Conservation of Biodiversity: Guilds, Microhabitat Use and Dispersal of Canopy Arthropods in the Ancient Sitka Spruce Forests of the Carmanah Valley, Vancouver Island, British Columbia.

by

Neville N. Winchester
BSc., University of Victoria, 1980
MSc., University of Victoria, 1984

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Supervisor: Dr. Richard A. Ring

Abstract

The high canopy (33m-65m) from an ancient Sitka spruce forest in the Carmanah Valley on Vancouver Island, British Columbia, was investigated to examine the structure and diversity of the arthropod fauna. A fixed-access canopy system was developed to facilitate arthropod sampling in this habitat.

Within the canopies of 5 ancient Sitka spruce trees, arthropods associated with branches were collected by cutting 270 branches over 6 time intervals. Branches were enclosed in plastic bags and contents were examined in the laboratory where 1,268 individuals were enumerated and assigned to feeding guilds. Arthropods associated with the branches in the canopy were dominated by individuals in the phytophagous, predator and parasitoid guilds. Individual trees and seasonality both contributed significantly to the proportional structuring of the phytophagous and predator guilds. Vertical partitioning was not a significant factor in guild proportionality. Interaction effects were only significant for the phytophagous guild. The documentation of high predator loading in a structurally and functionally diverse ecosystem such as ancient forest canopies is in concert with previous studies and supports observations on reduced herbivory in mature, structurally complex forests. I suggest that canopy habitats provide a template important for examining questions about the maintenance of biodiversity in ancient forests. Further understanding of the factors involved may provide us with predictive information that could be used to examine patterns in community structure and provide answers to process-driven biodiversity and conservation questions.

I collected samples bi-weekly throughout the growing season, from replicated moss/soil samples and malaise traps from 5 study sites associated with the ancient Sitka spruce forests: 2 ancient forest Sitka spruce canopies, ancient forest interior, transition zone (edge between ancient forest and clear-cut), and clear-cut (6 years old). I recorded 71 species of Oribatida (2,117 specimens), representing 51 genera and 34 families. Taxonomic distinctness was most pronounced in the canopy moss/soil mats where oribatid mites are members of a distinct arboreal community that is not just a random sub-set of the ground fauna. Comparisons between the high-canopy and three ground sites indicated that overall, species percent similarity was low. Thirty and 28 species of oribatids were recorded from the 2 canopy sites, of which 12 species are canopy specific. Species exhibiting strict arboreal specificity are all in the Brachyphlina, from the families Thyrisomidae, Damaeidae, Eremaeidae, Oripodidae, Gymnodamaeidae, Oppiidae, Peloppiidae, Galumnatidae, and Cymbaeremaeidae. I consider oribatids of the canopy to be inhabitants of islands, in the sense that they are isolated from their ground counterparts and have a distinct fauna that is characterized by two ecological groups of species; wandering species with dispersal capabilities and arboreal species with low dispersal capabilities. I conclude that oribatid mites can be used as a surrogate for other ancient forest soil microarthropods, and predict that arboreal specificity will also be pronounced in these taxa.

I explored dispersal capabilities further, where 36 species of Oribatida (2596 specimens), representing 29 genera and 21 families were recorded from replicated malaise traps positioned in the canopy and on the forest floor. Colonization of malaise traps was 100% in the canopy, 91% in the forest floor and 47% in the clear-cut. Nine of these species were not recorded using high gradient extractions of moss/soil from the canopy or forest floor or clear-cut. Thirty of these species are Brachypylina, with the families Eremaeidae, Peloppiidae and Ceratozetidae represented by three or more species. Colonizing specimens were predominantly adult, and represent sexually vreproducing taxa: immatures comprised only 0.9% to 4.2% of specimens. *Ceratoppia* spp., *Eporibatula* sp. 1, *Dorycranosus* sp.1, *Sphaerozetes* sp. 1 and *Oribatella* sp. 1 had a frequency > 50% in the forest floor malaise traps, and *Eporibatula* sp. 1, *Sphaerozetes* sp. 1 and *Dendrozetes* sp. 1 had a frequency > 50% in canopy malaise traps. Phoresy as a source of the oribatid fauna in the malaise traps is unlikely as only *Paraleius* sp. 1 of the species represented is modified for this mode of dispersal. The number of species recorded from malaise traps, and the frequency, relative abundance and seasonality of many of them support the hypothesis that active aerial dispersal by random movement is an important mode of colonization of canopy habitats.

I examined features related to the Centinelan extinction concept and asked whether or not this is applicable to northern temperate ancient forest arthropods. Habitat loss in these forest systems on Vancouver Island is well documented and at present, of 89 ancient forest watersheds over 5000 ha in size, only 6 remain undisturbed by logging. Examination of identified arthropod species (1,311 to date), indicates that the structurally complex habitat acts as a reservoir for biological diversity. Of particular importance to the maintenance of arthropod biodiversity is the documentation of those species that are new to science or species that are restricted to habitats only found in ancient forests. The new species (approx. 120) so far recorded represent a contribution towards categorizing the endemic arthropod fauna of this ancient forest. I expect that, with continued taxonomic resolution, this list of undescribed species will be significantly increased. Specific examples include *Hypogastrura arborea* Fjellberg, *Anacliliea vallis* Coher and *A. winchesteri* Coher, *Cinara n. sp.* Voegtlin, and *Miniliomosina n. sp.* Marshall. This type of habitat specificity is well documented for the oribatid mites and for the staphylinid beetles where I have documented 8 new species of Omaliinae which appear to rely on ancient forests as a source area to maintain reproductively viable subpopulations. Without proper documentation, I suggest that the arthropod fauna of ancient forests contain species that are candidates for the Centinelan extinction concept -- extinction of species unknown before their demise and hence unrecorded.

In conclusion, my studies present evidence from several arthropod groups to indicate that the ancient forests of the Carmanah Valley act as a source habitat for several species, many of which are currently undescribed. Habitat specificity is most pronounced in the canopy where soil micro-arthropods such as the oribatid mites exhibit arboreal specificity. The importance of describing these species assemblages coupled with the inclusion of dynamic processes such as dispersal into the framework of how we think about arthropods in ancient forests is a challenge that lies ahead for the entomological research community. Recognizing these components should assist efforts in addressing the conservation of biodiversity in these ancient forests.

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THESIS PAPERS

PAPERS 1-4

This thesis is based on the following papers, which will be referred to by their Arabic numbers and are contained in chapters 1-4.

1. **CHAPTER 1.**

   Winchester, N.N. 1997. Canopy arthropods of coastal Sitka spruce trees on Vancouver Island, British Columbia, Canada. Pp. 151-168 *In* N.E. Stork, J.A. Adis, and R.K. Didham, (Eds.), Canopy Arthropods, Chapman and Hall, London.

2. **CHAPTER 2.**

   Winchester, N.N., V. Behan-Pelletier and R.A. Ring. Arboreal specificity, diversity and abundance of canopy-dwelling oribatid mites. Manuscript for Pedobiologia.

3. **CHAPTER 3.**

   Behan-Pelletier, V. and N.N. Winchester 1997. Arboreal oribatid mite diversity: colonizing the canopy. Journal of Soil Ecology (accepted paper).

4. **CHAPTER 4.**

   Winchester, N.N. and R.A. Ring 1996. Centinelan extinctions: extirpation of Northern temperate old-growth rainforest arthropod communities. Selbyana 17(1): 50-57.

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I acknowledge with thanks the Western Canada Wilderness Committee who made available the research facility and the fixed canopy access system in the Upper Carmanah Valley. Field work was supported by FRDA research grants from the B.C. Ministry of Forests, Research Branch. Acknowledgement is made to A. Mackinnon and B. Nyberg of that Branch for their continued support.

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I am indebted to numerous taxonomic experts for identifications and the continued advice that they provide for this thesis and for my other canopy projects. Taxonomic contributions are invaluable and form the essence for understanding arthropod biodiversity in ancient forests and I extend thanks to: R.S. Anderson, G.E. Ball, V. Behan-Pelletier, R.G. Bennett, Y. Bousquet, D.E. Bright, F. Brodo, D. Buckle, J.F. Burger, J.M. Campbell, R.A. Cannings, D.S. Chandler, E.I. Coher, B.E. Cooper, A. Davies, R. Duncan, the late G. Eickwort, A. T. Finnamore, A. Fjellberg, B. Foottit, G.A.P. Gibson, H. Goulet, K.G.A. Hamilton, J. Huber, L.M. Humble, E.E. Lindquist, S.A. Marshall, L. Masner, E.L. Mockford, A.P. Nimmo, J.D. Oswald, S.J. Peck, D. Pollock, F. Rafi,

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Finally, to my supervisor, colleague and friend, Dr. R.A. Ring, a special thanks for your continued support and involvement in all aspects of this project. I look forward to many more years of collaboration and exploration in one of the last great unexplored frontiers- ancient rainforest canopies. Spirit of the Raven!

DEDICATION

IN MEMORY OF

RANDY STOLTMANN

&

MARK WARING

-TO ALL TIRELESS DEFENDERS OF NATURE-

" Carmanah-Walbran-Clayoquot were like a chain reaction. I have a hunch that if there hadn't been a Carmanah struggle, there would never have been a Protected Area Strategy"

R. Stoltmann 1995

General Introduction

In this thesis I present the results of 4 papers that investigate the ecological relationships of forest canopy arthropods to habitat characteristics of ancient forests. Specifically, paper 1 examines the functional roles of canopy arthropods by using feeding guilds to provide an understanding of patterns in community structure--(functional biodiversity). Papers 2 and 3 compare the resident oribatid fauna that inhabits the canopy of ancient Sitka spruce trees with the surrounding forest habitat types: ancient forest floor, edge (area between the ancient forest floor and clear-cut), and clear cut--(compositional biodiversity). Fundamental to the basic elements of conservation of biodiversity is the documentation of abrupt changes in ecosystems. Anthropogenic activity (mainly logging) has altered the ancient forest landscape, causing changes in habitat structure and arthropods respond to these changes in a myriad of different ways. In paper 4, I explore responses that arthropod species assemblages exhibit in relation to habitat changes in the context of the Centinelan extinction concept.

Conservation of Biodiversity in Northern Temperate Rainforests

The global biodiversity crisis continues to be accelerated by habitat loss (Wilson 1988, 1989, 1992; Soulé, 1991; Raven and Wilson 1992; Deharveng, 1996; Laurance 1997) and consequent extinctions of floral and faunal species assemblages (Lockwood 1987; Erwin 1991b; Whitmore and Sayer, 1992) that cannot adjust to rapid, and often large-scale, habitat alterations (Winchester and Ring 1996a,b; Stork *et al.* 1997; Winchester 1997a). The ultimate goal in recording biological diversity is to build a factual foundation for answering basic questions about evolution and ecology (May 1992). The setting for building this foundation is the natural landscape which represents a mosaic of geological, environmental, ecological and evolutionary processes. With increased human disturbance across virtually all natural landscapes, the focus to study and preserve biological diversity has been centered in the tropics where rapid habitat loss is most pronounced in forests.

These biotopes are thought to contain more than half of the world's species (Wilson 1988, 1992; Ehrlich 1988).

However, it is a global reality that forests throughout the world are being compromised by human-induced perturbations (see Laurance 1997). In temperate zones some of the last remaining tracts of intact ancient coniferous forests occur in the Pacific Northwest of North America (Franklin 1988) and the "coastal temperate rainforest" of British Columbia represent approximately 25% of the worldwide coastal temperate rainforests (Kellogg 1992). In British Columbia, intact coastal ancient forests are becoming endangered systems (Winchester 1993, 1997c; Winchester and Ring 1996a,b) and figures suggest that 49% by area "old growth" (vs. 53% "mature" from satellite imagery) remain as of 1995 (MacKinnon and Eng 1995). Nowhere is the reduction of ancient forests more apparent than on Vancouver Island where during the last 60 years an increase in logging activities has reduced intact watersheds so that only 6 of 89 remain (> 5000 hectares) (Winchester 1993, 1997c; Winchester and Ring 1996a,b). The ongoing fragmentation of these landscapes has heightened the awareness for a need to understand/determine the endemic fauna and flora (Scudder 1994) and apply system-based conservation approaches across a wide range of forest types (Murray *et al.* 1993; Harding and McCullum, 1994).

Arthropods in Northern Temperate Rainforests

Historically little research concerning the conservation of biodiversity has been done in the ancient forests of the Pacific Northwest (Winchester 1993; Winchester and Ring 1996b) and this research has generally failed to link results to ecosystem processes. In British Columbia these forests are thought to contain much of the biodiversity of the province (Fenger and Harcombe 1989; Bunnell, 1990; Pojar *et al.* 1990; Winchester and Ring 1996a,b). They often have diffuse boundaries with other ecosystems, and this temporal and spatial mosaic creates a dynamic and complex set of habitats that are utilized by a variety of species. The faunal elements associated with these forests form a heterogeneous group, and nowhere is this more evident than in the arthropods. Arthropods, primarily insects, are an integral part of most old-growth forests and may comprise 80-90% of the total species in these systems (Asquith *et al.* 1990). They play a primary role in the function of natural ecosystems (Ehrlich and Mooney 1983; Lattin and Moldenke 1990; Moldenke and Lattin 1990; Wiggins *et al.* 1991; Schultz and Mooney 1993; Lerdau 1997), may regulate nutrient cycling (Mattson and Addy 1975; O'Neill 1976; Moldenke and Lattin 1990; Naeem *et al.* 1994, 1995) and are now frequently mentioned as important components of diversity that need to be identified and conserved (May 1986; Wilson 1988; di Castri *et al.* 1992; Samways 1992, 1994).

Canopy Arthropods

The study of forest canopies in determining the structure of arthropod assemblages and the systematics of canopy arthropods has increased rapidly during the last 20 years (Stork and Best 1994; Stork *et al.* 1997). In general, canopies of rainforests contain a large percentage of the species present in these forest systems and the most speciose group is the arthropods (see Stork *et al.* 1997). Canopies of natural forests in temperate (Schowalter 1989; Winchester and Ring 1996a,b; Behan-Pelletier and Winchester 1997; Winchester 1997a,b) and tropical regions (Erwin and Scott 1980; Erwin 1983; Stork 1988; Bassett and Kitching 1991; Basset 1997, 1996, 1994; Didham 1997; Davies *et al.* 1997; Hammond *et al.* 1997; Kitching *et al.* 1997) contain largely undescribed and little understood assemblages of arthropods that have greatly expanded estimates of the total number of insect-arthropod species. Estimates of total species numbers range considerably and have reached as high as 100,000 million species concordant with the assumption that tropical forest canopies provide the habitat template for this incredible diversity (Wilson 1988; Erwin 1988, 1991a; Stork 1988, 1993; Gaston 1991; Kitching *et al.* 1997; Stork *et al.* 1997). In Canada, approximately half of the estimated 66,000 insects have been described

(Danks 1993), and in British Columbia there may be as many as 40,000 arthropod species (Cannings 1992), many of which are undescribed, associated with ancient forests (Winchester and Ring 1996a,b; Cannings and Cannings 1997; Winchester 1997a,b). Even with the increased focus on global rainforest canopy research, within the forests of the Pacific Northwest one of the least explored habitats is the forest canopy. Only a handful of studies on ancient forest-canopy invertebrates of the Pacific Northwest have been completed to date (Denison *et al.* 1972; Pike *et al.* 1972; Pike *et al.* 1975; Voegtlin 1982; Schowalter 1986, 1989, 1995) These studies were carried out in old-growth Douglas fir-hemlock forests in Oregon.

Given the importance of arthropods in these ancient forests and the lack of taxonomic knowledge of this biotope, in this thesis I answer the following questions:

Questions Addressed

1. Guild structure. In paper 1, I compare the proportional guild structure of arthropods in the Sitka spruce canopy of the Upper Carmanah Valley to investigate effects of tree, time and height on the proportions of individuals in guilds.

2. Arboreal specificity. Discovery in the Sitka spruce canopy of an unexpected habitat feature (4-28 cm deep moss mats) which is supported by a well developed soil layer led to hypotheses relating soil microarthropods to canopy specificity. Paper 2 measures alpha and beta diversity to determine if the canopy contains a distinct and unique arboreal fauna of oribatid mites. Paper 3 tests the hypothesis concerned with oribatid dispersal in order to address whether or not random movement has an effect on colonization of canopy habitats.

3. Centinelan extinction. The discovery of many undescribed species across a wide range of arthropod taxa adds to the evidence for Centinelan extinctions-- extinctions of species unknown before their demise and hence unrecorded (*sensu* Wilson 1992). In paper 4 I

address whether or not this is occurring in ancient northern temperate rainforests by using species data from two taxonomic groups, the staphylinid beetles and the oribatid mites.

The combined answers to the questions listed above have enabled me to draw conclusions about how abrupt changes in forest habitats influence the biology of canopy arthropod species assemblages and about their contribution to the biodiversity (form and function) of these habitats. This study demonstrates the importance of these areas as rich sources of biodiversity and specifically details the uniqueness of the arboreal arthropod community. The broad approach that I have taken will allow for further development of biodiversity questions that are process-driven and will provide a database for the further development of ecological and evolutionary questions pertaining to arthropods in ancient northern temperate rainforest canopies.

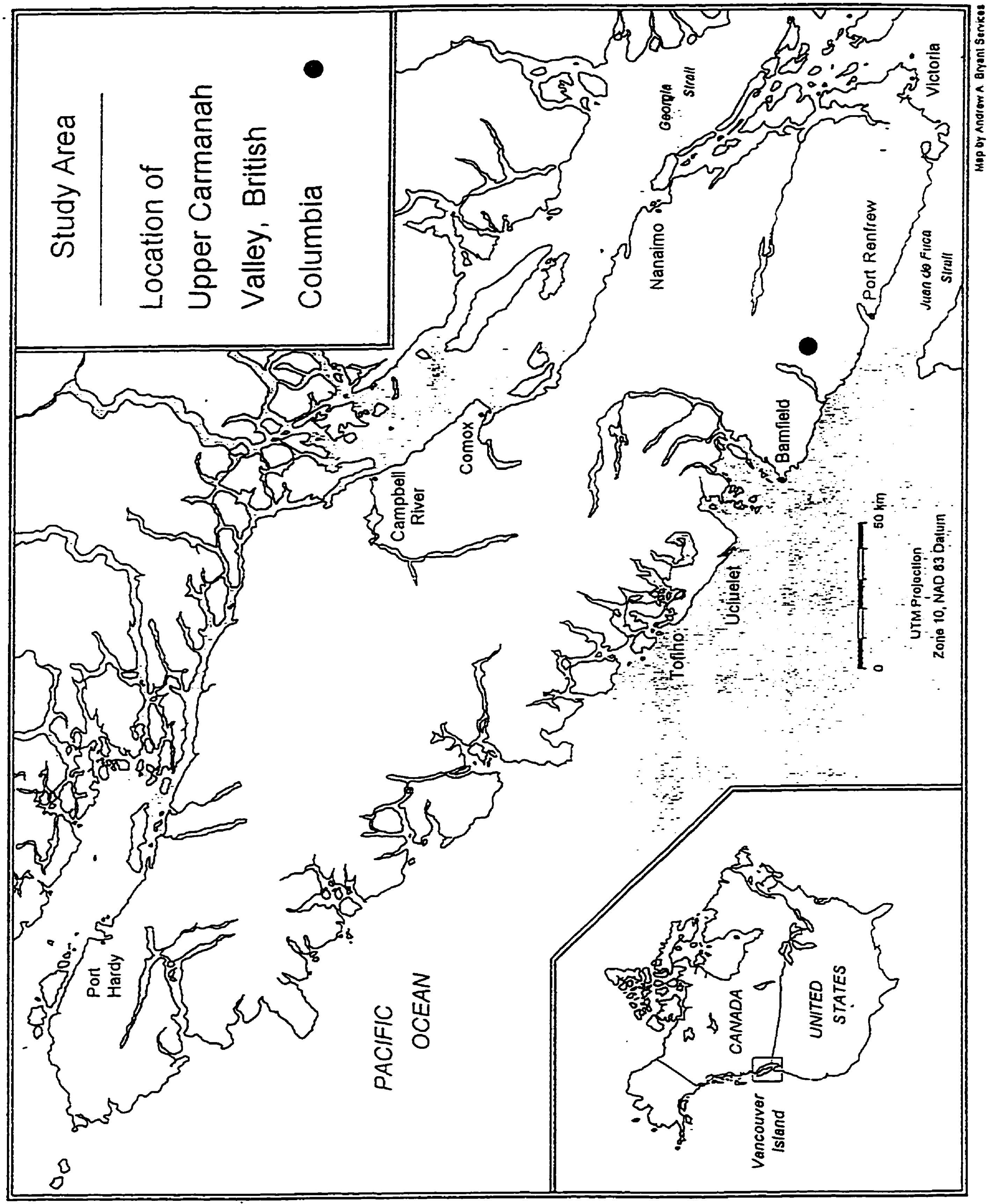
General Methods

Study Area

The study area is located in the Upper Carmanah Valley drainage (48° 44'N; 124° 37'W) on the south-west coast of Vancouver Island, British Columbia, Canada (Figure 1). This typical U-shaped coastal valley, approximately 6,731 ha in extent, is situated between the villages of Port Renfrew and Bamfield. The entire valley lies within the Coastal Western Hemlock Biogeoclimatic Zone with the exception of two high-elevation areas (Meidinger and Pojar, 1991). A maritime climate prevails, with wet, humid cool summers and mild winters with little snow. Precipitation can vary, but the mean annual precipitation is in excess of 2000mm.

For each chapter, data were collected at one or more of four study sites: ancient canopy (10U CJ 801991), ancient forest floor (10U CJ 802998) (the oldest trees at both ancient forest sites are approximately 700 years old), transition zone (10U CJ 803006) (edge between ancient forest and clear-cut), and clear-cut (10U CK 803006). All study sites are located adjacent to each other along an approximately 4 km transect.

Figure 1. Map location of the Upper Carmanah Valley canopy research site, Vancouver Island, British Columbia, Canada.


