing diversity and Hymenoptera populations in the soil.

Considering the immense diversity within the arthropod community, it is unsurprising that different groups would respond distinctly to various environmental conditions. To coexist in these habitats in such great numbers necessitates adaptations and adjustments in their ecological roles and niches (Lawton and Strong 1981). Therefore, investigating trophic relationships can give insight into community structures and trophic webs. For example, if there are two highly abundant groups, this could suggest that they share similar ecological functions. On the other hand, if one group thrives where another group is scarce, it may indicate potential resource competition within the habitat or cascading trophic effects.

The relationships that stood out provide insights into arthropod community dynamics. The positive correlation between total abundance and Collembola abundance, observed in both tree and soil habitats, suggests that Collembola could serve as a surrogate for overall abundance. Additionally, the negative relationship between total abundance and diversity, indicates that

areas with high abundance may not necessarily correspond to higher diversity. In addition, the measurements of abundance of several groups were correlated between the tree and the soil. For example, the abundance of soil Diptera and Opiliones positively correlated with the abundance of tree Diptera and Opiliones, respectively. These connections indicate the possibility of cooperative or competitive relationships between these habitats and underscore the intricacies and continuum of ecological dynamics.

While community diversity was less responsive to environmental characteristics in both chapters, the strong response of overall arthropod abundance highlights its significance as a valuable community measure. It is important to recognize that undue focus solely on species diversity may lead to an incomplete understanding of ecosystem dynamics by concentrating on ecological parts, while disregarding ecological wholes. As argued by Karr (2000), ecosystems can exhibit full ecological functioning even in areas with relatively low biodiversity, such as desert ponds, temperate forests, rocky outcrops, and small wetlands. These habitats deserve equal protection as areas with higher numbers of species. By considering both abundance and diversity measures, ecologists can obtain a more comprehensive view of arthropod community structure and function.

4.2 Limitations and Future Research

A limitation of arthropod research lies in their immense diversity and the difficulties in identifying them to species level. The identification process requires significant time, expertise, and resources, making data collection a laborious task. However, this limitation also presents a compelling argument for the use of indicators in monitoring arthropods. Using indicators, such as simple structural components of the environment or focusing on specific taxonomic groups, offers a more feasible approach for ecologists (McGeogh 1998, Lindenmayer et al. 2000, Timms et al. 2013, Cosović et al. 2020). DNA barcoding, using standardized, short DNA regions for specimen identification, also presents a fast and reliable method to overcome this challenge in ecological research (Antil et al. 2023). However, barcoding first requires the creation of a reference library, an arduous undertaking in itself. As the technology becomes more accessible, it will undoubtedly become the preferred method of taxonomic identification, although it remains an expensive option for smaller studies.

Another alternative is to shift the focus from species diversity towards functional diversity. Identifying arthropods to a taxonomic level that allows for grouping based on similar ecological roles provides an efficient and perhaps more informative measurement for future research. Functional diversity can provide essential information to assess the health of arthropod communities (Lawton and Strong 1981, Nielsen et al. 2010).

There are several exciting paths forward for continuing research of arthropod communities in Newfoundland forests. One direction is to measure and include additional parameters into the models. Soil, for example, is much more complex than just its acidity, and incorporating other measures such as temperature, bacterial communities, and nutrient levels, can create a more comprehensive understanding of the relationship between arthropods and soil. Additionally, structural diversity, quantified by factors like stand structure, plant traits, and canopy complexity, has been proposed as being a strong predictor of ecosystem functioning (LaRue et al. 2019). Measuring other broader environmental predictors that contribute to forest structural diversity and investigating their relationships with arthropod community traits can provide more context on how habitat heterogeneity impacts these communities and identify potential bioindicators.

Furthermore, the province's diverse climate and ecoregions offer a unique opportunity for replication across different parts of the island and over time. Conducting similar investigations can help validate and generalize the findings of this study and expand the knowledge of arthropod communities in Newfoundland. Longitudinal studies can track how these communities respond to environmental changes and disturbances. Furthermore, in investigating arthropod communities on replicated trees that serve as 'microlandscapes', the current study provides baseline date for future manipulative experiments in the province. While the sheer numbers of arthropods that can be collected provides a rich source of ecological data, it is essential to consider identification efforts for future studies.

4.3 Conclusion

To summarize, this study offers valuable insights into the complex interactions between arthropod groups and their environment in both soil and tree habitats. In particular, the amount of lichen on trees emerged as an important factor in forming arthropod communities in tree habitats. Other direct microhabitat variables such as bark texture and soil pH appeared to significantly shape these communities, with varying responses among different taxonomic groups. Furthermore, effects such as canopy cover and tree height, while exerting their effects in more indirect and complex ways, were also important and measurable parameters. Another noteworthy finding was the variation in responses at each site in both chapters, indicating that arthropod communities are sensitive to landscape-level changes. Finally, trophic relationships were observed in both habitats, reflecting the possibility of interactions between groups or shared sensitivities and ecological roles within their environments. The two complex systems I focused on, trees and soil, may appear distinct, but are intricately connected and continuous in their ecological interactions. Trees, seemingly discrete habitat islands, and soil, resembling an ocean of countless niches, both support diverse faunal communities. The influence of habitat characteristics on the arthropod communities within them highlights the potential to establish structural indicators of arthropod community traits, such as overall abundance. In addition, this research has revealed that certain taxonomic groups may serve as surrogates for community traits. Bioindicators can provide rapid and cost-effective biodiversity assessments to identify priority areas, monitor existing populations, and obtain conservation objectives in the future. Overall, this research provides the foundation for more extensive exploration of arthropod communities in Newfoundland forests.

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