

# Effect of gap harvesting on epiphytes and bark-dwelling arthropods in the Acadian forest of central Maine

Kathryn M. Miller, Robert G. Wagner, and Stephen A. Woods

**Abstract:** Using a long-term silvicultural experiment, we (i) investigated how epiphyte and arthropod communities were affected by height on the stem, bark texture, and stem diameter of red maple (*Acer rubrum* L.) trees, (ii) examined how harvest gaps influenced epiphyte and arthropod communities on red maple boles, and (iii) explored whether these effects influenced the relationship between the epiphyte and arthropod communities. Arthropod and epiphyte assemblages dwelling on the bark of red maple trees located in undisturbed forest and harvest gaps varied with height. Bryophytes, *Cladonia* spp., and cyanolichens were most abundant near the base of the tree, while noncyano, foliose lichens and fruticose lichens were most abundant 4–6 m above the ground. Acari, Araneae, and Collembola were most abundant near the base of the tree, while Diptera were most abundant above 2 m. A previously undocumented assemblage of dipterans (flies), primarily in the suborder Nematocera, was found. Gap harvesting reduced the abundance of bryophytes, Collembola (springtails), Araneae (spiders), and total arthropods on the bark of red maple. Canonical correlation analysis revealed a positive association between bryophytes, Collembola, and Araneae. A strong correlation between Collembola and Araneae suggested a possible trophic interaction that may be affected by gap harvesting through a reduction in bryophyte abundance.

**Résumé :** Nous avons utilisé une expérience sylvicole à long terme pour (i) étudier comment les communautés d'épiphytes et d'arthropodes sont affectées par la hauteur sur le tronc, la texture de l'écorce et le diamètre du tronc de l'érable rouge (*Acer rubrum* L.), (ii) examiner comment les trouées créées par les coupes influencent les communautés d'épiphytes et d'arthropodes sur le tronc des érables rouges et (iii) explorer si ces effets influencent la relation entre les communautés d'épiphytes et d'arthropodes. Les assemblages d'arthropodes et d'épiphytes qui vivent sur l'écorce du tronc des érables rouges situés dans la forêt non perturbée et les trouées créées par la coupe varient selon la hauteur. Les bryophytes, *Cladonia* spp. et les cyanolichens étaient surtout abondants près de la base des arbres tandis que les lichens foliacés et fruticuleux, qui n'appartiennent pas au groupe des cyanolichens, étaient plus abondants 4-6 m au-dessus du sol. Les acariens, les aranéides et les collembolés étaient plus abondants près de la base des arbres tandis que les diptères étaient surtout abondants au-dessus de 2 m. Un assemblage non encore rapporté de diptères (mouches), principalement dans le sous-ordre Nematocera, a été observé. La coupe par trouées a réduit l'abondance des bryophytes, des collembolés, des aranéides (araignées) et la quantité totale d'arthropodes sur l'écorce de l'érable rouge. L'analyse de corrélation canonique a révélé qu'il y avait une association positive entre les bryophytes, les collembolés et les aranéides. Une forte corrélation entre les collembolés et les aranéides indique qu'il existe possiblement une interaction trophique qui pourrait être affectée par la coupe par trouées à cause d'une réduction de l'abondance des bryophytes.

[Traduit par la Rédaction]

## Introduction

Managing forests in a sustainable manner requires a comprehensive understanding of how forestry practices influence forest ecosystems. Current knowledge in this regard is far from complete and is especially deficient for organisms lacking in charisma or economic value. Arboreal arthropods and epiphytes in temperate forests are prime examples of taxa where additional monitoring and research are needed. Relatively little research has been devoted to arboreal communities, owing in part to the difficulties of sampling them (Barker and Sutton 1997; Schowalter and Ganio 1998).

Lichen epiphytes have been shown to influence nutrient cycling (Knops et al. 1996), to contribute to the annual nitrogen budget of a forest (Becker 1980), to provide nest material and food for vertebrates (Hayward and Rosentreter 1994), and to have an associated unique arthropod fauna (Gerson and Seaward 1977; Stubbs 1989). This lichen-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 and Crossley 1988; Chen and Wise 1997), and in the regulation of arthropod pest populations (Riechert 1974; Riechert and Bishop 1990). Little research,

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however, has focused on the sensitivity of lichen-associated arthropods to specific forestry practices (Pettersson et al. 1995). Epiphytic bryophytes and their associated arthropods have received even less attention.

The sensitivity of epiphytic lichens to timber harvesting has resulted in a marked loss of lichen biomass and diversity in managed and secondary forests (Lesica et al. 1991; 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). The factors generally considered to cause lichen decline following harvesting include poor dispersal ability (Hazell and Gustafsson 1999; Sillett et al. 2000), restricted microclimate requirements (Gauslaa and Solhaug 1996), and lack of colonizable substrates (Esseen et al. 1996). Bryophytes have also been shown to be sensitive to forest management (Ross-Davis and Frego 2002; Fenton et al. 2003). Frisvoll and Presto (1997) found changes in availability of suitable substrate and humid microclimate as a result of forest management to negatively affect bryophyte diversity on the forest floor.

Research on the sensitivity of nonpest arthropod communities to forest management has received some attention over the last few decades (Schowalter and Ganio 1998; Peck and Niwa 2005); however, little work has examined lichen-associated arthropod responses to forest management (Pettersson et al. 1995). Schowalter (1995) found old-growth canopies to support the greatest diversity of canopy arthropods, while partially harvested stands supported greater arthropod diversity than plantations. Another study in the Pacific Northwest has investigated multiple organism responses, including epiphytes and moths, to forest thinning, which aimed to increase structural complexity in a young, even-aged forest (Muir et al. 2002). Regarding epiphyte-associated arthropods, Pettersson (1996) found that unmanaged, lichen-rich forests supported higher arboreal spider abundance and diversity than lichen-poor, selectively logged forests. A similar study reported that unmanaged forests supported fivefold more invertebrates per tree branch and greater invertebrate diversity than mature managed forests (Pettersson et al. 1995).

Finally, a fair amount of the research on lichen sensitivity to forest management has used comparisons among extreme conditions, such as old-growth forests versus regenerated clearcuts (McCune 1993; Esseen et al. 1996). While such research has contributed substantially to what is known about epiphytic lichen communities, nearly all actively managed forests in New England are secondary forests, and very little old-growth forest remains for comparison. In addition, various forms of partial cutting now dominate in New England forests. In the state of Maine, for example, 97% of the annual forest harvest is now by partial and shelterwood cutting, with clearcuts occurring on only 3% of harvested lands (Maine Forest Service 2005). Since the presettlement Acadian spruce-fir forest of New England, 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

(Seymour et al. 2002), it is important to understand how current partial and gap harvesting practices may affect epiphyte and arboreal arthropod communities.

In this study, we (i) investigated how epiphyte and arthropod communities were affected by height on the stem, bark texture, and stem diameter of red maple (*Acer rubrum* L.) trees, (ii) examined how harvest gaps influenced epiphyte and arthropod communities on red maple boles, and (iii) explored whether these effects influenced the relationship between the epiphyte and arthropod communities.

## Methods

### Study site

This study took place in the Penobscot Experimental Forest 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 (*Picea mariana* (Mill.) BSP), 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, paper birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.), and bigtooth aspen (*Populus grandidentata* Michx.). The Penobscot Experimental Forest has a complicated history of repeated partial cuttings and insect outbreaks that resulted in multicohort 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 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. The Acadian Forest Ecosystem Research Program is a long-term study designed to compare two silvicultural systems that were inspired by the natural gap-dynamic 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 using 0.07–0.2 ha gaps with 10%–30% of the basal area retained within the harvest gap. The research plots used in this study are 9.4 ha (plot 1) and 10.1 ha (plot 6) in size, each containing eight harvest gaps that average 0.15 ha in size. The mean basal area of trees in the closed canopy matrix was 10.4 m<sup>2</sup>/ha (SD = 5.4) for hardwoods and 23.3 m<sup>2</sup>/ha (SD = 11.2) for softwoods. Mean basal area for retention trees in the harvest gaps was 1.5 m<sup>2</sup>/ha (SD = 0.74) for hardwoods and 6.8 m<sup>2</sup>/ha (SD = 5.5) for softwoods. The gaps used in plots 1 and 6 were created in 1995 and 1996, respectively.