Study Area
Location of Upper Carmanah Valley, British Columbia
Port Hardy
PACIFIC OCEAN
Campbell River
Comox
Tofino
Ucluelet
Bamfield
Nanaimo
Georgia Strait
Port Renfrew
Juan de Fuca Strait
Victoria
0
50 km
UTM Projection
Zone 10, NAD 83 Datum
CANADA
UNITED STATES
Vancouver Island
Map by Andrew A. Bryant Services

Vegetation plot surveys supported the observation that there was no observable gradients (moisture and nutrient regimes) among or between the ground study sites before harvesting. Vegetation at the Upper Carmanah Valley is dominated by undisturbed ancient forest with dominant trees in excess of 700 years of age. Ancient trees commonly exceed 60 meters in height and 135 cm dbh. The dominant conifers in the Carmanah drainage are western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.),Sitka spruce (*Picea sitchensis* (Bong) Carr.), Pacific silver fir (*Abies amabilis* (Dougl.) Forb.), and western red cedar (*Thuja plicata* D.Don), accounting for 30, 25, 25 and 10% total cover, respectively. Ground shrubs are dominated by salmonberry (*Rubus spectabilis* Pursh), Devil's club (*Oplopanax horridus* (Smith) Miq.), Alaskan blueberry (*Vaccinum alaskaense* Howell) and false azalea (*Menziezia ferruginea* Sm.).

This watershed represents an intact, ancient forest that has evolved since the Wisconsin glaciation (circa 10,000 yrs before present). In 1985 the clear-cut site (c.a. four hectares in extent) was harvested and is the only area in the entire Carmanah watershed to be logged.

Canopy Access

A 2000 m linear transect was placed along Carmanah Creek and all Sitka spruce trees taller than 30 m were identified. From these trees, a cluster of five were chosen randomly to be incorporated into a canopy access system. Access to the canopy is by means of a 2:1 mechanical advantage pulley system. Four wooden platforms strapped onto the branches and trunk of the main tree provide consistent heights (31 to 67 metres) from which to sample. A series of burma bridges and bridges provides access to four other Sitka spruce trees (Ring and Winchester 1996). At the inception of this study this station was the only permanent access system of this type available for long-term canopy work in northern temperate rainforests.

Survey Design

Owing to the diverse nature of arthropods and their varied habits, no single survey method or sampling technique can be used for a complete study. The variety of techniques used in this study is summarized in Winchester and Scudder (1993) and in a report of the Biological Survey of Canada (1994). Survey design, sampling and statistical methodologies are detailed in each paper.

CHAPTER 1

PAPER 1

CANOPY ARTHROPODS OF COASTAL SITKA SPRUCE TREES ON VANCOUVER ISLAND, BRITISH COLUMBIA, CANADA

N.N. Winchester

Abstract

Arthropod biodiversity was investigated in the Carmanah Valley on Vancouver Island, British Columbia. One component of this study, the arboreal arthropods, were collected within the canopy of five old-growth Sitka spruce trees using branch-clipping and substrate coring. Arthropods associated with the branches in the canopy were dominated by individuals in the phytophagous, predator and parasitoid guilds. Individual tree characteristics and seasonality both contributed significantly to the proportional structuring of the phytophagous and predator guilds. Vertical partitioning was not a significant factor in guild proportionality. Interaction effects were only significant for the phytophagous guild. Taxonomic distinctness was most pronounced in the canopy moss mats where oribatid mites are members of a distinct arboreal community. A total of 56 species were resident in the canopy, of which 15 undescribed species were canopy specific. Comparisons between the high-canopy and three ground sites indicated that, overall, species percent similarity was low. Describing species assemblages, documenting their habitat preferences and including processes into the framework of arthropods in old-growth forests are challenges that lie ahead. Recognizing these components should assist efforts in addressing the issues that surround the maintenance of biological diversity (form and function) in these old-growth forests.

Canopy Arthropods. Edited by N.E. Stork, J. Adis and R.K. Didham. Published in 1997 by Chapman & Hall, London. ISBN 0 412 74900 9P

INTRODUCTION

The ultimate goal in recording biological diversity is to build a factual foundation for answering basic questions about evolution and ecology (May, 1992). The setting for building this foundation is the natural landscape which represents a mosaic of geological, environmental, ecological and evolutionary processes. With increased human disturbance across virtually all natural landscapes, the focus to study and preserve biological diversity has been centered in the tropics. These areas, which are rapidly being lost, contain more than half of the world's species (Wilson 1988, 1992; Ehrlich 1988). Tropical biotopes most at risk are the species-rich forests. However, it is a global reality that forests throughout the world are being compromised by human-induced perturbations. In temperate zones some of the last remaining tracts of intact old-growth coniferous forests occur in the Pacific Northwest of North America (Franklin, 1988). The ongoing fragmentation of these landscapes has heightened the awareness for a need to understand the endemic fauna and flora and apply system-based conservation approaches across a wide range of forest types.

Historically, little research concerning the conservation of biodiversity has been done in the old-growth forests of the Pacific Northwest (Winchester & Ring, 1996) and this research has generally failed to link results to ecosystem processes. In British Columbia these forests are thought to contain much of the biodiversity of the province (Bunnell, 1990; Fenger and Harcombe, 1989; Winchester and Ring, 1996). They often have diffuse boundaries with other ecosystems, and this temporal and spatial mosaic creates a dynamic and complex set of habitats that are utilized by a variety of species. The faunal elements associated with these old-growth forests form a heterogeneous group, and nowhere is this more evident than in the arthropods. Arthropods, primarily insects, are an integral part of most old-growth systems and may comprise 80-90% of the total species in these systems (Asquith *et al.* 1990). They play a primary role in the functioning of natural ecosystems, may regulate nutrient cycling (Mattson and Addy, 1975; O'Neill, 1976) and are now frequently mentioned as important components of diversity that need to be identified (May, 1986; Wilson, 1988; di Castri *et al.* 1992; Samways, 1994).

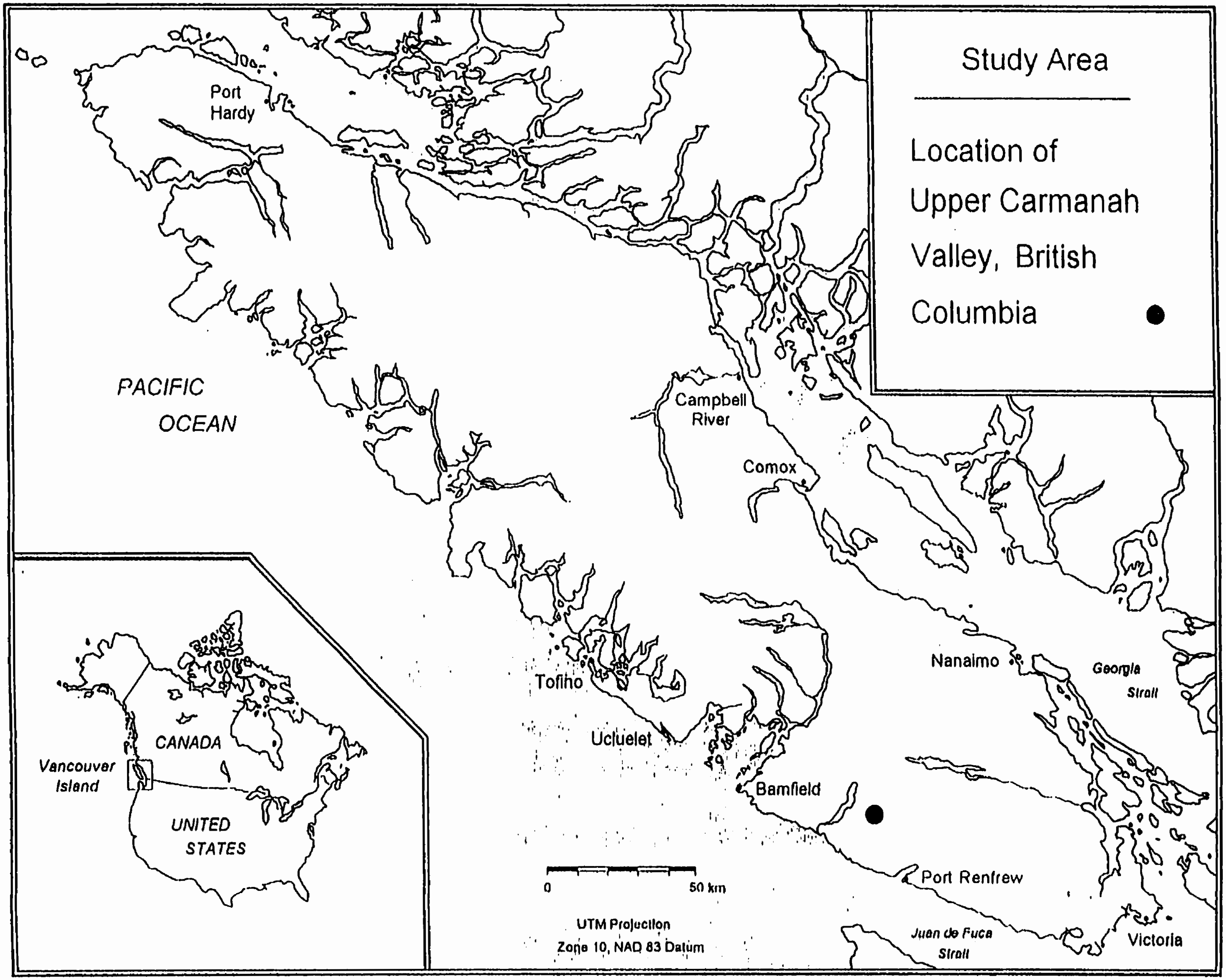
Within the forests of the Pacific Northwest one of the least explored habitats is the forest canopy. Only a handful of studies on old-growth forest canopy invertebrates of the Pacific Northwest have been completed to date (Voegtlin, 1982; Schowalter, 1986, 1989). These studies were carried out in old-growth Douglas fir-hemlock forests in Oregon. Given the importance of arthropods in these old-growth forests coupled with the lack of taxonomic knowledge of the canopy, the objective of this paper is to present results from the canopy segment of a larger study (Winchester, 1993; Ring and Winchester, 1996) which documents the arthropod fauna from an old-growth Sitka spruce forest. Specifically, I will use guild structure and habitat-specificity to address the following questions:

1. What is the proportional guild structure of arthropods in the Sitka spruce canopy?
2. What are the effects of tree, time and height on the proportions of individuals in guilds?
3. Are new species present in the canopy and is there evidence to support habitat specificity?

STUDY AREA

The study area is located in the Upper Carmanah Valley drainage (48° 44'N; 124° 37'W) on the south-west coast of Vancouver Island, British Columbia, Canada (Figure 1). This typical U-shaped coastal valley, approximately 6,731 ha in extent, is situated between the villages of Port Renfrew and Bamfield. The entire valley lies within the Coastal Western Hemlock Biogeoclimatic Zone with the exception of two high-elevation areas (Meidinger and Pojar, 1991). A maritime climate prevails, with wet, humid cool summers

Figure 1. Map location of the Upper Carmanah Valley canopy research site, Vancouver Island, British Columbia, Canada.



Map by Andrew A Bryant Services

and mild winters with little snow. Precipitation can vary, but the mean annual precipitation is in excess of 2000mm.

The sample area in the Upper Carmanah Valley drainage includes four study sites: ancient forest canopy, ancient forest floor (both undisturbed ancient forest sites contain trees that are approximately 700 years old), transition zone (edge between ancient forest and clear-cut) and clear-cut. All study sites are located adjacent to each other along an approximately 4 km transect.

Vegetation plot surveys supported the observation that there was no observable gradients (moisture and nutrient regimes) among or between the ground study sites before harvesting. Vegetation at the Upper Carmanah Valley is dominated by undisturbed ancient forest with dominant trees in excess of 700 years of age. Ancient trees commonly exceed 60 meters in height and 135 cm dbh. The dominant conifers in the Carmanah drainage are western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.),Sitka spruce (*Picea sitchensis* (Bong) Carr.), Pacific silver fir (*Abies amabilis* (Dougl.) Forb.), and western red cedar (*Thuja plicata* D.Don), accounting for 30, 25, 25 and 10% total cover, respectively. Ground shrubs are dominated by salmonberry (*Rubus spectabilis* Pursh), Devil's club (*Oplopanax horridus* (Smith) Miq.), Alaskan blueberry (*Vaccinum alaskaense* Howell) and false azalea (*Menziezia ferruginea* Sm.).

This watershed represents an intact ancient forest that has evolved since the Wisconsin glaciation. In 1985 the clear-cut site (approx. 4 hectares) was harvested and is the only area in the entire Carmanah watershed to be logged.

CANOPY ACCESS

A 2000 m linear transect was placed along Carmanah Creek and all Sitka spruce trees taller than 30 m were identified. From these trees, a cluster of five were chosen randomly to be incorporated into a canopy access system. Access to the canopy is by means of a 2:1 mechanical advantage pulley system. Four wooden platforms strapped onto the branches and trunk of the main tree provide consistent heights (31 to 67 metres) from which to sample. A series of burma bridges provides access from the main tree to the other four Sitka spruce trees, complete with platforms (Ring and Winchester 1996). At the inception of this study this station was the only permanent access system of this type available for long-term canopy work in northern temperate rainforests.

SURVEY DESIGN

Owing to the diverse nature of arthropods and their varied habits, no single survey method or sampling technique can be used for a complete study. The variety of techniques used in this study are summarized in Winchester and Scudder (1993) and the Biological Survey of Canada (1994). This paper will only deal with aspects of the 1991 sampling protocol which are listed below.

SAMPLING PROTOCOL

BRANCH CLIPPINGS

The branch clipping program was conducted in the five Sitka spruce trees in the fixed-access canopy system. The sampling procedure was modified from Schowalter (1989). In each tree, three samples were taken at each of three heights (33, 45, and 54 m). A total of 45 branches were collected in each of six sample periods. Samples were collected at 1-month intervals from May - October, 1991. All insects were removed from each sample and prepared for identification. Immature individuals of all species were reared to maturity. Single branches from each tree and level were run through Tullgren funnels to extract Collembola and Acari. After sorting, all branches were dried and then total branch weight and needle weight were recorded.

MOSS CORES

A hand-held moss/soil corer (ca. 3 cm x 5 cm) was used to collect 5 moss/soil cores at random from the canopy site (tree 1 and 2) and the 3 ground sites once a month from May - October, 1991. A total of 120 cores were collected. Arthropods were extracted in the laboratory using Tullgren funnels for 48 hours. Samples were preserved in 75% ethanol. Volume displacement and dry weight were recorded for each core sample.

SAMPLE SORTING AND DATA ANALYSIS

An informative view of canopy arthropods can be gained by placing them in guilds defined in terms of feeding habits. The guilds used in this study were structured after work by Root (1967, 1973) and further elaborated upon by Moran and Southwood (1982) and Stork (1987, 1988). The six guilds recognized in this study were: phytophages, epiphyte fauna, scavengers, predators, parasitoids and tourists. All arthropods except the Acarina and Collembola collected from the branch-clipping program were identified to family and arranged by guild. Guilds were expressed as a percentage of total individuals for the variables tree, time and height.

A mixed model three-way analysis of variance (SAS Institute Inc.1982) was used to test for differences in the phytophage, predator, and parasitoid guilds. The low number of individuals in all other guilds (i.e. cells in the ANOVA) precluded statistical verification (see Simberloff, 1976, 1978). Data were expressed as mean number of individuals/kg dry plant material. Tree, time and height were the main effects (tree was random, time and height were fixed) and a significance level of 0.05 was used. In factorial designs it is misleading to present significance tests that address the main effects if the interactions terms are significant (Krebs 1989); therefore, interaction terms are reported where significant.

Species-level identifications were completed for most of the oribatid mites. Numerical relationships between the oribatid species and four study sites were calculated using all individuals from the moss cores, pooled over all collection times.

CANOPY GUILD STRUCTURE

Relative abundances of different guilds, expressed as percentage of mean number of individuals/kg dried plant material for all individuals from the branch-clipping sampling programme, is presented in Table 1. The canopy arthropod fauna in this study is dominated by the phytophagous (41.3%), predator (37.3%) and parasitoid (11.8%) guilds. Phytophagous guild representation is similar to the percentage contribution reported for temperate trees by Moran and Southwood (1982), but considerably higher than that reported by Stork (1987) for tropical trees. Predator and parasitoid guild proportions in our study are higher than those reported by Moran and Southwood (1982) and Stork (1987). Numerical dominance of functional groups in this study supported previous findings from deciduous forests by Schowalter and Crossley (1987) and coniferous forests by Schowalter (1989). The phytophagous guild was composed of a small number of species (e.g. Lepidoptera, 13 species) which contained a large number of individuals (N. Winchester, unpublished data). This appears typical of plant-feeding species in this system and may relate to the reduced number of food options (mainly developing vegetative buds and female cones). The predator guild contains more species than the phytophagous guild and is composed primarily of 38 arachnid species which do not contain a large number of individuals (N. Winchester, unpublished data). Numerical dominance of spiders has been reported from other temperate studies (Nielsen, 1975; Ohmart and Voigt, 1981; Voegtlin, 1982; Bigot and Kabakibi, 1987; Basset, 1991a). The maintenance of high predator loading in a structurally and functionally diverse ecosystem such as the Carmanah Valley supports previous findings by Kareiva (1983), Risch (1981) and Schowalter (1986, 1989). The parasitoid guild is represented by a large number of species (e.g. Braconidae, 118 species, N. Winchester, unpublished data) with low numbers of individuals. The main prey components of the parasitoids are species from the Lepidoptera and Aphididae. Numbers of parasitoid species are not influenced is by taxonomic richness in the

Table 1. Guild structure of the arthropod fauna collected from the branch clipping program. Data for tree, time and height were pooled and expressed as the percentage of mean number of individuals per kilogram of dry plant material. All samples were collected in 1991 from the Upper Carmanah Valley, British Columbia.

Guild	Percentage
Phytophages	41.3
Predators	37.2
Parasitoids	11.8
Epiphyte fauna	8.3
Scavengers	1.0
Tourists	0.4

phytophagous guild, but by the type of host-stage that is attacked. From the branch-clippings, several parasitoid species have been reared that attack the egg or larva or pupa of a variety of lepidopteran species. This variety of available host stages may contribute to an increase in parasitoid species that inhabit the canopy. Conspicuous by their absence in the canopy are Formicidae, with only four winged individuals collected during the entire study. Ants can exert considerable impact on other insects in arboreal habitats (Stork, 1987), although percentage contributions of species and indivividuals in temperate forests are generally low (Southwood *et al.*, 1982; Bassett, 1991a). The paucity of tourists is related to the transitory nature of these arthropods and branch-clipping does not adequately sample this faunal component.

Basset (1991a) noted that interception traps collected many more vagile arthropods, whereas restricted canopy fogging yielded more sedentary, apterous and juvenile specimens. This point is supported by our work using canopy Malaise traps which collected 20,000 individuals, most of which are tourists (N. Winchester, unpublished data).

TREES/HEIGHT/TIME

Guild patterns have been shown to vary considerably, depending upon which variables or combination of variables are being considered (Southwood, 1960, 1961; Moran & Southwood, 1982; Kennedy & Southwood, 1984; Stork, 1987). Guild proportionality was explored for the phytophagous, predator and parasitoid guilds by using numbers of individuals and separating guild structure based on three factors: (i) tree individuality; (ii) vertical partitioning; and (iii) temporal sequencing.

TREES

Do trees act as individuals (*sensu* Moran & Southwood, 1982)? There was a significant effect of tree on the phytophagous guild ($F_{4,179} > 7.22$, $P < 0.0001$), and the predator guild ($F_{4,179} > 2.75$, $P < 0.05$), but no effect on the parasitoid guild $F_{4,179} > 0.25$, n.s.). The numbers of insects on individual trees has been shown to vary with population size and proportional distribution among guilds (Southwood *et al.*, 1982). There appeared to be a remarkable consistency within guilds among the first three trees (Table 2). Where differences in proportional representation of insects in guilds between trees were evident, accumulations of individuals in single species in the phytophagous guild (usually aphids) occurred. The accumulation of single species, such as the aphid *Euceraphis punctipennis* (Zetterstedt), was recorded by Southwood *et al.* (1982). This difference was most pronounced in trees 4 and 5 where proportional representation reaches 46.3% and 60.6%, respectively. It is likely that observed variation in guild proportionality between trees, arises primarily from species which accumulate individuals in the phytophagous guild. The species in these trees are virtually identical (N. Winchester, unpublished data), confirming the observation by Moran and Southwood (1982) that the major guilds in the arboreal community are shaped by habitat characteristics of the tree which serve to impose a proportional consistency. Therefore, mature Sitka spruce present a habitat template that may dictate the guild composition of species, but not individuals. Individuals in the phytophagous and predator guilds exhibit non-uniformity between trees, which may be the result of a myriad of factors that are coupled with the physical characteristics of the tree. Factors may include plant chemistry (Southwood *et al.*, 1982), plant architecture (Lawton, 1983, 1986; Morse *et al.*, 1985) and plant health. Trees may act as individuals, in the sense that there are differences in guild proportionality and these differences are most evident in the phytophagous guild.

HEIGHT

Does tree height affect guild proportionality among individuals? Guild proportionality between heights, pooling trees and time, indicates that all guilds were similar (Table 3). The effect of height was not significant for the phytophagous, predator

Table 2. The percentage of arthropod individuals recorded from five Sitka spruce trees (time and height are pooled) in the Carmanah Valley, arranged by guild.

GUILD	TREE 1	TREE 2	TREE 3	TREE 4	TREE 5
Phytophages	32.9	30.1	38.2	46.3	60.6
Predators	46.1	41.3	46.2	32.3	24.3
Parasitoids	9.7	18.8	7.6	8.2	10.1
Epiphyte fauna	9.7	8.5	6.3	12.3	4.6
Scavengers	1.4	1.3	0.4	0.2	0
Tourists	0	0	1.3	0.6	0.5

Table 3. The percentage of arthropod individuals recorded from three heights (time and tree are pooled) in the Carmanah Valley, arranged by guild.

Guild	High	Mid	Low
Phytophages	42.7	42.7	36.2
Predators	39.1	35.2	41
Parasitoids	11.3	13.2	5.7
Epiphyte fauna	6.0	7.3	15.2
Scavengers	0.9	1.6	1.2
Tourists	0.0	0.0	0.7

or parasitoid guilds ($P>0.05$). This may reflect the ability of the phytophagous guild to track the availability of developing vegetative buds which occur throughout the vertical profile of the canopy. Predators, comprising mainly web-constructing arachnids, also seem able to utilize the entire vertical profile of the canopy. The guild proportionality of parasitoids is virtually identical between the high and mid-canopy zones, but is reduced, although not significantly, in the lower zone. This reduction may be a result of host-specificity, as the phytophage guild appeared to be composed of a higher proportion of Lepidoptera in the high and mid-canopy. The epiphytic guild has the highest guild proportionality in the lower canopy and may be associated with features of the habitat, including reduced moisture and a higher loading of the moss/lichen component. It is, known however, that certain groups studied here (e.g. oribatid mites) do segregate on a vertical gradient (Winchester, 1993), and one should approach with caution statements regarding vertical partitioning across a wide range of taxa.

