Ancient temperate rain forest research in British Columbia[1]

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Abstract—This paper is a tribute to Dr. R.A. Ring upon his retirement. During the past 12 years (1993–2005), an emerging canopy research program has established a wealth of baseline information on the structure and functioning of temperate rain forest canopy arthropod communities. Studies from research sites on Vancouver Island, British Columbia, have shown that ancient temperate rain forest canopy ecosystems contain a largely undescribed fauna that is specific to habitat features found only in these canopies. In particular, diverse assemblages of free-living mites have been shown to dominate conifer species and canopy microhabitats. For example, oribatid mites are the dominant arthropod fauna on branches, branches with attached lichens, and suspended soil accumulations. Species composition differs significantly between the ground and the canopy at both the family and the species level. Arboreal specificity may be due to intrinsic variation in habitat quality, habitat architecture, patchiness, and (or) resource availability. The prevalent patterns of habitat specialization, low vagility, and restricted distribution displayed by a large percentage of the resident canopy microarthropods are features often associated with forest ecoregions that have enjoyed relatively stable conditions for long periods of time, as have the ancient forests on Vancouver Island. Investigators in the "one-Ring lab" continue to document the diversity and abundance of canopy arthropods of temperate forests in British Columbia. In particular, studies are concerned with defining the organizing principles that elicit community patterns associated with the various levels of complexity in arboreal communities. Our long-term goal is to provide a greater degree of predictability when addressing temperate forest diversity issues. To meet the stated goals of sustainable forest management and retention of biodiversity, an extensive plan of ecological research that features arthropods is needed. This plan, fostered by Dr. Ring, should have as a priority the inventory and cataloguing of species assemblages and should address dynamic processes such as organismal dispersal and the effects of habitat loss and fragmentation on arthropods in ancient forests.

Résumé—Ce travail est un hommage au Prof. R.A. Ring. Il traite de la richesse des données de base accumulées sur la structure et le fonctionnement de la canopée de la forêt pluvieuse tempérée au cours des 12 dernières années (1993–2005) dans un programme en émergence de recherche sur la canopée. Les études faites à des sites de recherche sur l'île de Vancouver, Colombie-Britannique, montrent que les écosystèmes de la canopée de l'ancienne forêt pluvieuse tempérée contiennent une faune qui est, en grande partie, non décrite et qui est spécifique aux habitats particuliers que l'on ne trouve que là. Notamment, il y a divers peuplements d'acariens libres qui prédominent chez les espèces de conifères et dans les microhabitats de la canopée. Par exemple, les oribates forment le groupe dominant de la faune d'arthropodes sur les branches, les branches porteuses de lichens et dans les accumulations de sol suspendu. La composition spécifique dans les sols et celle de la canopée diffèrent significativement, tant au niveau des familles qu'à celui des espèces. La spécificité en fonction des arbres peut être due à des variations intrinsèques de la qualité de l'habitat, de l'architecture de l'habitat, de sa distribution contagieuse et (ou) de la disponibilité des ressources. Les patrons dominants de spécialisation des habitats, la mobilité réduite et les répartitions restreintes d'un pourcentage important des microarthropodes résidant dans la canopée sont des caractéristiques souvent associées aux écorégions forestières qui ont bénéficié de conditions stables pendant de longues périodes, comme c'est le cas des forêts anciennes de l'île de Vancouver. Les chercheurs du « one-Ring lab » continuent d'accumuler des informations sur la diversité et l'abondance des arthropodes de la canopée dans les forêts de

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la Colombie-Britannique. En particulier, certaines études cherchent à découvrir les principes d'organisation qui génèrent les patrons de communauté associés aux différents niveaux de complexité des communautés dans les arbres. Notre objectif à long terme est d'obtenir un plus grand pouvoir de prédiction dans les études qui s'intéressent à la question de la diversité des forêts tempérées. Afin d'atteindre les objectifs fixés de gestion durable des forêts et de maintien de la biodiversité, il faudra un programme élargi de recherche écologique qui inclut les arthropodes. Ce programme, mis de l'avant par le Prof. Ring, doit avoir comme priorités l'inventaire et le catalogage des regroupements d'espèces et doit s'intéresser aux processus dynamiques, tels que la dispersion des organismes et les effets de la perte d'habitats et de la fragmentation, sur les arthropodes des forêts anciennes.