### Experimental design

We randomly selected five harvest gaps from each research plot (10 gaps total) to sample. Four red maple 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

**Table 1.** List of epiphytes by guild found on red maple (*Acer rubrum*) trees from the base to 6 m above the ground on the south side of the bole.

Guild	Species	Code	Mean % cover (SE)	Frequency (%)	
Bryophyte	Measured at this level in field	BRYOPHT	20.118 (1.096)	98.33	
Crustose	Measured at this level in field	CRUSTOSE	18.354 (1.062)	97.92	
Cyanolichen	<i>Collema subflaccidum</i>	COLSUB	0.154 (0.089)	3.33	
	<i>Leptogium corticola</i> *	LEPCOR	0.033 (0.023)	1.25	
	<i>Leptogium cyanescens</i>	LEPCYA	0.617 (0.180)	11.25	
	<i>Leptogium saturninum</i> *	LEPSAT	0.042 (0.029)	0.83	
	<i>Lobaria pulmonaria</i>	LOBPUL	2.021 (0.578)	12.50	
	<i>Lobaria quercizans</i>	LOBQUE	0.887 (0.242)	7.92	
	<i>Peltigera horizontalis</i> **	PELHOR	0.096 (0.057)	1.25	
	<i>Peltigera polydactylon</i> **	PELPOL	0.004 (0.004)	0.42	
	<i>Peltigera praetextata</i> **	PELPRA	0.013 (0.013)	0.42	
	Large foliose*†	<i>Platismatia tuckermanii</i>	PLATUC	0.450 (0.154)	6.67
<i>Tuckermannopsis ciliaris</i> group*		TUCCIL	0.017 (0.013)	0.83	
<i>Cetrelia olivetorum</i> *		CETOLI	0.013 (0.013)	0.42	
Fruticose	<i>Bryoria furcellata</i>	BRYFUR	0.100 (0.032)	5.42	
	<i>Bryoria nadvornikiana</i> *	BRYNAD	0.017 (0.012)	0.83	
	<i>Evernia mesomorpha</i>	EVMES	0.084 (0.031)	4.17	
	<i>Ramalina americana</i> **	RAMAME	0.010 (0.006)	2.08	
	<i>Ramalina dilacerata</i> **	RAMDIL	0.021 (0.021)	0.42	
	<i>Ramalina intermedia</i> **	RAMINT	<0.001 (<0.001)	0.42	
	<i>Usnea filipendula</i>	USNFIL	0.504 (0.193)	6.25	
	<i>Usnea lapponica</i> *	USNLAP	0.004 (0.004)	0.42	
	<i>Usnea strigosa</i>	USNSTR	0.125 (0.052)	2.50	
	<i>Usnea subfloridana</i>	USNSUB	0.595 (0.114)	17.08	
	Small foliose	<i>Hypogymnia physodes</i>	HYPPHY	1.126 (0.223)	18.75
		<i>Melanelia subaurifera</i>	MELSUB	0.134 (0.033)	9.58
		<i>Myelochroa galbina</i>	MYEGAL	1.106 (0.147)	35.42
<i>Parmelia squarrosa</i>		PARSQU	2.678 (0.373)	33.33	
<i>Parmelia sulcata</i>		PARSUL	4.673 (0.559)	48.33	
<i>Punctelia rudecta</i>		PUNRUD	0.450 (0.142)	5.83	
<i>Pyxine soorediata</i> *		PYXSOR	0.046 (0.026)	1.67	
Squamulose†	<i>Cladonia</i> spp.	CLACHL	1.458 (0.258)	20.83	

**Note:** Mean % cover with  $\pm 1$  SE, epiphyte percent frequency (no. of occurrences/240  $\times$  100), and codes used in NMS ordination (Fig. 1) are presented for each epiphyte. Species denoted with an asterisk were not included in the NMS ordination analysis because of too few occurrences ( $n < 4$  out of 240). Species denoted by double asterisks were combined at the genus level. A dagger symbol signifies guilds with no occurrences at one or more height intervals and were omitted from GLM analysis.

plots and because cyanolichens were observed to be common on the bark of red maple. 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 and allowed for only minor influence of edge effects on closed canopy trees (Hagan and Whitman 2001; Roberts and Frego 2005). To avoid a 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. The relatively large size of the gaps (0.15 ha) combined with the proximity of gaps to one another created a situation where trees in the same gap were often as close to one another as trees in adjacent gaps and in the closed forest. Thus, we minimized any opportunity for spatial correlation among sample trees in the harvest gaps on each plot. All sample trees were between 15 and 50 cm diameter at breast height (DBH) and

able to safely support a climbing ladder. A total of 80 trees were sampled from 25 July to 20 August 2004. All sampling occurred on rain-free days between 9:00 a.m. and 3:00 p.m.

Each tree was sampled using 6.7 m (three 2.4 m sections) aluminum climbing ladders. The bole of each sample tree was divided into three, 2 m height intervals: 0–2 2–4 and 4–6 m. All sampling for epiphytes and arthropods occurred on the south-facing surface of the tree bole. Each tree was measured for 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.

## Data collection

### Epiphytes

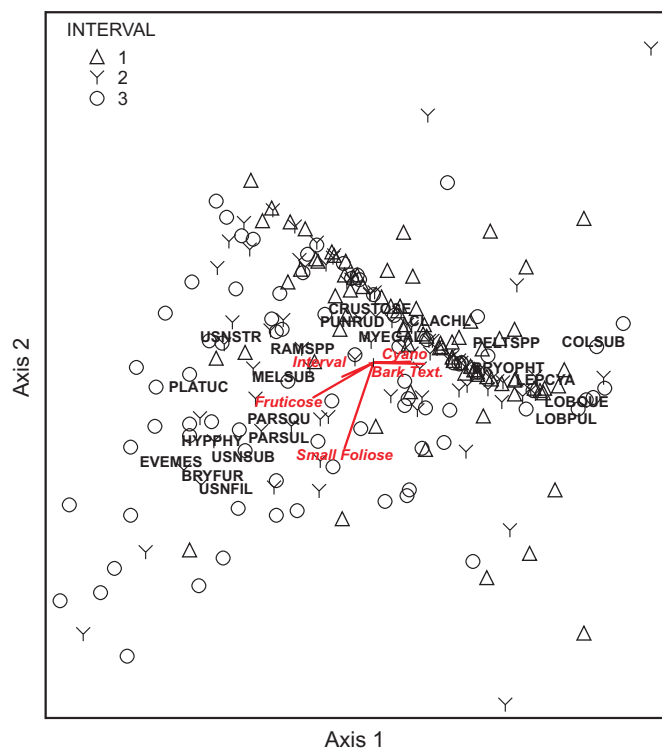
Percent cover of epiphytes within the first metre of each height interval and on the south side of the bole was as-

**Table 2.** List of arthropod orders collected on red maple trees from the base to 6 m above the ground on the south-facing side of the bole.

Class	Order	Common name	Mean count/m <sup>2</sup> (SE)	Frequency (%)
<b>Major arthropods</b>				
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 and wasps	5.72 (0.48)	63.33
Insecta	Psocoptera	Bark lice	10.00 (0.71)	80.42
<b>Other arthropods</b>				
Insecta	Coleoptera	Beetles	0.52 (0.10)	11.25
Insecta	Hemiptera	True bugs	0.73 (0.27)	9.58
Insecta	Homoptera	Aphids and scales	1.05 (0.40)	11.67
Insecta	Lepidoptera	Moths and 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*		Millipedes	0.03 (0.02)	0.83

**Note:** Mean count/m<sup>2</sup> with ±1 SE and percent frequency (no. of occurrences/240 × 100) are presented for each order. Arthropods denoted with an asterisk were identified at the class level. Orders under the major arthropods heading were analyzed using GLM repeated-measures analysis. Other arthropods were omitted from further analyses.

**Fig. 1.** Ordination scatterplot (NMS) of epiphytes using percent cover values (Table 1) at three height intervals from 80 trees (i.e., 240 “plots”) (vector cutoff value = 0.150). Epiphyte codings are described in Table 1 and are capitalized in the scatterplot. Plot symbols denote vertical intervals such that triangles occurred at interval 1 (0–1 m), “Y” symbols at interval 2 (2–3 m), and circles at interval 3 (4–5 m). Both axes contained significant structure (Monte Carlo *p* values = 0.0196) and accounted for 83.8% of the variance.