TIME

Does time affect the guild proportionality among individuals? Time alludes to seasonality and has been shown to have an effect on species and individual composition (Erwin and Scott, 1980; Schowalter *et al.*, 1988). This is a factor that should be considered when addressing consistencies in guild proportionalities (Stork, 1988). Considerable differences are exhibited in guild proportionality through time, and these changes are similar in direction but not magnitude (Table 4).

The significant effect of time on number of individuals in the phytophagous guild ($F_{5,20}>6.91$, $P<0.0001$) is likely related to the flush of vegetative buds and development of female cones, and supports the observation of seasonal structure for phytophagous insects noted by Lawton (1983). Early in the growing season (June to early July) vegetative buds and female cones provide a food source that supports a relative increase of numbers of individuals in the phytophagous guild (54.6%-57.7%). This pattern has also

Table 4. The percentage of arthropod individuals recorded from 6 time intervals (tree and height are pooled) in the Carmanah Valley, arranged by guild. Times are: 1 = 4/June/91; 2 = 3/July/91; 3 = 30/July/91; 4 = 27/August/91; 5 = 21/September/91; 6 = 27/October/91.

Guild	Time					
	1	2	3	4	5	6
Phytophages	54.6	57.8	32.8	24.9	24.9	35.7
Predators	28.5	23.9	41.4	42.3	53.3	52.9
Parasitoids	4.1	11.1	20.1	11.7	17.8	10.2
Epiphyte fauna	11.7	6.1	5.1	19.6	2.2	0.0
Scavengers	0.4	0.5	0.6	1.1	1.8	1.2
Tourists	0.7	0.6	0.0	0.4	0.0	0.0

been noted in other canopy studies by Nielsen and Ejlersen (1977), Schowalter *et al.*(1988) and Basset (1991b). During late July, percentage of phytophagous individuals starts to decline (32.8%) while the proportional representation of predators continues to increase until late September (53.25%). There is no significant effect of time on the number of individuals in the predator guild ($P>0.05$) which indicates that the recorded increased proportional representation from early July (23.88%) to late September (53.25%) is a reflection of changes in the phytophagous guild. A high proportion of the predator guild is composed of spiders which are present in relatively even numbers over the length of the growing season. Temperate spiders have been shown to be poorly synchronized with herbivore accumulations (Renault and Miller, 1972; Basset, 1991b) and may be able to wait or switch prey items based on availability. Input from the forest floor or adjacent riparian zones has been suggested by D.Voegtlin (unpublished data) as areas which provide a food source during times of low numbers of resident herbivores. The parasitoids are more difficult to follow and are closely associated with the number and stage of their hosts, principally Lepidoptera and Aphididae. Time has a significant effect on the parasitoid guild ($F_{5,20}>3.14$), $P<0.05$). There appear to be two peaks of emergence for parasitoids, one in late July and the other in early September. Synchronization of emergence is closely associated with host biology (see Price, 1991; Hawkins, 1993). Reared material (N. Winchester, unpublished data) indicates that the first peak is composed of parasitoids that attack the larval stages of Lepidoptera while the second peak appears to consist of parasitoids that attack the pupal stage.

INTERACTION EFFECTS

Interaction effects were only significant for the phytophagous guild: (tree x height, $F_{8,179}>4.33$, $P<0.0001$; tree x time, $F_{20,179}>2.63$, $P<.0005$; and tree x height x time, $F_{40,179}>1.87$, $P<.005$). Interaction terms are difficult to interpret and I present these results to indicate that these interactions need to be considered when addressing the significance attributed to the main effects. Further study is required to ascertain the biological meaning of these interactions. Currently I am detailing life histories of several species from the phytophagous guild in order to address the biological significance of the interaction terms. Interaction effects were not significant ($P>0.05$) for any of the other guilds.

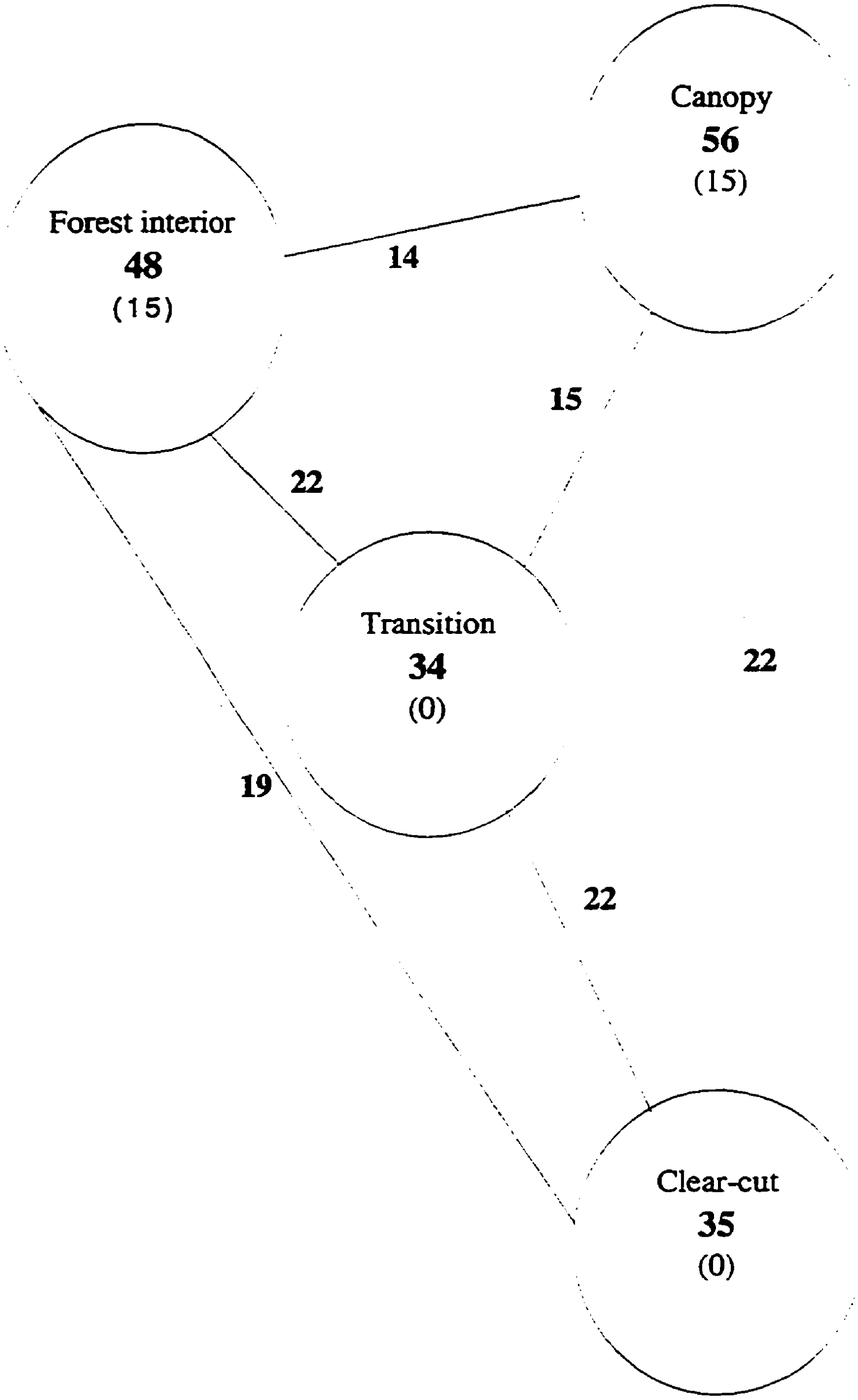
ACARINA

Of the 7,219 soil microarthropods collected by coring the thick, moss mats of the canopy, the numerically dominant group, both in terms of individuals (5,937) and species (85+), is the Acarina. Although not specifically dealing with the canopy, mites were found to be one of the largest arthropod components in studies conducted in the rainforests of Peru (Beck,1963), Nigeria (Madge, 1965) and Costa Rica (Nadkarni & Longino, 1990). Within the Acarina, the Oribatida ('beetle mites') is the dominant Suborder in our samples. A similar situation was found in the tropics by Beck (1963) and in mature northern temperate forests by Wallwork (1983) and Moldenke & Lattin (1990). Numerical relationships of the oribatid mite fauna (Figure 2) indicate that the canopy has the highest number of species (56), followed by the forest floor (48). The total number of species present in the transition zone (34) is similar to the clear-cut zone (35). Percentage similarity is lowest between the canopy and forest floor (18%) and highest between the canopy and clear-cut (41%). Overall, percent similarity is generally high between any of the other ground pair-wise site comparisons (range 42% - 88%). Of the 30 confirmed new species, 15 were specific to the forest floor and 15 were specific to the canopy.

CANOPY ORIBATIDA

Perhaps the most interesting and least explored habitats in the Sitka spruce canopy are the 4-28 cm deep moss mats which support a well developed soil layer. These mats are primarily composed of three moss species, *Isothecium myosuroides* Brid., *Antitrichia*

Figure 2. Numerical relationship between oribatid species from four study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time periods. Numbers within the circles represent the number of species occupying a given site, numbers along the lines represent those species shared in common between sites and those in brackets are the numbers of undescribed species.


Canopy
56
(15)
Forest interior
48
(15)
14
15
22
Transition
34
(0)
22
19
22
Clear-cut
35
(0)

curtipendula (Hedw.) Brid. and *Dicranum fuscescens* Sm., which are also abundant on the forest floor. Soil microarthropods dominate this canopy soil/litter habitat, a fact which has not been well documented in these forests but has been noted in other canopy studies (Nadkarni & Longino, 1990, Paoletti *et al.*, 1990). From the oribatid mites that have been processed to date, there is strong evidence that we are dealing with a distinct arboreal fauna. A high number of species with low percent similarity to ground sites (Figure 2), is consistent with the findings of Behan-Pelletier *et al.* (1993). The discovery of several new oribatid species is not surprising (see Behan-Pelletier, 1993) given the scope of this study. Fifteen undescribed species appear confined to habitats found only in the old-growth forest canopy. For example, *Dendrozetes* represents the first record for this genus in North America and this new species has modifications for an arboreal existence (V. Behan-Pelletier personal communication). *Parapirnodus*, *Paraleius*, and *Anachipteria* are genera that are known to be arboreal (V. Behan-Pelletier personal communication) and in this study each are represented by an undescribed, strictly arboreal species. Similarly, new species with unique habitat associations have been recorded in Oregon (Voegtlin, 1982), northern Venezuela (Behan-Pelletier *et al.*, 1993), Peru (Wunderle, 1992) and in Australia (Walter *et al.*, 1994). The microhabitats associated with the canopy of the ancient Sitka spruce trees are not replicated in any second-growth forest canopies that we have surveyed to date, and it is unlikely that these habitat features will develop in second-growth forests that are in an 80-120 year rotation. These canopy microhabitats appear to harbour taxonomically discrete species assemblages that may be lost if these canopy habitats are not retained, or allowed to develop in second-growth forests. Canopy specificity indicates that arboreal oribatids are not just a subset of the ground fauna. Studies from distinct geographic areas indicate that, in general, the percent overlap between arboreal oribatid species and their ground-dwelling counterparts is less than 40%.

SUMMARY

The resident canopy arthropod fauna in this study is dominated by the phytophagous and predator-parasitoid guilds, supporting previous studies in temperate forests (Schowalter and Crossley, 1987; Schowalter 1989). The phytophagous guild is composed mainly of species that are feeding on the developing vegetative buds and female cones. These species appear to have little effect on the host with a negligible loss in developing plant tissue. I infer from this guild structure that herbivory in this mature, structurally-complex forest is relatively insignificant and, through a series of checks and balances, large-scale herbivore damage caused by insect outbreaks is negligible. This supports previous findings by Reichle *et al.* (1973), Nielson (1978), Ohmart *et al.* (1983) and Schowalter (1989) who noted that herbivory was less than 10% of the standing crop in mature forests. The maintenance of a high predator loading in a structurally and functionally diverse ecosystem such as the Carmanah Valley supports previous findings by Kareiva (1983), Risch (1981) and Schowalter (1986, 1989).

I present evidence to suggest that several species - many new to science - exhibit habitat specificity that restricts their distribution to structural features contained only in the old-growth forest, both on the forest floor and in the canopy. Canopy specificity is most pronounced in the microarthropods that inhabit the moss-mats. This arboreal community is dominated, in both numbers of individuals and species, by oribatid mites. Of all the arthropod groups that have been examined, the oribatids contain the greatest number of new species. Patterns of community structure on trees, examined at the guild level, indicate that in terms of number of individuals, the phytophage and predator-parasitoid guilds are numerically dominant. The high proportion of the predator-parasitoid complement indicates that herbivory in these mature, structurally complex forests is relatively insignificant. Members of the phytophage guild are primarily composed of species from the Lepidoptera and Aphididae and are associated with the developing vegetative buds and female cones. Guild proportionality exhibits temporal variation over time. Vertical height, however, does not effect guild proportionality. Differences between trees, while not pronounced, are significant and relate to increased numbers of individuals in the phytophage guild. The summarizing of these key patterns and documentation of changes due to disturbance should identify ecological roles of arthropods that are at the heart of the biodiversity challenge. The arthropod specimens collected in this study will help provide an understanding of the diversity, habitat requirements and ecosystem processes that occur within these northern temperate old-growth rainforests.

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CHAPTER 2

PAPER 2

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Arboreal specificity, diversity and abundance of canopy-dwelling oribatid mites

Neville N. Winchester[1]

Department of Biology, University of Victoria, P.O. Box 3020,
Victoria, British Columbia, Canada
V8W 3N5

Valerie Behan-Pelletier

Biodiversity Assessment and Evaluation, Agriculture Canada
Research Branch
K.W. Neatby Bldg., Carling Ave., Ottawa, Ontario, Canada
K1A 0C6

Richard A. Ring

Department of Biology, University of Victoria, P.O. Box 3020,
Victoria, British Columbia, Canada
V8W 3N5

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[1] Corresponding Author

ABSTRACT

Seventy-one species of Oribatida (2,117 specimens), representing 51 genera and 34 families were recorded from replicated moss/soil samples. Samples were collected from 5 study sites located in the ancient Sitka spruce forest of the Upper Carmanah Valley, Vancouver Island, British Columbia, Canada: 2 ancient forest canopies, an ancient forest interior, a transition zone (edge between ancient forest and clear-cut), and a clear-cut (6 years old). Thirty and twenty-eight species of oribatids were recorded from the 2 canopy sites respectively, of these, 12 species were canopy specific. Species exhibiting strict arboreal specificity were all in the Brachyphlina, from the families Thyrisomidae, Damaeidae, Eremaeidae, Oripodidae, Gymnodamaeidae, Oppiidae, Peloppiidae, Galumnatidae, and Cymbaeremaeidae. We consider oribatids of the canopy to be inhabitants of islands, in the sense that they are isolated from their ground counterparts and make up a distinct faunal assemblage that is characterized by two ecological groups of species: wandering species with good dispersal capabilities, and arboreal species with poor dispersal capabilities. We suggest that oribatid mites can be used as a surrogate for other ancient forest soil microarthropods, and predict that arboreal specificity will also be pronounced in these taxa.

INTRODUCTION

The Acari are the most speciose and abundant group in the Arachnida, and densities in temperate forest soils have been reported in excess of several hundred thousand individuals per square metre (Anderson 1975, 1978; Norton 1994). Within this soil fauna the oribatid mites (Suborder Oribatida, also known as Cryptostigmata), commonly called "beetle-mites", typically form the most diverse taxonomic assemblage (Aoki 1967; Huhta and Koskenniemi 1975: Pande and Berthet 1975; Crossley 1977; Behan-Pelletier *et al.* 1978; Wallwork 1983). Many oribatid species show little evidence of trophic specialization and species ostensibly co-exist (Anderson and Healy 1972; Anderson 1978), adopting a variety of feeding habits (Travé 1963; Spain and Harrison 1968; Mitchell and Parkinson 1976; Anderson 1978; André 1983; Norton 1983; Walter and Behan-Pelletier 1993) which have been classified into six main feeding types (see Wallwork 1983).

Microhabitat specialization has been proposed as a hypothesis to explain oribatid coexistence (Aoki 1967; Anderson 1971) and subsequently used in several studies of oribatid faunas in forest floors to explain how potentially competitive species reduce interactions by becoming spatially separated (e.g. Hammer 1972; Fujikawa 1974; Pandre and Berthet 1975). The association of oribatid species with micro- and macroflora has been reviewed by Seyd and Seaward (1984) and it is now clear that distinct species assemblages are present in 'suspended soils' (*sensu* Wallwork 1976). For example, specific oribatid species are associated with lichens (Gerson and Seaward 1977; Seyd and Seaward 1984), moss (Seniczak and Plichta 1978), and corticolous habitats (André 1984, 1985).

Despite early observations on some 'tree-climbing' oribatids (Travé 1963; Aoki 1971), exploration of canopy oribatid assemblages have largely been ignored (Walter and Dowd 1995a,b). A handful of studies have reported that a relatively rich oribatid fauna exists in the canopies of a variety of trees, mainly in tropical rainforests (Norton and Palacios-Vargas 1987; Nadkarni and Longino 1990; Wunderle 1991; Walter and Behan-Pelletier

1993; Walter *et al.* 1994; Walter and O'Dowd 1995a). To date, species in at least 85 genera from 35 families have been recorded from arboreal habitats (Behan-Pelletier and Winchester 1997). Studies in northern temperate rainforests lag far behind their tropical counterparts even though oribatid mites have been recorded in old-growth canopies (e.g. Aoki 1974; Voegtlin 1982) and have been recorded as being the numerically dominant group in Sitka spruce canopies (Behan-Pelletier and Winchester 1997; Winchester 1996; Winchester and Ring 1996a).

Here we examine the composition of the arboreal oribatid mite community associated with the moss-mats that are supported by a well developed suspended soil layer. Arboreal mites appear to be tightly associated with structural aspects of the surrounding plant architecture. For example, relationships between foliar mites and leaf surface structures (e.g. leaf domatia) have been discussed by Walter (1992); Walter and Dowd (1992a b); Walter and Behan-Pelletier (1993). The Carmanah canopy research project is the first to explore the association between mites and suspended soils/moss mats in the canopies of coniferous forests (Winchester and Ring 1996 a,b; Winchester 1997 a,b; Behan-Pelletier and Winchester 1997).

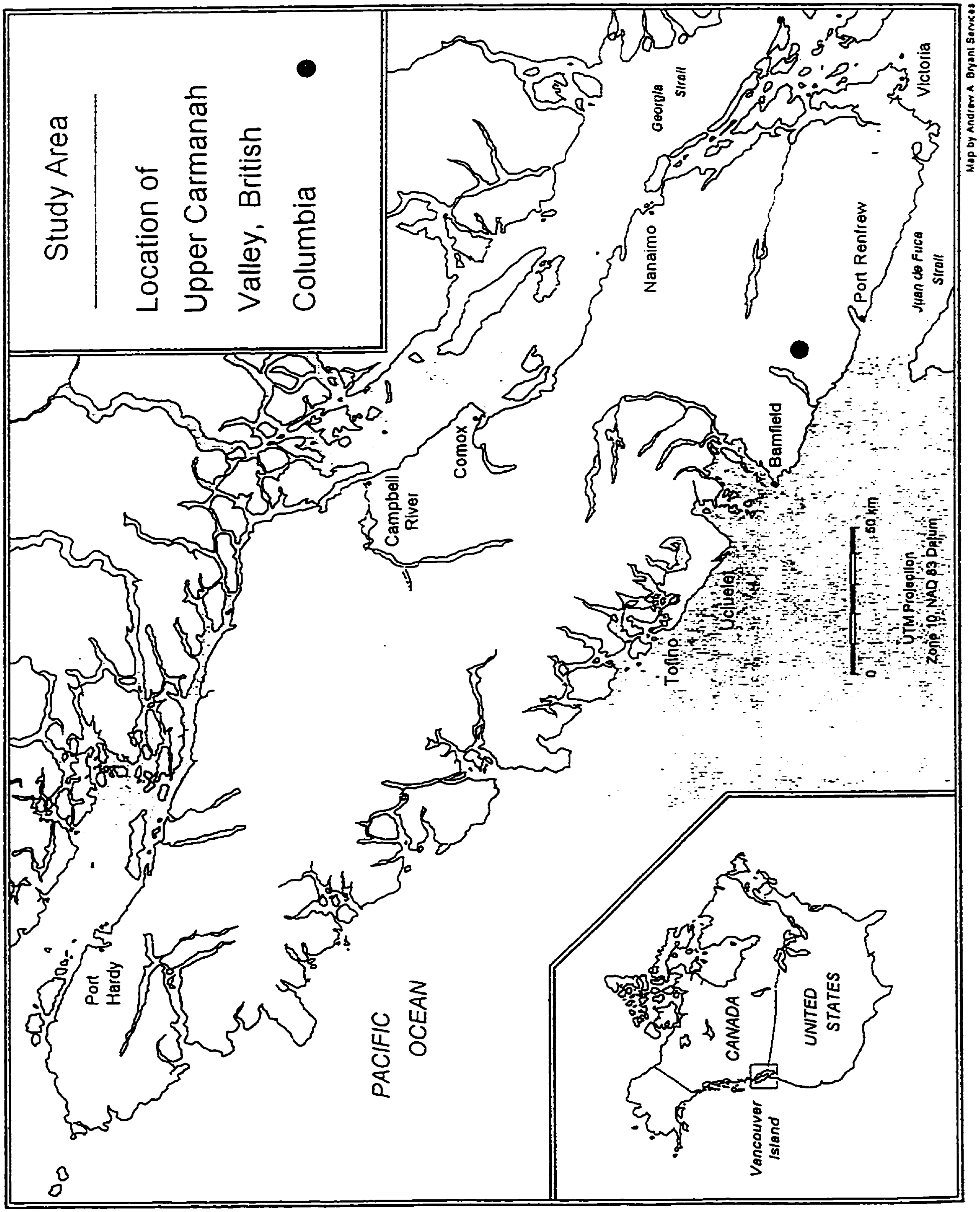
In this paper we test the hypothesis that the suspended soils/moss mats in old-growth Sitka spruce trees act as a reservoir for arboreal oribatid diversity by comparing the oribatid fauna in the high canopy to that of 3 ground sites. We have also determined the percentage of the arboreal fauna that is canopy specific.

METHODS AND MATERIALS

STUDY AREA

The study area is located in the Upper Carmanah Valley drainage (48° 44'N; 124° 37'W) on the south-west coast of Vancouver Island, British Columbia, Canada (Figure 1). This typical U-shaped coastal valley, approximately 6,731 ha in extent, is

Figure 1. Map location of the Upper Carmanah Valley canopy research site, Vancouver Island, British Columbia, Canada.