[Traduit par la Rédaction]

Introduction

Exploration of the last terrestrial biotic frontier (*sensu* Erwin 1983) has seen a proliferation of collaborative forest canopy research projects throughout the world (*e.g.*, Basset *et al.* 2003; Roslin 2003). Standard terminology (Moffett 2000) and joint international research projects such as the IBISCA project (Investigating the Biodiversity of Soil and Canopy Arthropods 2003–2005) in Panama are directing canopy researchers to explore an increasing number of biodiversity-related questions such as those listed by Roslin (2003) and Ozanne *et al.* (2003). The nature and limits of canopy biology outlined by Moffett (2001) offer a constructive set of steps that contribute to "putting the canopy into canopy biology" — a useful exercise for canopy biologists to consider when exploring the high frontier.

With significant input from the canopy research community, our focus on canopy arthropods from study sites on Vancouver Island, British Columbia, has enabled us to compile an extensive database (*e.g.*, Ring and Winchester 1996; Winchester 1997; Behan-Pelletier and Winchester 1998; Fagan 1999; Fagan and Winchester 1999; Winchester and Ring 1999; Winchester *et al.* 1999) showing that these canopy ecosystems contain a largely undescribed arthropod fauna that is specific to habitat features found only there. Deforestation and habitat loss are causing a significant decline in species worldwide (Didham and Lawton 1999; Luck *et al.* 2003; Sax and Gaines 2003), and forest canopies are among the most species-rich and highly threatened terrestrial habitats (Ozanne *et al.* 2003). At a regional scale, current patterns of forest harvesting in Canada, particularly in British Columbia, contribute to habitat loss for canopy-dependent species. This in turn may result in changes in species richness and evenness where large-scale habitat loss and fragmentation exert significant stressors on communities (see Didham 1997). For example, many of the lowland forests on Vancouver Island have been cleared and are now in various stages of regrowth. As the demand for timber products grows, the extent of habitat loss in coastal forests also increases, and there has been a steady shift in timber extraction from low-elevation to high-elevation sites (Fagan 1999). Changes in forest structure through logging and subsequent management plans have undesirable consequences for other components of forest ecosystems (Spies 1998). For example, the disruption of the complex vertical stratification that is a prevalent feature of ancient forests (Ozanne *et al.* 2003) and the fragmentation of these landscapes (Didham 1997) have heightened awareness of the need to understand the endemic fauna and flora (Scudder 1994; Humble *et al.* 2000) and apply system-based conservation approaches across a wide range of forest types (Harding and McCullum 1994).

Historically, little research on the conservation of biodiversity has been done in the canopies of ancient forests in British Columbia (Winchester and Ring 1996*a*, 1999). As a consequence, the exact impacts of habitat change on the arthropod communities of these canopies are poorly documented and theoretically not well understood. In British Columbia, canopy habitats are thought to contain a significant portion of the invertebrate biodiversity in these forests (see Winchester and Ring 1996*a*, 1996*b*). Canopies often have diffuse boundaries with other components of forest ecosystems and this spatial (and temporal) mosaic creates a dynamic and complex set of microhabitats utilized by a variety of species.

The arthropod species associated with these ancient forests form a heterogeneous assemblage, and nowhere is this more evident than in the canopy. In particular, Acari are the dominant

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fauna in the temperate canopies of the Pacific Northwest (Moldenke and Fichter 1988; Moldenke and Lattin 1990; Behan-Pelletier and Winchester 1998; Schowalter and Ganio 1998; Winchester and Ring 1999) and have been shown to dominate conifer species and canopy microhabitats (Behan-Pelletier and Walter 2000). For example, oribatid mites are the dominant fauna on branches, branches with attached lichens, and suspended soil accumulations (Winchester and Ring 1999).

Arthropods are an integral part of these aerial ecosystems and may regulate nutrient cycling (Ozanne *et al.* 2003; Wardle *et al.* 2003; Didham and Fagan 2004) and decomposition (Fagan 1999; Wardle *et al.* 2003). Traditionally, the forest canopy has been viewed simply as a source of organic material for decomposition processes that occur after litter falls to the forest floor (Dickinson and Pugh 1974). However, decomposition processes also occur within the canopy and provide a substrate that supports a diverse oribatid community (Winchester and Behan-Pelletier 2003). These rich accumulations of debris and litter, or "suspended soils" (*sensu* Delamare-Debouteville 1951), provide the habitat for a high abundance and diversity of soil-dwelling arthropods, particularly oribatid mites (Winchester *et al.* 1999). For example, Winchester (1997) found only 18% similarity between the canopy and ground species of oribatid communities of a Sitka spruce (*Picea sitchensis* (Bong.) Carr.; Pinaceae) forest on Vancouver Island. Many oribatid species appear to be restricted to microhabitats that are associated only with ancient forests.