**Table 3.** Correlation of secondary matrix variables with NMS ordination of epiphyte percent cover axes.

	Axis 1	Axis 2
Interval	-0.309	-0.205
DBH	0.336	0.050
Bark texture	0.393	-0.056
Cyanolichen	0.332	-0.040
Small foliose	-0.299	-0.512
Fruticose	-0.428	-0.322

**Note:** Epiphyte guild variables are the sum of percent cover for all epiphyte species in a guild.

essed using a 1 m × 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 percent cover of epiphytes was visually estimated to the nearest 5%. Estimation occurred at the species level for macrolichens and also quantified overall percent cover for crustose lichens and bryophytes. Lichen nomenclature followed Esslinger (1999). Lichen voucher specimens are located in the University of Maine Herbarium.

**Arthropods**

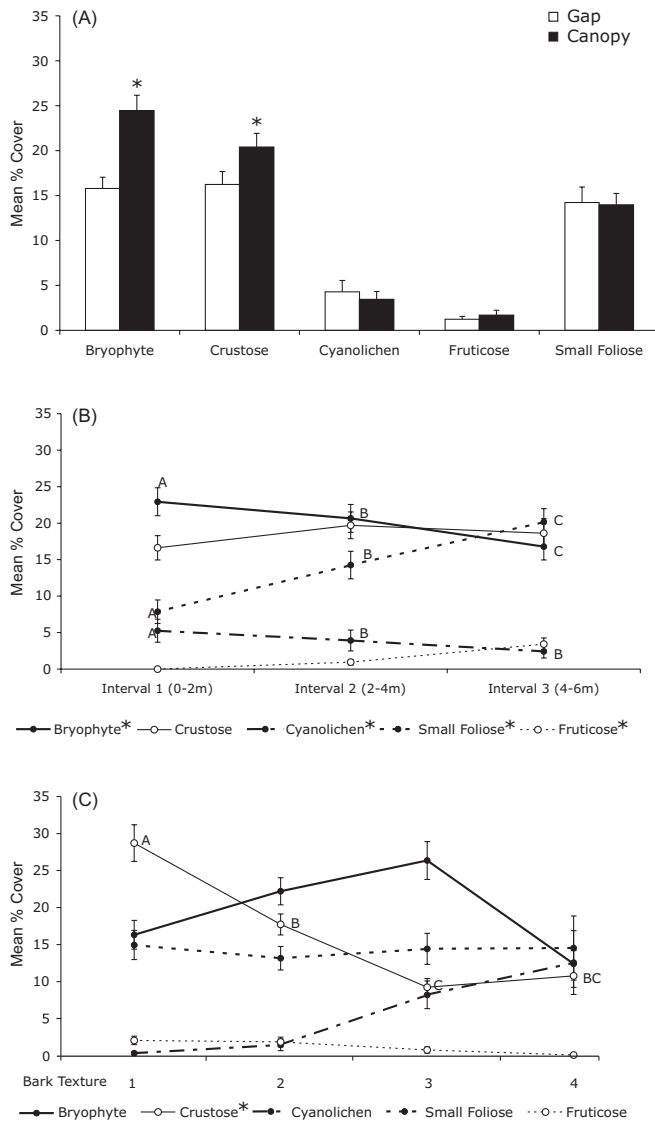
Arthropods were sampled over the entire length of the 2 m height interval. The sample area had a width that was the same as that of the epiphyte sample quadrat (0.125 m) and was also located on the south side of the bole. Each 2 m interval was sampled for invertebrates using an Echo PV-413 backpack leaf blower with vacuum attachments. The vacuum was modified by adding a 10 m pool-vac hose

**Table 4.** ANOVA table for GLM analysis for the influence of canopy condition (levels: gap and closed canopy), bark texture (levels: 1 = smooth, 2 = fissures <5 cm, 3 = fissures >5 cm, and 4 = thick and flaky), height interval (levels: 0–2, 2–4, and 4–6 m), research plot (categories: plot 1 and plot 6), and harvest gap (categories 1–10) on percent cover of each epiphyte guild.

Source of variation	df	Bryophyte			Crustose			Cyanolichen			Small foliose			Fruticose		
		MS	F	p	MS	F	p	MS	F	p	MS	F	p	MS	F	p
<b>Between subjects</b>																
Canopy condition	1	14.62	12.18	0.00	9.90	6.62	0.02	0.69	1.31	0.27	0.42	0.10	0.75	0.00	0.00	0.03
Plot	1	22.58	18.82	0.00	4.52	3.02	0.10	0.51	0.97	0.34	30.93	7.63	0.01	8.17	5.78	0.86
Plot × canopy condition	1	0.22	0.18	0.68	1.26	0.85	0.37	0.11	0.20	0.66	3.71	0.91	0.35	0.05	0.03	0.00
Harvest gap (plot × canopy condition)	16	1.20	1.03	0.44	1.50	1.78	0.06	0.52	0.71	0.77	4.06	1.86	0.05	1.41	4.04	0.00
Texture	3	0.37	0.32	0.81	10.18	12.12	0.00	0.73	0.99	0.40	0.35	0.16	0.92	0.25	0.70	0.56
Canopy condition × texture	3	3.49	3.00	0.04	0.31	0.37	0.77	0.75	1.02	0.39	3.76	1.72	0.18	1.76	5.03	0.00
Plot × texture	3	0.33	0.29	0.83	6.33	7.53	0.00	0.62	0.84	0.48	2.27	1.04	0.38	0.13	0.37	0.78
Plot × canopy condition × texture	3	0.93	0.80	0.50	1.49	1.78	0.16	0.52	0.70	0.55	3.02	1.38	0.26	0.57	1.62	0.20
Error	48	1.16			0.84			0.74			2.19			0.35		
<b>Within subjects</b>																
Interval	2	1.90	3.99	0.03	0.33	0.94	0.40	1.41	4.46	0.02	15.82	25.76	0.00	6.63	11.47	0.00
Interval × canopy condition	2	0.47	0.99	0.38	0.11	0.30	0.74	0.03	0.08	0.92	0.07	0.12	0.89	0.24	0.41	0.67
Interval × plot	2	1.06	2.22	0.13	0.08	0.23	0.79	0.52	1.64	0.21	1.03	1.67	0.20	2.42	4.19	0.02
Interval × plot × canopy condition	2	0.07	0.15	0.86	0.86	2.42	0.11	0.11	0.36	0.70	0.15	0.25	0.78	0.08	0.14	0.87
Interval × harvest gap (plot × canopy condition)	32	0.48	1.22	0.23	0.35	1.11	0.34	0.32	1.53	0.06	0.61	1.03	0.43	0.58	2.49	0.00
Interval × texture	6	0.32	0.82	0.56	0.36	1.12	0.36	0.20	0.95	0.46	0.67	1.13	0.35	0.25	1.06	0.39
Interval × canopy condition × texture	6	0.66	1.69	0.13	0.16	0.50	0.81	0.13	0.64	0.70	0.59	1.00	0.43	0.61	2.64	0.02
Interval × plot × texture	6	0.35	0.88	0.51	0.34	1.05	0.40	0.17	0.81	0.56	0.97	1.64	0.15	0.28	1.20	0.31
Interval × plot × canopy condition × texture	6	0.50	1.27	0.28	0.11	0.35	0.91	0.18	0.89	0.50	0.24	0.40	0.88	0.19	0.82	0.56
Error	96	0.39			0.32			0.21			0.59			0.23		

**Note:** Analyses were run separately for each guild and interval was considered as a repeated measure. Guilds were transformed using a natural log to meet the assumption of constant variance. Effects were considered significant at the  $p < 0.05$  level.

**Fig. 2.** Mean percent cover of lichen guilds by (A) canopy condition (levels: gap and closed canopy), (B) height interval, and (C) bark texture (levels: 1 = smooth, 2 = fissures <5 cm, 3 = fissures >5 cm, and 4 = thick and flaky). Data were analyzed separately for each guild using GLM repeated-measures analysis with height interval treated as a repeated measure. An asterisk indicates a significant main effect. Different letters within guilds represent differences in cover among factor levels. Error bars denote  $\pm 1$  SE about the mean. Significance was considered at the  $p < 0.05$  level. Pairwise comparison probabilities were Bonferroni adjusted for multiple comparisons.



to the intake so that sampling only required maneuvering the hose about the tree rather than the entire machine. The utility/blower shop-vac nozzle was attached to the end of the pool-vac hose. Arthropods were collected using a bag made of knee-high nylon stocking material that was placed between the nozzle and the pool-vac hose.

