Arboreal arthropod associations with epiphytes following gap harvesting in the Acadian forest of Maine

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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 a closed canopy forest and within harvest gaps. A positive correlation among bryophytes, Collembola (springtails) and Araneae (spiders) suggested a potential trophic interaction where arboreal spiders, during early developmental stages, were dependent upon availability of Collembolan prey. This relationship appeared to be sensitive to a decline in bryophyte abundance that occurred following gap harvesting. Fifteen families of Diptera (flies) 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 lichens. A potential association was identified between six Dipteran families and a Collembolan morphospecies in the family Entomobryidae, suggesting a diverse arthropod community that exploits different attributes of the arboreal habitat and exhibits varied responses to harvest gaps.

KEYWORDS. Acadian forest, arboreal arthropods, lichens, bryophytes, gap harvesting, Collembola, epiphytes, Maine.

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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, relatively little is known about forest invertebrates in terms of their life histories and sensitivity to forest management.

A number of arboreal arthropods have been shown to be associated with epiphytes, though the details of these relationships are poorly understood (André 1985; Broadhead 1958; Gerson & Seaward 1977; Pettersson et al. 1995; Stubbs 1987, 1989). This epiphyte-associated arthropod fauna may play an important role in arboreal food chains containing birds (Norberg 1978; Pettersson et al. 1995), in litter decomposition and nitrogen dynamics on the forest floor (Blair & Crossley 1988; Chen & Wise 1997), and in the regulation of arthropod pest populations (Riechert 1974; Riechert & 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 (Esseen & Renhorn 1996; Lesica et al. 1991; McCune 1993; Neitlich 1993; Pettersson et al. 1995; Pipp et al. 2001). The effect of epiphyte decline on epiphyte-dependent organisms, however, has not been well documented.

Pettersson et al. (1995) were the first to examine how decline of epiphyte abundance in managed forests may affect associated invertebrates. Their study found that unmanaged forests supported five times more invertebrates per tree branch and greater invertebrate diversity than mature, secondary forests. A later study found that unmanaged, lichen-rich forests supported higher spider diversity and abundance than lichen-poor, selectively logged forests (Pettersson 1996). Little research, however, has focused on describing lichen-associated arthropods below the order level, or 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 or their sensitivity to forest management.

Our previous study focused on the influence of forest gap harvesting and other factors on epiphyte and order-level arthropod communities (Miller et al. 2007). Results from that study identified two important questions that warranted further 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, we detected a strong positive correlation between bryophytes, Collembola (springtails) and Araneae (spiders). The three taxa were all negatively influenced by gap harvesting. The objectives of this study were to: (1) further examine the influence of gap harvesting on Collembola and their associations with epiphtyes and arthropods, especially bryophytes and spiders, using morphospecies analysis within Collembolan families, and (2) describe Dipteran family assemblages collected in an arboreal habitat, and their associations with epiphytes.

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 including red spruce (*Picea rubens*), black spruce (*P. mariana*), balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*) and northern white cedar (*Thuja occidentalis*). Common hardwoods include red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), gray birch (*B. populifolia*), quaking aspen (*Populus tremuloides*) and bigtooth aspen (*P. grandidentata*). 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 loams and sandy loams (Brissette 1996).

Sampling for this study used two research plots established by the University of Maine's Acadian Forest Ecosystem Research Program (AFERP). AFERP is a long-term study designed to compare two silvicultural systems that were designed based on patterns of natural disturbance in the Acadian forest (Saunders & Wagner 2005). The silvicultural systems include expanding gaps of various sizes and rates of harvest with permanent reserve trees. This study used the larger gap treatment, which consisted of 20% removal of the canopy using 0.07 to 0.2 ha harvest gaps with 10% to 30% of the basal area retained within the gap. Research plots are 9.4 ha (plot 1) and 10.1 ha (plot 6) in size. Both research plots sampled each contained eight harvest gaps that averaged

0.15 ha (SE = 0.01). The mean basal area of trees in the closed canopy matrix was 10.4 m²/ha (s = 5.4) for hardwoods, and 23.3 m²/ha (s = 11.2) for softwoods. Mean basal area for retention trees in the harvest gaps was 1.5 m²/ha (s = 0.74) for hardwoods, and 6.8 m²/ha (s = 5.5) for softwoods. The gaps used in plots 1 and 6 were created in 1995 and 1996, respectively.