Investigators in the "one-Ring lab" continue to document the diversity and abundance of canopy arthropods of temperate forests in British Columbia. In 2005, Stacey Wilkerson completed her master's research examining the effect of variable retention stands on trophic feeding guilds and microarthropod diversity in the canopy of Pacific silver fir trees (*Abies amabilis* (Dougl. *ex* Loud.) Dougl. *ex* Forbes; Pinaceae). Research on microhabitats in the high canopy of ancient forests is a current Ph.D. project of Zoë Lindo; she is investigating island biogeographic principles and metacommunity dynamics of oribatid mites in suspended soils of ancient Western red cedar trees (*Thuja plicata* Donn *ex* D. Don; Cupressaceae). The long-term goals of our laboratory are to collect data on species diversity patterns of canopy oribatids at local and regional scales to test assumptions of neutral theory proposed by Hubbell in 2001 and summarize empirical patterns of species abundance and spatial species turnover (beta-diversity). In this paper I summarize the following: (*i*) patterns of invertebrate diversity associated with canopy habitats in temperate forests; and (*ii*) results from an experimental approach on colonization of needle litter in a montane forest.

Methods and materials

The investigation of temperate ancient rain forests and the arthropod communities associated with suspended soils in them is an avenue of research and development of sampling protocols and canopy access that has been "fine-tuned" since 1992 (see Winchester 2002) and applied to eight sites on Vancouver Island, British Columbia. Characteristics of the primary study sites and details of our canopy sampling procedures can be found in Winchester (1997) (Carmanah Valley) and Fagan (1999) (Mount Cain).

Results and discussion

Invertebrate responses to canopy habitats: the structural complexity association

Canopy habitats are three-dimensional systems (Parker and Brown 2000) whose physical architecture provides a habitat template (*sensu* Southwood 1996) for invertebrates. Tree architecture is one of the most important variables to take into account in the study of arboreal species assemblages (Didham and Fagan 2004). Increasing structural complexity results in an increase in invertebrate diversity (Southwood 1996). This is related to both architectural complexity (*e.g.*, resource heterogeneity) and spatial complexity (arrangement of microhabitats in tree crowns), leading to a concomitant increase in living space that is almost inevitably positively correlated with an increase in arthropod diversity (Southwood *et al.* 1979, 2004). For example, Southwood (1996) noted that an old beech tree occupying 6 m^2 of ground surface had a summer surface area of 11 000 m^2, which, for small animals (*e.g.*, insects), provided a structurally complex habitat that resulted in increased diversity. Similarly, Winchester (1997) and Fagan and Winchester (1999) found that Collembola diversity increased significantly as habitat complexity increased. Bultman and Uetz (1984) found that

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Table 1. Taxonomic comparison of the suborder Oribatida from six study sites in the Pacific Northwest, North America.

Site	Forest type	Canopy habitat	No. of families	No. of genera	No. of species
MASS (49°55′N, 125°25′W)	Montane	Branch–needle	17	20	25
MASS (49°55′N, 125°25′W)	Montane	Lichen	18	25	27
Wind River (48°44′N, 124°37′W)	Inland	Lichen	13	14	16
Mount Cain (50°13′N, 126°18′W)	Montane	Needle–debris	23	35	43
Maquilla Peak (50°13′N, 126°18′W)	Montane	Needle–debris	12	17	20
Carmanah (48°44′N, 124°37′W)	Coastal	Suspended soil	23	26	37
Walbran (48°39′N, 124°35′W)	Coastal	Suspended soil	31	45	54

Note: All sites are located on Vancouver Island, British Columbia, Canada, except for the Wind River site, which is in Washington, United States of America. MASS, Montane Alternative Silviculture Site. Structural complexity increases from branch–needle to lichen to needle–debris to suspended soil habitats.

litter complexity and not nutritional content was the most influential variable affecting Araneae abundance. Work by Bengtsson (2003) on the temporal predictability of ground-level forest soil communities indicated that the higher taxa of communities not subjected to environmental impacts (*e.g.*, forest management practices) are quite predictable over time. Results from these and other studies have yet to be tested in the canopy, where they may provide insights into the relationships between habitat structure and community composition.

