ARBOREAL ARTHROPOD ASSOCIATIONS WITH EPIPHYTES AND THE EFFECTS OF GAP HARVESTING IN THE ACADIAN FOREST OF CENTRAL MAINE

by

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B.S. Northland College, 2002

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Science)

The Graduate School

The University of Maine

May, 2006

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Thesis Advisor: Dr. Robert G. Wagner

An Abstract of the Thesis Presented
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Epiphytes and arthropods play important roles in forest ecosystems and are important sources of biodiversity. However, their life history characteristics, habitat requirements, and response to forest management are poorly understood. I investigated associations between epiphytes and arthropods, and assessed the effect of gap harvesting using a long-term silvicultural experiment.

Arboreal arthropods and epiphytes on the bark of red maple (*Acer rubrum*) trees located in undisturbed forest and harvest gaps were compared at three height intervals (0-2, 2-4, and 4-6 m). A strong vertical gradient was observed for both epiphytes and arthropods. Bryophytes, *Cladonia* spp., and cyanolichens were most abundant near the base of the tree, while foliose and fruticose lichens were most abundant at 4-6 m. Acari (mites), Araneae (spiders) and Collembola (springtails) were most abundant near the base of the tree, whereas Diptera (flies) were most abundant above 2 m.

Gap harvesting reduced the abundance of bryophytes, Collembola, and Araneae on the bark of trees. A positive correlation in the abundance of bryophytes, Collembola, and Araneae suggested that there may be a trophic interaction among the three. During their early developmental stages, arboreal spiders appeared to be dependent upon availability of Collembola prey, which in turn were dependant upon bryophytes. This relationship appeared to be sensitive to a decline in bryophyte abundance that occurred following gap harvesting.

This study was the first to identify Diptera as a major component of the arboreal community. Fifteen Diptera families were identified, eight of which were common. The eight common families utilized the arboreal habitat differently depending on height along the bole and abundance of crustose and "other" lichen. A potential interaction was identified between Diptera and a Collembola morphospecies in the family Entomobryidae. These findings suggest a diverse arthropod community that exploits different characteristics of the arboreal habitat and exhibits varied responses to harvest gaps.

ACKNOWLEDGMENTS

I sincerely thank Bob Wagner for providing financial support for my research and especially for his willingness to take on the role as my advisor during the final stages of my research. His enthusiasm and input were invaluable to me. I would like to thank Connie Stubbs for also stepping in as a Committee Member at the last minute. Her thorough editing skills were greatly appreciated. I also thank the other members of my committee, Mac Hunter and Steve Selva for offering valuable advice and support when needed. I also thank Steve Woods for luring me to the University of Maine with an exciting research project on lichen and insects. I appreciate his effort and support in getting me started on my research. Thanks to Bill Halteman for all of his statistical advice, and for teaching so many great statistics courses.

A special thanks to my first mentor, Jim Meeker, who got me interested in ecology and natural history at Northland College. Following him around in the Northwoods of Wisconsin was my most valuable learning experience. Without Jim I would not have fully realized my passion and potential for studying the natural world.

I owe a great debt to my parents for their encouragement and for supplementing the meager graduate student income when needed. I also thank my grandmother, Pauli Jezzard for her tenacity in paving the way for women in higher education by obtaining a bachelor's degree in English, at a time when this was unheard of.

I thank all the graduate students and their partners that I had the pleasure of knowing and learning from. Thanks to Kerry Gray for her hard work as my field assistant. Most importantly, I thank my partner, Tara King, for all her patience and help throughout my degree. She was my first editor, field assistant, computer guru, and biggest supporter. Without her, I couldn't have made it this far.

Finally, I would like to thank natural selection and random mutation for the diversity of life. I can't imagine a dull moment in my life, when all the entertainment and inspiration I need surrounds me in the natural world.

This research was funded through a Teaching Fellowship with the National Science Foundation, and grants through the USDA National Research Initiative Competitive Grants Program, and the University of Maine's Association of Graduate Students.

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PROLOGUE

The focus of this thesis is the arboreal community of epiphytes and arthropods located on trees in the Acadian forest of central Maine. My interest in this topic was initially sparked by Dr. Steve Woods' observations of Psocoptera (bark lice) while climbing trees for his PhD research on gyspy moths in southern New England. The research began describing arboreal Psocoptera life histories and their associations with lichens, and later evolved to include a more community-level investigation of epiphytes and arthropods. The final project: (1) investigated how epiphytes and arthropods vary with height on the tree, bark texture, and stem diameter, (2) examined the influence of harvest gaps on the arboreal community, and (3) explored epiphyte/arthropod associations.

This research is unique in several respects. First, much of the work examining the influence of forest management on epiphytes and arthropods has focused on comparisons between extreme conditions such as regenerated clearcuts and old-growth forests. I examined the influence of harvest gaps, a low-intensity silvicultural approach that was designed to emulate natural disturbances, on the arboreal community. Second, research regarding arboreal arthropods is far from complete, and has generally focused on either a particular species (e.g., forest pests) while overlooking the rest of the arthropod community, or order level trends (Stubbs 1987 and 1989, Pettersson et al. 1995). This approach has been especially true for investigations of epiphyte-associated arthropods. I investigated family-level trends for two major arboreal arthropod orders: Collembola (springtails) and Diptera (flies). Finally, while there is extensive evidence that epiphytes change with height on a tree (Hale 1952, Liu et al 2000, Pike et al. 1975, McCune and

Antos 1982, McCune 1993, McCune et al 1997), much of the research investigating effects of forest management on epiphytes and arthropods has not considered the influence of height. The research presented here explores the arboreal community from the base of the tree up to 7 m.

This thesis is divided into two chapters. The first chapter examines the influence of tree height, bark texture, and harvest gap on epiphytes and arboreal arthropods at the order level. Two initial observations about epiphyte/arthropod associations from Chapter 1 were pursued in more detail in Chapter 2 using family-level and morphospecies analyses. The first observation involved a new assemblage of arthropods comprised of Diptera (flies), which was previously undocumented in an arboreal context. Family-level analyses were used to explore arboreal Diptera trends, and to detect potential epiphyte associations. The second observation was a possible trophic interaction involving bryophytes, Collembola, and Araneae (spiders). A morphospecies analysis of Collembola was used to investigate this relationship further, and also to test for tree height, bark texture, and harvest gap effects, as well as other epiphyte associations. The completed work provides a relatively thorough examination of epiphytes and arboreal arthropods, and offers additional insight into the ecological relationship between two poorly understood groups of organisms.

CHAPTER 1

EFFECT OF GAP HARVESTING ON EPIPHYTES AND ARBOREAL ARTHROPODS IN THE ACADIAN FOREST OF CENTRAL MAINE

ABSTRACT

Epiphytes and arthropods play important roles in forest ecosystems and are important sources of biodiversity. However, their life history characteristics, habitat requirements, and response to forest management are poorly understood. We investigated associations between epiphytes and arthropods, and assessed the effect of gap harvesting using a long-term silvicultural experiment. Arthropod and epiphyte assemblages dwelling on the bark of red maple (*Acer rubrum*) trees located in undisturbed forest and harvest gaps were compared at three height intervals (0-2, 2-4, and 4-6 m). A strong vertical gradient was observed for both epiphytes and arthropods. Bryophytes, *Cladonia* spp., and cyanolichens were most abundant near the base of the tree, while non-cyano, foliose lichen and fruticose lichen were most abundant at 4-6 m. Acari, Araneae and Collembola were all most abundant near the base of the tree, whereas Diptera were most abundant above 2 m. A previously undocumented assemblage of Dipterans (flies), primarily in the Nematocera suborder, was found. Gap harvesting reduced the abundance of bryophytes, Collembola (springtails), Araneae (spiders), and total arthropods. Canonical Correlation Analysis indicated that there was a positive association between bryophytes, Collembola, and Araneae. A strong correlation between Collembola and Araneae suggested a trophic interaction that may be affected by gap harvesting through reduction of bryophyte abundance. The composition of the epiphyte

and arthropod communities on eastern hemlock (*Tsuga canadense*) were similar to that found on red maple. However, epiphyte cover and arthropod abundance were much lower on hemlock than red maple, and cyanolichens were absent on hemlock.

INTRODUCTION

Practicing sustainable forestry requires a comprehensive knowledge of the forest community and the impacts of forest management. This knowledge is far from complete, and is especially deficient for organisms lacking in charisma or potential economic value. Arboreal arthropods and epiphytes in temperate forests are a prime example of taxa where monitoring and research are much needed, and would add greatly to our understanding about the impact of forest management. Relatively little research has been devoted to arboreal communities, due in part to the difficulties in accessing them (Barker and Sutton 1997, Schowalter and Ganio 1998).

Lichen epiphytes have been shown to influence nutrient cycling (Knops et al. 1996), contribute to the annual nitrogen budget of a forest (Forman and Dowden 1977, Becker 1980), provide nest material and food for vertebrates (Hayward and Rosentreter 1994, Sharnoff and Rosentreter 1998), and to have an associated unique arthropod fauna (Broadhead 1958, Gerson and Seaward 1977, André 1985, Stubbs 1987 and 1989, Pettersson et al. 1995). This lichen-associated arthropod fauna may play an important role in arboreal food chains containing birds (Norberg 1978, Pettersson et al. 1995), litter decomposition and nitrogen dynamics on the forest floor (Blair and Crossley 1988, Chen and Wise 1997), and in the regulation of arthropod pest populations (Reichert 1974, Reichert and Bishop 1990). However, little research has focused on lichen-associated arthropods and their sensitivity to specific forestry practices (Stubbs 1987 and 1989, Pettersson et al. 1995). Epiphytic bryophytes and their associated arthropods have received even less attention.

The sensitivity of epiphytic lichen to timber harvesting has resulted in a marked loss of lichen biomass and diversity in managed and secondary forests (Lesica et al. 1991, McCune 1993, Neitlich 1993, Pettersson et al. 1995, Esseen and Renhorn 1996, Pipp et al. 2001). This trend has been observed throughout the world, with some lichen species considered to be restricted to old-growth forests (Selva 1994, Esseen and Renhorn 1998). Numerous studies have examined potential factors associated with lichen decline, with somewhat conflicting results (Renhorn et al. 1997). Factors generally attributed to lichen decline following harvesting include poor dispersal ability (Esseen and Renhorn 1998, Hazell and Gustafsson 1999, Sillett et al. 2000, Hilmo and Sastad 2001), restricted microclimate requirements (Gauslaa and Solhaug 1996), and lack of colonizable substrates (Esseen and Renhorn 1996).

Research involving non-pest arthropod sensitivity to forest management has largely been overlooked until recent years, especially for arboreal and lichen-associated arthropods (Schowalter 1989, Niemela 1997, Schowalter and Ganio 1998, Peck and Niwa 2005). Pettersson (1996) found unmanaged, lichen-rich forests to support higher spider diversity and abundance than lichen-poor, selectively logged forests. Another study found unmanaged forests to support five times more invertebrates per tree branch and greater invertebrate diversity than mature managed forests (Pettersson et al. 1995).

Finally, much of the research on lichen sensitivity to forest management uses comparisons between extreme environments, such as a reference old-growth forest versus regenerated clearcuts. While this research is valuable and has contributed a great deal to what is known about the epiphytic lichen community, nearly all of the actively managed forests in New England are secondary forests, and very little old growth forest remains for comparisons. One approach, then, is to study the effect of harvesting techniques that emulate patterns of natural disturbance. The presettlement Acadian spruce-fir forest, which occupies a broad ecotone between the boreal forest biome and the eastern deciduous forest, was dominated by frequent disturbances of relatively low severity and small spatial scale (Lorimer 1977, Seymour et al. 2002). Therefore, studying influence of silvicultural approaches using gap harvesting in the Acadian spruce-fir forest is important to understanding and perhaps helping to maintain epiphyte and arboreal arthropod communities.

This study: (1) investigated how the epiphyte and arthropod communities changed with height on the tree, bark texture, and stem diameter, (2) examined the influence of harvest gaps on epiphyte and arthropod communities, and (3) explored epiphyte/ arthropod associations.

METHODS

Study Site

This study took place in the Penobscot Experimental Forest (PEF) in east-central Maine (44°50'; N, 68°35' W). The forest is dominated by northern conifers such as red spruce (*Picea rubens* Sarg.), black spruce (*P. mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and northern white cedar (*Thuja occidentalis* L.). Common hardwoods include red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), gray birch (*B. populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.), and bigtooth aspen (*P. grandidentata* Michx.). The PEF has a complicated history of repeated partial cuttings and insect outbreaks that resulted in multi-cohort stand structures with many species (R. Seymour, unpublished data). The soils consist primarily of poorly to very poorly drained loams and silt loams in flat areas that are situated between glacial till ridges composed of well-drained or sandy loam (Brissette 1996).

Sampling for this study used two research plots established by the University of Maine's Forest Ecosystem Research Program (FERP). FERP is a long-term study designed to compare two silvicultural systems that emulate the natural disturbance regime of the Acadian forest (Saunders and Wagner 2005). The silvicultural regimes include an expanding-gap harvest system with permanent reserve trees. This study utilized the heavier harvest treatment, which consisted of 20% removal of the canopy with 10% of the basal area permanently reserved within the harvest gap. Research plots are 9.4 ha (plot 1), and 10.1 ha (plot 6). Both research plots sampled contain eight harvest gaps, which average 0.15 ha (SE=0.01). Harvesting occurred in 1995 for research plot 1, and in 1996 for research plot 6.

Experimental Design

During the 2004 field season, five harvest gaps were randomly selected from each research plot. Four red maple (*A. rubrum*) trees located at the north end (south-exposed) of each harvest gap were randomly selected for sampling. Four additional trees were randomly selected in the adjacent undisturbed forest 20 to 50 m away from the southern edge of each harvest gap. This placement of trees provided the greatest contrast in exposure between harvest gap and trees in the closed canopy. All sample trees were between 15 and 50 cm diameter at breast height, and able to safely support a climbing ladder. A total of 80 trees were sampled from July 25 to August 20, 2004. All sampling occurred on rain-free days between 9:00 am and 3:00 pm.

Each tree was sampled using 6.7 m (three 2.4 m sections) aluminum climbing ladders. Each section was secured to the bole of the tree using a nylon webbed tie-down strap with 182 kg rated capacity. Personnel wore an arborist saddle that was secured to the ladder using two 45 cm lanyards.

The bole of each sample tree was divided into three, 2 m height intervals: 1) 0-2 m, 2) 2-4 m, and 3) 4-6 m. All sampling for epiphytes and arthropods occurred on the south-exposed surface of the tree bole. Each tree was measured for diameter at breast height (dbh), and assigned a single bark texture value. Bark texture was an index that ranged from 1 to 4, and was determined as follows: 1) smooth bark without fissures, 2) shallow fissures (<5 cm thick), 3) deep fissures (>5 cm thick), and 4) flaky and easily sloughed off. Additionally, each sample tree was flagged and the GPS coordinates recorded using a Magellan GPS unit.

During the 2005 field season, a total of 24 red maple trees were resampled from 2004. An additional height interval (6-7 m) was sampled on these trees. There were little to no differences between the epiphyte and arthropod communities between the two research plots sampled in 2004. Therefore, only trees in research plot 1 were sampled, as it was more accessible than research plot 6. Trees were selected for resampling by randomly selecting three of the five sampled gaps from research plot 1 to return to.

Eastern hemlock (*T. canadense*) trees were also sampled in 2005. Hemlock trees were chosen in a similar fashion as the red maple from the previous year, with a total of sixteen sampled. Eight of the trees were located in two of the three canopy gaps resampled for red maple, and eight were located 20-50 m from the southern edge of the gaps in a closed canopy. Many of the hemlock trees contained large branches around 2.5 m from the ground, which formed an obstacle to properly securing the second and third ladder sections to the tree. Therefore, only the 0-1 and 2-3 m heights were sampled. Sampling of the hemlock and red maple occurred from July 25 to August 12, 2005.