Experimental design. Five harvest gaps were randomly selected from each research plot (10 gaps total) to sample. Four red maple (*Acer rubrum*) trees were randomly selected on the north side (south-exposed) of each harvest gap (40 trees total). Red maple was selected for study because it was one of the most abundant and evenly distributed hardwood species across the research plots. To compare trees in gaps with those in closed forest conditions, four red maple trees were randomly selected in the adjacent closed canopy forest 20–50 m away from the southern edge of each harvest gap (40 trees total). This placement of trees provided the greatest contrast in exposure between trees in harvest gaps and in the closed canopy. To avoid spatial clustering of trees in gaps, and thus avoid potential concerns about pseudoreplication when using individual trees as experimental units, care was taken to ensure that trees in gaps were well dispersed across the harvest gaps. All sample trees were 15–50 cm diameter at breast height (1.37 m), and able to safely support a climbing ladder. The average dbh was 23.79 cm (SE = 0.84), and did not vary between gap and closed canopy (p = 0.11). A total of 80 trees were sampled on July 25–August 20, 2004. All sampling occurred on rain-free days between 9:00 am and 3:00 pm.

Data collection. 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 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, after Stubbs (1989). This study took place within 20 km of our study site, used comparable methods to examine lichen and arthropod

associations, and found the south side of trees to support greater lichen biomass and abundances of arthropods, than the north-exposed side. Each tree was measured for diameter at breast height (dbh), and assigned a single bark texture value. Bark texture was classified using an index that ranged from 1 to 4, and was determined as follows: 1) smooth without fissures, 2) shallow fissures (<5 cm thick), 3) deep fissures (>5 cm thick) and 4) flaky and easily sloughed off. The location of each sample tree was GPS-located using a Magellan GPS unit.

Epiphytes.—Epiphyte cover within the first meter of each height interval was sampled using a 1 × 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. The percentage cover of epiphytes was visually estimated for each quadrat. 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 with a utility/blower shop-vac nozzle to facilitate sampling up the bole. Samples were collected in knee-high nylon stockings that were placed between the nozzle and the pool-vac hose. The open end of the stocking overlapped the coupling at the end of the pool-vac hose, and the shop-vac nozzle was placed over the coupling. This apparatus allowed for air flow through the stocking to create suction, while the stocking captured the arthropods.

During the 2005 field season, pitfall traps were established near 24 of the sample trees from 2004 to determine if the arthropods collected in arboreal habitat were also found in the soil/leaf litter. One pitfall trap was set on the south side of each sample tree at 1.0–1.5 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 (Miller et al. 2007). Therefore, we compared the 2005 pitfall trap results to 2004 arboreal arthropod results to determine whether arthropods collected from arboreal habitat were exclusively arboreal or whether they also occupied soil/leaf litter habitat. 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 immediately in an ice-filled cooler in the field and later transferred to a freezer kept at $-17°$C. Arthropods were 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 families were also identified for Collembola. Morphospecies are non-taxonomical groupings based on similar morphology to provide a relative estimate of species diversity within a family (Oliver & Beattie 1996). Spiders 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 further. Although adults were identified to species, species counts were too sparse to include in our 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 1–4), 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 $p < 0.05$. Only significant variables were included in the models. 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 parameter estimate results and were Bonferroni adjusted at the family-wise $\alpha = 0.05$ level.

Three models were developed: one evaluating Collembolan morphospecies and two addressing questions about Dipteran families (**Table 1**). The objectives for these models were to evaluate relationships between epiphytes and arthropods, and to detect any possible effects of bark texture, height and harvest gaps. A number of families/ morphospecies were excluded from the analysis because of too few counts, which prevented the model from converging.