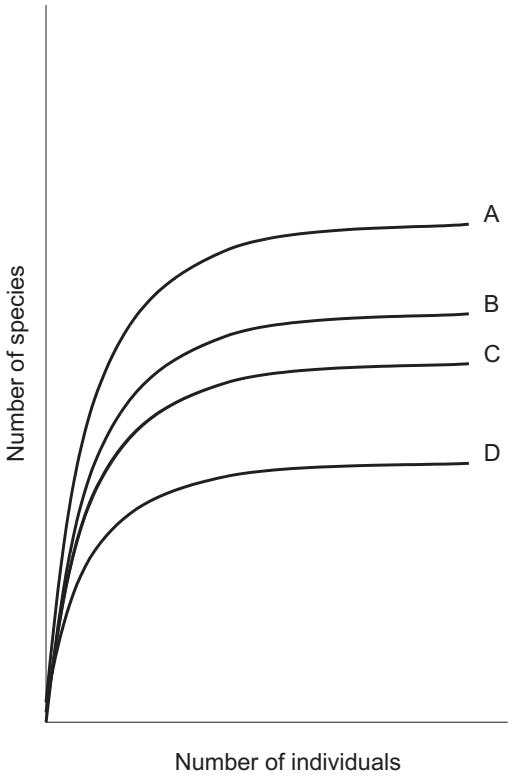
Structural space, often referred to as "ecospace" (Southwood 1996), is enhanced in old tree crowns (Franklin and Van Pelt 2004), where the accumulation of suspended soil mats (Winchester and Ring 1999), lichen species, and biomass (McCune *et al.* 2000; Goward 2003) is positively associated with tree age. Communities within apparently similar habitats in different parts of the ecospace may be quite distinctive (Southwood 1996). Results from 12 years of research on Vancouver Island have consistently documented less than 30% species similarity between the oribatid mite communities in suspended soils and those in ground-level soils (Winchester 1997; Behan-Pelletier and Winchester 1998; Fagan 1999). These canopy microhabitat – diversity relationships are currently being investigated (*e.g.*, Walbran Valley, Montane Alternative Silviculture Site (MASS), Vancouver Island); with increased site replication, standardized sampling, and detailed examination of canopy microhabitats, these investigations address, in part, some of the concepts related to community diversity presented by Winchester (1997), Behan-Pelletier and Winchester (1998), Schowalter and Ganio (1998), and Fagan (1999), who explored correlations between oribatid diversity and architectural complexity in canopy habitats (Table 1, Fig. 1).

A detailed study of temperate arboreal communities was conducted by Fagan (1999), who found that temperate montane Pacific silver fir trees supported a diverse community of ground and canopy invertebrates composed primarily of Acari, Collembola, Homoptera (*e.g.*, aphids and scale insects), Psocoptera, Tardigrada, Diptera, and Arachnida (*e.g.*, spiders and pseudoscorpions), in decreasing order of abundance (Table 2). This general pattern of faunal composition is in close agreement with findings from other studies of temperate arboreal communities (*e.g.*, Pettersson *et al.* 1995; Schowalter and Ganio 1998) and is supported by the ordinal patterns recorded during previous work on Vancouver Island (*e.g.*, Winchester *et al.* 1999). Of note is that the species of Oribatida in the coastal lowland Sitka spruce and western red cedar canopies on Vancouver Island tend to exceed those in the montane Pacific silver fir canopy, largely because Sitka spruce and western red cedar tree crowns often support deep (>5 cm) moss mats that provide a significant habitat resource for invertebrates and are thus capable of supporting a larger fauna (Table 1) (Winchester 1997; Winchester and Ring 1999; Winchester *et al.* 1999). In addition, increasing accumulations of conifer needle litter on branches and in the forks of branches in the crown region support a greater diversity of arthropods (Winchester 1997). Hypotheses to explain microarthropod diversity in arboreal habitats are currently being tested by investigating the diversity patterns (increasing species

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Fig. 1. An architectural complexity template indicating the relationship between species richness, number of individuals, and architectural complexity found in the high canopy of ancient temperate rain forest trees. Microarthropod richness is positively associated with architectural complexity. Architectural complexity decreases from A (suspended soils) to B (needle litter) to C (lichen) to D (branches and needles).



richness and abundance with increasing architectural complexity) observed by Winchester (1997) and Fagan (1999) (Fig. 1).