Data Collection

Epiphytes

In 2004 epiphyte percent cover within the first meter of each height interval and on the south exposed side of the bole was sampled using a 1m x 0.125 m sample quadrat. The vertical sides (1 m) of the quadrat were rigid and made of 1.27 cm pvc pipe. The horizontal sides (12.5 cm) were made of twine, so that the area measured, regardless of tree diameter, was equal for every tree and height interval. In each quadrat, the percentage cover of epiphytes was visually estimated to the nearest five percent. Estimation occurred at the species level for macrolichens, and also quantified overall percent cover for crustose lichen and bryophytes. Lichen nomenclature followed Esslinger (1999).

Arthropods

In 2004 arthropods were sampled over the entire length of the 2 m height interval. The width of the sample area was the same as the lichen sample quadrat (0.125 cm), and was also located on the south exposed side of the bole. Each 2 m interval was sampled for invertebrates using an Echo PV-413 backpack leaf blower with vacuum attachments. The vacuum was modified by adding a 10 m pool-vac hose to the intake so that sampling only required maneuvering the hose about the tree, rather than the entire machine. Additionally, a utility/blower shop-vac nozzle was attached to the end of the pool-vac hose. Samples were collected in knee-high nylon stockings that were located between the nozzle and the pool-vac hose.

Arthropods were sampled in 2005 using the same equipment as in 2004, but with a slight revision in methods. Arthropods in 2005 were sampled only in the first meter of the interval. That is, arthropod collection only occurred in the same area that the epiphyte community was estimated for percent cover. Also, because the second interval was merely a transition between interval 1 and interval 3 in both epiphytes and arthropods in 2004, only intervals 1, 3, and 4 (the new interval) were sampled for arthropods in 2005.

Pitfall traps also were established near each resampled red maple tree to compare the soil arthropod community to that collected on the tree. Specifically, one pitfall trap was set on the south side of each sample tree between 1 and 1.5 m from the base. Collection jars within each pitfall trap contained propylene glycol, and remained in the field August 1-10, 2005.

All arthropod samples were placed in a cooler with ice in the field, and later transferred to a freezer kept at -17 °C. Arthropods were later sorted in the lab from debris to order, and placed in 70% ethanol for long term storage.

Analytical Approach

Epiphytes

To examine the influence of height and canopy condition on the epiphyte community, the 2004 epiphyte data were analyzed using Nonmetric Multidimensional Scaling (NMS) in PC-ORD (McCune and Mefford 1999). The primary matrix used in the ordination contained the percent cover of epiphytes collected on all 80 trees over three height intervals (i.e., 240 sample units). Because the data were between 0 and 100%, Relative Sorenson distance matrix was used for the NMS ordination. Epiphyte species observed in less than four quadrats were not included in the NMS, except in the case of *Peltigera* spp. and *Ramalina* spp., which were combined at the genus level to include in the ordination (Table 1.1). The secondary matrix used in the NMS ordination included the percent cover of epiphyte guilds for each sample unit, and the following categorical variables: height interval, canopy condition (gap or canopy), bark texture, and dbh. The epiphyte guild data included the total percent cover of epiphyte species in each guild per sample unit. Guilds are non-taxonomic groups of species that have similar habitat requirements and morphologies, and tend occupy similar niches. In this study, guilds were modified from functional groups described by McCune 1993 (Table 1.1). Small and large foliose lichen species were contained in separate guilds rather than all being included in "other" lichens. *Cladonia* spp. were placed in a squamulose group.

Table 1.1. List of all epiphytes by guild observed on red maple (*Acer rubrum*) trees from the base to 6 m on the south-facing bole. The mean % cover with ± 1 standard error (SE), epiphyte percent frequency (# occurrences/240*100%) and codes used in NMS ordination scatter plot (Figure 1) are presented for each epiphyte. Species denoted by a star (*) were not included in the NMS ordination analysis because of too few occurrences (n < 4 out of 240). Species denoted by two stars (**) were combined at the genus level. A dagger (†) signifies guilds with no occurrences at one or more intervals, and were omitted from the repeated measures GLM analysis.

GUILD	SPECIES	CODE	Mean % Cover (SE)	% Frequency
BRYOPHYTE	measured at this level in field	BRYOPHT	20.12 (1.10)	98.33
CRUSTOSE	measured at this level in field	CRUSTOSE	18.35 (1.06)	97.92
CYANOLICHEN	*Collema subflaccidum*	COLSUB	0.15 (0.09)	3.33
	*Leptogium corticola**	LEPCOR	0.03 (0.02)	1.25
	Leptogium cyanescens	LEPCYA	0.62 (0.18)	11.25
	*Leptogium saturninum**	LEPSAT	0.04 (0.03)	0.83
	Lobaria pulmonaria	LOBPUL	2.02 (0.58)	12.50
	Lobaria quercizans	LOBQUE	0.89 (0.24)	7.92
	*Peltigera horizontalis***	PELHOR	0.10 (0.06)	1.25
	*Peltigera polydactylon***	PELPOL	<0.01 (<0.01)	0.42
	*Peltigera praetextata***	PELPRA	0.01 (0.01)	0.42
LARGE FOLIOSE*	*Platismatia tuckermanii*	PLATUC	0.45 (0.15)	6.67
	Tuckermannopsis ciliaris grp.*	TUCCIL	0.02 (0.01)	0.83
	*Cetrelia olivetorum**	CETOLI	0.01 (0.01)	0.42
FRUTICOSE	*Bryoria furcellata*	BRYFUR	0.10 (0.03)	5.42
	*Bryoria nadvornikiana**	BRYNAD	0.02 (0.01)	0.83
	Evernia mesomorpha	EVEMES	0.08 (0.03)	4.17
	*Ramalina americana***	RAMAME	0.01 (0.01)	2.08
	*Ramalina dilacerata***	RAMDIL	0.02 (0.02)	0.42
	*Ramalina intermedia***	RAMINT	<0.01 (<0.01)	0.42
	Usnea filipendula	USNFIL	0.50 (0.19)	6.25
	*Usnea lapponica**	USNLAP	<0.01 (<0.01)	0.42
	Usnea strigosa	USNSTR	0.13 (0.05)	2.50
	Usnea subfloridana	USNSUB	0.60 (0.11)	17.08
SMALL FOLIOSE	*Flavoparmelia caperata**	FLACAP	<0.01 (<0.01)	0.42
	Hypogymnia physodes	HYPPHY	1.13 (0.22)	18.75
	Melanelia subaurifera	MELSUB	0.13 (0.03)	9.58
	Myelochroa galbina	MYEGAL	1.11 (0.15)	35.42
	Parmelia squarrosa	PARSQU	2.68 (0.37)	33.33
	Parmelia sulcata	PARSUL	4.67 (0.56)	48.33
	Punctelia rudecta	PUNRUD	0.45 (0.14)	5.83
	*Pyxine sorediata**	PYXSOR	0.05 (0.03)	1.67
SQUAMULOSE	*Cladonia* spp.	CLACHL	1.46 (0.26)	20.83

Results from the NMS ordination suggested that epiphytes responded more similarly to height and bark texture gradients within guild than among species in other guilds, and therefore subsequent analyses considered guilds rather than species. Some information may be lost by lumping species into guilds. However, species within a guild are often highly correlated, which causes rather serious multicolinearity issues. By analyzing guilds of epiphytes, we are eliminating most of the multicolinearity problems. To investigate guild relationships to height, bark texture, and response to harvest gaps, separate general linear models (GLM) were developed using Systat (Systat 2004). Each model contained the following factors: canopy condition (levels: gap and canopy), bark texture (levels: 1, 2, 3, and 4) and height interval (levels: 1, 2, and 3). Height interval was treated as a repeated measure. Guilds were examined for constant variance across factors using modified Levene's tests, and were transformed using ln (% cover + 1) to correct for constant variance. Pairwise comparisons across bark texture were Bonferroni adjusted at the family-wise $\alpha=0.05$ level. Comparisons between height intervals were adjusted using Sidak correction for multiple comparisons and considered significant at the $p<0.05$ level. All main effects were considered significant at the $p<0.01$ level.

The relation between stem diameter and the epiphyte community was also of interest. However, because dbh was correlated ($r^2=0.393$, $p<0.0001$) with bark texture, and since bark texture was a better predictor, dbh was excluded from GLM repeated measures models. The relation between bark texture and dbh was examined using linear regression, and the implications of this relationship were related to the epiphyte community.

Several analyses were performed on the data collected in 2005. First, the epiphyte community was compared between red maple and hemlock tree species using NMS ordination of the interval 1 and 2 data for all red maple and hemlock trees sampled (n=192). Next, the epiphyte community at interval 4 was compared to the other intervals. This dataset only contained the epiphyte percent cover data for the 24 resampled trees (*n*=96). The data were transformed using Beals Smoothing, then analyzed using NMS.

Arthropods

The arthropod analyses included count data collected in 2004, and unless otherwise noted, were the data used for analyses. The first level of arthropod analysis considered total count. These data were analyzed using GLM repeated measures, with height interval handled as a repeated measure. The model also contained canopy condition and bark texture. The data were checked for constant variance using modified Levene's tests, and were transformed using ln (count + 1).

Arthropod analysis next occurred at the order level and used GLM repeated measures for each order. Orders included in the analysis are listed in Table 1.2. The data were checked for constant variance across factors using modified Levene's tests, and resulted in the following transformations: $(\text{Araneae}+1)^{-1}$ and ln (Collembola + 1). For both total count and order level analyses, pairwise comparisons across bark texture were Bonferroni adjusted at the family-wise $\alpha=0.05$ level. Comparisons between intervals were adjusted using Sidak correction for multiple comparisons and considered significant at the $p<0.05$ level.

The 2004 and 2005 counts were analyzed to examine year to year variability in the arthropod community. First, the data for the major orders were compared between 2004 and 2005 for intervals 1 and 3. The data were converted to count/square meter to make values across different years comparable, then transformed using ln (count + 1) to correct for constant variance. Finally, GLM repeated measures analysis was performed separately for each interval, with year as the repeated measure.

Epiphyte/Arthropod Associations

Canonical correlation (CANCOR) was used to detect associations between the guilds and arthropod orders (Systat 2004). All variables were standardized so that each variable ranged from 0-1. The dependent variable set contained the six major arthropod orders (Table 1.2). The independent variable set contained all the epiphyte guilds (Table 1.1). Significant canonical correlations were rotated. Variables with canonical loadings greater then 0.3 were considered significant.

RESULTS

Epiphytes

A total of 33 epiphytes were observed in 2004 (Table 1.1). The most abundant and common epiphytes were bryophyte and crustose lichen. The most common lichen species was *Parmelia sulcata*.

The NMS ordination accounted for 83.8% of the variance, and resulted in two axes with significant structure (Figure 1.1). The first axis accounted for 57.8% of the variance, and the second axis accounted for 26.0% of the variance. The first axis was correlated with height interval, cyanolichen cover, fruticose lichen cover, foliose lichen cover, and bark texture (Table 1.3). This axis described a gradient where an increase in height was associated with increased fruticose cover (e.g., *Usnea* spp. and *Bryoria* spp.) and foliose cover (e.g. *P. sulcata* and *Hypogymnia physodes*). At the other end of the gradient, lower height intervals, larger dbh, and thicker, flakier bark were positively associated with abundance of cyanolichen cover, bryophyte cover, and *Cladonia* spp. Additionally, the ordination demonstrated that lichen species tended to behave similarly within their respective guild (Figure 1.1).

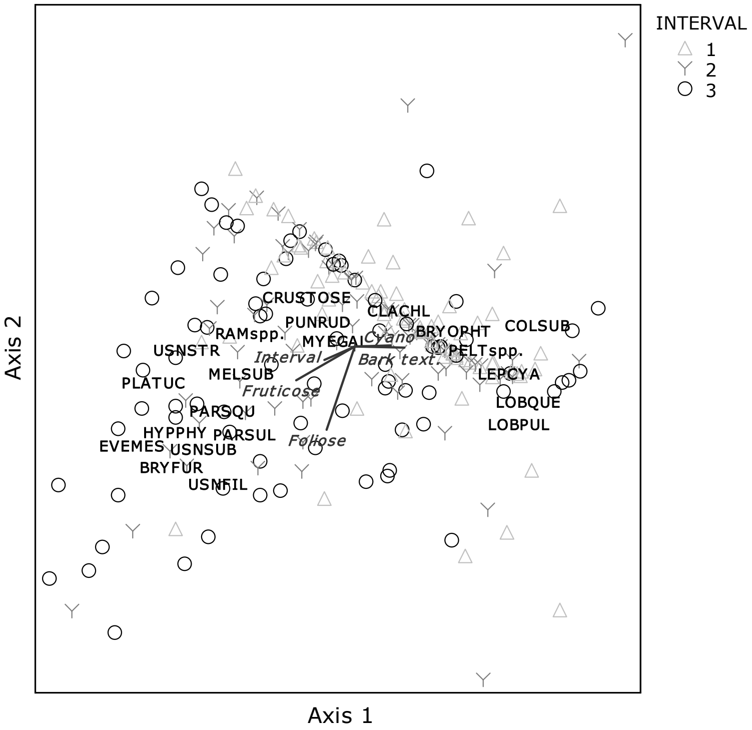

Figure 1.1. Ordination scatterplot (NMS) of 3 intervals per 80 trees (i.e. 240 "plots") (vector cutoff value=0.150) generated using percent cover values of epiphytes listed in Table 1.1. Epiphyte codings are described in Table 1.1 and are capitalized in the scatterplot. Plot symbols denote vertical intervals such that (△) occurred at interval 1 (sampled 0-1 m), (Y) at interval 2 (sampled 2-3 m), and (O) at interval 3 (sampled 4-5 m). Both axes contained significant structure (Monte Carlo p-values =0.0196), and accounted for 83.8% of the variance.

Table 1.2. List of all arthropod orders collected on red maple (*Acer rubrum*) trees from the base to 6 m on the south-facing bole. The mean count per square m with ± 1 standard error (SE), and percent frequency (# occurrences/240* 100%) are presented for each order for 2004. Arthropods denoted by a star (*) were identified at the class level. Orders under the major arthropods heading were analyzed using GLM repeated measures. Other arthropods were omitted from further analyses.

CLASS	ORDER	Common Name	Mean Count/m^2 (SE)	% Frequency
MAJOR ARTHROPODS				
Arachnida	ACARI	Mites	177.28 (11.62)	99.58
Arachnida	ARANEAE	Spiders	7.72 (0.72)	72.08
Parainsecta	COLLEMBOLA	Springtails	75.77 (6.28)	97.92
Insecta	DIPTERA	Flies	22.88 (1.48)	95.42
Insecta	HYMENOPTERA	Bees & Wasps	5.72 (0.48)	63.33
Insecta	PSOCOPTERA	Bark lice	10.00 (0.71)	80.42
OTHER ARTHROPODS				
Insecta	COLEOPTERA	Beetles	0.52 (0.10)	11.25
Insecta	HEMIPTERA	True Bugs	0.73 (0.27)	9.58
Insecta	HOMOPTERA	Aphids & Scales	1.05 (0.40)	11.67
Insecta	LEPIDOPTERA	Moths & Butterflies	1.15 (0.17)	22.92
Insecta	NEUROPTERA	Lacewing	0.02 (0.02)	0.42
Arachnida	OPILIONES	Harvestmen	0.45 (0.10)	8.75
Insecta	ORTHOPTERA	Grasshoppers	0.02 (0.02)	0.42
Insecta	THYSANOPTERA	Thrips	0.02 (0.02)	0.42
Chilopoda*		Centipedes	0.05 (0.03)	1.25
Diplopoda*		Millipede	0.03 (0.02)	0.83

Table 1.3. Correlation of secondary matrix variables with NMS ordination of epiphyte percent cover axes. Epiphyte guild variables are the sum of the percent cover of epiphyte species in a guild.