RESULTS

Collembola morphospecies. In the order Collembola (springtails), six families were identified (**Table 1**). Two sets of morphospecies were established, with three morphospecies in the family Entomobryidae, and two morphospecies in the Isotomidae (**Table 1**). The model converged and fit the data well (goodness of fit p = 0.287). Significant epiphyte predictors in the model were percent cover of bryophytes, *Lobaria quercizans, Parmelia squarrosa* and *Usnea subfloridana.* Other significant predictors were count of immature spiders, height interval, canopy condition, dbh and bark texture (**Table 2**). Numbers of morphospecies Entomobryidae-2, Entomobryidae-3 and Isotomidae-1 collected were higher (p < 0.01) on trees located in closed canopy; however, this trend was apparent for all Collembolan morphospecies (**Fig. 1A**). While Entomobryidae-3 and Onychiuridae were evenly distributed among height intervals, all other morphospecies were most abundant at the 0–2 m height (**Fig. 2A**). As the roughness and flakiness of the bark texture increased, Entomobryidae-2 and Onychiuridae increased in abundance (**Fig. 3A**). Pitfall traps regularly captured five of the six most common morphospecies found on the trees, though they were collected at relatively low numbers in the traps (**Table 3**).

Bryophyte abundance was positively correlated with numbers of all morphospecies except for Isotomidae-1. Isotomidae-1 abundance also decreased with increasing abundance of *Lobaria quercizans* and *Parmelia squarrosa*, and increased with the abundance of *Usnea subfloridana* (**Table 4**). Entomobryidae-1 abundance was negatively correlated with *Parmelia squarrosa* and *Usnea subfloridana*. Additionally, Entomobryidae-1,

Table 1. List of all Collembola and Diptera families collected on red maple (*Acer rubrum*) trees from 0–6 m high on the south-facing bole. Mean count with ± 1 standard error (SE), percent frequency (# of occurrences/240*100%) and figure labels are presented for each family/morphospecies included in a model. An asterisk (*) 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	ENTO-1
		Entomobryidae 2	2.379 (0.434)	38.33	ENTO-2
		Entomobryidae 3	8.817 (0.565)	93.33	ENTO-3
		Isotomidae 1	0.692 (0.227)	9.58	ISOTO-1
		Isotomidae 2	1.104 (0.223)	27.08	ISOTO-2
		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	

Entomobryidae-3 and Isotomidae-2 were all positively correlated with immature spiders (SPI-IMM).

Diptera families. Fifteen families in the order Diptera (flies) were identified, eight of which were common (**Table 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 1**). Significant predictors ($p < 0.01$) in this model included crustose lichen cover, canopy condition (gap vs. closed canopy), height interval, bark texture and count of the Collembolan morphospecies Entomobryidae-3 (**Table 2**). Other than Chironomidae, few arboreal flies were collected in pitfall traps, providing further evidence that these taxa tended to occur primarily at bole heights above 2 m (**Table 3**).

Dipteran abundance in Model 1 was positively correlated with the Collembolan morphospecies Entomobryidae-3 (estimate = 0.0264; p = 0.0078). Empididae abundance decreased with increased cover of crustose lichens, while all other families in Model 1 were positively correlated with crustose lichen cover (**Table 5**). Empididae and Dolichopodidae abundances were higher on trees in harvest gaps (**Fig. 1B**). Chironomidae and Empididae abundance increased at taller height intervals (**Fig. 2B**). Finally, Dipteran count in Model 1 was associated with bark texture values >2, indicating a preference for bark surfaces with shallow to deep fissures (**Fig. 3B**).

Based on Diptera Model 2, Phoridae family abundance was higher ($p < 0.01$) on trees located in

Table 2. Generalized linear models 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 consisted of a hierarchical fitting of the model based on order specified. Type 3 analysis was independent of order, and computed likelihood ratios for each term.

Parameter	2*log likelihood	df	Type 1		Type 3	
			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*SPI-IMM	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-ENTO-3	−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.

a closed canopy (**Fig. 1B**) and at the taller height intervals (**Fig. 2B**). Phoridae was also positively correlated with the cover of "other" lichens, and negatively correlated with the cover of crustose lichens (**Table 5**). The class "other" lichen refers to all non-cyano, foliose and fruticose (e.g., alectorioid) lichen species.