All arthropod samples were placed in a cooler with ice in the field and later transferred to a freezer kept at  $-17^{\circ}\text{C}$ . Arthropods were later sorted in the laboratory from debris to order and placed in 70% ethanol for long-term storage.

Arthropod identifications followed Triplehorn and Johnson (2004).

**Analytical approach**

**Epiphytes**

To examine the influence of height on the stem and canopy condition (gap versus closed canopy) on the epiphyte community, we used 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 composed of values between 0% and 100%, a relative Sørensen 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). The secondary matrix used in the NMS ordination included the percent cover of epiphyte guilds (except bryophytes and crustose lichens, which were included in the primary matrix) for each sample unit, DBH, and the following categorical variables: height interval, canopy condition (gap or closed canopy), and bark texture. The epiphyte guild data included the total percent cover of epiphyte species in each guild per sample unit. Guilds are nontaxonomic groups of species that have similar habitat requirements and morphologies and tend to occupy similar niches. In this study, guilds were modified from functional groups described by McCune 1993 (Table 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.

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 grouping species into guilds. However, species within a guild are often highly correlated, creating problems with multicollinearity. By analyzing guilds of epiphytes, we eliminated most of the multicollinearity problems. To investigate guild relationships to height on stem, bark texture, and response to harvest gaps, separate general linear models (GLM) were developed using Systat (SYSTAT Software Inc. 2004). Each model contained the following factors: canopy condition (levels: gap and closed canopy), bark texture (levels: 1, 2, 3, and 4), height interval (levels: 1 (0–2 m), 2 (2–4 m), and 3 (4–6 m)), harvest gap indicator ( $n = 10$ ), and research plot indicator ( $n = 2$ ).

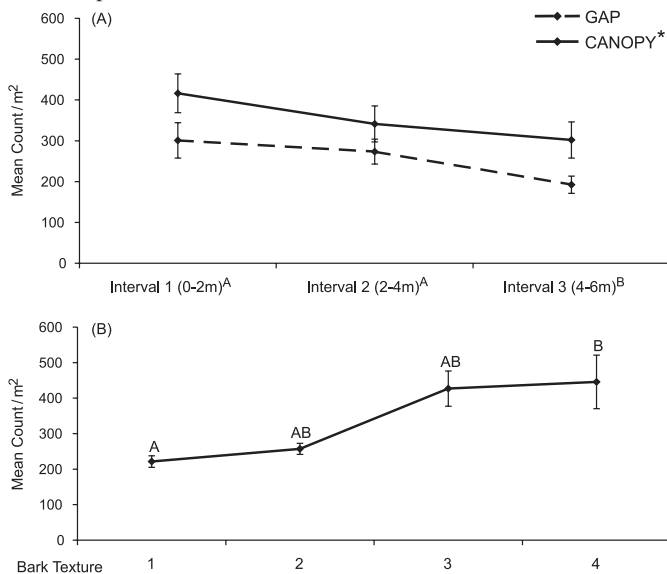
To account for any possible variation associated with sample trees being located in a particular harvest gap or research plot, indicator variables describing gap and research plot were included in the GLMs. Height interval was treated as a repeated measure, which is essentially the same as incomplete randomized block design, to account for the lack of independence within a tree. Guilds were examined for constant variance across factors using modified Levene tests and were transformed using  $\ln(\% \text{ cover} + 1)$  to correct for constant variance. Pairwise comparisons were Bonferroni adjusted at the family-wise  $\alpha = 0.05$  level. Statistical signifi-

**Table 5.** ANOVA table for GLM analysis for the influence of canopy condition (levels: gap and closed canopy), bark texture (levels: 1 = smooth, 2 = fissures <5 cm, 3 = fissures >5 cm, and 4 = thick and flaky), height interval (levels: 0–2, 2–4, and 4–6 m), research plot (categories: plot 1 and plot 6), and harvest gap (categories 1–10) on total arthropod count.

Source of variation	df	MS	F	p
<b>Between subjects</b>				
Canopy condition	1	5.00	6.20	0.02
Plot	1	0.09	0.11	0.74
Plot × canopy condition	1	0.97	1.20	0.29
Harvest gap (plot × canopy condition)	16	0.81	1.18	0.32
Texture	3	3.48	5.07	0.00
Canopy condition × texture	3	0.64	0.93	0.44
Plot × texture	3	0.94	1.38	0.26
Plot × canopy condition × texture	3	1.40	2.04	0.12
Error	48	0.69		
<b>Within subjects</b>				
Interval	2	1.79	6.94	0.00
Interval × canopy condition	2	0.45	1.74	0.19
Interval × plot	2	0.41	1.58	0.22
Interval × plot × canopy condition	2	0.17	0.65	0.53
Interval × harvest gap (plot × canopy condition)	32	0.26	1.68	0.03
Interval × texture	6	0.14	0.91	0.49
Interval × canopy condition × texture	6	0.16	1.02	0.42
Interval × plot × texture	6	0.10	0.64	0.70
Interval × plot × canopy condition × texture	6	0.23	1.52	0.18
Error	96	0.15		

**Note:** Total arthropod count was transformed using a natural log to meet the assumption of constant variance. Effects were considered significant at the  $p < 0.05$  level.

**Fig. 3.** Mean arthropod count by (A) canopy condition (levels: gap and closed canopy) and height interval and (B) bark texture index (levels: 1 = smooth, 2 = fissures <5 cm, 3 = fissures >5 cm, and 4 = thick and flaky). Differences were analyzed using GLM repeated-measures analysis with height interval treated as a repeated measure and canopy condition and bark texture index as predictor variables. An asterisk indicates a significant main effect. Different letters indicate differences among height intervals and bark texture index. Significance was considered at the  $p < 0.05$  level. Pairwise comparison probabilities were Bonferroni adjusted for multiple comparisons. Lines on points denote  $\pm 1$  SE about the mean.



cance was determined at the  $p < 0.05$  level. When interactions in the GLM were significant, we examined the direction of trends. When interactions reflected minor changes in slope, we identified presence of an interaction but discussed the trend in terms of main effects.

The relationship between stem diameter and the epiphyte community was also of interest. However, because DBH was correlated with bark texture ( $r^2 = 0.394$ ,  $p < 0.0001$ ), and since bark texture was a better predictor, DBH was excluded from GLM repeated-measures models. The relationship between bark texture and DBH was examined using Pearson correlations, and the implications of this relationship were related to the epiphyte community.

**Arthropods**

The first level of arthropod analysis considered total count. These data were analyzed using the GLM repeated-measures model discussed for epiphyte guilds. The data were checked for constant variance using modified Levene tests and were transformed using  $\ln(\text{count} + 1)$ .

Arthropod analysis next occurred at the order level and also used GLM repeated-measures model for each order. Orders included in the analysis are listed in Table 2. The data were checked for constant variance across factors using modified Levene tests and resulted in the following transformations:  $(\text{Araneae} + 1)^{-1}$  and  $\ln(\text{Collembola} + 1)$ . Pairwise comparisons were Bonferroni adjusted at the family-wise  $\alpha = 0.05$  level. Statistical significance was determined at the  $p < 0.05$  level. Where interactions in the GLM were significant, we examined the direction of trends. When in-

**Table 6.** ANOVA table for GLM analysis on the influence of canopy condition (levels: gap and closed canopy), bark texture (levels: 1 = and 4–6 m), research plot (categories: plot 1 and plot 6), and harvest gap (categories 1–10) on arthropod orders.

Source of variation	df	Acari			Araneae <sup>-1</sup>		
		MS	F	p	MS	F	p
<b>Between subjects</b>							
Canopy condition	1	5307.43	1.91	0.19	0.67	5.96	0.03
Plot	1	2669.97	0.96	0.34	0.05	0.47	0.05
Plot × canopy condition	1	41842.19	15.02	0.00	0.02	0.16	0.70
Harvest gap (plot × canopy condition)	16	2785.87	1.11	0.37	0.11	1.02	0.46
Texture	3	19113.19	7.64	0.00	0.13	1.15	0.34
Canopy condition × texture	3	453.64	0.18	0.91	0.16	1.41	0.25
Plot × texture	3	4236.85	1.69	0.18	0.10	0.87	0.47
Plot × canopy condition × texture	3	20694.09	8.27	0.00	0.12	1.09	0.37
Error	48	2502.43			0.11		
<b>Within subjects</b>							
Interval	2	6662.46	12.18	0.00	0.86	14.83	0.00
Interval × canopy condition	2	3000.99	5.49	0.01	0.11	1.88	0.17
Interval × plot	2	2275.97	4.16	0.03	0.07	1.26	0.30
Interval × plot × canopy condition	2	1539.65	2.82	0.08	0.07	1.19	0.32
Interval × harvest gap (plot × canopy condition)	32	546.84	0.93	0.58	0.06	0.71	0.86
Interval × texture	6	1923.31	3.27	0.01	0.03	0.37	0.90
Interval × canopy condition × texture	6	1572.05	2.68	0.02	0.02	0.27	0.95
Interval × plot × texture	6	1267.11	2.16	0.05	0.02	0.21	0.97
Interval × plot × canopy condition × texture	6	1054.63	1.80	0.11	0.02	0.30	0.94
Error	96	587.57			0.08		

**Note:** GLMs were performed separately for each order with interval as a repeated measure and at the  $p < 0.05$  significance level. Araneae and Collembola

teractions merely reflected minor changes in slope, we indicated the presence of an interaction but discussed the trend in terms of the main effects. If interactions reflected a major change in a trend, we explain the trend at the interaction level.