Study Area

Location of Upper Carmanah Valley, British Columbia

Map by Andrew A. Bryant Services

situated between the villages of Port Renfrew and Bamfield. The entire valley lies within the Coastal Western Hemlock Biogeoclimatic Zone with the exception of two high-elevation areas (Meidinger and Pojar, 1991). A maritime climate prevails, with wet, humid cool summers and mild winters with little snow. Precipitation can vary, but the mean annual precipitation is in excess of 2000mm.

The sample area in the Upper Carmanah Valley drainage includes four study sites: ancient forest canopy, ancient forest floor (both undisturbed ancient forest sites contain trees that are approximately 700 years old), transition zone (edge between ancient forest and clear-cut) and clear-cut. All study sites are located adjacent to each other along an approximately 4 km transect.

Vegetation plot surveys supported the observation that there was no observable gradients (moisture and nutrient regimes) among or between the ground study sites before harvesting. Vegetation at the Upper Carmanah Valley is dominated by undisturbed ancient forest with dominant trees in excess of 700 years of age. Ancient trees commonly exceed 60 meters in height and 135 cm dbh. The dominant conifers in the Carmanah drainage are western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.),Sitka spruce (*Picea sitchensis* (Bong) Carr.), Pacific silver fir (*Abies amabilis* (Dougl.) Forb.), and western red cedar (*Thuja plicata* D.Don), accounting for 30, 25, 25 and 10% total cover, respectively. Ground shrubs are dominated by salmonberry (*Rubus spectabilis* Pursh), Devil's club (*Oplopanax horridus* (Smith) Miq.), Alaskan blueberry (*Vaccinum alaskaense* Howell) and false azalea (*Menziezia ferruginea* Sm.).

This watershed represents an intact ancient forest that has evolved since the Wisconsin glaciation. In 1985 the clear-cut site (approx. 4 hectares) was harvested and is the only area in the entire Carmanah watershed to be logged.

MOSS CORES

A hand held moss/soil corer (3 cm X 5 cm) was used to collect 5 moss/soil cores at random from the canopy of 2 trees (trees 1 and 2) in the fixed access system and from 3 ground sample sites once a month from May - October, 1991 (6 months). Each sample core was composed of approximately 1cm of soil and 4 cm of moss and this structure did not appear to vary between sites. A total of 120 cores were collected. In the laboratory each core was broken up and arthropods were extracted from each core using Tullgren funnels which were run for 48 hours. Arthropods extracted were preserved in 75% ethyl alcohol. Volume displacement and moss/soil dry weight were recorded for each core sample.

MALAISE TRAPS

Five Malaise traps (Martin 1977; Winchester and Scudder 1993) were placed at random in each of three habitats: Sitka spruce canopy at heights of 32m, 32m, 33m, 35m, 39m; forest interior of Sitka spruce; and 6 year old clear-cut, approximately 600m from the forest edge. Malaise traps have a black centre baffle with black sides and a white top. The Malaise trap supports were touching vegetation in the three habitats. Arthropods were collected into 75% ethyl alcohol. Malaise trap samples were collected approximately every two weeks from 3 July to 27 October (9 collection dates). Arthropods, including oribatid mites were sorted from these samples, counted and identified to species where possible (see below).

SORTING AND IDENTIFICATION

Extracted arthropods were sorted into the following groups: Acari, Araneae, Collembola, Coleoptera, soil microarthropods (Pseudoscorpionida, Diplura, Chilopoda, Diplopoda, Symphyla, Protura), and Others (Hymenoptera, Hemiptera, Lepidoptera, Thysanoptera). All Acari were counted, from which all mature Oribatida were separated and representative specimens were slide mounted using the procedures outlined by Krantz

(1978). Representative slide mounted specimens were identified by Dr. Behan-Pelletier, and N. Winchester related these to non-mounted specimens. Slides were deposited at the Canadian National Collection, Ottawa and at the Pacific Forestry Centre, Victoria.

DATA ANALYSES

Oribatid species composition from trap type (moss/soil cores and Malaise traps) for all sites were tabulated. Relative abundance of soil arthropods was expressed as the percentage of mean number of indiviuduals per gram of dried core material (replicate cores were averaged) plotted over all sites (5) and dates (6). For each site (5), mean and standard deviation for the number of oribatid species collected were calculated by combining replicate core samples (5) with time (6). In addition, a rank abundance plot of the numbers of individuals for five study sites was plotted (pooled over all collection times (6) and replicate moss cores (5) per each collection time). The relationship between core weight and number of Acari individuals was analyzed using the Pearson product-moment correlation coefficient (Zar 1984). A two-way Anova was used to test for the effects of site and time on mean number of species present. A species-accumulation curve for each sample site (5) was generated to evaluate the cumulative number of species discovered, as a function of sampling effort. In addition to the basic species-accumulation curves, I calculated the total theoretical oribatid species richness for each habitat using the first-order jackknife estimator (Heltshe and Forrester 1983; Palmer 1990) and the second-order jackknife estimator (Burnham and Overton 1979; Palmer 1991). Both jackknife estimates function to augment the number of species actually observed by the number of species unique to any sample, weighted by the number of samples. To classify both species and sites simultaneously, I performed cluster analyses using Jaccard's and Morisita's similarity measures, squared Euclidean distance with average linkages within groups, using SPSS (1994). Measurements of diversity were calculated from cumulative species plots using the Q statistic (Kempton and Taylor 1976).

RESULTS

ORIBATIDA DIVERSITY

A total of 71 oribatid species representing 51 genera and 34 families were recovered from the Tullgren extractions (Table 1). Thirty, 28, 38, 37, and 32 species were recorded from tree 1, tree 2, forest floor, edge, and clear-cut sites, respectively (Figure 2). Species shared in common between each site ranged from a high of 23, tree 1 and tree 2; edge and clear-cut, to a low of 11, tree 1 and forest floor (Figure 2). Forty-nine species were recorded only from the extractions (Table 2), while 23 species were recorded from both Tullgren extractions and the Malaise traps (Table 2). At each site, species abundance profiles were similar (Figure 3). For all sites, approximately one quarter of the species contained three-quarters of the individuals. Accumulation curves of species richness (Figure 4 a-e) illustrate differences between sites and predict the absolute difference in the number of species should increase with increasing sample effort. The total theoretical richness of the sampled sites increases to 42.6 species at the Tree 1 site, 41.4 species at the Tree 2 site, 56.4 species at the forest ground site, 57.4 species at the edge and 50.5 species at the clear cut site (Table 3). The Q statistic values ranged from a high of 25.6 in the forest ground site to a low of 14.1 in the clear cut site (Table 4). The 2 arboreal sites cluster together with a high degree of similarity. The 3 ground sites cluster together, with the edge and clearcut most similar to each other (Figure 5). A total of 18 species were common between the arboreal and ground sites (Figure 2).

FREQUENCY AND RELATIVE ABUNDANCE

The correlation between moss core weight and the number of individual mites was not significant, ($r = ^{-}.024$; $P>0.50$, Figure 6). Acari, composed primarily of oribatids, had the highest relative abundance in all sites over all time intervals (Figure 7, a-f). Relative frequency was highest in the canopy where the occurrence of mites was over 90% in both

Table 1. Oribatida collected from moss/soil samples collected in 1991 from the Upper Carmanah Valley, Vancouver Island, British Columbia, Canada.

COHORT	SUPERFAMILY	FAMILY	SPECIES
Enarthronota	Brachychthonioidea	Brachychthoniidae	*Synchthonius* sp.
Mixonomata	Phthiracaroidea	Phthiracaridae	*Phthiracarus (Archiphthiracarus)* sp.
"	"	"	*Phthiracarus (Phthiracarus)* sp.
"	Euphthiracaroidea	Oribotritiidae	*Maerkelotritia nr. alaskensis* Hammer 1967
"	"	Euphthiracaridae	*Microtritia nr. paeneminima* (Walker 1965)
"	"	"	*Euphthiracarus nr. longirostralis* Walker 1965
"	"	"	*Euphthiracarus nr. cernuus* Walker 1965
"	"	"	*Euphthiracarus monyx* Walker 1965
"	Epilohmannioidea	Epilohmanniidae	*Epilohmannia* sp.
Desmonomata	Crotonioidea	Camisiidae	*Heminothrus* sp.
"	"	"	*Platynothrus nr. sibiricus* Sitnikova 1975
"	"	Nanhermannidae	*Nanhermannia elegantula* Berlese 1913
"	"	"	*Nanhermannia* sp. 2
"	Hermannioidea	Hermanniidae	*Hermannia gibba* (C.L. Koch 1839)
Brachypylina	Hermanniellioidea	Hermanniellidae	*Hermanniella robusta* Ewing 1918
"	"	"	*Hermanniella occidentalis* ? Ewing 1918
"	Plateremaeoidea	Gymnodamaeidae	*Gymnodamaeus* sp.
"	Damaeoidea	Damaeidae	*Belba* sp.
"	"	"	*Belbodamaeus* sp.
"	"	"	*Epidamaeus* sp. 1
"	"	"	*Epidamaeus nr. floccosus* Behan-Pelletier & Norton 1995
"	Cepheoidea	Cepheidae	*Sphodrocepheus anthelionus* Woolley & Higgins 1968
"	"	"	*Eupterotegaeus rhamphosus* Higgins & Woolley 1968

Table 1 cont.

"	"	"	*Conoppia* sp.
"	Eremaeoidea	Eremaeidae	*Eueremaeus acostulatus* Behan-Pelletier 1993
"	"	"	*Eueremaeus aysineep* Behan-Pelletier 1993
"	"	"	*Eueremaeus marshalli* Behan-Pelletier 1993
"	"	Megeremaeidae	*Megeremaeus montanus* Higgins & Wooleu 1965
"	Gustavioidea	Liacaridae	*Liacarus bidentatus* Ewing 1918
"	"	"	*Liacarus* sp. 2
"	"	"	*Dorycranosus* sp. 1
"	"	"	*Dorycranosus* sp. 2
"	"	Peloppiidae	*Ceratoppia* sp. 1
"	"	"	*Ceratoppia* sp. 2
"	"	"	*Ceratoppia* sp. 3
"	"	"	*Dendrozetes* sp.
"	"	"	*Metrioppia* sp.
"	"	"	*Parapyroppia* sp.
"	"	Kodiakellidae	*Kodiakella lutea* Hammer 1967
"	Tectocepheoidea	Tectocepheidae	*Tectocepheus velatus* (Michael 1888)
"	"	"	*Tectocepheus* sp. 2
"	Oppioidea	Oppiidae	*Oppiella* sp. 1
"	"	"	*Oppiella* sp. 2
"	"	"	*Oppiella* sp. 3
"	"	"	*Oppiella* sp. 4
"	"	"	*Oppia* sp. 1
"	"	Quadroppiidae	*Quadroppia* sp.
"	"	Suctobelbidae	*Rhinosuctobelba* sp.
"	"	"	*Allosuctobelba gigantea* (Hammer 1955)
"	"	"	*Suctobelbella* sp. 1

Table 1 cont.

"	"	"	*Suctobelbella* sp. 2
"	"	"	*Suctobelbella* sp. 3
"	"	Autognetidae	*Autogneta longilamellata* (Michael 1885)
"	"	Thyrisomidae	*Banksinoma* sp.
"	Cymbaeremaeoidea	Cymbaeremaeidae	*Scapheremaeus palustris* Sellnick 1924
"	Oripodoidea	Oribatulidae	*Eporibatula* sp.
"	"	Oripodidae	Oripodidae? genus, sp. 1
"	"	"	Oripodidae? genus, sp. 2
"	"	Scheloribatidae	*Scheloribates* sp. 1
"	"	"	*Scheloribates* sp. 2
"	Ceratozetoidea	Chamobatidae	*Chamobates* sp.
"	"	Ceratozetidae	*Ceratozetes* sp.
"	"	"	*Sphaerozetes* sp.
"	"	"	*Melanozetes* sp.
"	Phenopelopoidea	Phenopelopidae	*Eupelops* sp.
"	Achipterioidea	Achipteriidae	*Achipteria nr. oregonensis* Ewing 1918
"	"	"	*Anachipteria acuta* (Ewing 1918)
"	"	"	*Anachipteria* sp. 2
"	"	"	*Dentachipteria* sp.
"	Oribatelloidea	Oribatellidae	*Oribatella* sp.
"	Galumnatoidea	Galumnatidae	*Pilogalumna* sp.

Figure 2. Numerical relationship between adult oribatid species from 5 study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time periods. Numbers along the lines represent those species in common between sites. Numbers within the circles represent species occupying a given site.

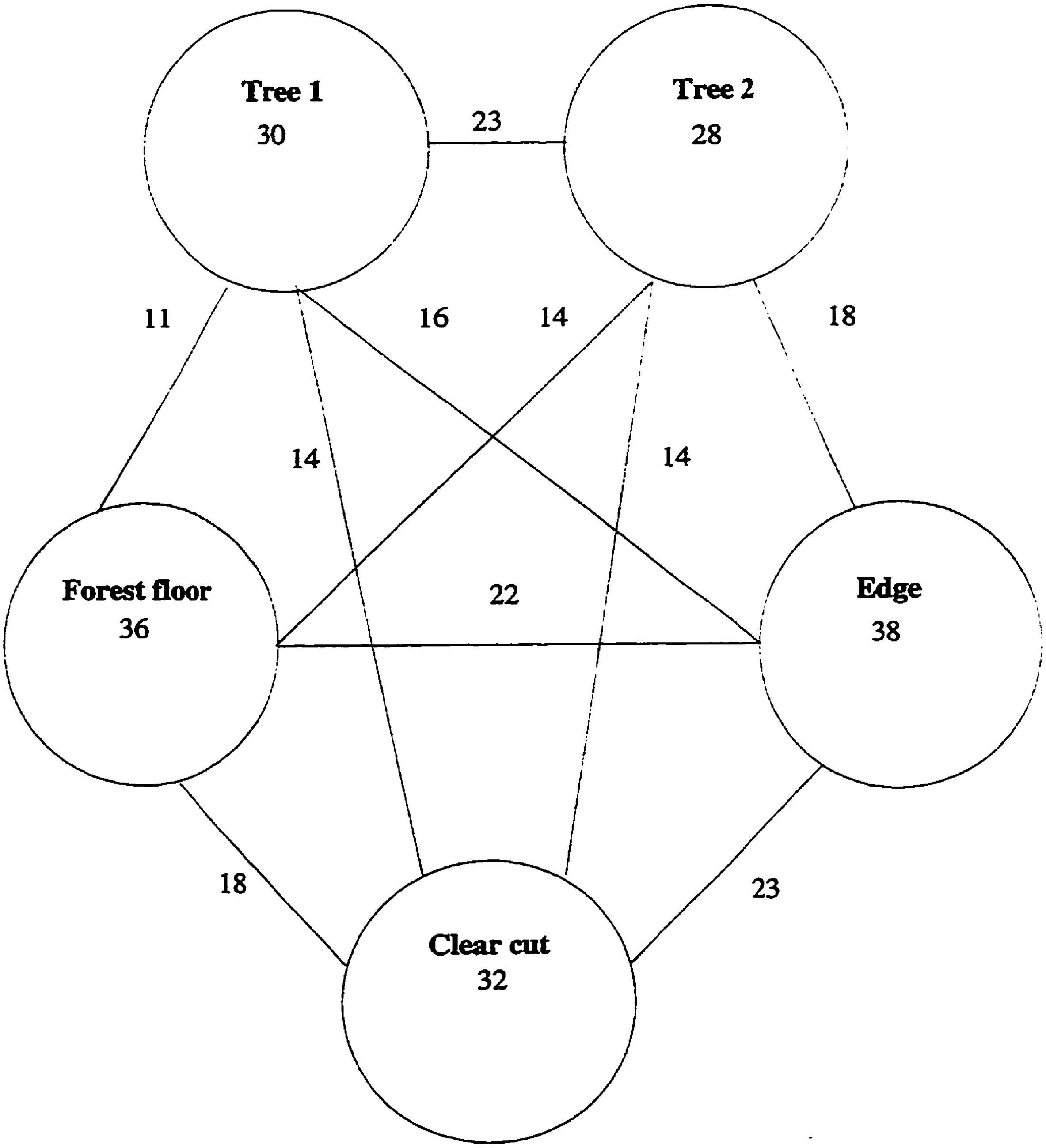

Tree 1
30
Tree 2
28
23
11
16
14
18
14
14
Forest floor
36
22
Edge
38
18
23
Clear cut
32

Table 2. Oribatid species compostion and occurrence in the Upper Carmanah Valley, Vancouver Island, British Columbia, Canada. Data are recorded from high-grade extraction for two canopy sites, tree 1, tree 2, and three ground sites, forest interior, edge and clear-cut.Species indicated by √ are recorded as present, - absent, and * are species recorded from Malaise traps.

SPECIES	TREE 1	TREE 2	FOREST INTERIOR	EDGE	CLEAR CUT
Synchthonius sp.	√	-	-	√	√
Phthiracarus (Archiphthiracarus) sp.	-	-	√	√	√
Phthiracarus (Phthiracarus) sp.	-	-	√	√	√
* *Maerkelotritia nr. alaskensis* Hammer 1967	√	√	√	√	√
Microtritia nr. paeneminima (Walker 1965)	-	-	√	-	-
Euphthiracarus nr. longirostralis Walker 1965	-	-	-	-	√
Euphthiracarus nr. cernuus Walker 1965	-	-	√	-	-
Euphthiracarus monyx Walker 1965	-	-	√	-	-
Epilohmannia sp.	-	-	√	-	-
Heminothrus sp.	-	-	√	√	-
Platynothrus nr. sibiricus Sitnikova 1975	-	-	√	-	-
Nanhermannia elegantula Berlese 1913	-	-	√	√	√
Nanhermannia sp. 2	√	-	-	√	√
* *Hermannia gibba* (C.L. Koch 1839)	√	√	√	√	√
Hermanniella robusta Ewing 1918	-	-	√	-	-
Hermanniella occidentalis ? Ewing 1918	-	-	√	√	-
Gymnodamaeus sp.	√	√	-	-	-
Belba sp.	√	√	-	√	-
Belbodamaeus sp.	-	-	-	-	√
Epidamaeus sp. 1	√	√	-	-	-
Epidamaeus nr. floccosus Behan-Pelletier & Norton 1985	√	√	-	-	-

Table 2 cont.

Sphodrocepheus anthelionus Woolley & Higgins 1968	-	-	√	√	-
* *Eupterotegaeus rhamphosus* Higgins & Woolley 1968	√	√	-	√	√
Conoppia sp.	-	-	-	-	√
* *Eueremaeus acostulatus* Behan-Pelletier 1993	√	√	√	-	-
* *Eueremaeus aysineep* Behan-Pelletier 1993	√	√	-	-	-
Eueremaeus marshalli Behan-Pelletier 1993	√	√	-	-	-
Megeremaeus montanus Higgins & Woolley 1965	-	-	-	√	-
Liacarus bidentatus Ewing 1918	-	-	√	√	√
Liacarus sp. 2	-	√	√	√	√
* *Dorycranosus* sp. 1	√	√	√	-	-
* *Dorycranosus* sp. 2	-	-	√	√	-
* *Ceratoppia* sp. 1	-	√	√	√	√
* *Ceratoppia* sp. 2	-	√	√	-	√
* *Ceratoppia* sp. 3	√	√	-	√	-
* *Dendrozetes* sp.	√	√	√	-	√
Metrioppia sp.	-	-	√	√	-
Parapyroppia sp.	-	√	-	-	-
Kodiakella lutea Hammer 1967	-	-	√	-	-
Tectocepheus velatus (Michael 1888)	√	√	√	√	√
Tectocepheus sp. 2	√	√	√	√	-
Oppiella sp. 1	√	√	-	-	-
Oppiella sp. 2	√	-	-	√	-
Oppiella sp. 3	-	-	√	-	-
Oppiella sp. 4	-	-	-	√	-

Table 2 cont.

Oppia sp. 1	√	√	-	√	√
Quadroppia sp.	√	√	-	√	√
Rhinosuctobelba sp.	-	-	-	√	-
Allosuctobelba gigantea (Hammer 1955)	-	-	-	√	√
Suctobelbella sp. 1	√	-	-	√	√
Suctobelbella sp. 2	-	-	√	√	-
Suctobelbella sp. 3	-	-	√	-	-
Autogneta longilamellata (Michael 1885)	√	√	-	-	√
* *Banksinoma* sp.	-	√	-	-	-
* *Scapheremaeus palustris* Sellnick 1924	√	-	-	-	-
* *Eporibatula* sp.	√	√	√	√	√
Oripodidae? genus, sp. 1	√	-	-	-	-
* Oripodidae? genus, sp. 2	-	√	-	-	-
* *Scheloribates* sp. 1	√	√	√	√	√
Scheloribates sp. 2	√	-	-	-	-
* *Chamobates* sp.	-	-	√	√	√
* *Ceratozetes* sp.	-	-	-	√	√
* *Sphaerozetes* sp.	√	√	√	√	√
Melanozetes sp.	-	-	√	√	√
Eupelops sp.	-	-	√	-	-
Achipteria nr. oregonensis Ewing 1918	-	-	-	√	√
Anachipteria acuta (Ewing 1918)	-	-	√	-	√
* *Anachipteria* sp. 2	-	-	-	-	√
* *Dentachipteria* sp.	-	-	√	√	√
* *Oribatella* sp.	√	√	√	-	√
Pilogalumna sp.	-	√	-	-	-

Figure 3. Rank abundance plots between the number of adult oribatid species and the number of individuals in sample cores, collected from moss/soil mats in the Upper Carmanah Valley, British Columbia. The abundance of each species is plotted on a logarithmic scale.