Axis	1	2
INTERVAL	-0.309	-0.205
DBH	0.336	0.050
BARKCODE	0.393	-0.056
CYANOLICHEN	0.332	-0.040
SMALL FOLIOSE	-0.299	-0.512
FRUTICOSE	-0.428	-0.322

The GLM repeated measures yielded no interactions, and therefore all results can be described as main effects (Table 1.4). Bryophytes were less abundant (p= 0.004) on trees in harvest gaps, while the abundance of other guilds were not affected by canopy condition (Figure 1.2A). Bryophyte and cyanolichen abundance was greatest at lower intervals, and small foliose was more abundant at higher intervals (Figure 1.2B). These trends were also supported by the NMS ordination (Figure 1.1). Bark texture influenced abundance of crustose and cyanolichens (Figure 1.2C). Crustose lichens were most abundant on smooth bark, while cyanolichen were most abundant on thick, flaky bark.

The relation between bark texture and dbh of sample trees was positively correlated (r=0.622; p<0.0001), indicating that as stem diameter increased, the thickness and flakiness of the bark increased (Figure 1.3). Relating this to epiphyte guilds, crustose lichens were most abundant in trees with small dbh, whereas cyanolichen abundance increased on trees with larger dbh.

At 6-7 m (interval 4) large foliose (e.g., *Platismatia tuckermanii*) and fruticose (e.g. *U. subfloridana* and *Evernia mesomorpha*) lichen abundance were greater than in interval 3. Small foliose were also common in interval 4 (Appendix A). The epiphyte community on hemlock was different from that found on red maple; the major differences in the epiphyte community were an absence of cyanolichen and less epiphyte cover on hemlock trees (Appendix B).

Arthropods

In 2004 over 18,200 arthropods were collected and in 2005 over 4,800 arthropods were collected. While sixteen orders were represented by the collections, the most

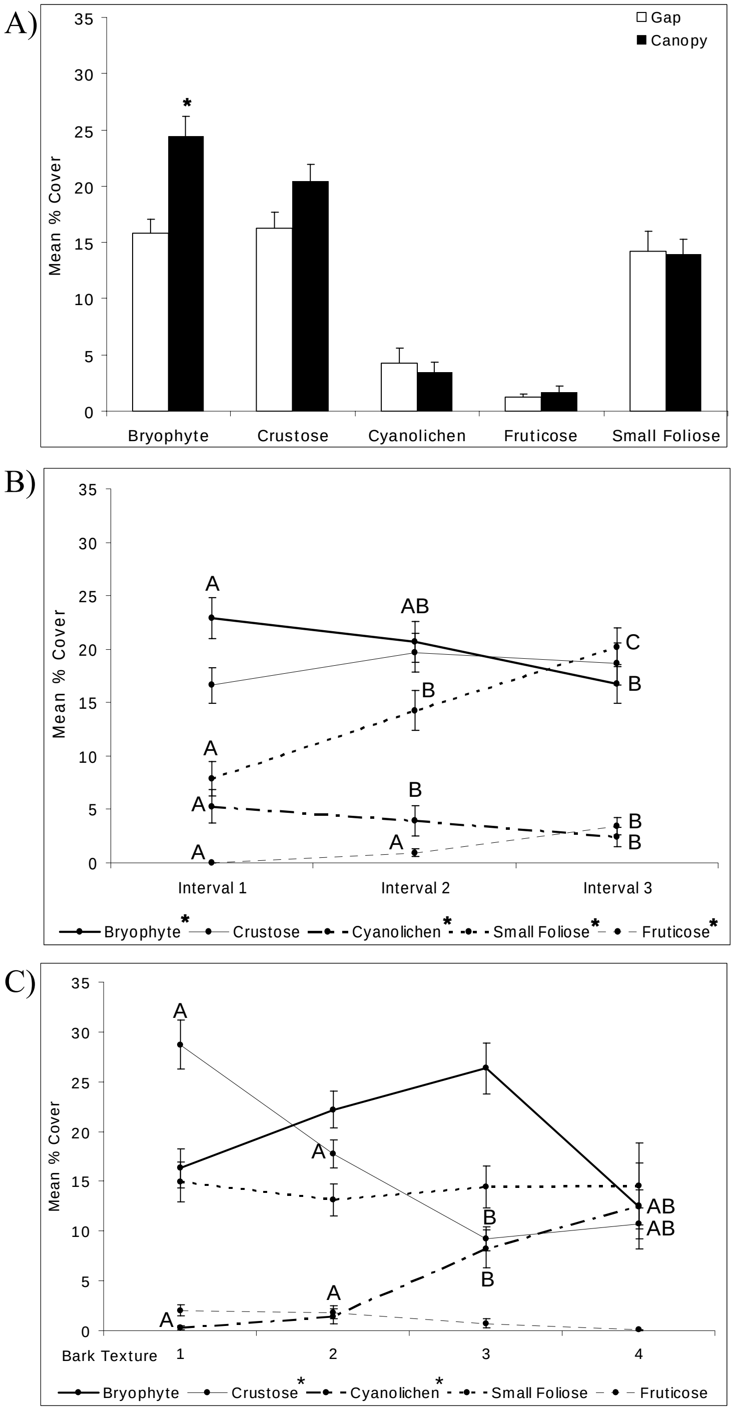

Figure 1.2. Mean percent cover of lichen guilds by canopy condition (A), interval (B), and bark texture (C). Data were analyzed separately for each guild using GLM repeated measures, with interval as the repeated measure. Stars (*) indicate a main effect significant at the $p<0.01$ level. Different letters within guilds represent differences in percent cover among factor levels. Error bars denote +/- 1 standard error around the mean. Significance was considered at the $p<0.05$ level after probabilities were adjusted for multiple comparisons using Sidak (interval) and Bonferroni (bark texture) corrections.

Table 1.4. ANOVA table for general linear model (GLM) repeated measures analysis of the effects of canopy condition (Gap), bark texture, and interval on epiphyte guild percent cover. Analyses were run separately for each guild, and interval was the repeated measure. Guilds were natural log transformed to meet the assumption of constant variance. Effects were considered significant at the p<0.01 level. Stars (*) indicate epiphyte guilds that only occurred in one interval, and were analyzed using GLM with canopy condition and bark texture as factors.

			BRYOPHYTE			CRUSTOSE			CYANOLICHEN			LARGE FOLIOSE*		
	Source of Variation	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Between Subjects	Gap	1	14.38	9.09	0.00	5.31	3.93	0.05	1.40	2.01	0.16	0.02	0.12	0.73
	Bark Texture	3	2.96	1.87	0.14	12.33	9.14	0.00	2.38	3.43	0.02	0.36	2.18	0.10
	Bark Texture*Gap	3	2.61	1.65	0.19	0.40	0.30	0.83	1.17	1.69	0.18	0.05	0.33	0.80
	Error	72	1.58			1.35			0.69			0.16		
Within Subjects	Interval	2	2.05	4.65	0.01	0.50	1.46	0.24	2.13	8.77	0.00			
	Interval*Gap	2	0.53	1.20	0.31	0.07	0.19	0.82	0.03	0.11	0.90			
	Interval*Bark Texture	6	1.41	3.19	0.01	0.58	1.70	0.13	0.19	0.77	0.59			
	Interval*Bark Texture*Gap	6	0.88	1.99	0.07	0.19	0.56	0.76	0.15	0.62	0.72			
	Error	144	0.44			0.34			0.24					

			FRUTICOSE			SMALL FOLIOSE			SQUAMULOSE*		
	Source of Variation	df	MS	F	P	MS	F	P	MS	F	P
Between Subjects	Gap	1	0.19	0.25	0.62	3.47	1.04	0.31	4.08	3.91	0.05
	Bark Texture	3	1.96	2.57	0.06	2.32	0.69	0.56	1.55	1.49	0.23
	Bark Texture*Gap	3	1.42	1.86	0.14	0.74	0.22	0.88	0.01	0.01	1.00
	Error	72	0.76			3.34			1.04		
Within Subjects	Interval	2	6.59	18.28	0.00	23.00	35.70	0.00			
	Interval*Gap	2	0.28	0.77	0.47	0.30	0.46	0.63			
	Interval*Bark Texture	6	1.02	2.82	0.01	0.96	1.50	0.18			
	Interval*Bark Texture*Gap	6	0.45	1.26	0.28	0.63	0.98	0.44			
	Error	144	0.36			0.64					

abundant orders collected were Acari (mites), Collembola (springtails), Diptera (flies), Psocoptera (bark lice), Araneae (spiders), and Hymenoptera (wasps) (Table 1.2).

Total arthropod count varied with canopy condition, bark texture, and height interval, and there were no interactions among factors (Table 1.5). Total arthropod countwas greater at lower height intervals and on trees in undisturbed forest (Figure 1.4A). Also, as bark texture increased in thickness and flakiness, so did arthropod count (Figure 1.4B). This also implies that larger trees tend to have more arthropods per square meter than smaller trees.

Table 1.5. ANOVA table for GLM Repeated measures analysis of the effects of canopy condition (Gap), bark texture, and interval on total arthropod count. Total arthropod count was natural log transformed to meet the assumption of constant variance. Effects were considered significant at the p<0.01 level.

Source of Variation		df	MS	F	P
Between Subjects	Gap	1	9.404	12.666	0.001
	Bark Texture	3	3.897	5.249	0.002
	Bark Texture*Gap	3	1.920	2.587	0.060
	Error	72	0.742		
Within Subjects	Interval	2	2.731	13.755	0.000
	Interval*Gap	2	0.308	1.549	0.216
	Interval*Bark Texture	6	0.125	0.629	0.707
	Interval*Bark Texture*Gap	6	0.040	0.200	0.976
	Error	144	0.199		

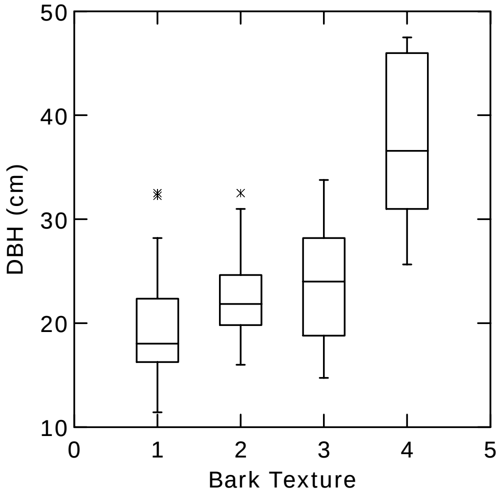

Figure 1.3. Box-plot demonstrating the relationship between bark texture and diameter at breast height (DBH). Correlation coefficient between variables was 0.627 (p <0.0001).

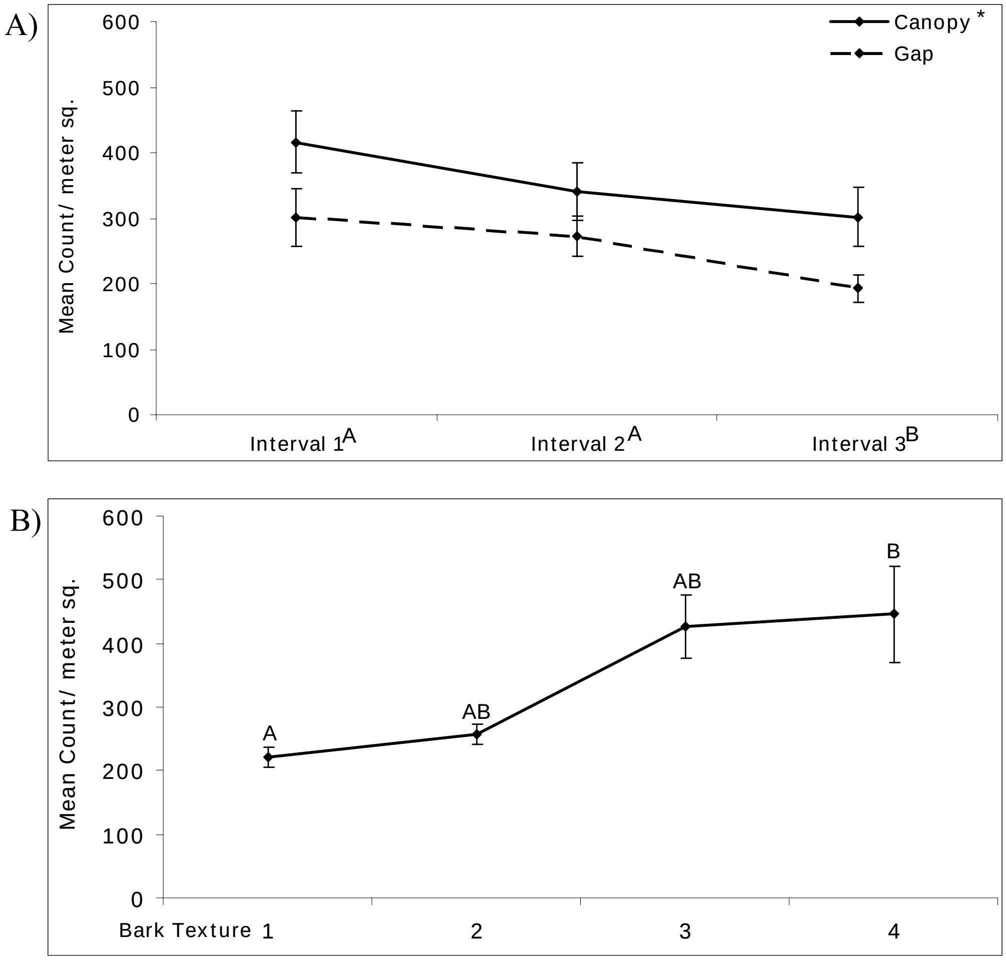

Figure 1.4. Mean of total arthropod count by canopy condition and interval (A), and bark texture (B). Data were analyzed using GLM repeated measures, with interval as the repeated measure and canopy condition and bark texture as factors. The star (*) represents a significant difference in count between gap and canopy trees at the $p<0.01$ level. Different letters indicate differences among intervals and bark texture. Significance was at the $p<0.05$ level after probabilities were adjusted using Sidak correction for multiple comparisons. Lines on points denote ± 1 standard error around the mean.

Canopy condition, bark texture, and height interval were important factors ($p < 0.01$) for four of the major arthropod orders (Table 1.6). Araneae and Collembola abundance was lower on trees in harvest gaps (Figure 1.5A). Acari, Araneae, and Collembola tended to increase in number at lower heights on the bole, whereas Diptera counts increased with height on the bole (Figure 1.5B). Acari and Collembola counts tended to increase in abundance with thicker, flakier bark (Figure 1.5C).

The six major orders collected on hemlock trees were proportionally similar to that found on red maple. The only major difference was that fewer arthropods per square meter were found on hemlock trees (Appendix D). The composition of the arthropod samples collected on the 24 red maple that were sampled in 2004 and 2005 demonstrated only minor variation in the arthropod community between years. The six major orders maintained the same rank of abundance, and the total count per square meter was similar for both years. Acari were the only arthropods that differed significantly between years at the $p<0.01$ significance level (Appendix E).