### Epiphyte–arthropod associations

Canonical correlation was used to detect associations between the guilds and arthropod orders (SYSTAT Software Inc. 2004). All variables were standardized so that each variable ranged from 0 to 1. The dependent variable set contained the six major arthropod orders (Table 2). The independent variable set contained all of the epiphyte guilds (Table 1). Canonical correlations were considered significant if their Bartlett  $\chi^2$  test of residual correlations was significant at the  $p < 0.05$  level. Significant canonical correlations were rotated. Variables with canonical loadings greater than 0.3 were considered significant.

## Results

### Epiphytes

A total of 33 epiphytes were observed (Table 1). Bryophytes and crustose lichens were the most frequent (98%) and abundant epiphytes, with 20.1% and 18.4% cover, respectively. *Parmelia sulcata* was the most common lichen species (48.3% frequency).

The NMS ordination accounted for 83.8% of the variance and resulted in two axes with significant structure (Fig. 1). Axis 1 accounted for 57.8% of the variance and the axis 2 accounted for 26.0% of the variance. Axis 1 was correlated with height interval, cyanolichen cover, fruticose lichen cover, small foliose lichen cover, and bark texture (Table 3). Axis 2 was correlated most strongly with small foliose li-

chen cover as well as fruticose lichen cover and interval. Axis 1 also described a gradient where an increase in height on the stem was associated with increased fruticose cover (e.g., *Usnea* spp. and *Bryoria* spp.) and small 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. It should also be noted that there was a fair amount of overlap between interval zones in the ordination as well as mixing between intervals 1 and 3. This pattern indicated that there was a substantial amount of variability in the epiphyte community that was not accounted for by height on the tree stem. The ordination also demonstrated that lichen species tended to respond similarly within their respective guild (Fig. 1).

The GLM repeated-measures analysis yielded several interactions for fruticose lichens and one for bryophytes and crustose lichens (Table 4). Most of the interactions for fruticose resulted from several harvest gaps having no fruticose lichens in research plot 1. To describe the major trends regarding influence of canopy condition, height interval, and bark texture on fruticose lichens, we would have needed a larger sample of fruticose lichen occurrences. A canopy condition by bark texture interaction was significant for bryophytes ( $p = 0.04$ ). This interaction indicated a minor difference in bryophyte response to harvest gaps by bark texture, although the overall trend was for greater bryophyte abundance on moderately thick-barked trees. An interaction between research plots and bark texture was significant for crustose lichens ( $p < 0.001$ ). This interaction reflected a relatively minor difference between research plots in the slope of the correlation between crustose lichen percent cover and bark texture, although the trend was similar for both plots.



smooth, 2 = fissures <5 cm, 3 = fissures >5 cm, and 4 = thick and flaky), height interval (levels: 0–2, 2–4,

ln (Collembola + 1)			Diptera			Hymenoptera			Psocoptera		
MS	F	p	MS	F	p	MS	F	p	MS	F	p
17.06	16.05	0.00	183.31	2.50	0.18	7.69	1.31	0.27	9.88	0.74	0.40
2.54	2.39	0.14	47.60	0.65	0.48	17.12	2.91	0.11	0.87	0.07	0.80
6.69	6.29	0.02	129.78	1.77	0.25	16.24	2.76	0.12	39.23	2.95	0.11
1.06	0.92	0.56	92.26	1.99	0.03	5.89	1.56	0.12	13.31	1.38	0.19
4.17	3.60	0.02	73.23	1.58	0.21	3.64	0.96	0.42	25.23	2.61	0.06
1.30	1.13	0.35	95.91	2.07	0.12	5.09	1.34	0.27	6.78	0.70	0.56
0.82	0.70	0.55	14.18	0.31	0.82	0.10	0.03	0.99	5.61	0.58	0.63
0.15	0.13	0.94	29.93	0.65	0.59	5.05	1.33	0.27	5.60	0.58	0.63
1.16			46.41			3.79			9.66		
5.59	10.22	0.00	124.33	9.51	0.02	4.78	1.29	0.29	7.69	1.15	0.33
0.32	0.58	0.57	81.03	6.20	0.06	1.08	0.29	0.75	10.02	1.50	0.24
1.37	2.50	0.10	10.58	0.81	0.67	0.65	0.18	0.84	9.48	1.42	0.26
0.25	0.46	0.64	25.85	1.98	0.39	1.06	0.29	0.75	0.51	0.08	0.93
0.55	1.39	0.11	26.37	1.67	0.03	3.71	1.56	0.05	6.69	1.32	0.15
0.21	0.52	0.79	13.07	0.83	0.55	2.42	1.02	0.42	2.37	0.47	0.83
0.73	1.85	0.10	22.65	1.44	0.21	1.52	0.64	0.70	7.30	1.44	0.21
0.24	0.60	0.73	13.11	0.83	0.55	0.60	0.25	0.96	6.45	1.27	0.28
0.48	1.21	0.31	15.89	1.01	0.42	2.28	0.96	0.46	1.90	0.38	0.89
0.39			15.75			2.37			5.07		

were transformed as noted in the table.

That is to say, crustose lichens were more abundant on smoother bark for both plots.

Bryophytes ( $p = 0.004$ ) and crustose lichens ( $p = 0.020$ ) were less abundant on trees in harvest gaps, while the abundance of other guilds was not affected by canopy condition (Fig. 2A). Bryophyte and cyanolichen abundance was greatest at lower stem heights, and small foliose lichens were more abundant at greater heights (Fig. 2B). These trends also were supported by results from the NMS ordination (Fig. 1). Bark texture influenced the abundance of crustose lichens, such that they were most abundant on trees with smooth bark (Fig. 2C).

Bark texture index and DBH of sample trees were positively correlated ( $r^2 = 0.394$ ,  $p < 0.0001$ ), indicating that as stem diameter increased, the thickness and flakiness of the bark increased. This relationship was especially pronounced for bark texture class 4. Thus, crustose lichens were most abundant on trees with smaller DBH.

### Arthropods

Approximately 18 200 arthropods were collected from 80 trees. While 16 orders were represented in the collections, the most abundant orders were Acari (mites), Collembola (springtails), Diptera (flies), Psocoptera (bark lice), Araneae (spiders), and Hymenoptera (wasps) (Table 2).