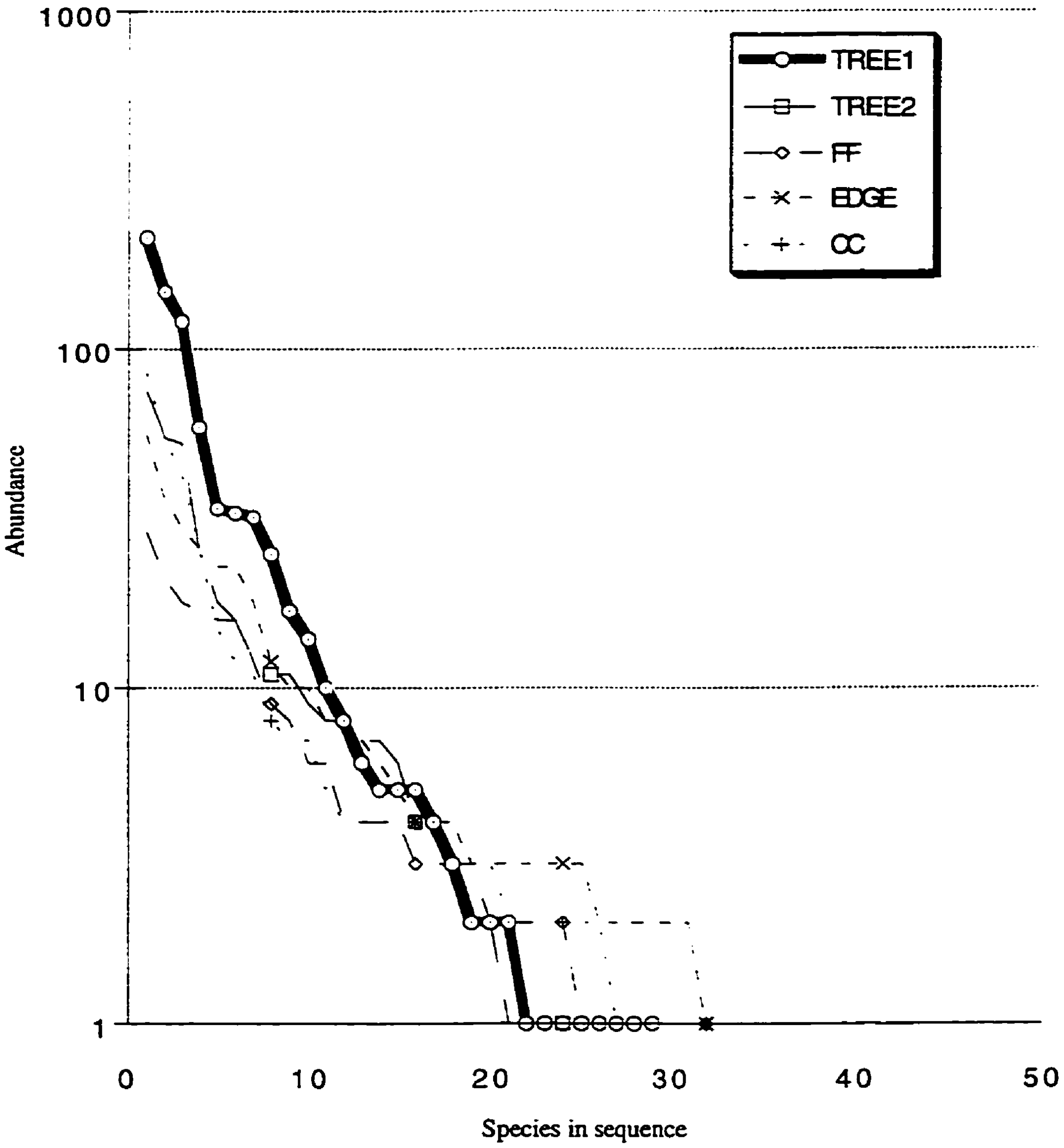
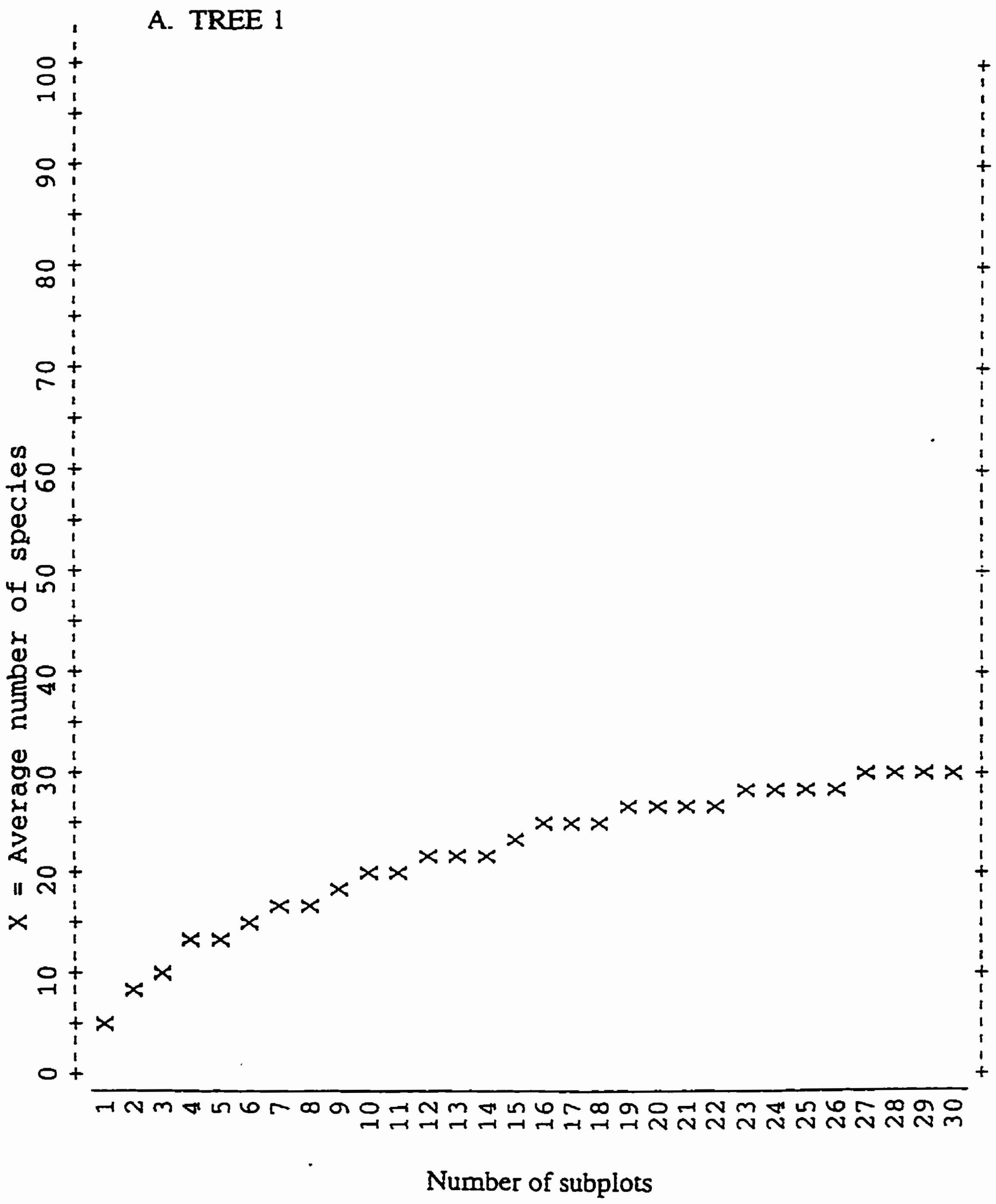
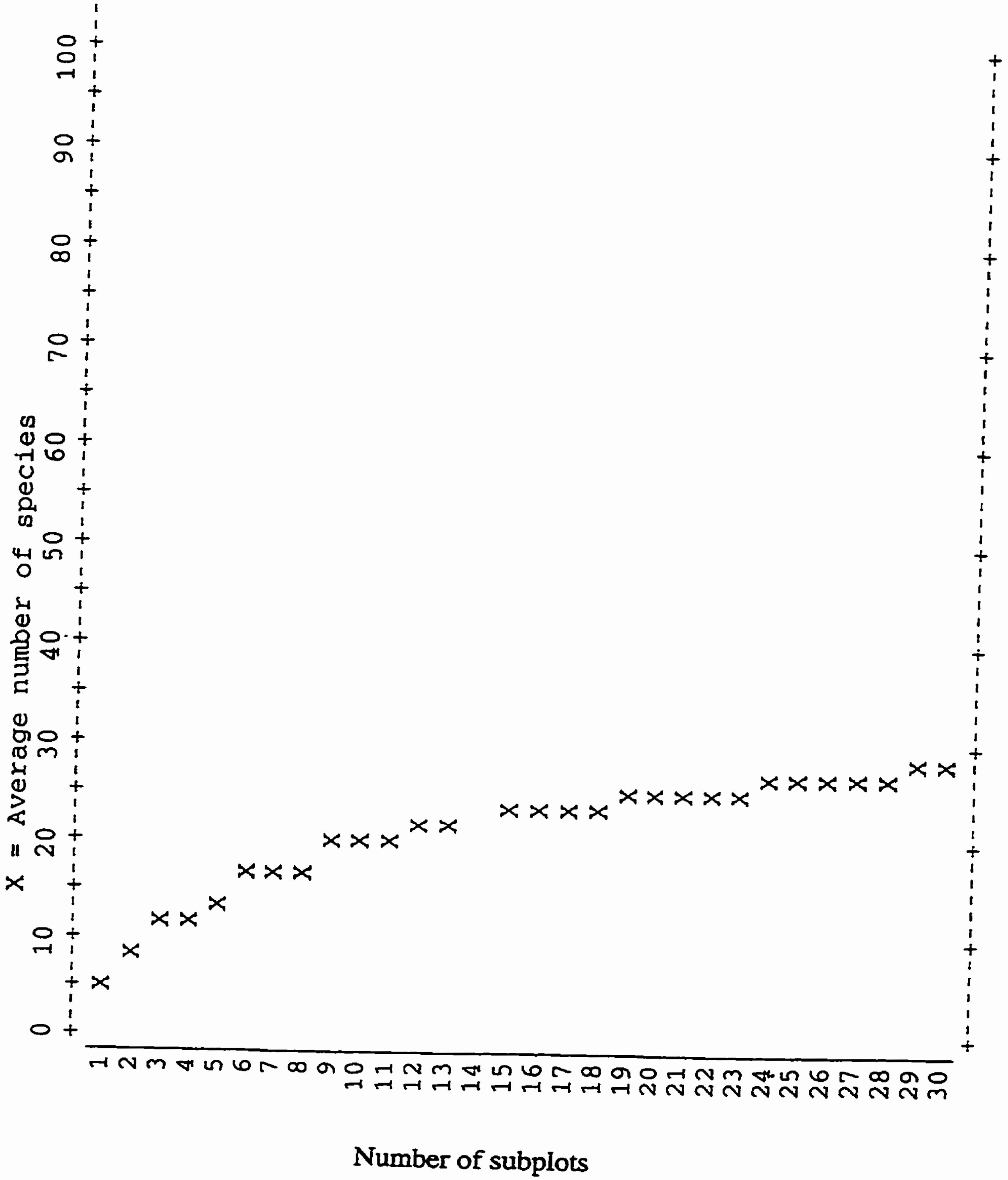

1000
100
10
1
Abundance
0
10
20
30
40
50
Species in sequence
TREE1
TREE2
FF
EDGE
CC

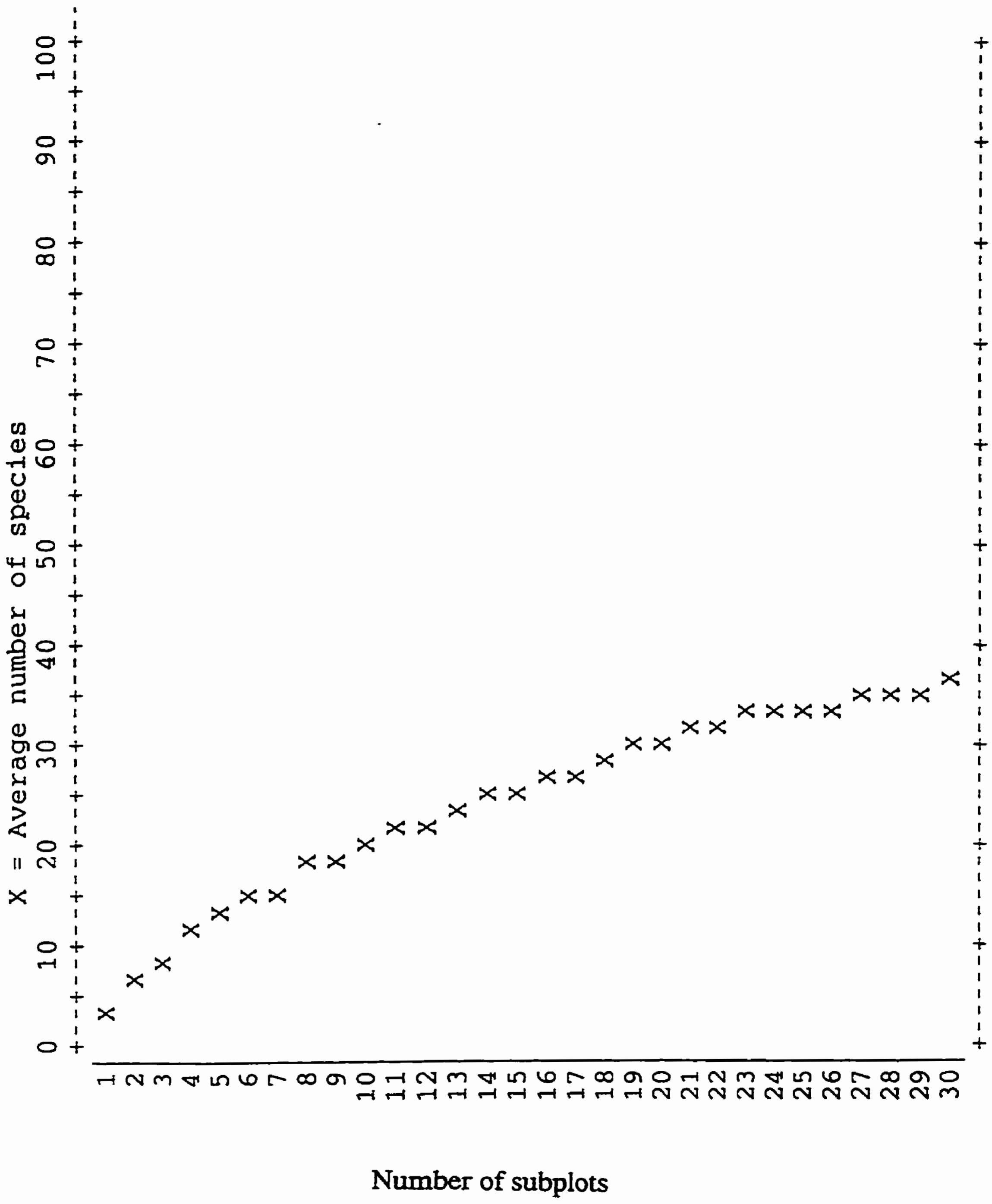
Figure 4 A-E. Accumulation curves of species richness for oribatid species from 5 study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time periods.


A. TREE 1
X = Average number of species
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Number of subplots

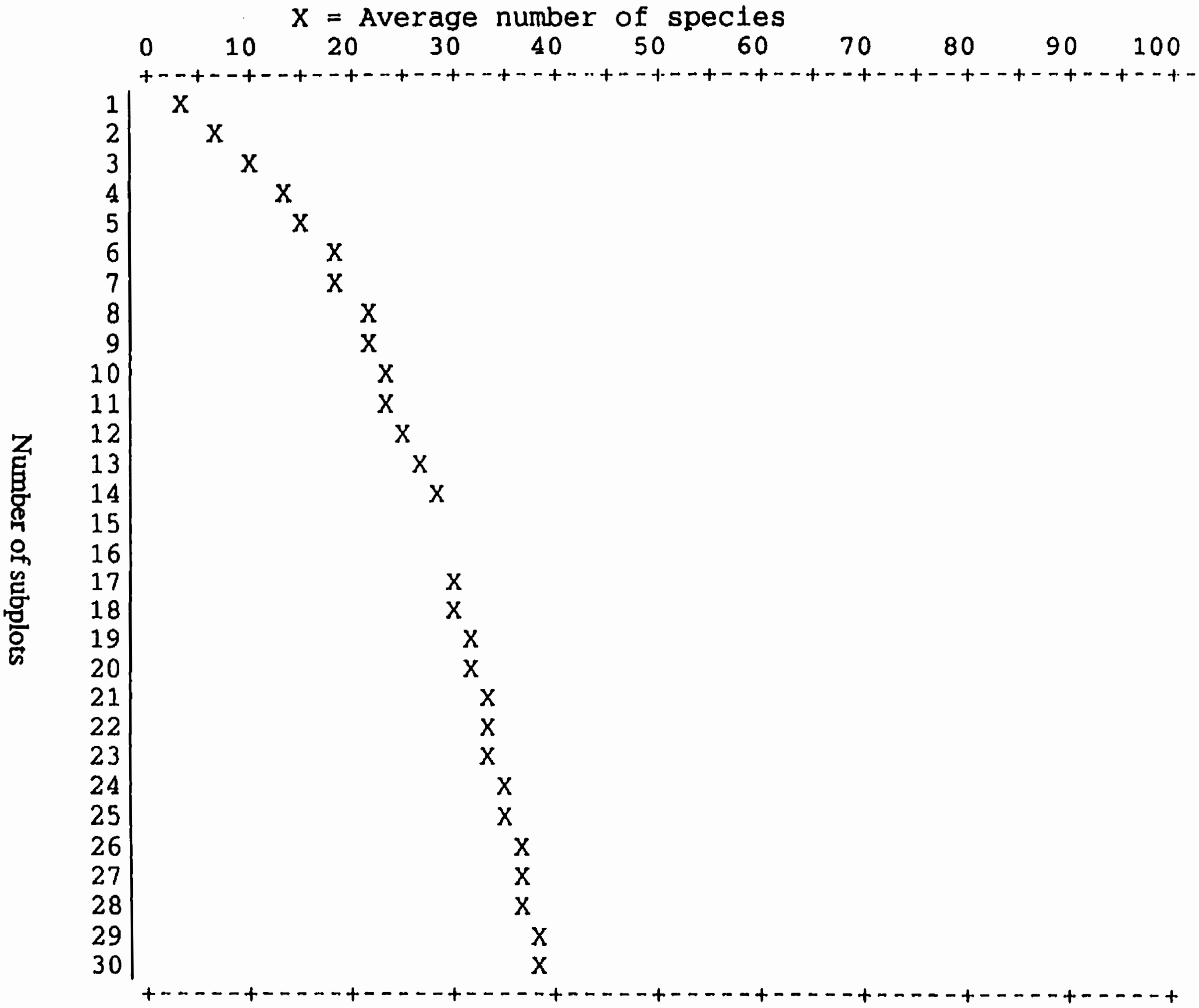
B. TREE 2


X = Average number of species
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Number of subplots

C. FOREST FLOOR



D. EDGE


X = Average number of species
0
10
20
30
40
50
60
70
80
90
100
Number of subplots
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30

E. CLEAR CUT

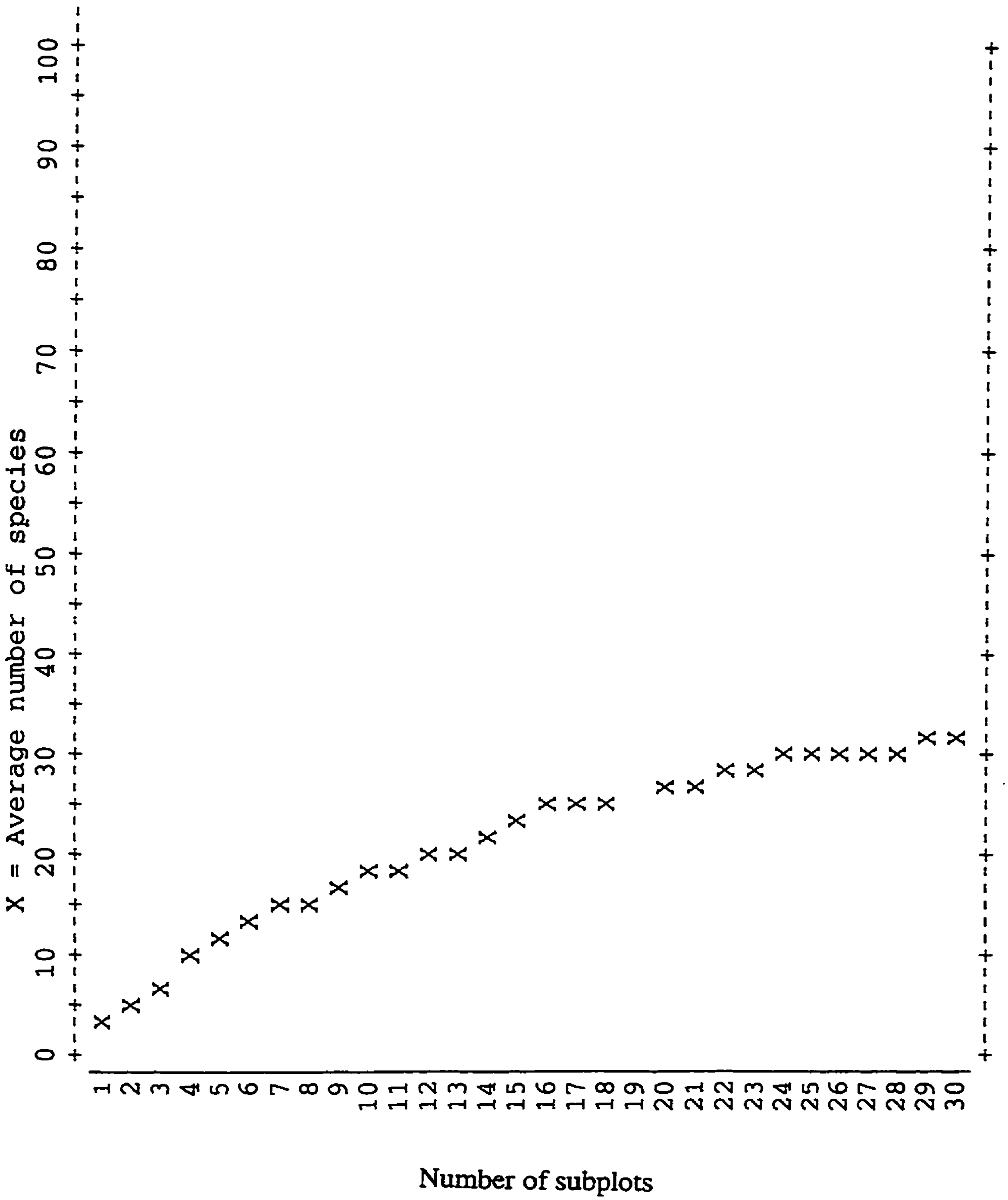

X = Average number of species
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Number of subplots

Table 3. First and second-order Jackknife estimates for the total theoretical oribatid species richness for each sample site in the Upper Carmanah Valley, Vancouver Island, British Columbia. Estimates are based on the 1991 moss/soil coring program.