Epiphyte/Arthropod Associations

Canonical Correlation Analysis yielded two canonical correlations with significant structure ($p<0.01$). The variables with the strongest loadings on the first canonical correlation were the arthropod orders Collembola, Acari, and Araneae and the epiphyte guilds cyanolichen and bryophyte (Figure 1.6A). This canonical correlation suggested a positive relationship among these variables. Hymenoptera and small foliose

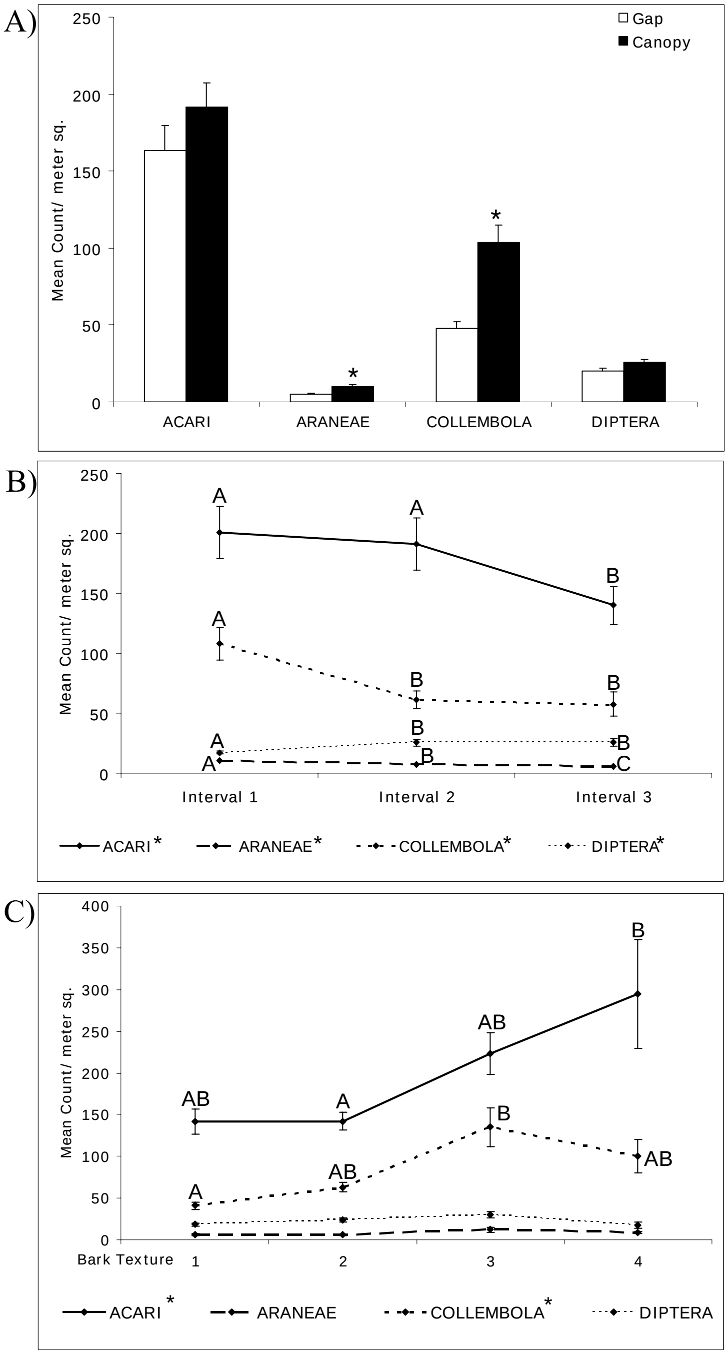

Figure 1.5. Mean count of major arthropod orders by canopy condition (A), interval (B), and bark texture (C). Data were analyzed separately for each order using GLM repeated measures, with interval as the repeated measure and canopy condition and bark texture as factors. Stars (*) indicate a main effect significant at the $p<0.01$ level. Different letters within order indicate differences in count among factor levels. Error bars denote +/- 1 standard error around the mean. Significance was considered at the $p<0.05$ level after probabilities were adjusted for multiple comparisons.

Table 1.6. ANOVA table for GLM Repeated measures analysis of the effects of canopy condition (Gap), bark texture, and interval on arthropod orders. GLM's were performed separately for each arthropod order, and interval was the repeated measure. Araneae and Collembola were transformed as noted in the table to achieve constant variance. Effects were considered significant at the p<0.01 level.

			ACARI			$(\text{ARANEAE}+1)^{-1}$			ln(COLLEMBOLA+1)		
Source of Variation		df	MS	F	P	MS	F	P	MS	F	P
Between Subjects	Gap	1	13568.48	3.48	0.07	0.74	6.60	0.01	30.66	24.21	0.00
	Bark Texture	3	17836.72	4.58	0.01	0.11	0.99	0.40	8.14	6.43	0.00
	Bark Texture*Gap	3	4863.08	1.25	0.30	0.18	1.64	0.19	3.34	2.64	0.06
	Error	72	3898.76			0.11			1.27		
Within Subjects	Interval	2	5720.77	7.13	0.00	1.17	15.65	0.00	8.08	17.56	0.00
	Interval*Gap	2	513.04	0.64	0.53	0.17	2.33	0.10	0.09	0.20	0.82
	Interval*Bark Texture	6	1269.20	1.58	0.16	0.05	0.64	0.70	0.27	0.58	0.74
	Interval*Bark Texture*Gap	6	823.81	1.03	0.41	0.03	0.34	0.92	0.17	0.37	0.90
	Error	144	802.46			0.08			0.46		

			DIPTERA			HYMENOPTERA			PSOCOPTERA		
Source of Variation		df	MS	F	P	MS	F	P	MS	F	P
Between Subjects	Gap	1	162.55	2.91	0.09	15.26	3.51	0.07	11.60	1.09	0.30
	Bark Texture	3	64.24	1.15	0.34	8.55	1.97	0.13	29.66	2.80	0.05
	Bark Texture*Gap	3	89.32	1.60	0.20	14.75	3.39	0.02	9.35	0.88	0.46
	Error	72	55.95			4.35			10.60		
Within Subjects	Interval	2	128.05	6.78	0.00	1.85	0.71	0.50	7.88	1.44	0.24
	Interval*Gap	2	60.01	3.18	0.05	0.63	0.24	0.79	4.75	0.87	0.42
	Interval*Bark Texture	6	9.19	0.49	0.82	3.12	1.19	0.32	5.04	0.92	0.48
	Interval*Bark Texture*Gap	6	19.70	1.04	0.40	1.29	0.49	0.82	3.78	0.69	0.66
	Error	144	18.89			2.63			5.48		

were less strongly positively associated with the first canonical correlation. Additionally, Collembola, Acari, Araneae, and Hymenoptera arthropods were negatively associated with crustose lichen.

The second canonical correlation described a positive relationship between Diptera and small foliose, large foliose, and fruticose epiphytes (Figure 1.6B). Acari was less strongly associated with this epiphyte community. As in the first canonical correlation, crustose lichen also appeared to be negatively associated with Diptera.

DISCUSSION

Epiphytes

We found that the epiphyte community was clearly influenced by height on the tree bole. The patterns we found were similar to those found by others (Hale 1952, Pike et al. 1975, McCune and Antos 1982, McCune 1993, McCune et al. 1997, Liu et al. 2000, Coxson and Coyle 2003), where bryophyte and cyanolichen dominated at the base of the tree (0-2 m). Small foliose and crustose lichens dominated the stem of the tree (2-6 m), and large foliose and fruticose lichens dominated the subcanopy community (4-7 m). We expected that the epiphyte community at lower heights would be most affected by gap harvesting. While cyanolichen did not appear to be affected by gap harvesting, bryophyte abundance was less abundant on trees in harvest gaps. This reduction in bryophyte abundance may adversely affect arboreal arthropods, and is discussed below.

Characteristics of the tree such as bark texture and stem diameter appeared to influence the epiphyte community. As bark texture increased in thickness and flakiness, the abundance of cyanolichen increased. It is possible that cyanolichen prefer certain

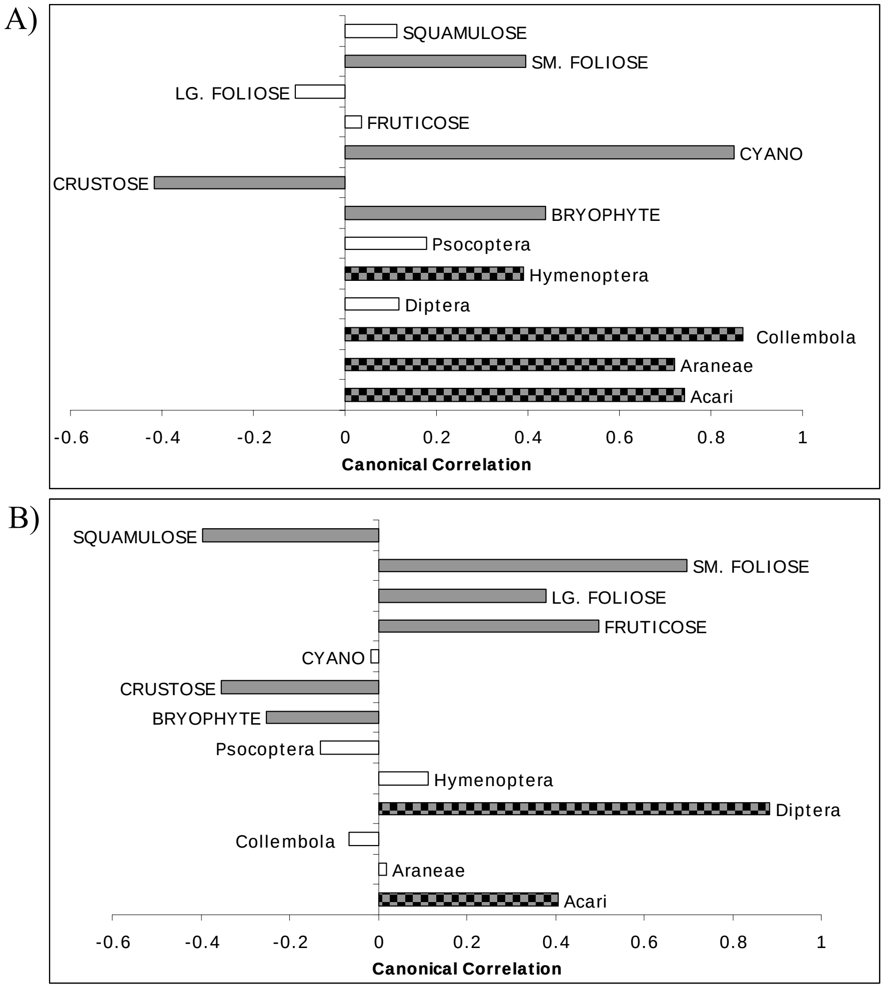

Figure 1.6. Figures represent rotated canonical correlation results between arthropod orders and epiphyte guilds for significant canonical correlations (Bartlett p-values <0.0001). Dependent variable set contained the six major arthropod orders listed in Table 1.1, and have checkered bars. Independent variable set contained all the epiphyte guilds listed in Table 1.4., and have solid bars. Bars represent the rotated canonical loadings for each variable, and are filled if loading is greater than 0.3. Graph A) contains the first canonical correlation results. Graph B) contains the second canonical correlation results.

bark characteristics. However, bark texture changes with age and size of the tree, such that most trees with bark texture values 3 and 4 have been around longer than those with textures of 1 and 2. Given that much of the research into the sensitivity of cyanolichen to forest management has determined dispersal limitations to be a major limiting factor for these lichens (Esseen and Renhorn 1998, Hazell and Gustafsson 1999, Sillett et al. 2000, Hilmo and Sastad 2001), and since gap harvesting did not appear to affect cyanolichen abundance, it may be that bark texture is a consequence of age. As suggested by Neitlich and McCune (1997), it is possible that gap harvesting is beneficial to cyanolichens by increasing structural complexity in managed forests that tend to be even-aged. In this management regime, it appears that choosing large trees, with thicker, flakier bark as reserve trees may be important for maintaining the cyanolichen community.

It should be noted here that only a single bark texture value was assigned to each sample tree, rather than to each height interval. Since bark texture tended to get smoother with increasing height on the bole, we could have been able to examine the relationship between bark texture and height in greater detail. For example, small foliose lichen were associated with smoother bark, and also with higher intervals. Had bark texture been measured at each height interval, there would likely have been an interaction between bark texture and height where small foliose lichen abundance was greatest at higher intervals with smoother bark.

Comparisons between red maple and hemlock suggested that hemlock tends to contain a sparser epiphyte community than red maple. Cyanolichens were also absent on hemlock. Further investigations into how the epiphyte community changes with tree species could help direct forest managers as to which tree species may be the best reserve trees for maintaining the epiphyte community.

Arthropods

The effect of harvest gaps was detected for both total arthropod counts and order-level analyses. Araneae and Collembola had significantly lower counts on gap trees (Figure 1.5A). However, this trend can be seen across the four most abundant orders, and so the overall trend is not driven by only one taxon. Given that Collembola and Araneae were also highly correlated ($r=0.691$, $p<0.0001$), gap effects on Araneae (spiders) may be the direct result of gap effects on Collembola, a potential prey item. The second phase of this research investigated this relationship further (see Chapter 2).

The six major orders collected on hemlock trees were proportionally similar to that found on red maple. However, hemlock contained fewer arthropods per square meter. This may be the result of a more developed epiphyte community on red maple, though more extensive sampling is necessary to make any strong conclusions.

Acari, Araneae, and Collembola were more abundant at lower heights. In contrast, Diptera tended to increase with height. These results suggest that at least two arthropod groupings occurred trees. The first group, including Acari, Araneae, and Collembola, has been described similarly by other comparable studies (Stubbs 1987 and 1989, Pettersson et al. 1995). On the other hand, Diptera were the third most abundant order in this study, but exhibited only a minor presence in other studies. This is the first time Diptera have been documented as comprising a considerable proportion of the arboreal arthropod community. The second phase of this research included a family-level analysis of Diptera to provide further insight into this community (see Chapter 2).

Epiphyte/Arthropod Associations

Although gap harvesting did not alter lichen epiphyte assemblages substantially, it did have a negative influence on bryophyte abundance. This change in the epiphyte community is potentially important, as arthropod taxa shown to be negatively affected by gap harvesting were also associated with bryophyte abundance. It is possible that Collembola and Araneae are sensitive to forest management due, in part, to their association with epiphytic bryophytes. A strong correlation between Collembola and Araneae also suggested a trophic interaction that may be influenced by gap harvesting, such that a decline in Araneae may be a result of depletion of prey (Collembola), that in turn were a result of bryophyte decline.

These findings also provide insight into insectivorous bird response to gap harvesting. For example, brown creepers (*Certhia americana*) may be affected by a change in arthropod community after harvest. This species is associated with interior forest (Austen et al. 2001), forages mostly on the lower bole of trees (Weikel and Hayes 1999), and has been positively correlated with abundance of arboreal spiders (Mariani and Manuwal 1990). Thus, food availability may be a factor in brown creeper response to gap harvesting. The potential relationships between bryophyte abundance, arthropods, and gap harvesting were investigated further in the next phase of this research (see Chapter 2).

Given the sampled length of the tree bole, gap harvesting appeared to have the greatest effect on the arboreal community at the base of the tree (0-2 m). It is probable that microclimate changes were most extreme on this community post-harvest, as it is more adapted to shadier and more humid conditions than the sub canopy community. It may be possible to reduce the negative impacts of gap harvesting by leaving groups of trees, or in the case of this forest by maintaining a dense buffer of regenerating conifers around the residual tree to help protect the basal arboreal community from microclimate changes. It is worth noting that the nature of this harvesting regime, which retains patches of undisturbed forest, will likely maintain the integrity of the arthropod and epiphyte communities at the stand level.