The oribatid fauna of rain forest canopies is composed of multiple phylogenetic lineages that have radiated extensively (Walter and Behan-Pelletier 1999). Just how many individuals an ancient forest tree supports is difficult to determine, but extrapolations for Sitka spruce trees indicate that the abundance of oribatid mites alone exceeds 3.5 million individuals (Table 3). How many oribatid species an ancient forest tree supports remains unknown. What governs species richness and relative abundance distributions within trees? If one considers trees to be ecological islands (*e.g.*, Southwood 1996) that contain spatially discrete microhabitats such as suspended soils (Winchester 1997) or epiphytes (Wardle *et al.* 2003), then basic concepts of island biogeography (MacArthur and Wilson 1967) may help to explain observed species richness and abundance patterns. Tree species are important in determining the composition of insect communities, but characteristics of individual trees determine the relative abundance of the taxa (Winchester 1997; Wardle *et al.* 2003).

An informative view of canopy arthropods can be gained by placing them in trophic guilds. The number of insects on individual trees has been shown to vary with tree species and size and the proportional distribution of insects among guilds (Southwood *et al.* 1982). Winchester and Ring (1999) observed consistency in the richness of species assemblages among individual Sitka spruce trees, but the proportions of insects in the phytophagous and predator guilds varied. Where trees differed in the proportions of insects represented by each guild, accumulation of a single species in the phytophagous guild (*e.g.*, aphids) was driving the pattern. Guilds in the arboreal community are shaped by characteristics of the trees, supporting the idea that these trees present a habitat template that may, within a community, dictate species richness but not evenness. Within guilds, the relative abundance of particular canopy arthropod species is not uniform among individual trees of the same species, and this is likely the result of myriad extrinsic factors coupled with the physical characteristics of the trees (*e.g.*, plant architecture or plant chemistry).

Abundance and richness of canopy invertebrates: a case study

Initial canopy research projects in Dr. Ring's laboratory focused on descriptive patterns of species abundance and distribution. Results from this work (*e.g.*, Winchester 1997) served to provide a framework for developing hypothesis-driven studies. To date, few canopy studies have been experimentally designed to look at the spatial and temporal variation in arthropod community structure (Didham 1997; Schowalter and Ganio 1998). The first such experiment in our laboratory was conducted by Fagan (1999), who used an experimental approach to address patterns of arthropod community structure in an ancient rain forest at the Mount Cain Coastal Montane Biodiversity Project (CMBP). The study area is a mosaic of high-elevation ancient forest (>700 years) with interspersed subalpine ponds and different-aged stands of intensively managed forest in the

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Table 2. General comparison of number of individuals of each taxon and percent contribution of each taxon to the insect fauna in pooled litter bags from Pacific silver fir (*Abies amabilis*) canopy and ground habitats sampled at Mount Cain (1997, 1998) and Maquilla Peak (1998), Vancouver Island, British Columbia; data from Fagan (1999).

	Canopy		Ground	
Taxon	No. of individuals	Percent contribution	No. of individuals	Percent contribution
Acari	1468	61.7	1516	63.1
Collembola	265	11.1	520	21.7
Homoptera	27	9.5	45	1.9
Psocoptera	124	5.2	0	0.0
Tardigrada	122	5.1	2	0.1
Diptera	38	1.6	112	4.7
Arachnida	29	1.2	26	1.1
Coleoptera	13	0.5	37	1.5
Thysanoptera	17	0.7	3	0.1
Hymenoptera	6	0.2	3	0.1
Neuroptera	1	0.1	0	0.0
Total	2381	100.0	2402	100.0
No. of litter bags	432*		75†	

*Mount Cain, 1997, 324 litter bags; Mount Cain, 1998, 54 litter bags; Maquilla Peak, 1998, 54 litter bags.

†Mount Cain, 1997, 39 litter bags; Mount Cain, 1998, 18 litter bags; Maquilla Peak, 1998, 18 litter bags.

Table 3. Estimated total number of oribatid mites supported by an ancient Sitka spruce (*Picea sitchensis*) tree.