DISCUSSION

Collembola morphospecies. Two overall conclusions can be drawn from the analysis of Collembolan morphospecies. First, Collembolan morphospecies appear to use arboreal habitats in widely different ways. While most morphospecies were associated with lower heights on the bole (0–
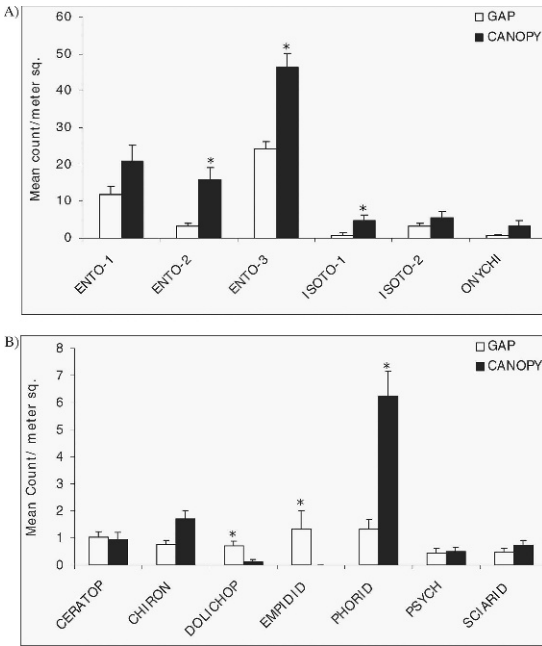
Figure 1. Mean count per m² of **A**) Collembola morphospecies and **B**) Diptera families on the bark of red maple trees in harvest gaps and closed canopy. An asterisk (*) above bars indicates a difference ($p < 0.05$) between gap and canopy trees within family or morphospecies. Error bars denote ± 1 standard error about the mean.

Figure 2. Mean count per m² of **A**) Collembola morphospecies, and **B**) Diptera families at three height intervals (1 = 0–2 m, 2 = 2–4 m and 3 = 4–6 m) on the bole of red maple trees. An asterisk (*) next to morphospecies indicates a difference ($p < 0.05$) among height intervals. Different letters within morphospecies or family indicates a difference in count among height intervals. Error bars denote ± 1 standard error about the mean. Significance levels were Bonferroni adjusted to maintain a family-wise error of $\alpha = 0.05$.

2 m), Entomobryidae-3 and Onychiuridae were uniformly distributed at all bole heights (0–6 m). While the abundance of most Collembolan morphospecies appeared to be correlated with the dense bryophyte mat at the base of sample trees, Isotomidae-1 abundance tended to decrease with increasing bryophyte cover. Morphospecies Isotomidae-1 was more closely associated with the epiphyte *Usnea subfloridana*, a species commonly found higher on the tree where there is greater light-exposure. The varied responses of these morphospecies suggest that analyses focusing on Collembola habitat use and potential food sources, especially at the species level, will likely increase our understanding about the arboreal ecology of this order, and the role of epiphytes in their life histories.

Collembolan 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
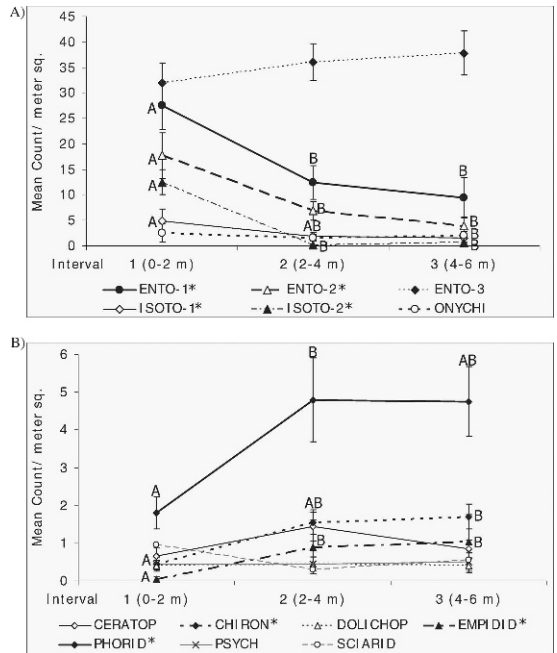
bole suggest an arboreal preference. Before any strong conclusions can be made in this regard, however, a more thorough field investigation involving more traps and more sample periods should be undertaken. It is possible that a more thorough sampling of the leaf litter, similar to that performed on the tree boles in this study, could have yielded substantially greater diversity and number of Collembola. Examination of diurnal and/or seasonal variation in Collembolan assemblages throughout the arboreal habitat also may increase our understanding about this taxon.