CHAPTER 2

ARBOREAL ARTHROPOD ASSOCIATIONS WITH EPIPHYTES FOLLOWING GAP HARVESTING IN THE ACADIAN FOREST OF MAINE

ABSTRACT

Arthropod and epiphyte assemblages were compared at three heights (0-2, 2-4, and 4-6 m) on the boles of red maple (*Acer rubrum*) trees located in closed canopy forest and within harvest gaps. A positive correlation between bryophytes, Collembola, and Araneae suggested that there was a trophic interaction where arboreal spiders, during early developmental stages, were dependent upon availability of Collembola prey. This relationship appeared to be sensitive to a decline in bryophyte abundance that occurred following gap harvesting. Fifteen Diptera families were identified, eight of which were common. The eight common families utilized the arboreal habitat differently depending on height along the bole and abundance of crustose and other lichen. A potential association was identified between Diptera and a Collembola morphospecies in the family Entomobryidae. These findings suggest a diverse arthropod community that exploits different attributes of the arboreal habitat and exhibits varied responses to harvest gaps.

INTRODUCTION

Invertebrates dominate the planet in terms of species, representing over 90% of the estimated 10 million-plus species on earth (Wilson 1987). Invertebrates play essential roles in forest ecosystems as herbivores, predators, parasites, pollinators, and detritivores, to name a few (Kellert 1993). However, little is still known about forest invertebrates in terms of their life histories and their sensitivity to forest management. Arboreal arthropods in temperate forests are a prime example of taxa where more monitoring and research are needed.

It has been proposed by several researchers that a number of arboreal arthropods are associated with epiphytes, though the details of these relationships are poorly understood (Broadhead 1958, Gerson and Seaward 1977, Stubbs 1987 and 1989, Pettersson et al. 1995). This epiphyte-associated arthropod fauna may play an important role in arboreal food chains containing birds (Norberg 1978, Pettersson et al. 1995), litter decomposition and nitrogen dynamics on the forest floor (Blair and Crossley 1988, Chen and Wise 1997), and in the regulation of arthropod pest populations (Reichert 1974, Reichert and Bishop 1990).

Response of temperate forest epiphytes to forest management has received considerable attention over the last few decades, demonstrating overwhelmingly that epiphytes are sensitive to forest management (Lesica et al. 1991, McCune 1993, Neitlich 1993, Pettersson et al. 1995, Esseen and Renhorn 1996, Pipp et al. 2001). The effect of epiphyte decline on epiphyte-dependant organisms, however, has been largely overlooked.

Pettersson et al. (1995) were the first to examine how decline of epiphyte abundance in managed forests may affect associated invertebrates. Their study found unmanaged forests to support five times more invertebrates per branch and greater invertebrate diversity than mature, secondary forests. A later study found unmanaged, lichen-rich forests to support higher spider diversity and abundance than lichen-poor, selectively logged forests (Pettersson 1996). Still, little research has focused on describing lichen-associated arthropods below the order level, nor in the context of silvicultural approaches designed to emulate natural disturbances. Consequently, little is known about the life histories of arboreal arthropods, their habitat requirements, and their sensitivity to forest management.

Our previous study focused on gap-harvesting effects, and major gradients in the epiphyte and order-level arthropod community (see Chapter 1). Results from that study identified two important questions that warranted more attention. First, a new assemblage of arthropods comprised of Diptera (flies), which was previously undocumented in an arboreal context was found high in the boles. Second, a potential trophic interaction involving bryophytes, Collembola (springtails), and Araneae (spiders) was detected. This potential interaction also appeared to be influenced by gap harvesting. Therefore, the objectives of this study research were to: (1) further investigate the arboreal food chain involving bryophyte, Collembola, and Araneae interactions, and the possible influence of gap harvesting, and (2) describe the Dipteran assemblages collected in arboreal habitat.

METHODS

Study Site

This study took place in the Penobscot Experimental Forest (PEF) in east-central Maine (44°50'N, 68°35'W). The forest is dominated by northern conifers such as red spruce (*Picea rubens* Sarg.), black spruce (*P. mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and northern white cedar (*Thuja occidentalis* L.). Common hardwoods include red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), gray birch (*B. populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.), and bigtooth aspen (*P. grandidentata* Michx.). The PEF has a complicated history of repeated partial cuttings and insect outbreaks that resulted in multi-cohort stand structures with many species (R. Seymour, unpublished data). The soils consist primarily of poorly to very poorly drained loams and silt loams in flat areas that are arranged between glacial till ridges composed of well-drained or sandy loam (Brissette 1996).

Sampling for this study used two research plots established by the University of Maine's Forest Ecosystem Research Program (FERP). FERP is a long-term study designed to compare two silvicultural systems that emulate the natural disturbance regime of the Acadian forest (Saunders and Wagner 2005). The silvicultural regimes include an expanding-gap harvest system with permanent reserve trees. This study utilized the heavier harvest treatment, which consisted of 20% removal of the canopy with 10% of the basal area permanently reserved within the harvest gap. Research plots are 9.4 ha (plot 1), and 10.1 ha (plot 6). Both research plots sampled contain eight harvest gaps, which average 0.15 ha (SE=0.01). Harvesting occurred in 1995 for research plot 1, and in 1996 for research plot 6.

Experimental Design

During the 2004 field season, five harvest gaps were randomly selected from each research plot. Four red maple (*Acer rubrum*) trees located at the north end (south-exposed) of each harvest gap were randomly selected for sampling. Four additional trees were randomly selected in the adjacent undisturbed (closed canopy) forest 20 to 50 m away from the southern edge of each harvest gap. This placement of trees provided the widest possible range of environmental conditions for trees in the harvest gaps and those under the closed canopy. All sample trees were between 15 and 50 cm diameter at breast height, and able to safely support a climbing ladder. A total of 80 trees were sampled from July 25 to August 20, 2004. All sampling occurred on rain-free days between 9:00 am and 3:00 pm.

Each tree was sampled using 6.7 m (three 2.4 m sections) aluminum climbing ladders. Each section was secured to the bole of the tree using a nylon webbed tie-down strap with 182 kg rated capacity. Personnel wore an arborist saddle that was secured to the ladder using two 45 cm lanyards.

The bole of each sample tree was divided into three, 2 m height intervals: 1) 0-2 m, 2) 2-4 m, and 3) 4-6 m. All sampling for epiphytes and arthropods occurred on the south-exposed surface of the tree bole. Each tree was measured for diameter at breast height (dbh), and assigned a single bark texture value. Bark texture was an index that ranged from 1 to 4, and was determined as follows: 1) smooth bark without fissures, 2) shallow fissures (<5cm thick), 3) deep fissures (>5cm thick), and 4) flaky and easily sloughed off. The location of each sample tree was GPS-located using a Magellan GPS unit.

Data Collection

Epiphytes

Epiphyte cover within the first meter of each height interval was sampled using a 1 m x 0.125 m sample quadrat. The vertical sides (1m) of the quadrat were rigid and made of 1.27 cm pvc pipe. The horizontal sides (12.5 cm) were made of twine, so that the area measured, regardless of tree diameter, was equal for every tree and height interval. In each quadrat the percentage cover of epiphytes was visually estimated. Estimation occurred at the species level for macrolichens, and also quantified crustose lichen, and bryophyte total cover. Lichen nomenclature followed Esslinger (1999).

Arthropods

Arthropods were sampled for the entire 2 m interval, though retained the same 0.125 m width as the lichen sample quadrat. Each 2 m interval was sampled for arthropods using an Echo PV-413 backpack leaf blower with vacuum attachments. The vacuum was modified by adding a 10 m pool-vac hose to the intake so that sampling only required maneuvering the hose about the tree, rather than the entire machine. Additionally, a utility/blower shop-vac nozzle was attached to the end of the pool-vac hose. Samples were collected in knee-high nylon stockings that were located between the nozzle and the pool-vac hose.

During the 2005 field season, pitfall traps were established near 24 of the sample trees from 2004 to compare the soil arthropod community to that collected on the tree. Specifically, one pitfall trap was set on the south side of each sample tree between 1 and 1.5 m from the base. Collection jars within each pitfall trap contained 2-3 ounces of propylene glycol, and remained in the field August 1-10, 2005. Our previous study found only marginal differences between sampling years at the order level (Appendix C). Therefore, we compared the 2005 pitfall trap results to 2004 arboreal arthropod results to examine whether there was any correlation between the soil and arboreal taxa. Because of time constraints, only arthropods that were collected both in arboreal habitat and pitfall traps were considered in this study.

Arthropod samples were placed in a cooler with ice in the field, and later transferred to a freezer kept at -17 °C. Arthropods were later sorted in the lab from debris to arthropod order, and placed in 70% ethanol for long term storage. Collembola and Diptera were identified to family following Triplehorn and Johnson (2004). Morphospecies within family were also identified for Collembola. Morphospecies are non-taxonomical groupings based on similar morphology to provide a rough estimate of species diversity within a family. Araneae were sorted as immature or adult. Individuals lacking well-developed spinnerets and/or the presence of reproductive organs were classified as immature and were not identified to family. Adults were identified to species, however species counts were too sparse to include in analyses.

Analytical Approach

All data were analyzed using generalized linear models in SAS, with arthropod count as the response variable (SAS 2000). Explanatory variables included epiphyte percent cover, height interval (0-2 m, 2-4 m, or 4-6 m), canopy condition (gap or closed canopy), bark texture (class 1 to 4), dbh, and family/morphospecies. Negative binomial distribution and log link were used to obtain maximum likelihood estimates for the model. Models were accepted only if the algorithm converged, and the goodness of fit p-value was non-significant at the $p<0.10$ level. Only significant variables were included in the models at the $p<0.05$ level. In addition to analyzing parameter estimates and their corresponding chi-square p-value for significance, contrasts were used for all pairwise comparisons within a factor, or interaction. Contrasts were used to check the parameter estimate results, and were Bonferroni adjusted at the family-wise $\alpha=0.05$ level.

Three models were developed: one evaluating Collembola morphospecies and two addressing questions about Diptera families (Table 2.1). The aims of these models were to evaluate relationships between epiphytes and arthropods, and to detect bark texture, height, and gap effects. A number of families/morphospecies were excluded from the analysis because of too few counts.

RESULTS

Collembola Morphospecies

Six families were identified in the order Collembola (Table 2.1). Two sets of morphospecies were established, with three morphospecies in family Entomobryidae, and two morphospecies in Isotomidae (Table 2.1). The model converged and the goodness of fit p-value was 0.287. Significant epiphyte predictors in the model were percent cover of bryophytes, *Lobaria quercizans* (LOBQUE), *Parmelia squarrosa* (PARSQU), and *Usnea subfloridana* (USNSUB). Additional variables were count of immature Araneae (ARAIMM), height interval, canopy condition, dbh, and bark texture (Table 2.2). The morphospecies ENTTIG, ENTYP, and ISOTOGR were significantly greater ($p<0.01$) on trees located in closed canopy, however this trend was apparent for all Collembola morphospecies (Figure 2.1A). While ENTYP and ONYCHI were evenly

Table 2.1. List of all Collembola and Diptera families collected on red maple (*Acer rubrum*) trees 0-6 m on the south-facing bole. The mean count with ± 1 standard error (SE), percent frequency (# occurrances/ 240*100%) and figure labels are presented for each family/morphospecies included in a model. A star (*) denotes families or morphospecies that were not included in any models because of too few counts. A dagger (†) denotes a family that produced a poor fitting model.

ORDER	MODEL	FAMILY	MEAN COUNT/m^2 (SE)	% FREQUENCY	LABEL
COLLEMBOLA	*Coll. Model*	Entomobryidae 1	4.117 (0.593)	55.00	ENTOMO
		Entomobryidae 2	2.379 (0.434)	38.33	ENTTIG
		Entomobryidae 3	8.817 (0.565)	93.33	ENTYP
		Isotomidae 1	0.692 (0.227)	9.58	ISOTOGR
		Isotomidae 2	1.104 (0.223)	27.08	ISOTOM
		Onychiuridae	0.512 (0.171)	14.58	ONYCHI
	*Other**	Hypogastruidae	0.038 (0.015)	2.92	
		Sminthuridae	0.450 (0.086)	19.17	
		Tomoceridae	0.025 (0.016)	1.25	
DIPTERA	*Model 1*	Ceratopoginidae	0.246 (0.041)	18.33	CERAT
		Chironomidae	0.308 (0.043)	22.50	CHIRON
		Dolichopodidae	0.104 (0.024)	8.33	DOLICHO
		Empididae	0.167 (0.084)	4.17	EMPID
		Psychodidae	0.117 (0.028)	8.75	PSYCH
		Sciaridae	0.150 (0.029)	11.67	SCIARID
	Model 2	Phoridae	0.946 (0.128)	35.00	PHORID
	*Other**	Cecidomyidae†	3.183 (0.232)	80.42	
		Choaboridae	0.021 (0.009)	2.08	
		Culicidae	0.079 (0.018)	7.50	
		Drosophilidae	0.008 (0.006)	0.83	
		Mycetophilidae	0.017 (0.008)	1.67	
		Simulidae	0.113 (0.032)	7.08	
		Syrphidae	0.008 (0.006)	0.83	
		Tabanidae	0.008 (0.006)	0.83	

Table 2.2. Generalized linear models (proc genmod) for predicting mean count of morphospecies (Morph) or family using log link and negative binomial distribution as a function of the epiphyte community and other factors. Only factors significant at the p<0.05 level were included in the model. Type 1 analysis consists of a hierarchical fitting of the model based on order specified. Type 3 analysis is independent of order, and computes likelihood ratios for each term.

			Type 1		Type 3	
Parameter	2*log likelihood	df	Chi-Square	p-value	Chi-Square	p-value
COLLEMBOLA MODEL*						
Intercept	9790.89					
Morph	10065.04	5	274.15	<0.0001	70.98	<0.0001
Interval	10149.49	2	84.45	<0.0001	100.51	<0.0001
Gap	10232.03	1	82.54	<0.0001	89.98	<0.0001
dbh	10272.76	1	40.73	<0.0001	7.32	0.0068
Bark Texture	10335.32	3	62.55	<0.0001	45.94	<0.0001
Morph*Interval	10450.17	10	114.85	<0.0001	136.15	<0.0001
Morph*Gap	10475.50	5	25.33	0.0001	43.91	<0.0001
Morph*dbh	10538.15	5	62.65	<0.0001	33.98	<0.0001
Morph*Bark Texture	10605.13	15	66.98	<0.0001	49.30	<0.0001
Morph**BRYOPHYTE*	10655.28	6	50.15	<0.0001	30.53	<0.0001
Morph**LOBQUE*	10673.45	6	18.17	0.0058	8.78	0.1863
Morph**PARSQU*	10697.47	6	24.02	0.0005	28.68	<0.0001
Morph**USNSUB*	10731.55	6	34.08	<0.0001	35.75	<0.0001
Morph*ARANIMM	10783.09	6	51.54	<0.0001	51.56	<0.0001
DIPTERA MODEL 1**						
Intercept	-1187.13					
Family	-1165.92	5	21.21	0.0007	17.72	0.0033
Gap	-1163.45	1	2.47	0.1157	15.32	<0.0001
Interval	-1157.07	2	6.37	0.0414	8.87	0.0119
Bark Texture	-1140.01	3	17.07	0.0007	15.97	0.0012
Collembola-ENTYP	-1135.34	1	4.67	0.031	6.92	0.0085
Family*Gap	-1083.71	5	51.63	<0.0001	44.40	<0.0001
Family*Interval	-1055.66	10	28.05	0.0018	28.08	0.0018
Family**CRUSTOSE*	-1036.26	6	19.40	0.0035	19.40	0.0035
DIPTERA MODEL 2***						
Intercept	-235.66					
Gap	-204.29	1	31.37	<0.0001	37.81	<0.0001
Interval	-195.33	2	8.96	0.0113	6.38	0.0411
CRUSTOSE	-190.37	1	4.96	0.0259	4.36	0.0368
"*OTHER*" LICHEN	-181.10	1	9.27	0.0023	9.27	0.0023

* Goodness of fit p-value= 0.287.