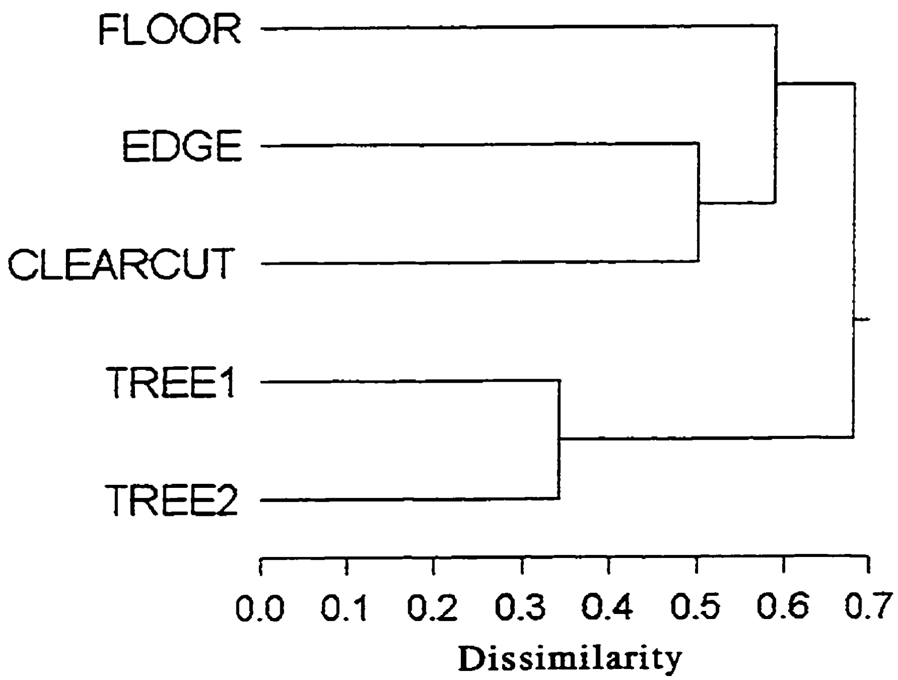
Sample site	# species observed	1st order estimate	2nd order estimate
Tree 1 canopy	30	38.7	42.6
Tree 2 canopy	28	35.7	41.4
Forest interior	36	50.5	56.4
Transition zone	38	51.5	57.4
Clear cut	32	45.5	50.5

Table 4. Measurement of the inter-quartile slope of the cumulative species abundance curves, Q statistic for the mature oribatid species from the 5 sample sites in the Upper Carmanah Valley, Vancouver Island , British Columbia, Canada.

Sample Site	Tree 1 canopy	Tree 2 canopy	Forest ground	Edge	Clear cut
Q statistic	24.2	15.5	25.6	19.1	14.1

Figure 5. Dendrograms showing the similarity between oribatid mites found at 5 sample sites in the Upper Carmanah Valley. Jaccard's similarity values were calculated from the number of identified species of oribatids collected at each site and Morisita's similarity values were calculated from the number of individuals in each identified oribatid species collected at each site.

A) Jaccard's Index



B) Morisita's Index

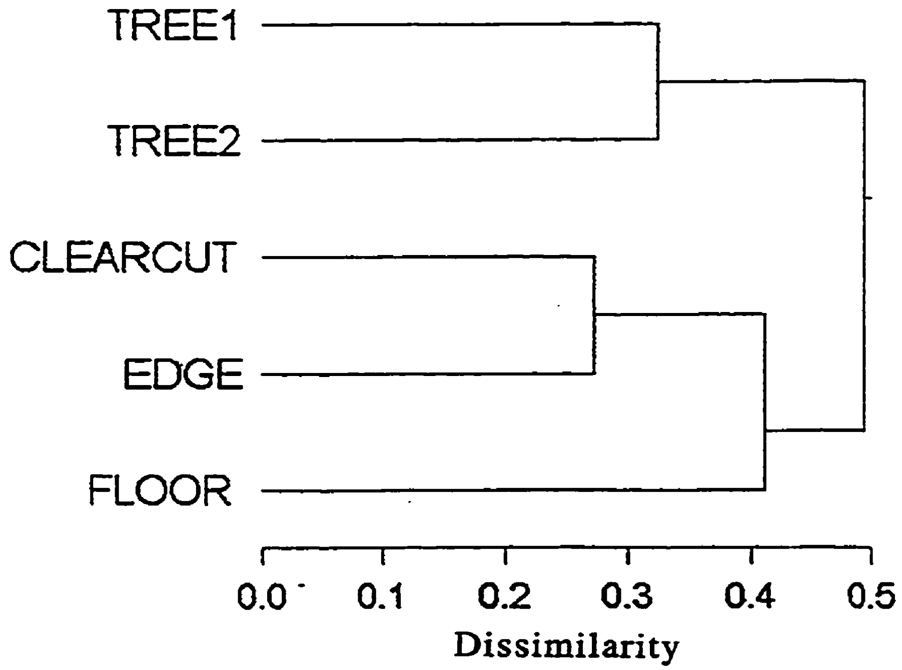


Figure 6. The relationship between the number of individuals (Acari) and moss/soil core dry weight for all samples pooled over all sampling times and over all core replicates. The Pearson product-moment correlation coefficent, $r = ^{-}.024$.

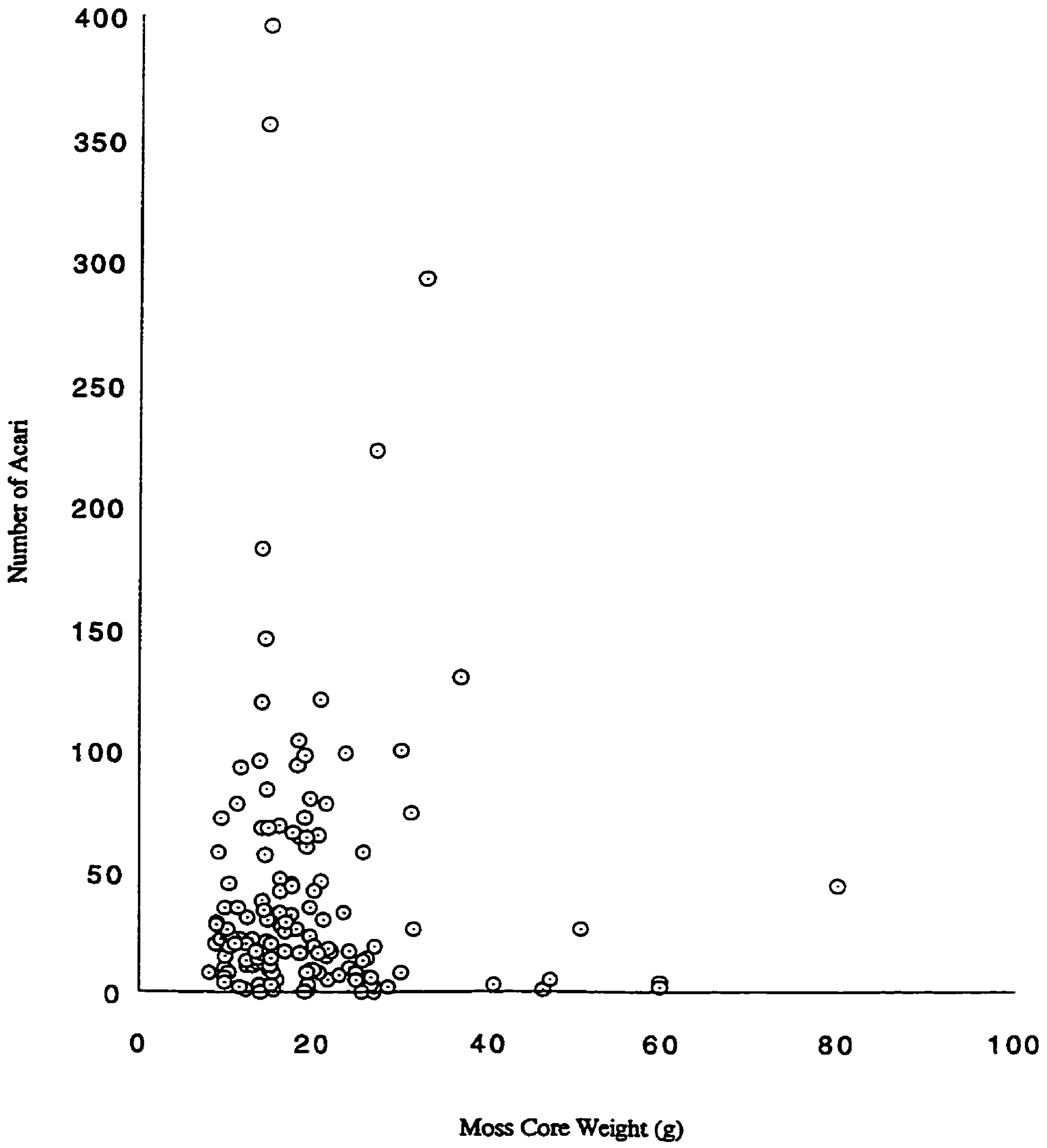
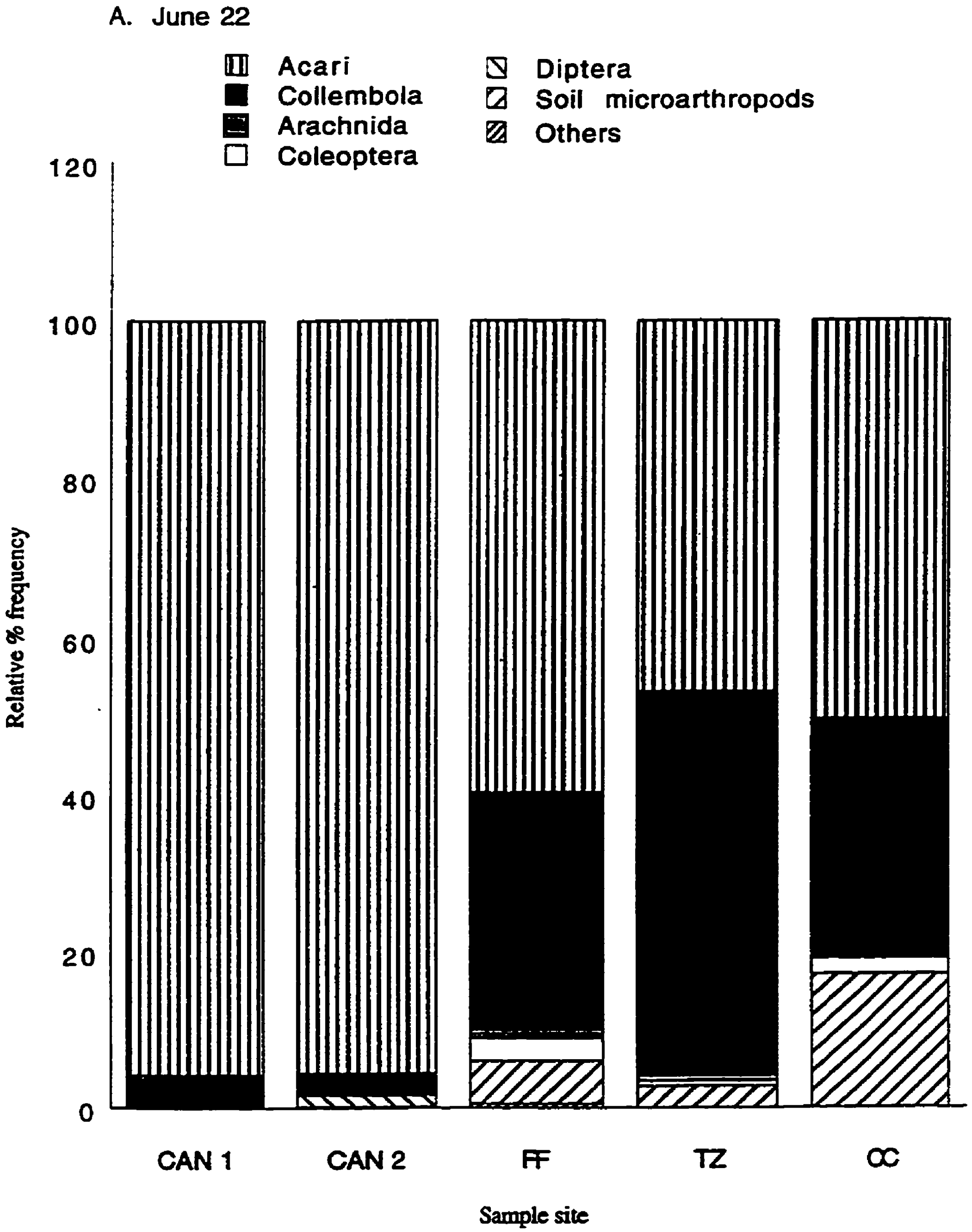
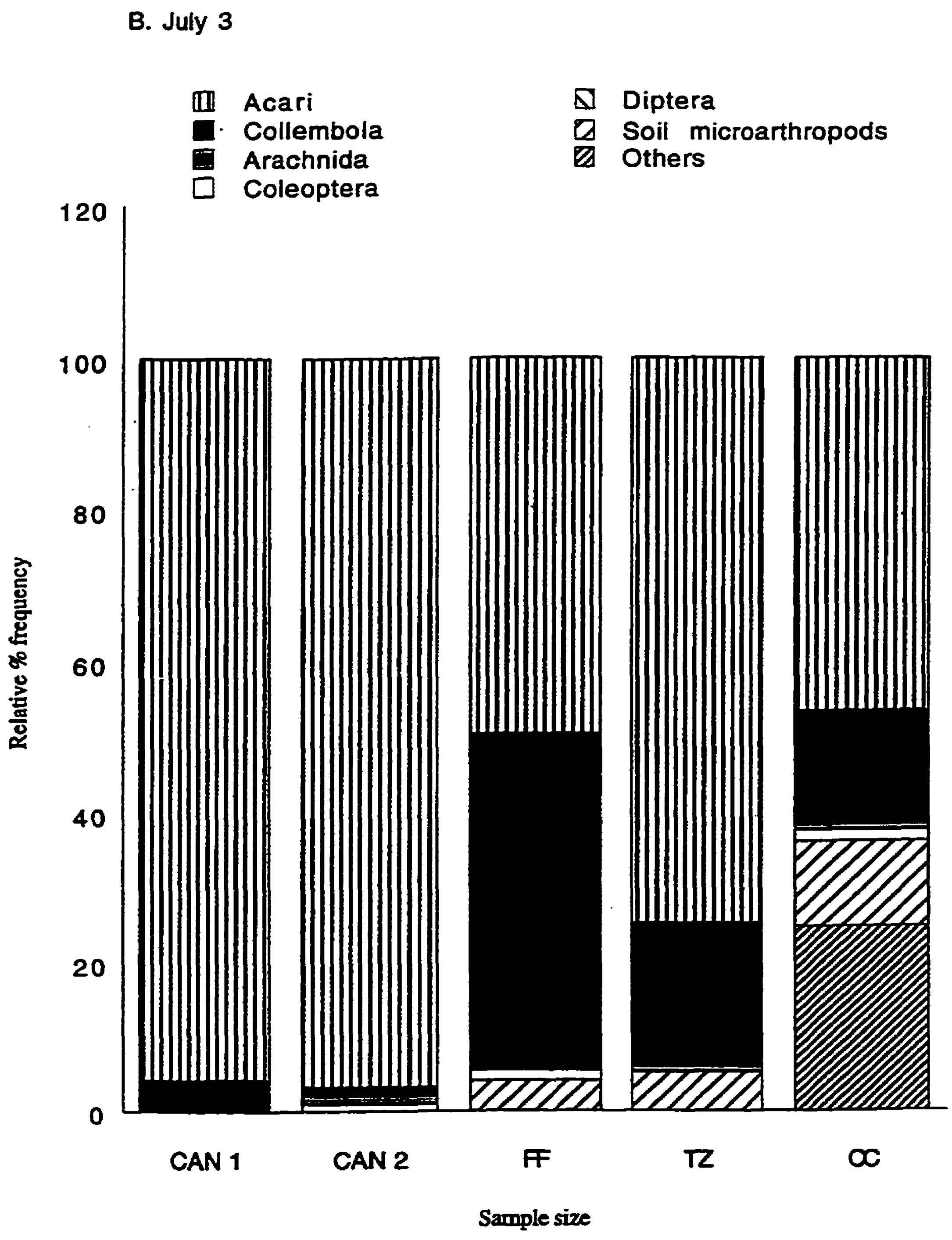
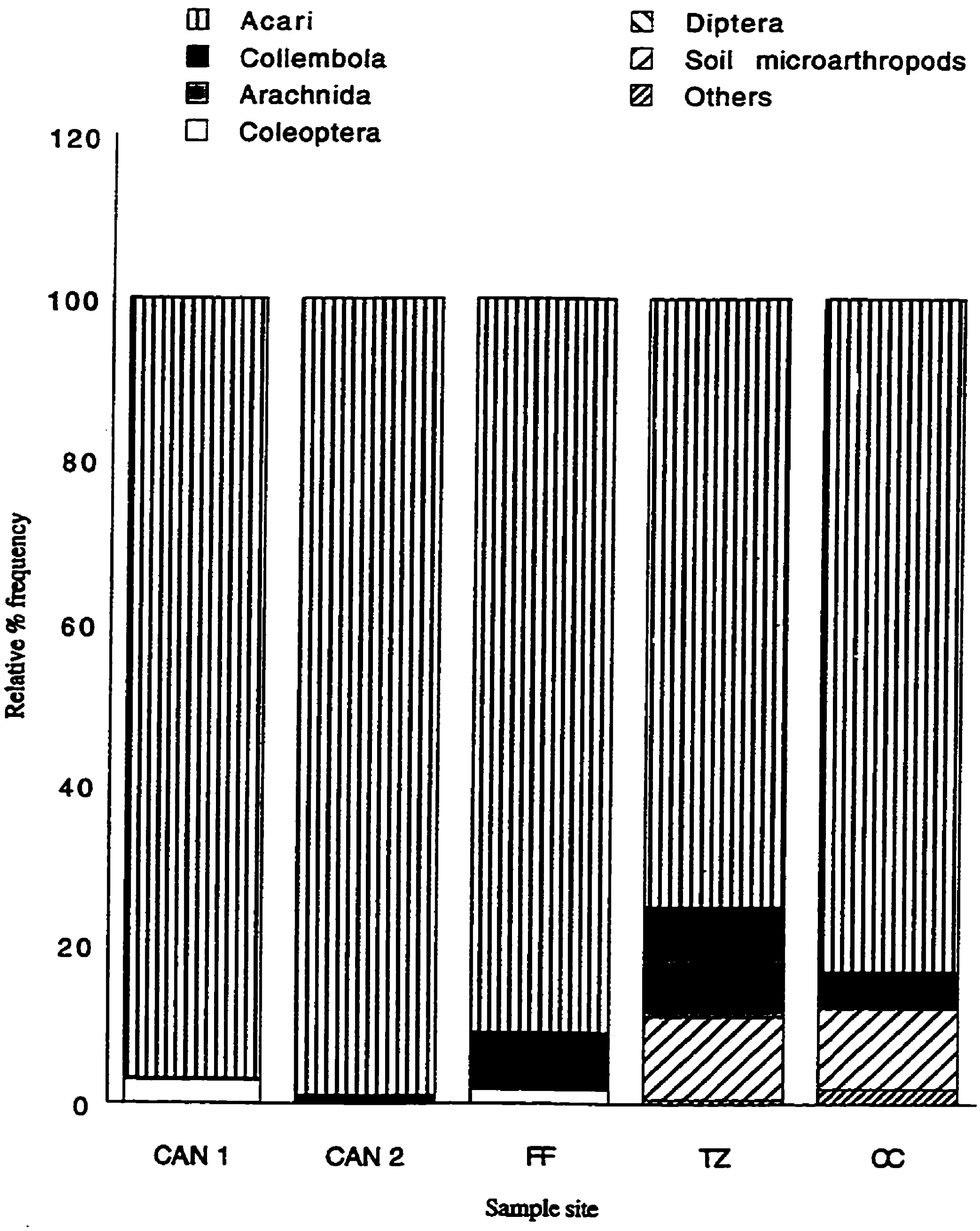

400
350
300
250
200
150
100
50
0
Number of Acari
0
20
40
60
80
100
Moss Core Weight (g)

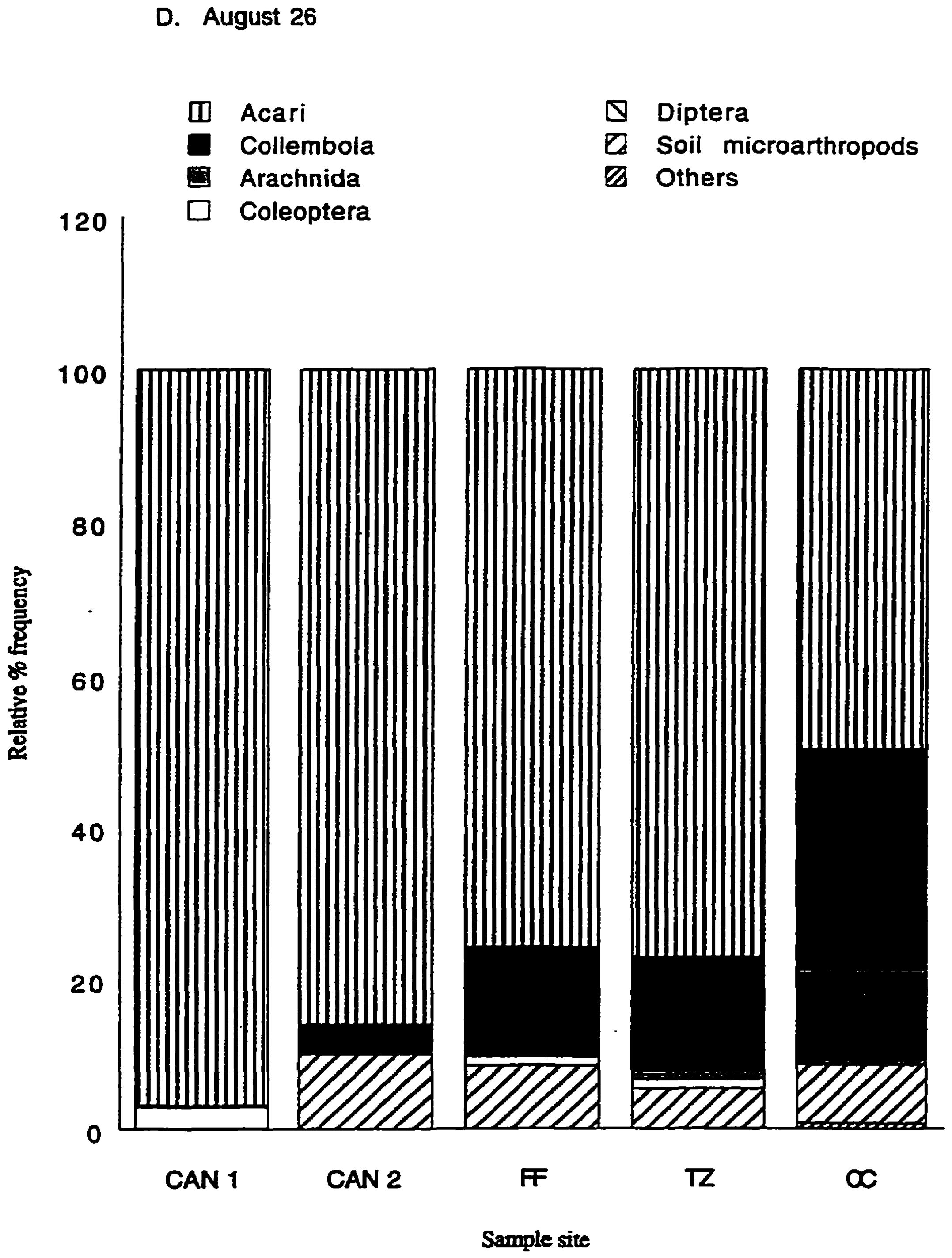
Figure: 7 A-F. Relative abundance of moss/soil microarthropods expressed as mean % of number of individuals per gram of dried core material for all sites over all sampling times.