Total arthropod count varied with canopy condition, bark texture index, and height interval (Table 5). There also was a significant interaction between height interval and harvest gap. The interaction reflected only a minor slope difference in the relationship between interval and arthropod count across the 10 harvest gaps and did not include a directional change in the trend across the harvest gaps. Total arthropod count was greater at lower height intervals and on trees in closed canopy forest (Fig. 3A). Arthropod count also increased as

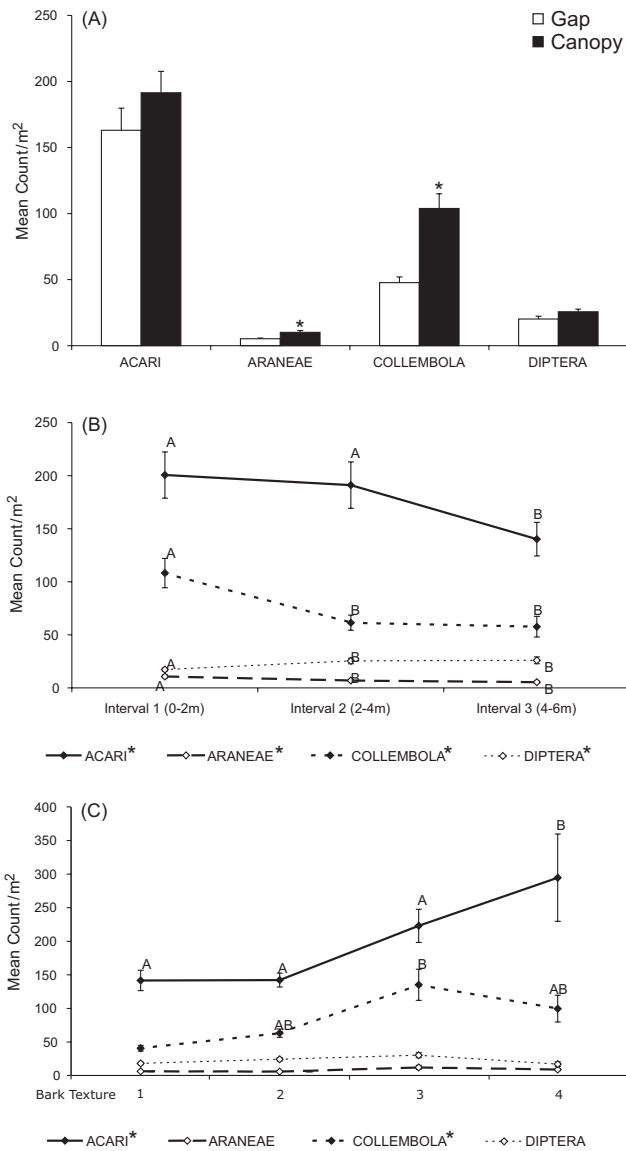
bark texture increased in thickness and flakiness (Fig. 3B). Thus, the bark of larger-diameter trees supported more arthropods per square metre than the bark of smaller trees.

Canopy condition, bark texture, and height interval were important factors ( $p < 0.05$ ) for four of the major arthropod orders (Table 6). A significant research plot by canopy condition interaction was detected for both Collembola and Acari (Table 6). In plot 1, trees in harvest gaps had greater numbers of Acari than trees in a closed canopy. This pattern was the opposite in plot 6, i.e., trees in gaps had fewer numbers of Acari than closed canopy trees. The plot by canopy condition interaction for Collembola was different from that for Acari in that both research plots had greater counts on closed canopy trees, although the difference between gap and closed canopy trees was more pronounced in plot 6. Araneae and Collembola abundance was lower on trees in harvest gaps (Fig. 4A). Acari, Araneae, and Collembola tended to be more abundant at lower heights on the bole, whereas Diptera counts increased with height on the bole (Fig. 4B). Acari and Collembola increased in abundance on thicker, flakier bark (Fig. 4C).

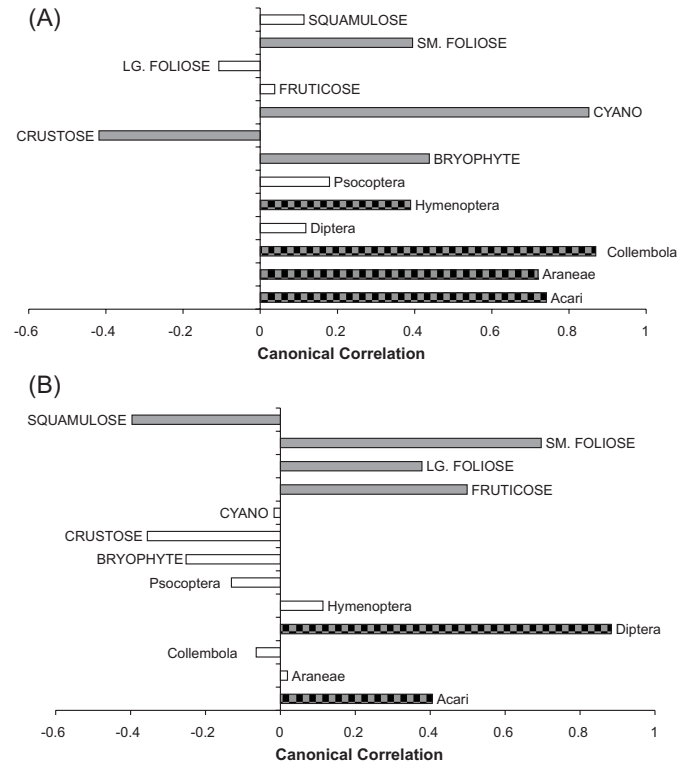
### Epiphyte–arthropod associations

Canonical correlation analysis yielded two canonical correlations with significant structure ( $p < 0.05$ ). The variables with the strongest loadings on the first canonical correlation were the arthropod orders Collembola, Acari, and Araneae and the epiphyte guild cyanolichens (Fig. 5A). This canonical correlation suggested a positive relationship among these variables. Bryophytes, small foliose lichens, and Hymenoptera were moderately positively associated with the first canonical correlation. Additionally, Collembola, Acari, Araneae, and Hymenoptera arthropods were negatively associated with crustose lichens.

**Fig. 4.** Mean count of major arthropod orders by (A) canopy condition (levels: gap and closed canopy), (B) height interval, and (C) bark texture (levels: 1 = smooth, 2 = fissures <5 cm, 3 = fissures >5 cm, and 4 = thick and flaky). Data were analyzed separately for each order using GLM repeated-measures analysis with height interval treated as a repeated measure and canopy condition and bark texture as predictor variables. An asterisk indicates a significant main effect. Different letters within guilds represent differences in cover among factor levels. Error bars denote  $\pm 1$  SE about the mean. Significance was considered at the  $p < 0.05$  level. Pairwise comparison probabilities were Bonferroni adjusted for multiple comparisons.



**Fig. 5.** Canonical correlation results between arthropod orders and epiphyte guilds for significant canonical correlations (Bartlett  $p < 0.0001$ ). The response variable set contains the six major arthropod orders listed in Table 1 and have checked bars. The predictor variable set contains all of the epiphyte guilds listed in Table 4 and have solid bars. Bars represent the rotated canonical loadings for each variable and are solid if loading is greater than 0.3. (A) First canonical correlation results; (B) second canonical correlation results.



The second canonical correlation described a positive relationship between Diptera and small foliose, large foliose, and fruticose lichens (Fig. 5B). Diptera were negatively associated with squamulose lichens and bryophytes. As in the first canonical correlation, crustose lichens also were negatively associated with Diptera. The order Acari was also positively associated with this epiphyte community, although the association was weaker than with the epiphyte community described by the first canonical correlation.

**Discussion**

**Epiphytes**

We found that the epiphyte community was clearly influenced by height on the tree bole. The patterns we observed were similar to those previously observed (Hale 1952; McCune et al. 1997), where bryophytes and cyanolichens were dominant at the base of the tree (0–2 m). Small foliose, large foliose, and fruticose lichens were most abundant 4–6 m high on the bole.

Since epiphytes favoring lower heights on the bole are generally adapted to shadier and more humid conditions than those in the subcanopy, we expected the epiphyte community at lower heights on the bole to be most affected by gap harvesting. Results from this study supported this hypothesis for the epiphyte guilds (small foliose, large foliose, and fruticose lichens) that were most abundant at the 4–6 m height interval. Our results were consistent with previous studies where small and large foliose lichens were found to be less sensitive to forest management (Gauslaa and Solhaug 1996; Coxson and Stevenson 2004). However, the two guilds that favored lower intervals (i.e., cyanolichens and bryophytes) responded differently to the harvest gaps. Cyanolichen abundance appeared to be relatively insensitive to harvest gaps. These results also were supported by previous studies that have determined dispersal limitation, rather than

changes in microclimate, to play a major role in the loss of cyanolichens after forest disturbance (Hazell and Gustafsson 1999; Sillett et al. 2000).

Bryophyte abundance was reduced by harvest gaps in our study. This finding contrasts somewhat with that of Fenton and Frego (2005), who observed that remnant forest patches in clearcuts can serve as refugia for forest floor bryophytes otherwise lost in surrounding clearcuts. However, we only examined bryophyte abundance and not species composition. It is possible that while bryophyte abundance declined in our study, most bryophyte species were retained by the residual trees. We suggest that future research investigate species-level responses of bryophytes to gap harvesting to better understand the influence of gap harvesting on epiphytic bryophytes.