** Goodness of fit p-value= 0.553.

*** Goodness of fit p-value= 0.293.

scattered among height intervals, all other morphospecies were most abundant at the 0-2 m height interval (Figure 2.2A). As the roughness and flakiness of the bark texture increased, ENTTIG and ONYCHI increased in abundance (Figure 2.3A). Pitfall traps regularly captured five of six major morphospecies, though they occurred at relatively low numbers in the traps (Table 2.5).

Bryophyte abundance was positively correlated with all morphospecies except for ISOTOGR. ISOTOGR abundance also decreased with increasing abundance of *Lobaria quercizans*, and *Parmelia squarrosa*, and increased with the abundance of *Usnea subfloridana* (Table 2.3). ENTOMO abundance was negatively correlated with *Parmelia squarrosa* and *Usnea subfloridana*. Additionally, ENTOMO, ENTIG, ENTYP, and ISOTOM were all positively correlated with immature Araneae (ARAIMM).

Diptera Families

Fifteen families within the order Diptera were identified, eight of which were common (Table 2.1). The models converged and the goodness of fit chi-square p-value was 0.553 for Diptera Model 1, and 0.292 for Diptera Model 2. Six families were modeled in Diptera Model 1, including Ceratopogonidae, Chironomidae, Dolichopodidae, Empididae, Psychodidae, and Sciaridae (Table 2.1). Significant predictors ($P<0.01$) in this model included crustose lichen cover, canopy condition (gap v. closed canopy), height interval, bark texture, and count of the Collembola morphospecies ENTYP (Table 2.2). Other than Chironomidae, few arboreal Dipterans were collected in pitfall traps, providing further evidence that these taxa tended to occur primarily at bole heights above 2 m (Table 2.5).

Table 2.3. Collembola morphospecies relationships with continuous variables based on parameter estimates and chi-square tests from model. Negative binomial distribution with log link were used to fit the data. Parameter estimates were significant at the p<0.01 level. A plus (+) denotes a positive correlation. A minus sign (–) indicates a negative correlation, and zero (0) indicates no relationship.

	Bryophyte	*LOBQUE*	*PARSQU*	*USNSUB*	ARAIMM
ENTOMO	+	0	–	–	+
ENTTIG	+	0	0	0	+
ENTYP	+	0	0	0	+
ISOTOGR	–	–	–	+	0
ISOTOM	+	0	0	0	+
ONYCHI	+	0	0	0	0

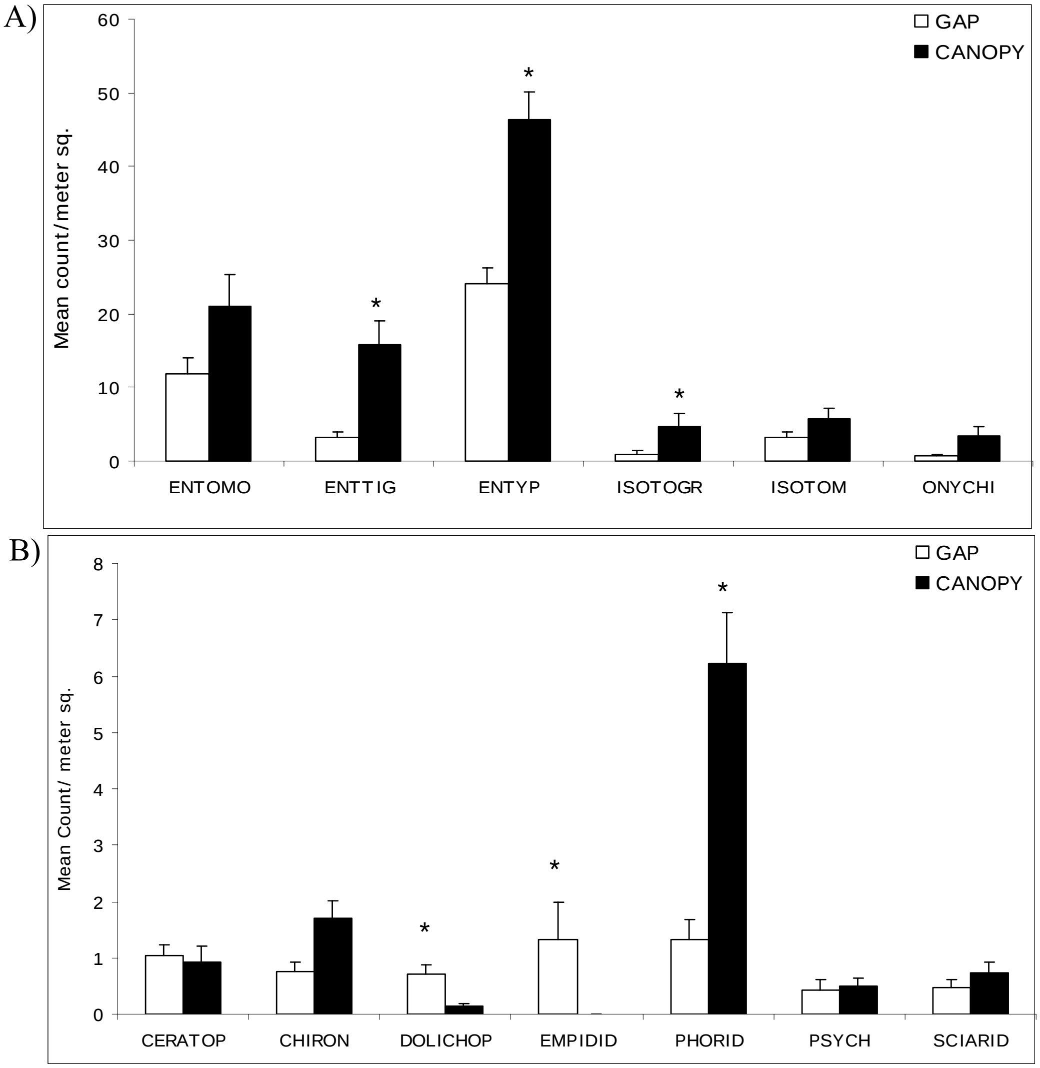

Figure 2.1. Mean count per square m of A) Collembola morpho-species and B) Diptera families by canopy condition. Stars (*) above bars indicate a significant difference between gap and canopy trees at the p<0.05 level within family or morphospecies. Error bars denote +/- 1 standard error around the mean.

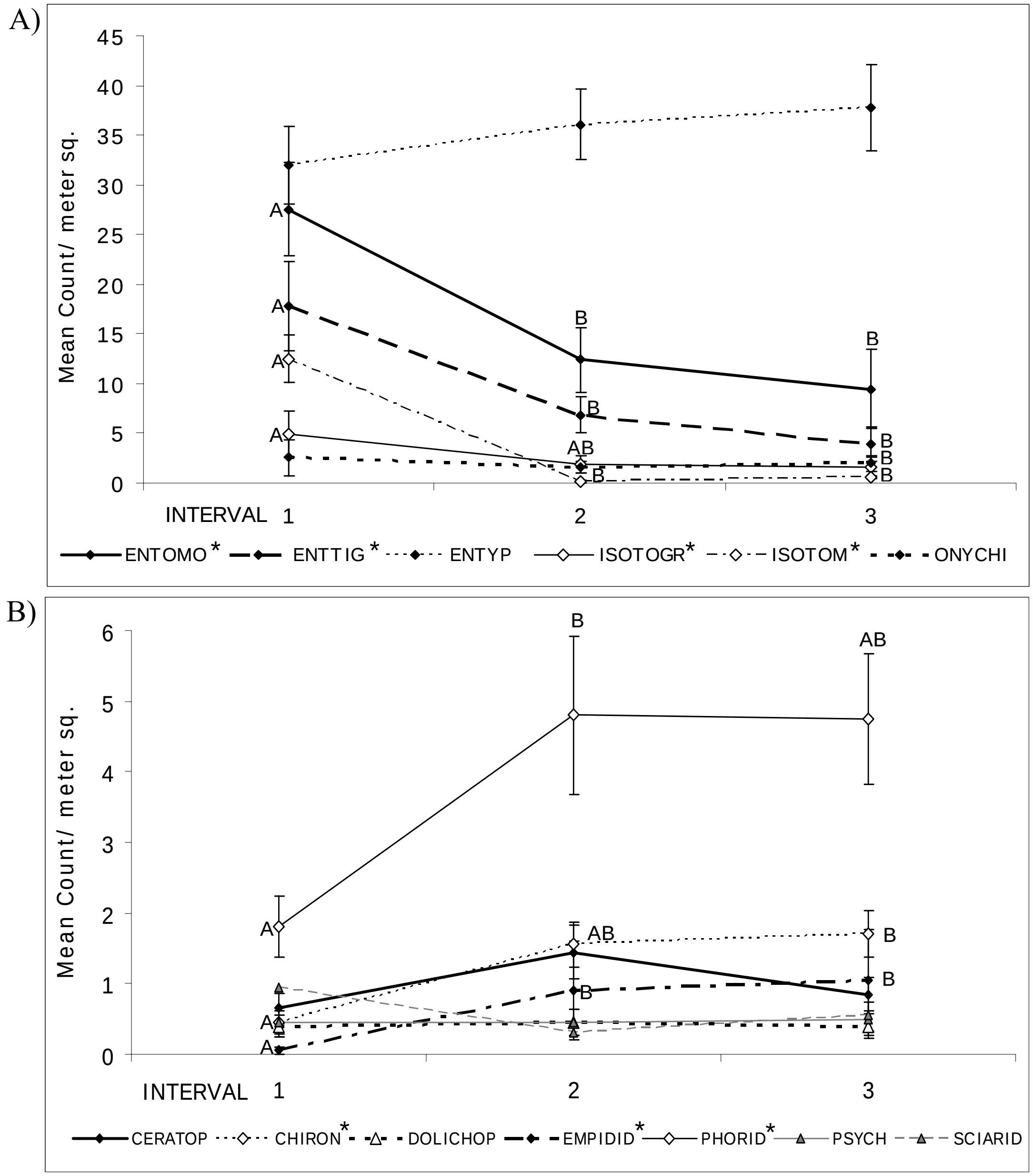

Figure 2.2. Mean count per square m of A) Collembola morpho-species, and B) Diptera families by interval. Stars (*) next to morphospecies indicate a significant difference between intervals at the $p<0.05$ level. Different letters within morphospecies or family indicate differences in mean count among intervals. Error bars denote +/- 1 standard error around the mean. Significance levels were Bonferroni adjusted to maintain a family-wise error of $\alpha=0.05$.

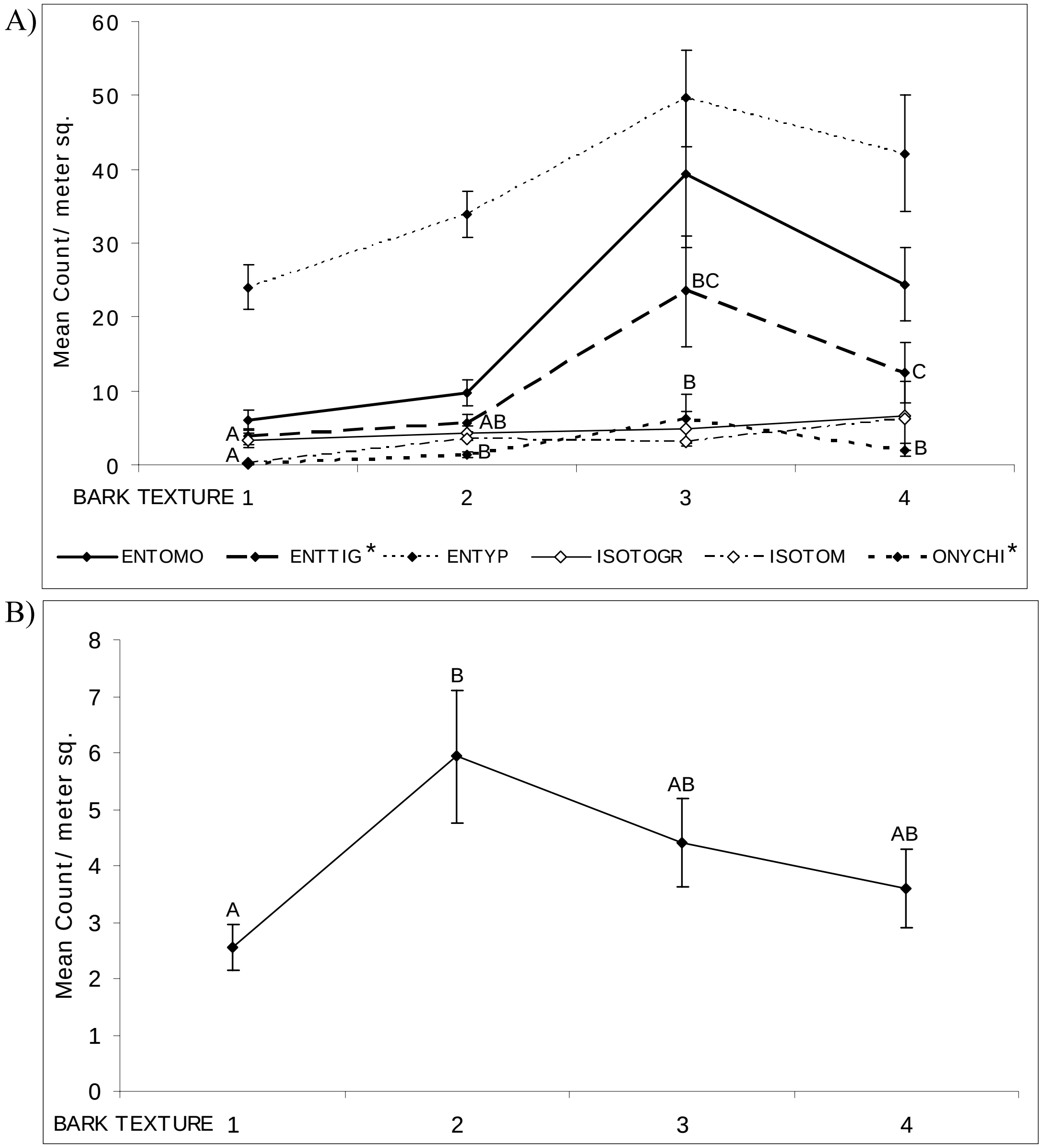

Figure 2.3. Mean count per square m of A) Collembola morpho-species and B) Diptera Model 1 count by bark texture. Stars (*) next to morphospecies indicate a significant difference between bark textures at the $p<0.05$ level. Different letters within morphospecies indicate significant differences in mean count among bark textures. Error bars denote +/- 1 standard error around the mean. Significance levels were Bonferroni adjusted to maintain a family-wise error of $\alpha=0.05$.

Diptera abundance in Model 1 was positively correlated with the Collembola morphospecies ENTYP (estimate= 0.0264; p=0.0078). Empididae abundance decreased with increased cover of crustose lichen, while all other families in Model 1 were positively correlated with crustose lichen cover (Table 2.4). Empididae and Dolichopodidae abundances were greater on trees in harvest gaps (Figure 2.1B). Chironomidae and Empididae abundances increased at taller height intervals (Figure 2.2B). Finally, Diptera count in Model 1 was with bark texture values 2 and greater, indicating preference for bark with shallow to deep fissures (Figure 2.3B).

Table 2.4. Diptera family relationships with continuous variables based on parameter estimates and chi-square tests from models. Negative binomial distribution with log link were used to fit the data. Parameter estimates were significant at the p<0.05 level. Both Crustose and "other" lichen were measured as percent cover. The class "other" lichen contains the percent cover of non-cyano foliose lichen and fruticose lichens. The variable ENTYP contains count of the Collembola morphospecies ENTYP (Family: Entomobryidae). A plus (+) denotes a positive correlation. A minus sign (–) indicates a negative relationship, and zero (0) indicates no significant relationship.