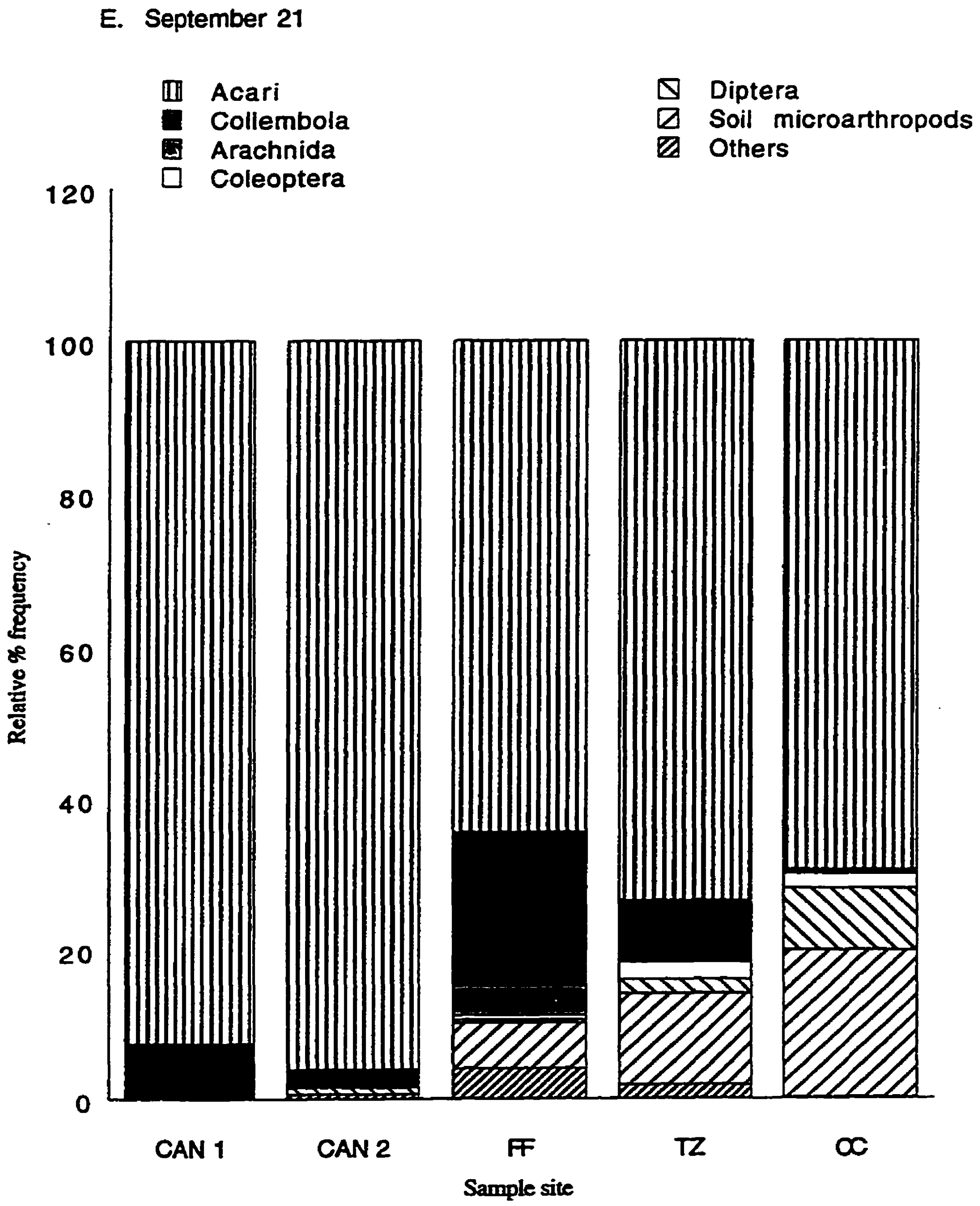

A. June 22
Acari
Collembola
Arachnida
Coleoptera
Diptera
Soil microarthropods
Others
120
100
80
60
40
20
0
Relative % frequency
CAN 1
CAN 2
FF
TZ
CC
Sample site


B. July 3
Acari
Collembola
Arachnida
Coleoptera
Diptera
Soil microarthropods
Others
120
100
80
60
40
20
0
Relative % frequency
CAN 1
CAN 2
FF
TZ
CC
Sample size

C. July 29

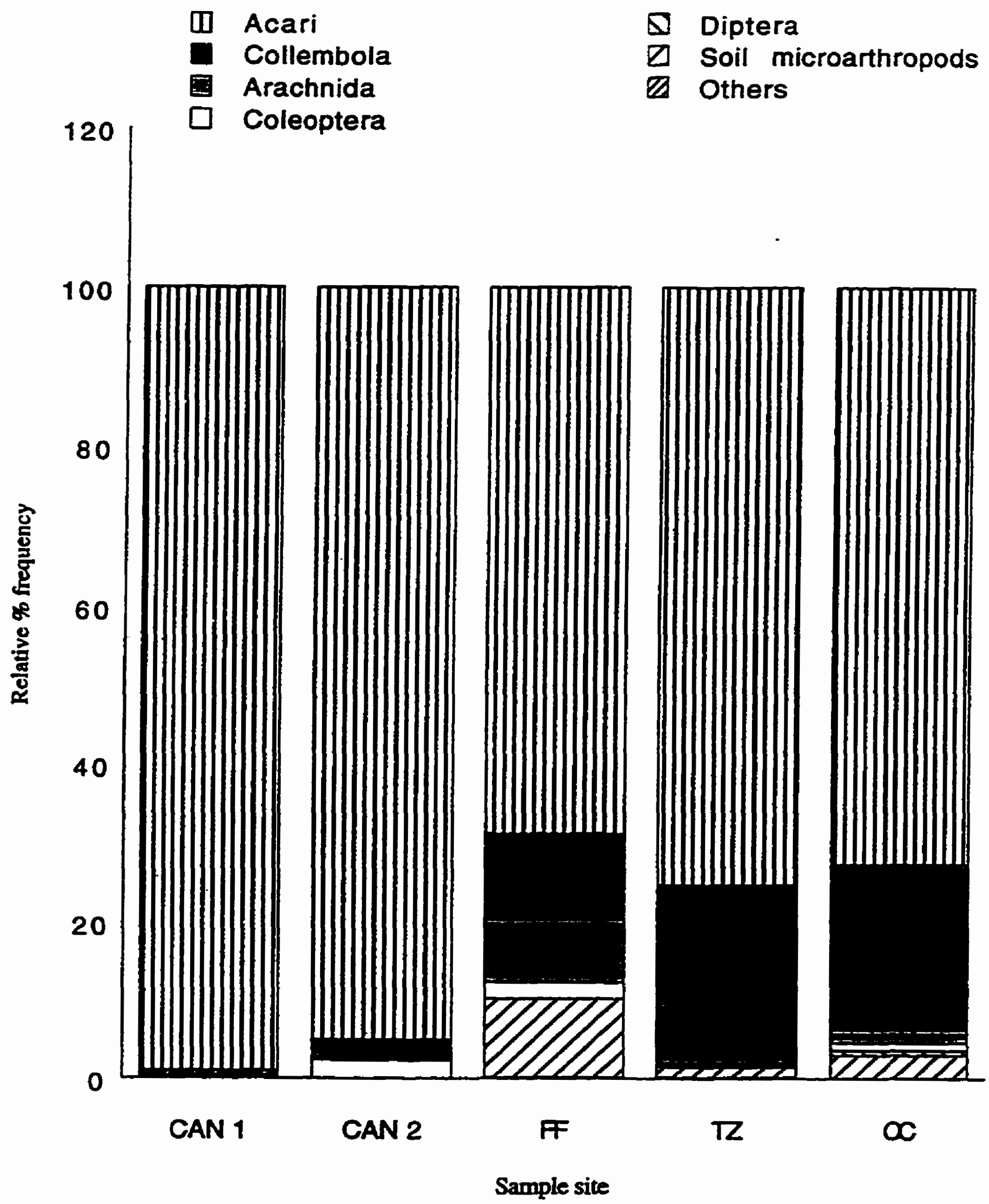

Acari
Collembola
Arachnida
Coleoptera
Diptera
Soil microarthropods
Others
120
100
80
60
40
20
0
Relative % frequency
CAN 1
CAN 2
FF
TZ
CC
Sample site


D. August 26
Acari
Collembola
Arachnida
Coleoptera
Diptera
Soil microarthropods
Others
120
100
80
60
40
20
0
Relative % frequency
CAN 1
CAN 2
FF
TZ
CC
Sample site



E. September 21

F. October 27


Acari
Collembola
Arachnida
Coleoptera
Diptera
Soil microarthropods
Others
120
100
80
60
40
20
0
Relative % frequency
CAN 1
CAN 2
FF
TZ
CC
Sample site

canopy sites at all sampling times. Collembola formed up to 50% relative abundance in the three ground sites early in the sampling season. As time progressed the oribatid relative frequency increased at all ground sites. I observed no statistically significant relationship between the occurrence of species per replicate per site and relationship between species presence over time (Table 5). I recorded significant effects of site ($F_{4,120} \geq 3.261$, $P < 0.025$), and time ($F_{5,120} \geq 2.891$, $P < 0.025$). Interaction effect (site X time) on mean number of species was not significant ($F_{20,120} \geq 1.602$, $P > 0.05$).

Table 5. Mean and standard deviation for the number of oribatid species collected from replicated moss/soil core samples for each of 6 sample periods in 1991: 1 = June 22; 2 = July 3; 3 = July 29; 4 = August 26; 5 = September 21; 6 = October 27. All samples were collected from the Sitka spruce forest in the Upper Carmanah Valley, Vancouver Island, British Columbia.

	Site				
Time	Tree 1	Tree 2	Forest Ground	Edge	Clear cut
1	4.0 ± 4.1	7.0 ± 4.1	4.0 ± 1.2	3.8 ± 3.0	2.6 ± 3.2
2	5.2 ± 3.0	5.4 ± 3.0	2.8 ± 2.2	3.0 ± 2.0	0.4 ± .0.6
3	6.0 ± 1.9	2.8 ± 3.1	2.8 ± 2.4	2.4 ± 1.1	4.8 ± 1.9
4	2.4 ± 2.0	2.8 ± 3.4	1.6 ± 2.3	5.6 ± 2.2	1.8 ± 1.9
5	5.8 ± 2.8	5.0 ± 1.4	3.6 ± 2.9	3.8 ± 2.7	2.8 ± 3.0
6	7.0 ± 2.2	3.8 ± 2.5	7.0 ± 3.5	5.2 ± 3.4	4.2 ± 2.3

DISCUSSION

Oribatid mites dominate the microarthropod fauna in moss mat habitats in the ancient forest of the Carmanah Valley. This finding is consistent with other faunal studies of mature forests (Cornaby et al. 1975, Huhta and Koskenniemi 1975, Behan-Pelletier *et al.* 1978, Wallwork 1983, Norton 1990) and also emphasizes the dominance of oribatid mites in coniferous soil ecosystems (Huhta and Koskenniemi 1975, Schenker 1984a,b, 1986, Seastedt et al. 1989, Teuben and Smidt 1992, Dwyer *et al.* 1997). The 71 oribatid species recorded in this study, of which 48 are undescribed, represent the highest number of species recorded from moss habitats in a northern temperate Sitka spruce forest. Northern forest systems, although relatively unexplored, contain a diverse assemblage of oribatids, as demonstrated by Dwyer *et al.* (1997) who found 83 oribatid species in samples covering a range of microhabitats in 2 commercial balsam fir forests. Our study is the first to sample the high canopy in an ancient forest where samples from 2 sites accounted for 30 and 28 species respectively, of which 12 species appear to be canopy specific. Our ground-based moss samples accounted for 57 species which is higher in comparison with other mature forest ground-based studies, where a wider range of microhabitats were sampled (e.g. litter debris, lichens, bark, rotten wood). Typical species richness values in these studies were in the order of 30 or 40 (Wallwork 1983, Andre´ 1984) and records of 28 species from a spruce forest were recorded (see Wallwork 1983). Comparable data for the tropics are scant although Wunderle (1992) recorded 42 species from soil samples taken at heights under 15 m from a lowland Peruvian rainforest, and a study whiche sampled a range of microhabitats from the canopy and ground in the forests of northern Venezuela by Behan-Pelletier *et al.* (1993) indicated that a total of 150 oribatid species were present. Greater species diversity in the tropics is not surprising given the complexity of soil and derived soil (e.g. bromeliads) microhabitats (Paoletti *et al.* 1990, Nadkarni and Longino 1990).

The range of microhabitats available for colonization by oribatids is impressive

(Wallwork 1983) and the importance of epiphytic cover as a determinant of species composition has been discussed (Andre´ 1984). To concentrate on macroscale habitat influences on species assemblages, we standardized our examination of microhabitats at each site by sampling only intact moss mats with similar species composition and coring only to the soil surface interface. We found that core weight was not a determining factor in the number of species or individuals present in a sample and observed changes in oribatid composition were attributable to time and site. Previous studies (Trave´ 1963, Spain 1969, Aoki 1971, 1973, 1974, Ehler and Frankie 1979, Andre´ 1984, Norton and Palacios-Vargas 1987, Wunderle 1991, 1992, Walter 1995, Behan-Pelletier and Winchester 1997,) have noted that oribatid distribution patterns extend to the epigeal (arboreal, above-ground) habitats. In temperate forests oribatids appear to have a distinct arboreal component (Gjelstrup 1979, Wallwork 1983, Winchester and Ring 1996a, Behan-Pelletier and Winchester 1997) and arboreal specificity in the tropics has been recorded (Behan-Pelletier *et al.* 1993, Paoletti *et al.* 1990, Wunderle 1991, 1992, Aoki 1967). Our results confirm the hypothesis that the Sitka spruce canopy contains a distinct species assemblage of oribatids, mainly Brachyphlina, (e.g., Oppiidae, Peloppiidae, Ermaeidae, Cymbaeremaeidae) and that these species are not just a random subset of the ground fauna. Our results are consistent both when viewed from a qualitative (presence/absence) or a quantitative (number of individuals per species) analysis and supports the observations on arboreal specificity made by Trave´ (1963), Spain and Harrison (1968), Spain (1969), Aoki (1971, 1973), Norton and Palacios-Vargas (1987), Wunderle (1991), Andre´ *et al.* (1992), and Behan-Pelletier and Winchester (1997). Walter (1995) found similar results in a subtropical rainforest where canopy inhabiting mites did not represent an extension of the soil-dwelling fauna. The 'suspended' soil (sensu Delamere-Deboutteville) habitat, in our study is located between 30 and 66m in the canopy of ancient Sitka spruce trees and is discontinuous with the ground although the numerically dominant moss cover in both habitats is composed of the same moss species.

We consider the oribatids of the canopy moss mats to be inhabitants of islands, in the sense that they are isolated from their ground counterparts and have a distinct fauna that is characterized by two ecological groups of species: group 1, those specific to arboreal habitats which have low dispersal capabilities (Behan-Pelletier and Winchester 1997); and group 2, those species that occur in the arboreal but are not specific to that habitat and have high dispersal capabilities (Behan-Pelletier and Winchester 1997). Species placed in group 1 have several genera in common with the truly arboreal forms given separate group status as an ecological life-form (i.e. strictly arboreal) by Aoki (1971) and include *Megeremaeus*, *Dendrozetes*, *Liacarus*, *Scapheremaeus* and *Achipteria*. Another life-form group proposed by Aoki (1971), the "wandering forms", are analogous to our group 2 designation and are composed of mites that expand their soil habitat to living trees and are able to wander between the two habitats. Several genera are common to both studies and include: *Hermannia gibba* , *Tectocepheus velatus* , *Ceratoppia*, and *Eupterotegaeus*. Regardless of site and group designation, approximately 26% of the species recorded contain 74% of the individuals, suggesting that each site is characterized by an assemblage of euryecious species (e.g., group 2, wandering forms) that are numerically dominant and common to all sample sites and a set of stenoecious species (group 1, e.g., strictly arboreal) which are specific to each sample site. Site specificity is most evident in the ancient forest where 33% of the total species recorded did not occur in the edge or clear cut sample sites. Within the ancient forest, 11 species were specific to forest interior habitats: *Anachipteria acuta* (Ewing), *Epilohmannia* sp., *Eupelops* sp., *Euphthiracarus monyx* Walker, *Euphthiracarus* nr. *cernuus* Walker, *Hermanniella robusta* Ewing, *Kodiakella lutea* Hammer, *Mictotritia* nr. *paeneminima* (Walker), *Oppiella* sp. 3, *Platynothrus* nr. *sibiricus* Sitnikova, *Suctobebella* sp. 3, and 12 species were specific to the arboreal habitat: *Banksinoma* sp., *Epidamaeus* nr. *floccosus* Behan-Pelletier and Norton, *Epidamaeus* sp. 1, *Eueremaeus aysineep* Behan-Pelletier, *Eueremaeus marshalli*, Oripodidae (genus undescribed), sp.1, sp.2, *Gymnodamaeus* sp. *Oppiella* sp. 1, *Parapyroppia* sp., *Pilogalumna* sp., and *Scapheremaeus palustris* Sellnick. Jackknife estimates indicate that increased sampling would increase the number of species found in all sites and based on the relationship between number of individuals and species we suggest that in the ancient forest sites these species would be from the specialist group and would further strengthen the argument that ancient forest habitats are source areas for oribatid biodiversity.

We observed significant differences in the mean number of species present across study sites and time and suggest that these differences, which led to increased patchiness in the ground sites, especially the clear cut site, can be viewed in terms of macroscale influences which apply to microscale patterns. This suggests that in times of microhabitat stress (e.g., desiccation of the moss mats) wandering early-colonizing species in the ground sites such as *Scheloribates* sp. 1, *Achipteria nr. oregonensis*, *Hermannia gibba* and *Tectocepheus velatus* become patchy as they disperse to suitable microhabitats. These results further support the observations by Behan-Pelletier and Winchester (1997) which indicated that oribatids (eg. *Trichoribates* sp. 1, and *Ceratoppia* sp 1) actively disperse by random movement and this is an important mode of colonization. Records in the clear cut of single individuals, coupled with species absence during the mid-summer, include *Autogneta longilamellata* (Michael), *Suctobelbella* sp. 1, *Liacarus* sp. 2, *Synchthonius* sp., *Belbodamaeus* sp. and *Maerkeloritia nr. alaskensis* Hammer, further suggesting that only generalist, early-colonizing oribatids persist under these conditions. Oribatid presence was not as patchy in the canopy site when compared to the ground sites, an observation attributable to the resident, non-dispersing oribatids and supported by the observations of Behan-Pelletier and Winchester (1997). Specialized canopy dwellers are also supported by the Q statistical results which indicate that the canopy has a comparable diversity values to the most diverse ground site (edge) and agree with observations by Aoki (1971, 1973, 1974), Norton and Palacios-Vargas (1987), Wunderle (1991), and Winchester (1997a). A component of the canopy fauna, however (e.g., *Ceratoppia* sp.1, *Dorycranosus* sp.1, sp.2, *Eporibaula* sp. *Sphaerozetes* sp., *Scheloribates* sp.1, and *Hermannia gibba*), also disperses over time and supports observations on broad distributions for mites in the arboreal noted by Walter (1995, 1992), Walter and Behan-Pelletier (1993), Walter *et al.* (1993), Walter *et al.* (1994), and Behan-Pelletier and Winchester (1997). Another way of considering how species are distributed across the forest gradient is in terms of " isovalent" species assemblages (see Wallwork 1983). Ecological flexibility is exhibited by those species that are not constrained by microhabitat conditions and these species are active in terms of their dispersal ability (see Behan-Pelletier and Winchester 1997), often occurring in large numbers across all habitat gradients. This high ecological valence (sensu Wallwork 1983) is typified by *Trichoribates* (Behan-Pelletier and Winchester 1997) which is found in all study sites and by *Sphaerozetes* sp. which comprises 20% of all the oribatid individuals sampled.

Malaise trap data may also be used to indicate dispersal ability, a mechanism that is one of the least known aspects of oribatid life histories (Norton 1994). Poor dispersal capabilities coupled with extremes in climatic conditions in the arboreal habitat suggests the development of a specialized oribatid fauna which graze among the moss mats (Wunderle 1992). In addition the moss mats in this study have a well developed underlying soil horizon which, as in the tropics, provides a habitat template where oribatids are speciose and occupy a variety of trophic levels such as microphytophagous, macrophytophagous, predatory and coprophagous.