Much of the research into the sensitivity of cyanolichens to forest management has determined that dispersal limitations are a limiting factor for these lichens and has emphasized the importance of residual trees in maintaining cyanolichens in intensive harvests (Hazell and Gustafsson 1999; Sillett et al. 2000). Our results support these claims, as we did not detect any difference in the abundance of cyanolichens on trees located in harvest gaps versus trees located in closed canopy forest. A recent analysis of the long-term effects of intensive management of a large forest property in the Acadian forest suggests that more trees with larger diameters may be maintained than with earlier practices (Etheridge et al. 2005). Thus, current forest management practices may not pose a serious threat to maintaining cyanolichen communities that are dependent on large-diameter trees.

A fair amount of research has been devoted to epiphyte substrate preferences, including tree species (Culbertson 1955), bark texture within a species (Gouch 1975), and bark chemistry (Gustafsson and Eriksson 1995). In this study, the abundance of crustose lichens decreased as bark texture increased in thickness and flakiness. Because this guild likely contains more species than in other lichen guilds, further examination (preferably species-level investigation) is needed to make conclusions about the influence of bark texture as well as how bark texture is associated with other tree characteristics.

It should be noted here that only a single bark texture index value was assigned to each sample tree rather than to each height interval. Since bark texture tended to become smoother with increasing height on the bole, we could have examined the relationship between bark texture and height in greater detail. For example, small foliose lichens 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 the abundance of small foliose lichens was greatest at higher intervals with smoother bark.

### Arthropods

The effect of harvest gaps was detected for both total arthropod counts and order-level analyses. Araneae and Collembola had substantially lower counts on trees in harvest gaps (Fig. 5A). However, this trend was observed across the four most abundant orders, and so the overall trend was not driven by just one taxon. However, Acari differed in re-

sponse to harvest gaps between the two research plots. We concluded that the factors influencing Acari are complex and that we would need to collect more environmental data as well as identify taxonomically below the order level to more fully understand Acari responses to gap harvesting.

The size of harvest gaps used in this study (0.15 ha) was similar to the midsize gaps used by Shure and Phillips (1991) to study arthropod response to varying-size disturbances. That study found that the control forest and 0.016 ha gaps supported significantly higher arthropod biomass than did larger gaps. Midsized patches, which were comparable with gaps in our study, tended to have higher densities of small herbivores such as homopterans, lower densities of larger consumers such as katydids (order Orthoptera, family Tettigoniidae), and smaller densities of predators such as ground spiders (order Araneae) and carabid beetles (order Coleoptera, family Carabidae). Overall, midsized patches had lower arthropod biomass and densities than the closed canopy (control forest). These results are consistent with our study where trees in the closed canopy supported more arthropods per tree and numbers of Araneae to be reduced by harvest gaps.

Because we found that Collembola and Araneae numbers were positively correlated ( $r^2 = 0.478$ ,  $p < 0.0001$ ), the effect of harvest gaps on Araneae (spiders) may have resulted from harvest gap influences on Collembola, a potential prey item. This relationship was investigated further by Miller (2006).

We found that Acari, Araneae, and Collembola were more abundant at lower heights on red maple boles. In contrast, Diptera numbers tended to increase with bole height. These results suggest that at least two arthropod groupings occurred on trees. The first group, including Acari, Araneae, and Collembola, has been described similarly by other comparable studies (Stubbs 1989; Pettersson et al. 1995). On the other hand, Diptera was 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 and may reflect the vertical gradient sampled or possibly the timing (season) of sampling that occurred in this study. The second phase of this research included a family-level analysis of Diptera to provide further insight into this community (Miller 2006).

### Epiphyte–arthropod associations

Although gap harvesting did not alter lichen epiphyte assemblages substantially, it did have a negative influence on the abundance of bryophytes. 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. While it may be that these taxa were all responding similarly to postharvest changes, it is also possible that Collembola and Araneae were sensitive to gap harvesting owing, in part, to their association with epiphytic bryophytes. A strong correlation between Collembola and Araneae may also suggest a trophic interaction that might be influenced by gap harvesting such that a decline in Araneae may have resulted from depletion of prey (Collembola), which in turn resulted from a decline in bryophytes.

Collembola are generally considered opportunistic feeders; common foods include fungi, detritus, and moss (Chen et al. 1995; 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 occurred on moss-covered rocks to feed on moss-inhabiting fungi (Varga et al. 2002). Several studies have also documented Collembola as a common prey item for ground-dwelling (not web-building) Araneae (Edgar 1969; Buddle 2002). In fact, Lawrence and Wise (2000) suggested that ground-dwelling spiders may affect decomposition in the forest floor by reducing Collembola densities. Miller (2006) investigated potential interactions between bryophytes, Araneae, and Collembola and the influence of gap harvesting using family and morphospecies analyses.

Gap harvesting appeared to have the greatest effect on epiphytes and bark-dwelling arthropods located at the base of the tree (0–2 m), with the exception of Acari. As these organisms tend to be adapted to shadier and more humid conditions than those occupying higher levels in the forest canopy, it may be possible to mitigate any negative effects of gap harvesting on epiphyte communities by leaving groups of trees or maintaining a buffer of regenerating conifers around residual trees to help protect the basal epiphyte/arthropod community from microclimatic extremes (Fenton and Frego 2005). The system of gap harvesting being used in this long-term study, which retains overstory trees and slowly expands the harvest gaps, may have the potential to maintain the arthropod and epiphyte communities in Acadian forest stands.

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## References

- Barker, M.G., and Sutton, S.L. 1997. Low-tech methods for forest canopy access. *Biotropica*, **29**: 243–247. doi:10.1111/j.1744-7429.1997.tb00032.x.
- Becker, V.E. 1980. Nitrogen fixing lichens in forests of the Southern Appalachian Mountains of North Carolina. *Bryologist*, **83**: 29–39. doi:10.2307/3242391.
- Blair, J.M., and Crossley, D.A., Jr. 1988. Litter decomposition, nitrogen dynamics and litter microarthropods in a Southern Appalachian hardwood forest 8 years following clearcutting. *J. Appl. Ecol.* **25**: 683–698.
- Brissette, J.C. 1996. Effects of intensity and frequency of harvesting on abundance, stocking and composition of natural regeneration in the Acadian forest of eastern North America. *Silva Fenn.* **30**: 301–314.
- Buddle, C.M. 2002. Interactions among young stages of the wolf spiders *Pardosa moesta* and *P. mackenziana* (Araneae:Lycosidae). *Oikos*, **96**: 130–136. doi:10.1034/j.1600-0706.2002.960114.x.
- Chen, B., and Wise, D.H. 1997. Response of forest-floor fungivores to experimental food enhancement. *Pedobiologia (Jena)*, **41**: 240–250.
- Chen, B., Snider, R.J., and Snider, R.M. 1995. Food preference and effects of food type on the life history of some soil Collembola. *Pedobiologia (Jena)*, **39**: 496–505.
- Coxson, D.S., and Stevenson, S.K. 2004. Retention of canopy lichens after partial-cut harvesting in wet-belt interior cedar-hemlock forests, British Columbia, Canada. *For. Ecol. Manag.* **204**: 97–112.
- Culberson, W.L. 1955. The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. *Ecol. Monogr.* **25**: 215–231. doi:10.2307/1943551.
- Edgar, W.D. 1969. Prey and predators of the wolf spider *Lycosa lugubris*. *J. Zool.* **159**: 405–411.
- Esseen, P.-A., and Renhorn, K.-E. 1998. Edge effects on an epiphytic lichen in fragmented forests. *Conserv. Biol.* **12**: 1307–1317. doi:10.1046/j.1523-1739.1998.97346.x.
- Esseen, P.-A., Renhorn, K.-E., and Pettersson, R.B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecol. Appl.* **6**: 228–238. doi:10.2307/2269566.
- Esslinger, T.L. 1999. A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. North Dakota State University. Available from [www.ndsu.nodak.edu/instruct/esslinge/chcklst/chcklst7.htm](http://www.ndsu.nodak.edu/instruct/esslinge/chcklst/chcklst7.htm)
- Etheridge, D.A., MacLean, D.A., Wagner, R.G., and Wilson, J.S. 2005. Changes in landscape composition and stand structure from 1945–2002 on an industrial forest in New Brunswick, Canada. *Can. J. For. Res.* **35**: 1965–1977. doi:10.1139/x05-110.
- Fenton, N.J., and Frego, K.A. 2005. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. *Biol. Conserv.* **122**: 417–430. doi:10.1016/j.biocon.2004.09.003.
- Fenton, N.J., Frego, K.A., and Sims, M.R. 2003. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Can. J. Bot.* **81**: 714–731. doi:10.1139/b03-063.
- Frisvoll, A.A., and Presto, T. 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. *Ecography*, **20**: 3–18. doi:10.1111/j.1600-0587.1997.tb00342.x.
- Gauslaa, Y., and Solhaug, K. 1996. Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. *Funct. Ecol.* **10**: 344–354. doi:10.2307/2390282.
- Gerson, U. 1969. Moss–arthropod associations. *Bryologist*, **72**: 495–500.
- Gerson, U., and Seaward, M.R.D. 1977. Lichen-invertebrate associations. *In* Lichen ecology *Edited by* M.R.D. Seward. Academic Press, London, U.K. pp. 69–119.
- Gouch, L.P. 1975. Cryptogam distributions on *Pseudotsuga menziesii* and *Abies lasiocarpa* in the Front Range, Boulder County, Colorado. *Bryologist*, **78**: 124–145.
- Gustafsson, L., and Eriksson, I. 1995. Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *J. Appl. Ecol.* **32**: 412–424.
- Hagan, J.M., and Whitman, A.A. 2001. Can patch retention maintain biodiversity in clearcuts and partially harvested forest? Cooperative Forestry Research Unit 2001 Annual Report MAFES Miscellaneous Report 428. Available from <http://library.umaine.edu/cfru/pubs/CFRU330.pdf>.
- Hale, M. 1952. Vertical distribution of cryptograms in a virgin forest in Wisconsin. *Ecology*, **33**: 398–406. doi:10.2307/1932835.