	Crustose	*"Other" lichen*	ENTYP
PHORID	–	+	0
CERAT	+	0	+
CHIRON	+	0	+
DOLICHO	+	0	+
EMPID	–	0	+
PSYCH	+	0	+
SCIARID	+	0	+

Based on Diptera Model 2, Phoridae family abundance was greater (p<0.01) on trees located in a closed canopy (Figure 2.1B) and at the taller height intervals (Figure 2.2B). Phoridae was also positively correlated with the cover of "other" lichens, and negatively correlated with the cover of crustose lichen (Table 2.4). The class "other" lichen refers to all non-cyano, foliose and fruticose (i.e., alectorioid) lichen species.

Table 2.5. Pitfall trap results for the Diptera families and Collembola morphospecies.

Diptera Family			Collembola Morphospecies		
	Mean Count	% Frequency		Mean Count	% Frequency
CERATOP	0.083	8.333	ENTOMO	0.125	12.500
CHIRON	0.458	33.333	ENTTIG	0.333	20.833
DOLICHOP	0.250	4.167	ENTYP	0.458	20.833
EMPIDID	0.000	0.000	ISOTOGR	0.000	0.000
PHORID	0.000	0.000	ISOTOM	1.333	58.333
PSYCH	0.000	0.000	ONYCHI	7.458	83.333
SCIARID	0.125	4.167			

DISCUSSION

Collembola Morphospecies

Two overall conclusions can be drawn from the Collembola morphospecies analysis. First, Collembola morphospecies appear to use arboreal habitats in widely different ways. While most morphospecies were associated with the lower heights on the bole (0 – 2 m), ENTYP and ONYCHI were uniformly scattered at all bole heights (0 – 6 m). While the abundance of most Collembola morphospecies appeared to be correlated with the dense bryophyte mat at the base of sample trees, ISOTOGR abundance tended to decrease with increasing bryophyte cover. Morphospecies ISOTOGR was more closely associated with the epiphyte *Usnea subfloridana*, a species commonly found at taller height intervals or in more light-exposed habitats. The varied responses of these morphospecies suggest that analyses focusing on Collembola habitat use and potential food sources, especially at the species level, will substantially increase our understanding about the arboreal ecology of this order.

Collembola morphospecies comprised nearly a quarter of the arthropod community between the ground and 6 m in the tree boles. Based on the pitfall trap results from this study, it appears that while the arboreal Collembola taxa can be found in the leaf litter, their substantially greater numbers on the tree bole suggest an arboreal preference. However, before any strong conclusions can be made in this regard, a more thorough field investigation involving more traps and more sample periods should be undertaken. It is possible that a more thorough sampling of the leaf litter, similar to that performed on the tree boles in this study, could have yielded substantially greater diversity and number of Collembola. Examination of diurnal and/or seasonal variation in Collembola assemblages throughout the arboreal habitat also could increase our understanding about this taxa.

A second major conclusion from this analysis is a potential arboreal food chain containing bryophyte, Collembola and Araneae that appeared to be influenced by gap harvesting at all three height intervals. At the base of this food chain are epiphytic bryophytes, which were found in a previous study to be less abundant on trees located near harvest gaps (see Chapter 1). Next, the morphospecies ENTOMO, ENTTIG, ENTYP, and ISOTOM were all positively correlated with bryophyte abundance, and immature Araneae counts. Both ENTTIG and ENTYP were found in lesser numbers on trees within harvest gaps. Numbers of immature Araneae also were reduced on trees in harvest gaps (p=0.033). These results suggest that harvest gaps may negatively influence an arboreal food chain on residual trees such that decline in Araneae may be the result of decreased prey (Collembola) populations, that in turn resulted from a decline in bryophytes. We found no correlation between numbers of Collembola and adult Araneae. Thus, it is likely that Collembola are important sources of prey for arboreal spiders during early stages of development.

There are several accounts of relationships between bryophytes and Collembola, and Collembola and Araneae in the literature, though none were documented in an arboreal context. Collembola are generally considered as opportunistic feeders; common foods include fungi, detritus, and moss (Varga et al. 2002, Chen et al. 1995, Peterson and Luxton 1982). A review of moss-associated arthropods by Gerson (1969) mentioned several studies that documented Collembola feeding on mosses. Another study found two species of Collembola that tend to occur on moss-covered rocks to prefer moss inhabiting fungi (Varga et al. 2002).

Several studies have documented Collembola as a common prey item for ground-dwelling (not web-building) Araneae (Edgar 1969, Lawrence and Wise 2000, Buddle 2002). In fact, Lawrence and Wise (2000) suggested that ground-dwelling spiders may affect decomposition in the forest floor by reducing Collembola densities. Important next steps to understand bryophyte, Collembola, and Araneae dynamics involve determining the amount of movement between the arboreal and forest floor habitats for common Collembola and Araneae species, species-specific examinations of bryophytes, and conducting food preference experiments for Collembola and Araneae.

The influence of harvest gaps on arthropods may in turn affect insectivorous birds through reduction of food availability. For example, brown creepers (*Certhia americana*) may be affected by changes in the arboreal arthropod community because it is commonly associated with interior forest (Austen et al. 2001), forages mostly on the lower bole of trees (Weikel and Hayes 1999), and has been shown to be positively correlated with abundance of arboreal spiders (Mariani and Manuwal 1990). Thus, food availability may be a factor in brown creeper response to gap harvesting.

It is noteworthy that our order-level analyses produced similar conclusions regarding the influence of harvest gaps, height on the tree bole, and the relation among bryophytes, Collembola and Araneae (see Chapter 1). Therefore, these taxa may be good candidates for monitoring changes in forest arthropods, as they are easily identifiable at the order level, and are generally most abundant near the base of the tree; providing easy access for sampling. Collembola and Araneae have been used in several studies to examine the effects of forestry practices on soil and litter arthropod communities (Willett 2001, Trofymow et al. 2003, Parisi et al. 2005). This study suggests that expanding the investigations to include the first two meters of tree boles may provide further insight into forest arthropod response to management.

Diptera Families

The Diptera order is quite diverse, and contains species with a broad range of life history strategies including parasites, nectar feeders, predators, parasitoids, and detritivores, to name a few. The Dipterans collected in this study also represent a diverse array of life history strategies, such as gall makers (Cecidomyiidae), fungivores (Sciaridae), predators (Dolichopodidae and Empididae), and blood-feeders (Ceratopoginidae) (Triplehorn and Johnson 2004). Many of the common families collected in this study have not been documented in an arboreal context, and therefore little is known about their life history characteristics. In this case, order-level analyses are not sufficient because of the diverse life history strategies among Dipterans. In this study, the abundance of some families was positively correlated with the cover of crustose lichen, while other families were negatively correlated with crustose lichen (Table 2.4). Also, the significant positive relationship between Model 1 families and the Collembola morphospecies ENTYP, may suggest some kind of interaction in the arthropod community. The relationship between some Dipterans and ENTYP is possible, as ENTYP was very common and found throughout the arboreal habitat we sampled. A thorough examination of the literature on temperate forest arboreal arthropods yielded few accounts of Diptera utilizing arboreal habitat (Gerson and Seaward 1977, Stubbs 1987 and 1989, Pettersson et al. 1995). Therefore, this study may be one of the first to suggest Diptera use of an arboreal habitat along the bole of the tree, as well as a potential association between some Diptera families, epiphytes and other arthropods.

Given the sheer numbers and diversity of arthropods, it is nearly impossible to monitor every arthropod species (Oliver and Beattie 1996). We are therefore left to examine a subset of all arthropods. As Majer (1997) suggested, using a subset of arthropods to monitor the entire arthropod community should include arthropods associated with different ecological functions. Given the diversity of life histories within the Diptera order, forest management activities are likely to produce a diverse array of responses and sensitivities. Therefore, Dipterans may be good candidates as indicators of forest management impacts on the larger arthropod community.

Future research targeting Diptera families in arboreal habitats would greatly add to our understanding about the arboreal arthropod community. The next steps in this process could involve examining Diptera assemblages along a continuum of harvesting intensities, identifying these taxa to species, and determining the most efficient and effective taxonomic level to investigate.

EPILOGUE

The objectives of this thesis were to (1) investigate how epiphytes and arthropods varied with height on the bole, bark texture, and dbh, (2) examine the influence of harvest gaps on the arboreal community, and (3) explore epiphyte/arthropod associations. I found that epiphytes and arthropods were clearly influenced by height on the bole, bark texture, and canopy condition of the tree. Bryophytes were the only epiphyte significantly reduced by gap harvesting, with a nearly 10 percent reduction in cover. Collembola (springtails) and Araneae (spiders) were the arthropods most affected by gap harvesting.

This research revealed two important and new findings concerning the arboreal community. First, a correlation between bryophyte, Collembola, and Araneae suggested an arboreal food chain that was sensitive to harvest gaps at all three height intervals. Araneae appeared to be dependent on Collembola as a source of prey during early stages of development and Collembola were associated with bryophytes.

The second major finding involved Diptera (flies). Outside of this research, Diptera had been documented only as a minor component of the arboreal arthropod community. The Dipterans collected in this study represented a diverse array of life history strategies, and resulted in a range of responses to harvest gaps, and a varied utilization of arboreal habitat. Therefore, Dipterans may be good candidates as indicators of forest management impacts on the greater arthropod community.

The methods used in this study generally worked well, though a few modifications could improve future research efforts. One important modification involves the height intervals located along the boles of sample trees. In 2004, epiphyte cover was only estimated for the first meter of the height interval, while arthropods were collected along 2 meters of the height interval. The second meter was added for arthropods to ensure that a substantial number of arthropods were collected. After processing the arthropod samples in the lab, I was surprised to find an average of 76 (SE=4.2) arthropods per sample (304 per m^2). In 2005, I only sampled arthropods in the same meter that epiphytes were sampled. Results were comparable, thus validating the 2004 data. Finally, sample trees were assigned only one bark texture. Assigning a bark texture value to every height interval would have allowed a more detailed assessment of epiphyte and arthropod preferences.

Results from this work suggest three important directions for future research. The first involves describing the arboreal community of major tree species in the Acadian forest. This study focused on the arboreal community located on red maple (*Acer rubrum*) because this species generally contains the greatest concentration of epiphyte abundance and diversity than any other tree species. I suspect that leaving red maples as residual trees in harvest gaps may be an important approach to maintaining the epiphyte community. Results from sampling hemlock trees also support this idea, since there was substantially less epiphyte cover and fewer arthropods per m^2 on hemlock trees than maple trees.

A second direction of investigation involves sampling epiphytes and arthropods along a range of forest management intensities, and to get a sense of temporal changes in the community post harvest. An example would be to sample the arboreal community on trees in shelterwood or seed tree cuts, and compare the results with the harvest gap and continuous forest results of this research. Another example would be to monitor changes in the arboreal community by sampling pre harvest, and multiple times post harvest.

Third, species-level analyses of bryophytes, Collembola, Araneae, and Diptera to corroborate whether the family-level trends demonstrated in this study are robust in other conditions. Although there has been a fair amount of research on leaf-litter Collembola and Araneae, additional species-level investigations of the arboreal Collembola and Araneae would elucidate whether the arthropods were exclusive to their arboreal habitat, or whether they move throughout the leaf litter and trees.

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APPENDIX: Table of Contents

APPENDIX A: Epiphyte Community at 6-7 m

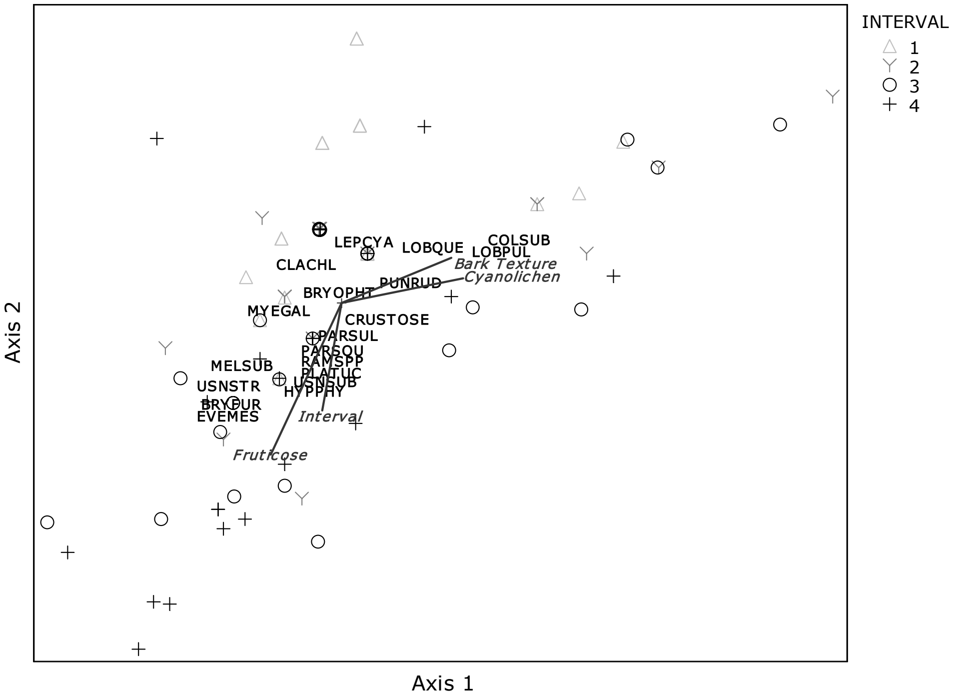

Figure A.1. Ordination scatterplot (NMS) of the 24 resampled trees in 2005, and generated using percent cover values of epiphytes listed in Table 1.1. Epiphyte coding is described in Table 1.1. and are capitalized in the scatterplot. Plots symbols denote vertical intervals such that (△) occurred at interval 1 (sampled 0-1 meters), (Y) at interval 2 (sampled 2-3 meters), (O) at interval 3 (sampled 4-5 meters), and (+) at interval 4 (sampled 6-7 meters). Vectors indicate the direction and strength of correlations between the axes scores and secondary variables. Vector labels are italicized. Both axes contained significant structure (Monte Carlo p-values =0.0196), and accounted for nearly 92% of the variance.

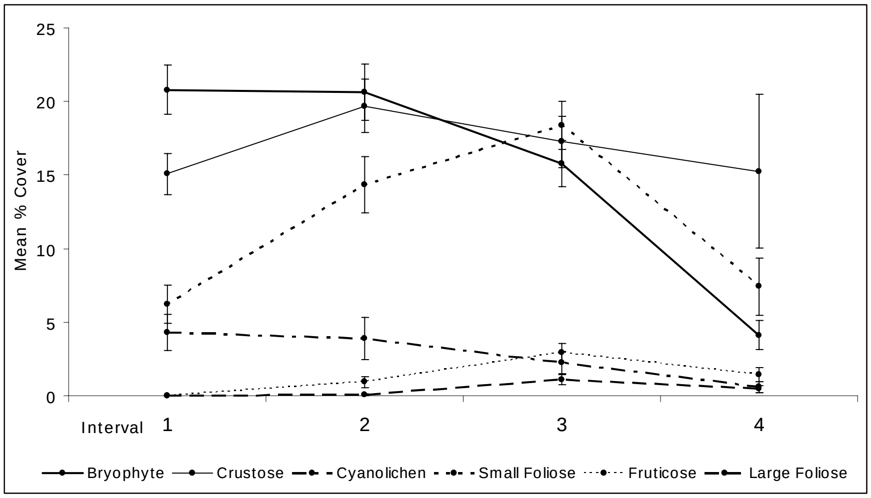

Figure A.2. Mean percent cover of lichen guilds by height interval. Lines on points denote ± 1 standard error around the mean. Means and standard errors were calculated using all trees sampled in 2004 and 2005.