Site	Ancient forest, Carmanah Valley
Tree age	>800 years
Tree height	>70 m
Mean branch length	3.9 m
Mean trunk diameter	1.4 m
Mean no. of live foliar units (branchlets)	30.5
Taxon	Oribatida (beetle mites)
Parameter estimates	1 foliar unit yields 800 mites
	30.5 foliar units per branch yield 24 000 mites
	Total number of limbs per tree = 145
	Total number of individuals = 145 × 24 000 = 3 538 000 mites

Note: Data are estimates taken from a single tree; the number of large branches was counted and the number of foliar units was estimated from a sample of 10 branches.

Coastal Western Hemlock and Mountain Hemlock biogeoclimatic zones (Meidinger and Pojar 1991). A detailed site description is provided by Fagan (1999).

Litter bags were placed in three randomly located Pacific silver fir trees at each of three elevations: 800 m, 1000 m, and 1200 m. Mesh litter bags (10 cm × 20 cm with 0.5 mm mesh) contained 10 ± 0.1 g of sterilized Pacific silver fir needle and branch material. At each tree, nine litter bags and three control bags were placed at random distances along three randomly chosen branches at fixed heights. In total, 108 litter bags were collected; microarthropods were extracted using a Lussenhop extractor and stored in 75% ethanol. For further details of the sampling design and protocol see Fagan (1999).

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A total of 2381 invertebrates were extracted from 432 canopy litter bags (Table 2). Dominant arthropod classes included Arachnida (62.9%), Insecta (17.8%), and Collembola (11.1%). Acari accounted for 50% of the total invertebrate abundance, and the mite fauna colonizing the litter bags was diverse. Overall, faunal composition was similar to that found in other temperate forest canopy studies in the Pacific Northwest (*e.g.*, Carmanah Valley, Winchester 1997). Oribatida dominated the fauna with a number of ubiquitous canopy species (*e.g.*, *Scapheremaeus* near *palustris* (Sellnick) (Acari: Cymbaeremaeidae), *Dendrozetes* sp. (Acari: Pelopidae)).

Total invertebrate abundance at each of the three elevations increased significantly over time (nested ANCOVA, $\alpha = 0.05$, $F_{1,237} = 111.93$, $P < 0.0001$) (Fig. 2). Colonization time is a significant factor affecting the abundance of most arthropod taxa (Bultman and Uetz 1984; Fagan 1999), and this may be due to a number of factors. In this study the majority of species showed a clear preference for colonizing needle litter bags at specific times in the decomposition sequence and at specific elevations. Very few of the canopy mite species were generalists with respect to their distribution in space and time. Increased abundances have been attributed to nutritional quality, as decomposition over time provides a nutritionally rich substrate for soil microarthropods (Bultman and Uetz 1984; Hasegawa 1997). In the CMBP study, resource quality (*e.g.*, fungal growth) within the litter bags increased over time, thereby providing a food source that in turn supported higher invertebrate abundances.

A total of 77 canopy species in the suborders Oribatida (including Astigmata; 1000 specimens and 48 species), Prostigmata (137 specimens and 15 species), and Gamasida (52 specimens and 14 species) were extracted from the litter bags (Fagan 1999); all species followed the same temporal pattern of colonization (nested ANCOVA, $\alpha = 0.05$, $F_{1,232} = 61.96$, $P < 0.001$) (Fig. 3). Fagan (1999) considered the relationship between Acari diversity and 18 spatial environmental variables and found that time (the time available for colonization) and elevation (high-elevation site, 1200 m) explained significant variation in mite species abundance data (Fig. 4). However, the total amount of variance in the data that was explained by these variables was small; the majority of the spatiotemporal variation in mite community structure may be due to unmeasured variables such as plant architecture, host tree specificity, and microenvironmental habitat heterogeneity (Fagan 1999). For example, distribution patterns of arboreal mites have been related to the presence and structure of epiphytes (Woltemade 1982; André 1985), increasing leaf structural complexity (Walter *et al.* 1994), and substrate characteristics such as moisture content, temperature, and pH (Wallwork 1983; Schenker 1984).

Conclusions

Determination of the organizing principles that elicit patterns associated with the various levels of complexity in arboreal communities will provide a greater degree of predictability when addressing temperate forest diversity issues. Canopy microhabitats are a critical component in the study of forest diversity. The forest canopy biota is diverse, specialized, and contains many species with very limited ranges (although beta-diversity and local endemism have yet to be rigorously addressed). However, evidence indicates that many canopy species are restricted to these arboreal islands, are poor dispersers, and are subject to extirpations at the population level (*e.g.*, Centinelan extinctions, Winchester and Ring 1996*a*). Given the catastrophic loss of coastal temperate rain forest canopy habitats, it is highly likely that these canopy communities have already experienced a wave of arthropod extinctions.