A second major conclusion from this analysis is a potential trophic interaction containing bryophytes, Collembola and spiders that appeared to be influenced by gap harvesting. At the base of this food chain are epiphytic bryophytes, which were found in a previous study to be less abundant on trees located in harvest gaps (Miller et al. 2007).
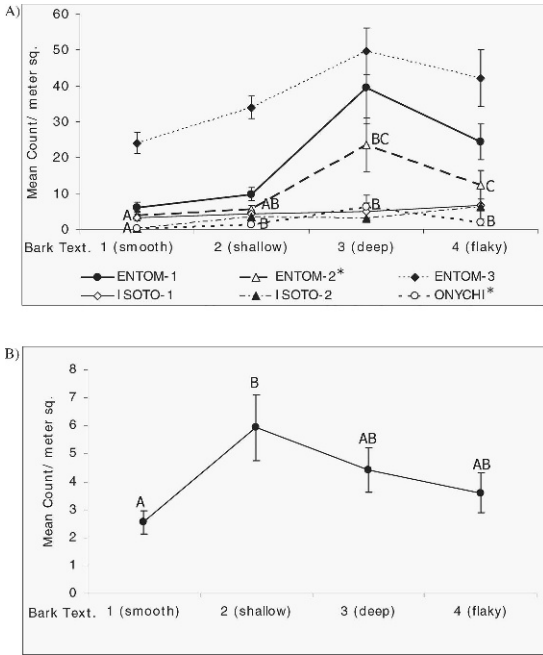
Figure 3. Mean count per m² of **A**) Collembola morphospecies and **B**) Diptera Model 1 count by bark texture index (1 = smooth without fissures, 2 = shallow fissures (<5 cm thick), 3 = deep fissures (>5 cm thick) and 4 = flaky and easily sloughed off). An asterisk (*) next to morphospecies indicates a difference (p < 0.05) among bark texture indices. Different letters within morphospecies indicates a difference in count among bark textures. Error bars denote ± 1 standard error about the mean. Significance levels were Bonferroni adjusted to maintain a family-wise error of α = 0.05.

Next, the morphospecies Entomobryidae-1, Entomobryidae-2, Entomobryidae-3 and Isotomidae-2 were all positively correlated with bryophyte abundance and immature spider counts. Both Entomobryidae-2 and Entomobryidae-3 were found in lesser numbers on trees within harvest gaps. Numbers of immature spiders also were lower on trees in harvest gaps (p = 0.033). These results suggest that harvest gaps may have negatively influenced these taxa on residual trees, such that a decline in spiders may have resulted from reduced prey (Collembola) populations, which in turn resulted from a decline in bryophytes. We found no correlation between numbers of Collembola and adult spiders. 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 spiders in the literature, though none was documented in an arboreal context. Collembola are generally considered opportunistic feeders; common foods include fungi, detritus and mosses (Chen et al. 1995; Peterson & Luxton 1982; Varga et al. 2002). A review of moss-associated arthropods by Gerson (1969) identified several studies that documented Collembola feeding on mosses. Another study found two species of Collembola that 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) spiders (Buddle 2002; Edgar 1969; Lawrence & Wise 2000). In fact, Lawrence and Wise (2000) suggested that ground-dwelling spiders may affect decomposition in the forest floor by reducing Collembolan densities. Important next steps to understand bryophyte, Collembola and spider dynamics involve determining the amount of movement between the arboreal and forest floor habitats for common Collembola and spider species, species-specific examinations of bryophytes, and conducting food preference experiments for Collembola and spiders.

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 & Hayes 1999), and has been shown to be positively correlated with abundance of arboreal spiders (Mariani & Manuwal 1990).

It is noteworthy that our order-level analyses produced similar conclusions regarding the influence of harvest gaps, height on tree bole and relationships among bryophytes, Collembola and spiders (Miller et al. 2007). 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 spiders have been used in several

Table 3. Mean count and frequency of captures from pitfall traps for Collembola morphospecies and Diptera families.