APPENDIX B: Epiphyte Communities on Red Maple and Eastern Hemlock

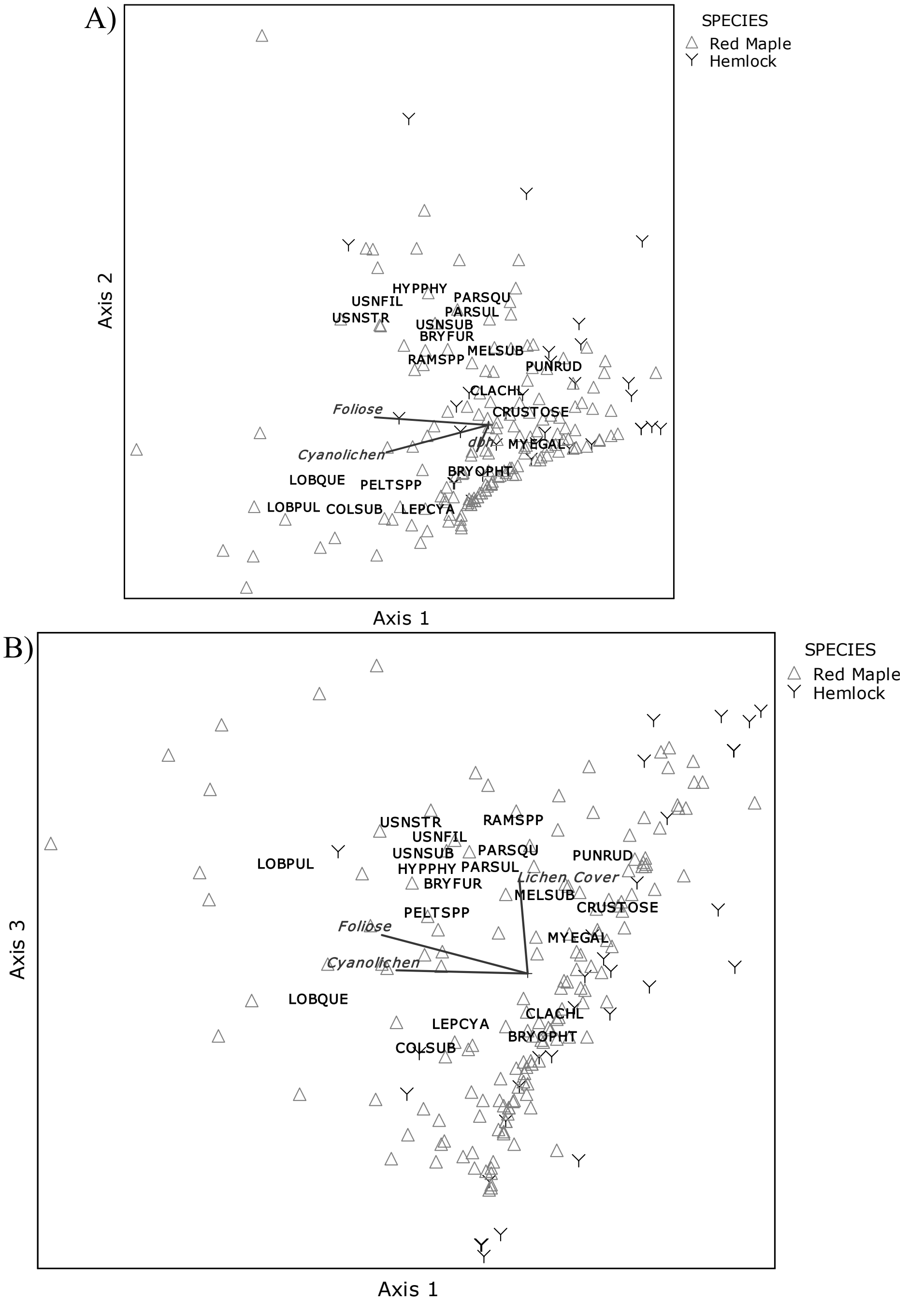

Figure B.1. NMS Ordination scatterplots for A) axis 1 by axis 2, and B) axis 1 by axis 3) of all sample trees (n=96) with two intervals per tree (i.e. 192 "plots") generated using percent cover values of epiphytes listed in Table 1.1. Sample trees include both red maple and Eastern hemlock, and intervals 1 (0-1 m) and 2 (2-3 m). Plots symbols denote sample tree species such that (△) are red maple, (Y) are Eastern hemlock. Vector labels are italicized. All three axes contained significant structure (Monte Carlo p-values =0.0196), and accounted for nearly 88% of the variance.

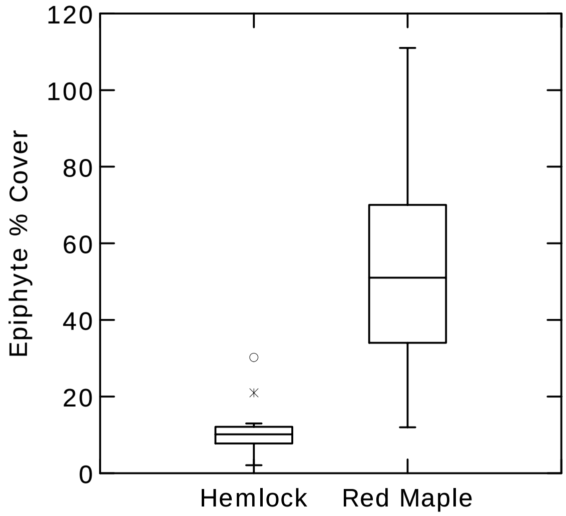

Figure B.2. Box and whisker plot of total epiphyte percent cover for interval 1 by tree species sampled.

APPENDIX C: Arthropod Community at 6-7 m

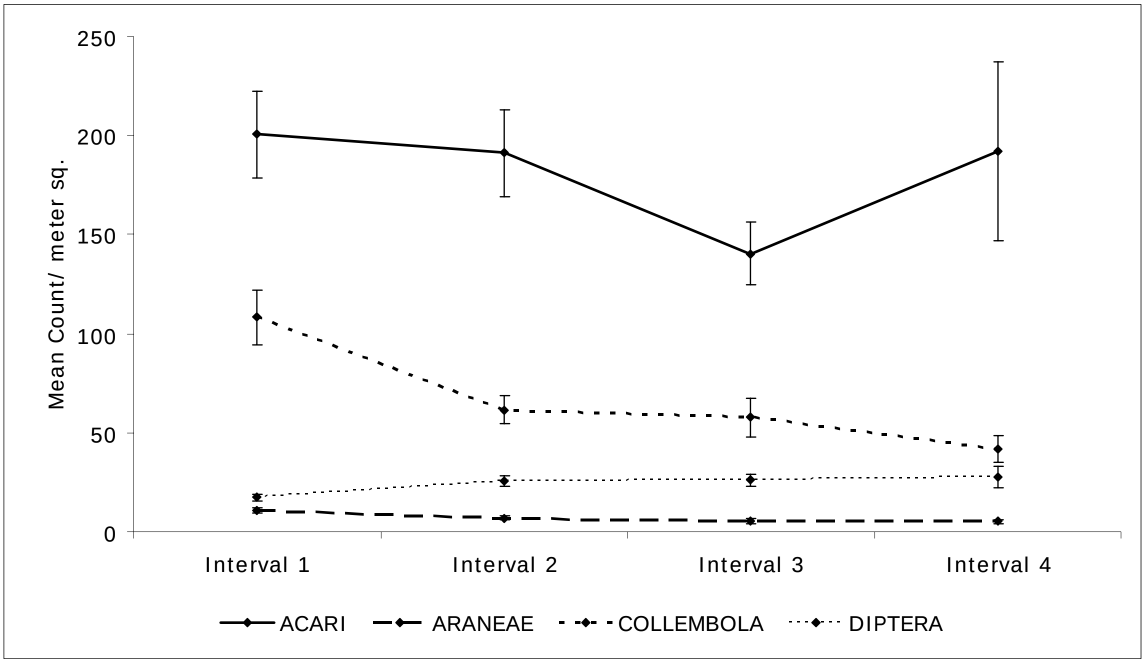

Figure C.1. Mean count per square m of major arthropod orders by height interval. Lines on points denote ± 1 standard error around the mean. Means and standard errors were calculated using all trees sampled in 2004 and 2005.

APPENDIX D. Arthropod Communities and Red Maple and Eastern Hemlock

Table D.1. ANOVA table for GLM analysis of total arthropod count by tree species sampled. Effects were considered significant at the p<0.05 level.

Source	df	Mean-Square	F-ratio	P
SPECIES	1	1.715	5.589	0.023
Error	37	0.307		

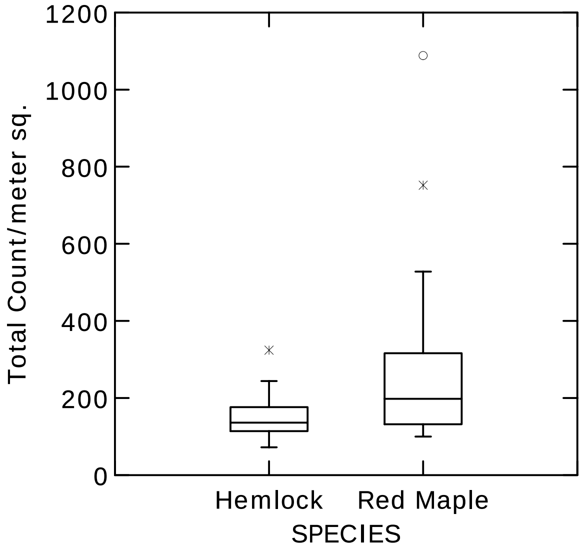

Figure D.1. Box and whisker plot of total arthropod count for interval 1 by tree species sampled.

APPENDIX E: Arthropod Changes by Year

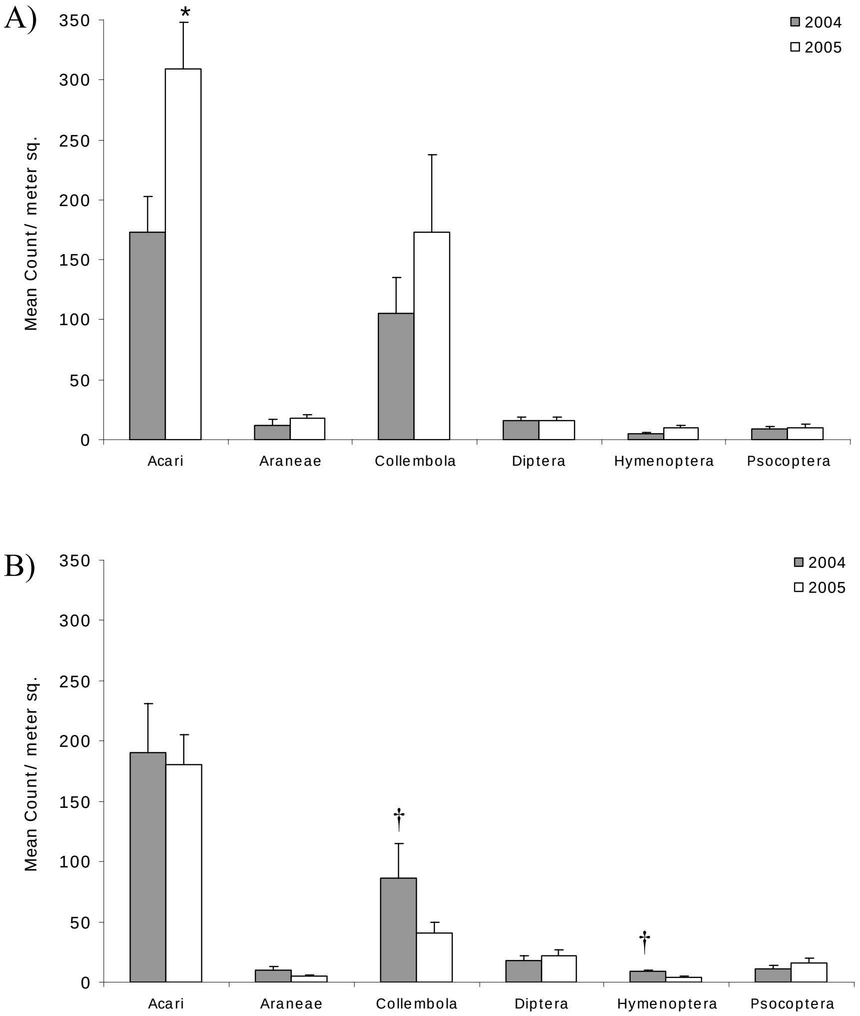

Figure E.1. Mean count of major arthropod orders by sample year and interval where A) is interval 1, and B) is interval 3. Data were analyzed separately for each order and by interval using GLM repeated measures, with sample year as the repeated measure. Stars (*) above bars indicate a significant difference in mean count between sample years at the $p<0.01$ level. Daggers (†) indicate a significant difference at the $p<0.05$ level. Lines above bars denote ± 1 standard error around the mean.

Table E.1. ANOVA table for GLM Repeated measures analysis on arthropod orders. Models were run separately for each arthropod order by interval, and sample year was the repeated measure. Araneae and Collembola were inverse transformed and all other orders were natural log transformed to achieve constant variance. Effects were considered significant at the p<0.01 level.

		ACARI			ARANEAE			COLLEMBOLA		
Source of Variation	df	MS	F	P	MS	F	P	MS	F	P
INTERVAL 1										
YEAR	1	5.50	13.70	0.00	0.34	4.71	0.04	0.07	0.04	0.84
Error	23	0.40			0.07			1.62		
INTERVAL 3										
YEAR	1	0.09	0.43	0.52	0.09	1.20	0.29	3.37	5.06	0.03
Error	23	0.20			0.07			0.67		

		DIPTERA			HYMENOPTERA			PSOCOPTERA		
Source of Variation	df	MS	F	P	MS	F	P	MS	F	P
INTERVAL 1										
YEAR	1	0.00	0.00	0.96	0.12	2.44	0.13	0.06	0.25	0.63
Error	23	0.29			0.05			0.24		
INTERVAL 3										
YEAR	1	0.09	0.25	0.63	0.48	7.02	0.01	0.51	2.16	0.16
Error	23	0.37			0.07			0.23		

BIOGRAPHY OF THE AUTHOR

Kathryn (Kate) Miller was born in Anderson, Indiana, on April 24, 1980. She was raised in Jasper, Indiana, where she graduated from Jasper High School in 1998. Soon after graduating from high school, she moved up to northern Wisconsin where she fell in love with the northwoods. She majored in Natural Resources with a minor in Biology and graduated with honors from Northland College in 2002. Kate has spent the last six years studying the flora and fauna of the northwoods. She has sampled plants in a variety of habitats including northern hardwood forests, pine barrens, Lake Superior and Lake Ontario coastal wetlands, and the Acadian forests of Maine. She has been a member of the Society for Conservation Biology (SCB), Entomological Society of America (ESA), Society of Wetland Scientists, and Natural Areas Association, and has presented her research at several scientific meetings, including ESA and SCB.

Kate is also passionate about science outreach and education, and has taught several Natural Resources courses at Northland College, Introductory Biology (BIO 100 and 200) and General Entomology labs at the University of Maine, and participated in the National Science Foundation Graduate K-12 Teaching Fellowship where she brought hands-on science into public school classrooms throughout central Maine.

Upon completion of her degree, she will be a crew leader for a project funded by the National Park Service and the State University of New York in Syracuse that will begin inventorying and monitoring the vegetation of National Parks throughout New England. Kathryn is a candidate for the Master of Science Degree in Ecology and Environmental Science from the University of Maine in May, 2006.