The prevalent patterns of habitat specialization (Shaw and Walter 2003; Walter 2004), low vagility (Winchester *et al.* 1999), and restricted distribution (Humble *et al.* 2000) displayed by a large percentage of canopy microarthropods are features often associated with forest ecoregions that have enjoyed relatively stable conditions for long periods of time, as have the ancient forests on Vancouver Island. Those studying canopy arthropods should not, however, assume that species assemblages are similar in geographically separated forest types (*e.g.*, montane *versus* coastal). Temperate canopy communities are considerably more complex than previously thought, and spatiotemporal variations in relative abundance and species composition may not be merely noise in the data. Both vertical and horizontal gradients within single trees can yield significant differences in invertebrate abundance and species richness.

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Fig. 2. Mean (±1 SE) abundance of all invertebrates as a function of increasing time since colonization of experimental needle litter bags in *Abies amabilis* tree crowns at Mount Cain, Vancouver Island, British Columbia, 1997. Circles and solid fitted regression line, 800 m elevation; squares and dashed fitted regression line, 1000 m elevation; triangles and dotted fitted regression line, 1200 m elevation. Figure is reproduced with permission from Fagan (1999).

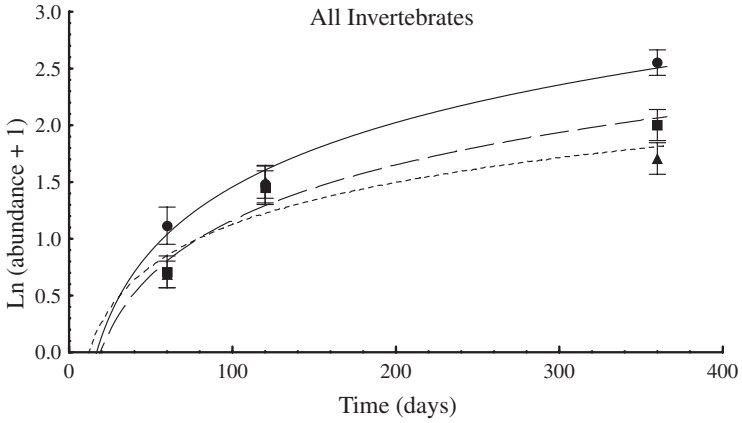
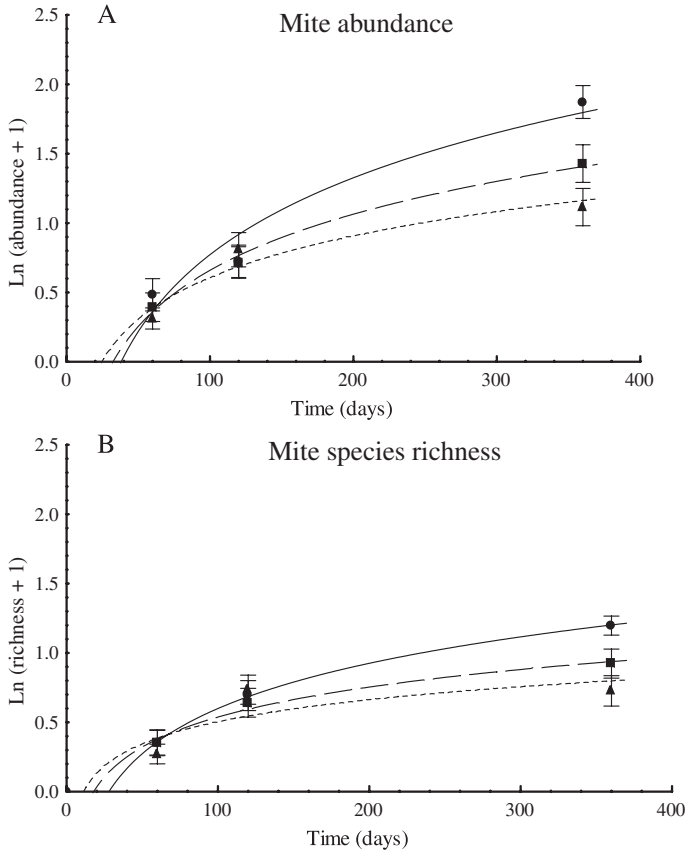