	Mean count	Frequency (%)
Collembola Morphospecies		
Entomobryidae-1	0.125	12.500
Entomobryidae-2	0.333	20.833
Entomobryidae-3	0.458	20.833
Isotomidae-1	0.000	0.000
Isotomidae-2	1.333	58.333
Onychiuridae	7.458	83.333
Diptera Family		
Ceratopoginidae	0.083	8.333
Chironomidae	0.458	33.333
Dolichopodidae	0.250	4.167
Empididae	0.000	0.000
Phoridae	0.000	0.000
Psychodidae	0.000	0.000
Sciaridae	0.125	4.167

studies to examine the effects of forestry practices on soil and litter arthropod communities (Parisi et al. 2005; Trofymow et al. 2003; Willett 2001). Results from this study suggested that expanding the investigations to include the first two meters of tree boles may provide further insight into arthropod responses to forest management.

It is also notable that all but one Collembolan morphospecies were positively correlated with bryophyte abundance, while no morphospecies were positively correlated with *Lobaria quercizans*. An NMS ordination of lichen species and bryophyte percent cover suggested similarities in occurrence with *L. quercizans*, bryophytes and other cyanolichens (Miller 2006). The results of the ordination reinforce our conclusions about an association between Collembola and bryophytes that is sensitive to gap harvesting. Collembola were strongly associated with bryophytes, and not the lichens commonly associated with that community. Additionally, cyanolichens were not found to be influenced by gap harvesting (Miller et al. 2007).

Diptera families. The Diptera order is quite diverse, containing 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 & Johnson 2004). Many of the common families collected in this study have not been documented in an arboreal context; therefore, little is known about their life history characteristics. Thus, 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 lichens, while other families were negatively correlated with crustose lichens (**Table 4**). Also, the significant positive relationship between Model 1 families and the Collembolan morphospecies Entomobryidae-3, may suggest an interaction in the arthropod community. The relationship between some Dipterans and Entomobryidae-3 is possible, as Entomobryidae-3 was very common and found throughout the arboreal habitat we sampled. A thorough examination of the literature on temperate forest

Table 4. Relationship between Collembola morphospecies and continuous predictor 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 p < 0.01. A "+" indicates a positive correlation, "−" indicates a negative relationship and "0" indicates no relationship.

	Bryophyte	*Lobaria quercizans*	*Parmelia squarrosa*	*Usnea subfloridana*	Immature spiders
Entomobryidae-1	+	0	−	−	+
Entomobryidae-2	+	0	0	0	+
Entomobryidae-3	+	0	0	0	+
Isotomidae-1	−	−	−	+	0
Isotomidae-2	+	0	0	0	+
Onychiuridae	+	0	0	0	0

Table 5. Relationship between Diptera family and continuous predictor 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 p < 0.05 level. Both crustose and "other" lichens were measured as percent cover. The class "other" lichen contains the percent cover of non-cyano foliose lichens and fruticose lichens. A "+" indicates a positive correlation, "−" indicates a negative relationship and "0" indicates no relationship.

	Crustose	"Other" lichen	Entomobryidae-3
Phoridae*	−	+	0
Ceratopoginidae	+	0	+
Chironomidae	+	0	+
Dolichopodidae	+	0	+
Empididae	−	0	+
Psychodidae	+	0	+
Sciaridae	+	0	+

* The family Phoridae was analyzed in a separate model from the remaining families.

arboreal arthropods yielded few accounts of Diptera utilizing arboreal habitats (Gerson & Seaward 1977; Pettersson et al. 1995; Stubbs 1987, 1989). Therefore, this study may be one of the first to identify Diptera use of an arboreal habitat along the bole of the tree, as well as a potential association between some Dipteran families, epiphytes and other arthropods.

Given the tremendous numbers and diversity of arthropods, it is nearly impossible to monitor every arthropod species (Oliver & 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 Dipteran families in arboreal habitats could add greatly to our understanding about the arboreal arthropod community. The next steps in this process should involve examining Dipteran assemblages along a continuum of harvesting intensities, identifying

these taxa to species, examining Dipteran species interactions with epiphytes, and determining the most efficient and effective taxonomic level to investigate.

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