- Hayward, G.D., and Rosentreter, R. 1994. Lichens as nesting material for northern flying squirrels in the Northern Rocky Mountains. *J. Mammal.* **75**: 663–673. doi:10.2307/1382514.
- Hazell, P., and Gustafsson, L. 1999. Retention of trees at final harvest — evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. *Biol. Conserv.* **90**: 133–142. doi:10.1016/S0006-3207(99)00024-5.
- Knops, J.M.H., Nash, T.H., III, and Schlesinger, W.H. 1996. The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecol. Monogr.* **66**: 159–179. doi:10.2307/2963473.
- Lawrence, K.L., and Wise, D.H. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia (Jena)*, **44**: 33–39.
- Lesica, P., McCune, B., Cooper, S.V., and Hong, W.S. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Can. J. Bot.* **69**: 1745–1755.
- Maine Forest Service. 2005. 2004 silvicultural activities report. Maine Department of Conservation, Augusta, Maine. Available from <http://mainegov-images.informe.org/doc/mfs/pubs/pdf/silvi/04silvi.pdf>.
- McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. *Bryologist*, **96**: 405–411. doi:10.2307/3243870.
- McCune, B., and Mefford, M.J. 1999. Multivariate analysis of ecological data. PC-ORD version 4.25. MjM Software, Gleneden Beach, Oreg.
- McCune, B., Amsberry, K., Camacho, F., Clery, S., Cole, C., Emerson, C., Felder, G., French, P., Green, D., Harris, R., Hutten, M., Larson, B., Lesko, M., Majors, S., Markwell, T., Parker, G., Pendergrass, K., Peterson, E.B., Peterson, E.T., Platt, J., Proctor, J., Rambo, T., Rosso, A., Shaw, D., Turner, R., and Widmer, M. 1997. Vertical profile of epiphytes in a Pacific Northwest oldgrowth forest. *Northwest Sci.* **71**: 145–152.
- Miller, K.M. 2006. Arboreal arthropod associations with epiphytes and the effects of gap harvesting in the Acadian forest of central Maine. M.S. thesis, University of Maine, Orono, Maine.
- Muir, P.S., Mattingly, R.L., Tappeiner, J.C., Bailey, J.D., Elliot, W.E., Hager, J.C., Miller, J.C., and Peterson, E.B. 2002. Managing for biodiversity in young Douglas-fir forests of western Oregon. USGS Biological Science Rep. BSR 2002-0006. Available from [http://fresc.usgs.gov/products/papers/mang\\_bio.pdf](http://fresc.usgs.gov/products/papers/mang_bio.pdf).
- Norberg, R.A. 1978. Energy content of some spiders and insects on branches of spruce (*Picea abies*) in winter; prey of certain passerine birds. *Oikos*, **31**: 222–229. doi:10.2307/3543566.
- Peck, R.W., and Niwa, C.G. 2005. Longer-term effects of selective thinning on microarthropod communities in a late-successional coniferous forest. *Environ. Entomol.* **34**: 646–655.
- Pettersson, R.B. 1996. Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. *Ecography*, **19**: 221–228. doi:10.1111/j.1600-0587.1996.tb00230.x.
- Pettersson, R.B., Ball, J., Renhorn, K.-E., Esseen, P.-A., and Sjöberg, K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biol. Conserv.* **74**: 57–63. doi:10.1016/0006-3207(95)00015-V.
- Pipp, A., Henderson, C., and Callaway, R. 2001. Effects of forest age and forest structure of epiphytic lichen biomass and diversity in a Douglas-fir forest. *Northwest Sci.* **75**: 12–24.
- Renhorn, K.-E., Esseen, P.-A., Palmqvist, K., and Sundberg, B. 1997. Growth and vitality of epiphytic lichens: I. Responses to microclimate along a forest edge–interior gradient. *Oecologia*, **109**: 1–9. doi:10.1007/s004420050051.
- Riechert, S.E. 1974. Thoughts on the ecological significance of spiders. *Bioscience*, **24**: 352–356.
- Riechert, S.E., and Bishop, L. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology*, **71**: 1441–1450.
- Roberts, M., and Frego, K.A. 2005. Tree islands: leave patches as refugia for vascular plants and bryophytes in harvest blocks. Fundy Model Forest publication. Available from <http://fundymodelforest.net/admin/data/docs/EffectsofForestryPracticesonPlantDiversityMonitoringVascularPlantsandBryophytes.pdf>.
- Ross-Davis, A.L., and Frego, K.A. 2002. Comparison of plantations and naturally regenerated clearcuts in the Acadian Forest: forest floor bryophyte community and habitat features. *Can. J. Bot.* **80**: 21–33. doi:10.1139/b01-129.
- Saunders, M.R., and Wagner, R.G. 2005. Ten-year results of the Forest Ecosystem Research Program (FERP) — successes and challenges. *In* Balancing ecosystem values: innovative experiments for sustainable forestry. Edited by C.E. Peterson and D.A. Maguire. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-635. pp. 147–153.
- Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *For. Ecol. Manag.* **78**: 115–125. doi:10.1016/0378-1127(95)03592-4.
- Schowalter, T.D., and Ganio, L.M. 1998. Vertical and seasonal variation in canopy arthropod communities in an old-growth conifer forest in southwestern Washington, USA. *Bull. Entomol. Res.* **88**: 633–640.
- Selva, S. 1994. Lichen diversity and stand continuity in the northern hardwoods and spruce–fir forests of northern New England and western New Brunswick. *Bryologist*, **97**: 424–429. doi:10.2307/3243911.
- Seymour, R.S., White, A.S., and deMaynadier, P.G. 2002. Natural disturbance regimes in northeastern North America — evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manag.* **155**: 357–367. doi:10.1016/S0378-1127(01)00572-2.
- Shure, D.J., and Phillips, D.L. 1991. Patch size of forest openings and arthropod populations. *Oecologia*, **86**: 325–334. doi:10.1007/BF00317597.
- Sillett, S.C., McCune, B., Peck, J., Rambo, T., and Ruchty, A. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* **10**: 789–799. doi:10.2307/2641045.
- Stubbs, C.S. 1989. Patterns of distribution and abundance of corticolous lichens and their invertebrate associates on *Quercus rubra* in Maine. *Bryologist*, **92**: 453–460. doi:10.2307/3243665.
- SYSTAT Software Inc. 2004. SYSTAT for Windows version 11.0. SYSTAT Software Inc., Richmond, Calif.
- Triplehorn, C., and Johnson, N. 2004. Borror and DeLong's introduction to the study of insects. 7th ed. Thomsom Brooks/Cole, Belmont, Calif.
- Varga, J., Naár, Z., and Dobolyi, C. 2002. Selective feeding of collembolan species *Tomocerus longicornis* (Müll.) and *Orchesella cincta* (L.) on moss inhabiting fungi. *Pedobiologia (Jena)*, **46**: 526–538.