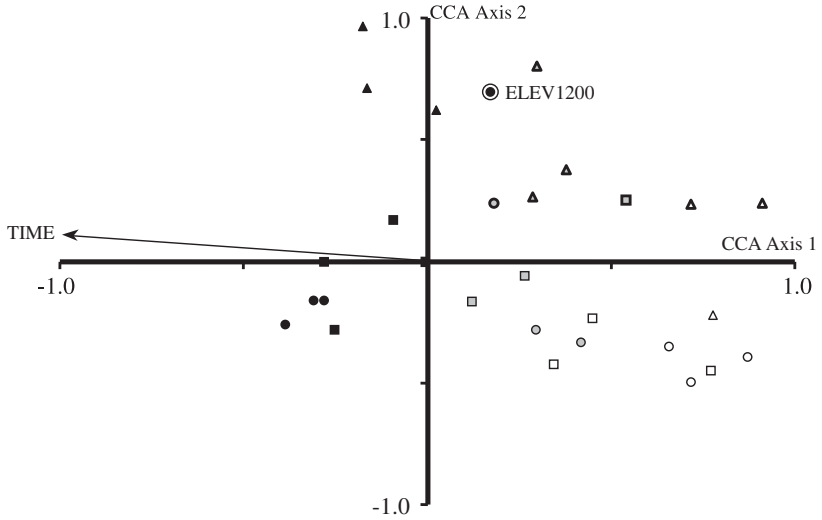
Fig. 3. Mean (±1 SE) abundance (A) and species richness (B) of Acari as a function of time available for colonization of needle litter bags in *Abies amabilis* tree crowns at Mount Cain, Vancouver Island, British Columbia, 1997. Circles and solid fitted regression lines, 800 m elevation; squares and dashed fitted regression lines, 1000 m elevation; triangles and dotted fitted regression lines, 1200 m elevation. Figure is reproduced with permission from Fagan (1999).



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Fig. 4. Canonical correspondence analysis biplot of variation in mite species community structure, showing significant environmental variables (arrow, continuous variables; centroid, nominal variables), sites (circles, 800 m elevation; squares, 1000 m elevation; triangles, 1200 m elevation), and time (open symbols, 60 days; shaded symbols, 120 days; solid symbols, 360 days). Figure is reproduced with permission from Fagan (1999).



The previous 10 years of canopy research in Dr. Ring's laboratory have established a wealth of baseline information on the structure and functioning of temperate rain forest canopy arthropod communities. Research is currently directed towards the design and implementation of biodiversity conservation measures in the ancient forests of Vancouver Island. Findings clearly indicate that the following points should be taken into account:

(1) arboreal habitats act as reservoirs for arthropod biodiversity;
(2) microhabitat features important for long-term residency of some species within the canopy are found only in intact coastal ancient rain forests;
(3) species assemblages will be lost if these ancient canopy habitats are not retained or are not allowed to develop in second-growth forests;
(4) oribatid mites can be used as exemplars for other suspended soil microarthropods; and
(5) conifer canopy specificity will also be pronounced in groups such as Collembola and other mite suborders.

Future directions of canopy research

Although many countries, including Canada, signed the Rio Convention on Biological Diversity in 1992, and the ecological, economic, and social importance of sustaining forest ecosystems has been clearly outlined in several policy initiatives (*e.g.*, Government of Canada 1995), current policy and subsequent actions have not resulted in the objective of "the maintenance of biodiversity (form and function)" being included in forestry practices in our national forests. Nowhere is this more evident than in forest canopies. We still assume that current silvicultural practices and second-growth forest management with harvest rotations of 80–120 years somehow mimic the natural dynamics of ancient forests. Clearly this is not supported by empirical data. Rotation lengths of 80–120 years are not sufficient for the re-establishment of the suspended soil microhabitats of ancient forests, which contain the majority of canopy arthropod diversity. To meet the stated goals of sustainable forest management and retention of biodiversity, an extensive plan of ecological research that features arthropods is needed. This plan should have as a priority the inventory and cataloguing of species assemblages and should address dynamic processes such as organismal dispersal and the effects of fragmentation of ancient forests. This is the challenge for policy makers, managers, and the canopy research community in Canada.

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