In summary, the microhabitats associated with the canopy of the ancient Sitka spruce trees contain a rich assemblage of oribatid mites that inhabit suspended moss/soil mats. We have demonstrated that the number of oribatid species in the canopy is comparable with that of ground sites, and that these habitats have a distinct arboreal oribatid assemblage. Differentiation into a separate arboreal fauna has been demonstrated in other forest types (e.g. Niedbala 1969, Travé 1963, Wunderle 1992) but until now, distinct species assemblages in ancient coniferous forests canopies have not been well documented (Winchester and Ring 1996a,b, Behan-Pelletier and Winchester 1997). Oribatid mites can be used as a surrogate for other soil microarthropods, and we predict that arboreal specificity will also be pronounced in groups such as Collembola, Diplura, Protura and gamasid mites. We conclude that, given the unique species of oribatid mites living in the canopy, continued loss of this habitat will have a negative impact on the naturally occurring arboreal species assemblages within the associated suspended moss/soil habitat. The results of our study also support previous conclusions by Winchester and Ring (1996a) and Winchester (1997a,b) that arboreal habitats act as reservoirs for arthropod biodiversity and that habitat features important for long term residency of some species within the canopy are only found in intact coastal ancient rainforests. Finally, we conclude that species assemblages will be lost if these canopy habitats are not retained, or allowed to develop over time in second growth forests.

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CHAPTER 3

PAPER 3

Arboreal oribatid mite diversity: colonizing the canopy [1]

Valarie Behan-Pelletier

Biodiversity Assessment and Evaluation, Agriculture Canada Research Branch

K.W. Neatby Bldg., Carling Ave., Ottawa, Ontario, Canada K1A 0C6

Neville N. Winchester [2]

Department of Biology, University of Victoria, P.O. Box 3020, Victoria,

British Columbia, Canada V8W 3N5

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[1] Accepted by Journal of Soil Ecology, 1997.

[2] Corresponding Author

ABSTRACT

Thirty-six species of Oribatida (2596 specimens), representing 29 genera and 21 families, were recorded from replicated Malaise traps positioned in the canopy and on the forest floor of old-growth Sitka spruce (*Picea sitchensis*) on western Vancouver Island, Canada, and in an adjacent clear-cut. Malaise traps were sampled bi-weekly throughout the growing season, and colonization of Malaise traps was 100% in the canopy, 91% in the forest floor and 47% in the clear-cut. Nine of these species were not recorded from the Upper Carmanah Valley study sites using high gradient extractions of moss/soil from the canopy or forest floor. Thirty of these species are Brachypylina, with the families Eremaeidae, Peloppiidae and Ceratozetidae represented by three or more species. Colonizing specimens were predominantly adult, and represent sexual taxa: immatures comprised only 0.9% to 4.2% of specimens. *Ceratoppia* spp., *Eporibatula* sp. 1, *Dorycranosus* sp.1, *Sphaerozetes* sp. 1 and *Oribatella* sp. 1 had a frequency > 50% in the forest floor Malaise traps, and *Eporibatula* sp. 1, *Sphaerozetes* sp. 1 and *Dendrozetes* sp. 1 had a frequency > 50% in Canopy Malaise traps. Phoresy as a source of the oribatid fauna in the Malaise traps is unlikely as only *Paraleius* sp. 1 is modified for this mode of dispersal. The number of species recorded from Malaise traps, and the frequency, relative abundance, and seasonality of many of them, support the hypothesis that active dispersal by random movement is an important mode of colonization of canopy habitats by oribatid mites.

Keywords: Arboreal Oribatida; Canopy; Sitka spruce; Active dispersal; Colonization; Malaise traps.

INTRODUCTION

Studies of Oribatida (excluding Astigmata) inhabiting the bark of trees and epiphytic mosses and lichens (Trave´ 1963; Andre´ 1984, 1985; Wunderle 1991), or those that fall from the trees when fogged with insecticide (Aoki 1973, 1974), indicate that diversity in arboreal habitats can be extensive. Fifteen genera of mostly undescribed oribatid mites were collected from the phylloplane in Australia (Walter and Behan-Pelletier 1993), and Walter (1996) estimated that at least 102 species of Oribatida inhabit the canopy of an Australian rainforest. Evidence for association of oribatid mites with arboreal habitats is ancient (O'Dowd *et al.* 1991), and to date, species in at least 85 genera representing 35 families are known to inhabit the canopy. Most of these species are members of the Brachypylina. Two genera of *Desmonomata* and one genus of *Mixonomata* also are known from the canopy, but few early derivative oribatid taxa have representatives here. Gut content analysis and laboratory rearing indicate that, the arboreal oribatid fauna utilizes resources that are broadly similar to those exploited by species in soil and litter (Trave 1963; Spain and Harrison 1968; Norton 1983; Walter and Behan-Pelletier 1993). Oribatida are only rarely associated with damage to intact leaves (Haq and Ramani 1984).

The canopy fauna is not a random subset of the forest floor fauna (Aoki 1973). Of the 28 oribatid species Walter *et al.* (1994) found on musk daisy trees in an Australian rainforest, only 7 also occurred in leaf litter under trees. Ongoing research on north temperate rainforest biodiversity on Vancouver Island shows that oribatid species richness in mosses in the canopy of old-growth Sitka spruce is significantly different from that found associated with the same species of moss on the forest floor (Winchester 1997a,b).

There are no data on colonization or successional stages (if any) in development of this fauna during tree growth, either in natural or managed forests. For example, Ehler and Frankie (1979) recorded the same oribatid species richness (18 species) on foliage of live-oak from a suburban shopping plaza, a university campus and a natural stand, but did not address the question of how the mites colonized trees in those urban stands.

It is possible that passive dispersal and/or phoresy play a role in canopy colonization. Oribatid mites undoubtedly are dispersed by wind currents from one patch of habitat to another. No oribatid mites have developed an obligatory relationship with vertebrates or their nests; however, rodents, birds and domestic animals are known to pick up oribatid mites and passively disperse them (Norton 1980; Miko and Stanko 1991). Active dispersal of non-astigmatid oribatid mites by phoresy was discussed in detail by Norton (1980). He recorded phoresy predominantly in the families Mesoplophoridae, Oppiidae, Oribatulidae and Scheloribatidae, by 31 insect species, primarily passalid beetles, but noted that unlike Astigmata, only species of *Mesoplophora* and *Paraleius* have structural modifications for phoresy.

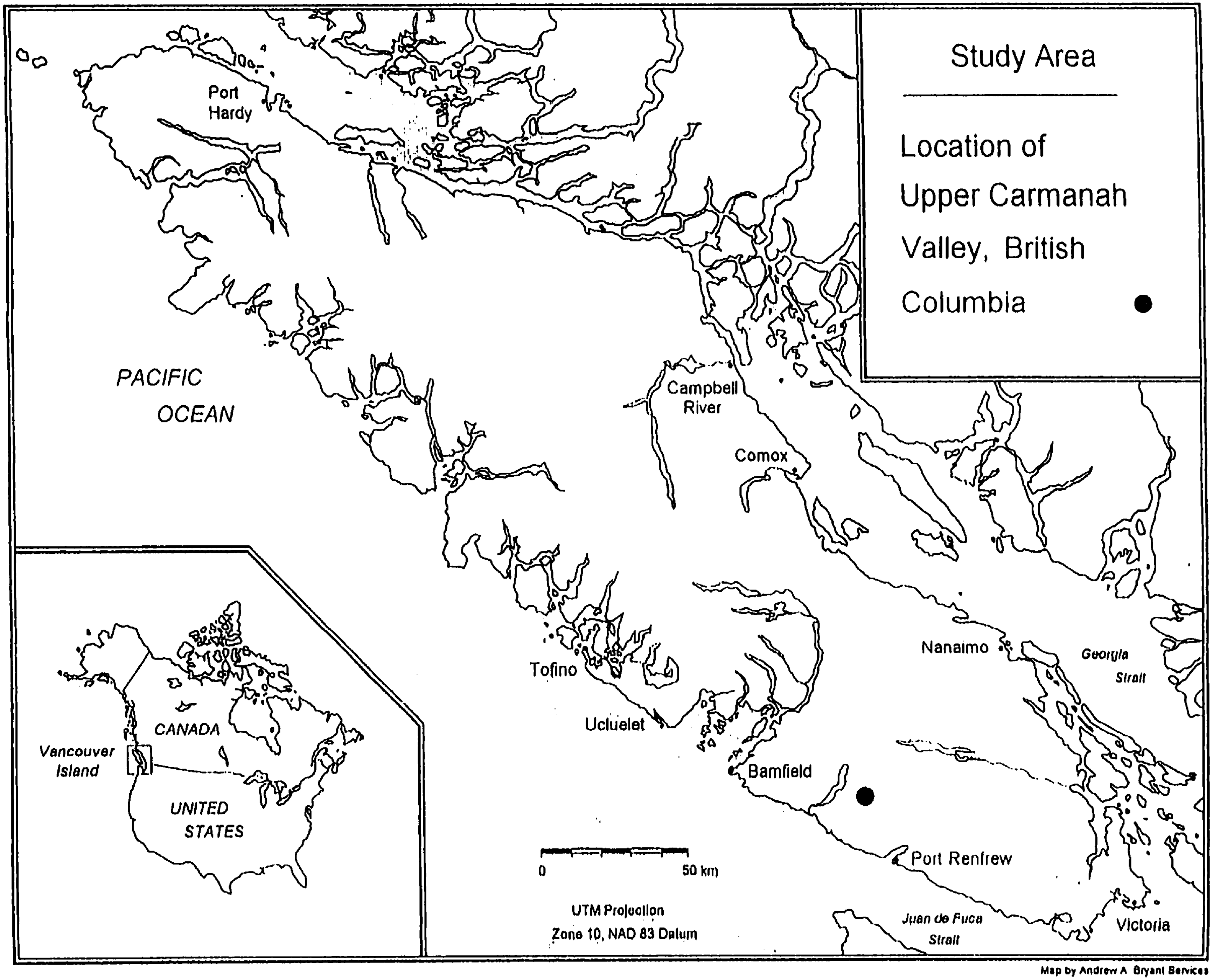
Another possibility is active dispersal through random movement, or negative geotropism leading to movement of oribatid mites from low vegetation to canopy habitats: a possibility addressed in this paper. Our hypothesis is that random movement can contribute to colonization of canopy habitats. We tested this hypothesis throughout a growing season in an ancient (700 years+) Sitka spruce (*Picea sitchensis*) forest in western Canada using a series of replicated Malaise traps in forest floor and canopy sites as well as in an adjacent 6 year old clear-cut.

MATERIALS and METHODS

1. Site Description

The study area is located in the Upper Carmanah Valley drainage (48° 44'N; 124° 37'W) on the south-west coast of Vancouver Island, British Columbia, Canada (Figure 1). This typical U-shaped coastal valley, approximately 6,731 ha in extent, is situated between the villages of Port Renfrew and Bamfield. The entire valley lies within the Coastal Western Hemlock Biogeoclimatic Zone with the exception of two high-elevation areas

Figure 1. Map location of the Upper Carmanah Valley canopy research site, Vancouver Island, British Columbia, Canada.


Study Area

Location of Upper Carmanah Valley, British Columbia ●

Map by Andrew A Bryant Services

(Meidinger and Pojar, 1991). A maritime climate prevails, with wet, humid cool summers and mild winters with little snow. Precipitation can vary, but the mean annual precipitation is in excess of 2000mm.

The sample area in the Upper Carmanah Valley drainage includes four study sites: ancient forest canopy, ancient forest floor (both undisturbed ancient forest sites contain trees that are approximately 700 years old), transition zone (edge between ancient forest and clear-cut) and clear-cut. All study sites are located adjacent to each other along an approximately 4 km transect.

Vegetation plot surveys supported the observation that there was no observable gradients (moisture and nutrient regimes) among or between the ground study sites before harvesting. Vegetation at the Upper Carmanah Valley is dominated by undisturbed ancient forest with dominant trees in excess of 700 years of age. Ancient trees commonly exceed 60 meters in height and 135 cm dbh. The dominant conifers in the Carmanah drainage are western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.),Sitka spruce (*Picea sitchensis* (Bong) Carr.), Pacific silver fir (*Abies amabilis* (Dougl.) Forb.), and western red cedar (*Thuja plicata* D.Don), accounting for 30, 25, 25 and 10% total cover, respectively. Ground shrubs are dominated by salmonberry (*Rubus spectabilis* Pursh), Devil's club (*Oplopanax horridus* (Smith) Miq.), Alaskan blueberry (*Vaccinum alaskaense* Howell) and false azalea (*Menziezia ferruginea* Sm.).

This watershed represents an intact ancient forest that has evolved since the Wisconsin glaciation. In 1985 the clear-cut site (approx. 4 hectares) was harvested and is the only area in the entire Carmanah watershed to be logged.

2 Malaise Traps

Five Malaise traps (Martin 1977; Winchester and Scudder 1993) were placed at random in each of the three habitats: Sitka spruce canopy at heights of 32m, 32m, 33m, 35m, 39m;

the forest floor of Sitka spruce; and the 6 year old clear-cut, approximately 600 m from the forest edge. Malaise traps have a black centre baffle with black sides and a white top. The Malaise trap supports were touching vegetation in the three habitats. In the canopy and forest floor the vegetation comprises moss mats (4-28cm in depth). These mats are primarily composed of three moss species: *Isothecium myosuroides* Brid., *Antitrichia curtipendula* (Hedw.) Brid. and *Dicranum fuscescens* S. Arthropods were collected into 75% EtOH. Malaise trap samples were collected approximately every two weeks from 3 July to 27 October, 1991 ie. 9 collection dates expressed as Julian days: 184/185 = 3/4 July; 196 = July; 211 = 30 July; 223 = 11 August; 239 = 27 August; 252/253 = 9/10 September; 272 = 29 September; 289 = 16 October; 299-300 = 26/27 October. On the same sampling dates, replicated 3 cm diam. core samples to a maximum depth of 20cm were collected from litter and moss in the canopy, forest floor and clear-cut, and arthropods extracted using high gradient extractors. Arthropods, including oribatid mites were sorted from these samples, counted and identified to species where possible.

RESULTS

1. Diversity of Oribatida in Malaise Traps

A total of 1751, 732 and 113 oribatid specimens were recovered from the forest floor, canopy and clear-cut Malaise traps, respectively (Table 1). Thirty-six oribatid species representing 29 genera and 21 families were recorded from the Malaise samples, with 33, 22 and 10 species recorded from forest floor, canopy and clear-cut Malaise traps, respectively (Table 1). None of the species indicated by * on Table 1 were recorded from the canopy, forest floor or clear-cut area using high gradient extractions (Winchester *et al.* in prep.). The remaining 27 species were recorded from the Sitka spruce forest using high gradient extractors and their occurrence in the three different habitats based on these extractions is indicated by ‡ in Table 1. Only three of the thirty-six species from the

Table 1. Oribatid species compostion from Malasie traps in Sitka spruce forest, British Columbia, Canada. Numbers following each taxon are the number of specimens, % frequency, and relative abundance. Species indicated by * were not recorded from this site using High gradient extraction. Species noted by ‡ were recorded from the habitats using High gradient extractions.

Site	Forest Floor	Canopy	Clear-cut
	no. of samples = 45	no. of samples = 45	no. of samples = 45
ORIBATIDA			
Maerkelotritia sp. 1	‡ 13:20%:0.7%	‡	‡
* *Camisia oregonae* Colloff	13:24%:0.7%	3:4%:0.4%	
Hermannia gibba (C.L. Koch)	‡ 5:11%:0.3%	‡1:2%:0.1%	‡
Hermanniella sp. 1	‡ 1:2%:0.06%		1:2%:0.9%
* *Platyliodes macroprionus* Woolley & Higgin	9:18%:0.5%	1:2%:0.1%	
Damaeidae sp. 1	3:4%:0.1%	‡ 1:2%:0.1%	
Damaeidae sp. 2	2:4%:0.1%	‡	
Damaeidae imm.		2:4%:0.3%	
* *Cepheus* sp. 1	20:31%:1.1%	1:2%:0.1%	3:7%:2.7%
Eupterotegaeus rhamphosus Higgins & Woolle	‡ 1:2%:0.06%	‡	‡
Eueremaeus acostulaus Behan-Pelletier		‡ 12:22%:1.6%	
Eueremaeus aysineep Behan-Pelletier	24:22%:1.4%	‡ 18:27%:2.5%	1:2%:0.9%
* *Eueremaeus* sp. 3	1:2%:0.06%		
Eueremaeus imm.	3:7%:0.2%	1:2%:0.1%	
Dorycranosus 2 spp.	‡ 52:56%:3%	‡ 13:18%:1.8%	1:2%:0.9%
Ceratoppia sp. 1	‡ 388:84%:22%	‡ 20:22%:2.7%	‡ 39:11%:34.5%
Ceratoppia sp. 2	‡ 691:71%:39%	‡ 38:33%:5.2%	1:2%:0.9%
Ceratoppia sp. 3	‡ 1:2%:0.06%		
Ceratoppia imm.	1:2%:0.06%	7:7%:1.0%	1:2%:0.9%
Dendrozetes sp. 1	26:40%:1.5%	‡ 59:60%:8.1%	‡

Peloppiidae imm.	7:2%:0.06%	‡	‡
Oppidae	1:2%:0.06%	‡	‡
Banksinoma sp. 1	2:4%:0.1%	‡ 1:2%:0.1%	
Scapheremaeus palustris Sellmick		‡ 3:7%:0.4%	
Eporibatula sp. 1	‡ 127:64%:7.2%	‡ 383:91%:52.3%	‡ 1:2%:0.9%
Eporibatula imm.		3:7%:0.4%	
Scheloribates sp. 1	22:27%:1.3%	‡ 15:33%:2.1%	‡
* *Paraleius* sp. 1	2:4%:0.1%	1:2%:0.1%	
* *Parapirnodus* sp. 1	3:7%:0.2%	8:11%:1.1%	
Oribatulidae ? Genus	1:2%0.06%		
Oripodoid imm.	1:2%:0.06%	1:2%:0.1%	
Chamobates sp. 1	‡ 16:20%:0.9%		‡
Ceratozetes sp. 1	3:7%:0.2%		‡
Sphaerozetes sp. 1	129:56%:7.4%	‡ 101:64%:13.8%	‡ 3:7%:2.7%
* *Trichoribates* sp. 1	11:20%:0.6%		59:36%:52.2%
* *Mycobates punctatus* Hammer	3:4%:0.2%	3:7%:0.4%	1:2%:0.9%
* *Jugatala tuberosa* Jacot	17:27%:1.0%	2:4%:0.2%	
Ceratozetoid imm.	8:13%:0.5%	6:9%:0.8%	
Oribatella sp. 1	‡ 123:56%:7.0%	‡ 10:20%:1.4%	‡
Achipteria sp. 1	7:11%:0.4%	3:7%:0.4%	‡
Anachipteria sp. 1	‡ 6:11%:0.3%		‡
Dentachipteria sp. 1	‡ 1:2%:0.06%		‡
TOTAL	1751:91%	732:100%	113:47%

Malaise traps are non-Brachypylina. Of these, *Camisia oregonae* has been recorded before from arboreal habitats (Colloff 1993), but *Maerkelotritia* sp. 1 and *Hermannia gibba* represent genera not associated previously with the canopy. Three families, Eremaeidae, Peloppiidae and Ceratozetidae were represented by three or more species in the Malaise traps.

2. Colonization of Malaise traps

All Malaise traps in the canopy, and all but three traps on the forest floor were colonized by at least one oribatid species per sampling period. In the clear-cut, however, two traps were never colonized and oribatid mites did not colonize any traps in the clear-cut during the last two sampling periods (days 289 and 299/300). The mean number of species colonizing Malaise traps per sampling period was highest in the forest floor traps, followed by those in the canopy (Table 2). In both forest floor and canopy Malaise traps the range of species colonizing per sampling period was wide. However, in the canopy the mean was quite consistent (4.2 to 5.8) for most of the sampling period (Table 2), suggesting that oribatid colonization in one sampling period had no effect on that of the next period.

3. Adults: Immatures

Immatures comprised only 1.08% (19 specimens), 4.23% (31 specimens) and 0.88% (1 specimen) of specimens in the forest floor, canopy and clear-cut Malaise traps, respectively. There was no significant seasonality evident in the occurrence of immatures. For example, in forest floor Malaise traps half the immatures were recorded from the Day 272 collection; in the canopy the majority of immatures were recorded from Days 196 and 211 collections.

Table 2. Mean number and range of oribatid species per Malaise trap per sampling period, in Sitka spruce forest, British Columbia, Canada.

Julian days, 1991	Canopy	Forest floor	Clear-cut
	(n=5): (range)	(n=5): (range)	(n=3): (range)
184/185	4.2: (3-6)	6.0 (0-11)	2.6: (1-5)
196	4.6: (2-7)	6.4: (0-11)	1.3: (1-2)
211	4.6: (3-6)	5.8: (3-9)	1.0: (1)
223	5.4: (3-7)	3.4: (0-7)	1.0: (1)
239	4.4: (2-6)	9.6: (5-12)	1.3: (1-2)
252/253	4.8: (3-7)	9.0: (5-12)	2.6: (2-4)
272	5.8: (3-8)	12.0: (8-15)	0.6: (0-2)
289	4.2: (2-5)	7.4: (4-11)	0
299/300	2.2: (1-4)	4.6: (1-7)	0

4. Frequency of occurrence, Relative Abundance and Seasonality

No species in the clear-cut Malaise traps had a frequency greater than 36 percent. Species with a frequency greater than 50 percent in the forest floor Malaise traps included *Ceratoppia* sp. 1 (84%), *Ceratoppia* sp. 2 (71%), *Eporibatula* sp. 1 (64%), *Dorycranosus* sp. 1 (56%), *Sphaerozetes* sp. 1 (56%), *Oribatella* sp. 1 (56%) (Table 1). Species with a frequency greater than 50% in the canopy included *Eporibatula* sp. 1 (91%), *Sphaerozetes* sp. 1 (64%) and *Dendrozetes* sp. 1 (60%) (Table 1).

Many of the species recorded in the Malaise trap samples were represented by one or only a few specimens (Table 1). Species with a relative abundance greater than 5 percent included: *Ceratoppia* sp. 2 (39%), *Ceratoppia* sp. 1 (22%), *Sphaerozetes* sp. 1 (7.4%), *Eporibatula* sp. 1 (7.2%), *Oribatella* sp. 1 (7%) in the forest floor Malaise traps; *Eporibatula* sp. 1 (52.3%), *Sphaerozetes* sp. 1 (13.8%), *Dendrozetes* sp. 1 (8.1%), *Ceratoppia* sp. 2 (5.2%) in the canopy Malaise traps; and *Trichoribates* sp. 1 (52.2%), *Ceratoppia* sp. 1 (34.5%) in the clear-cut Malaise traps.

There were no statistically significant differences in occurrence of species in Malaise trap samples throughout the collecting season, but some seasonal trends were evident. In Forest floor Malaise traps the mean number of specimens of *Ceratoppia* sp. 1, *Ceratoppia* sp. 2 and *Eporibatula* sp. 1 was highest between Days 223 and 272. Few specimens were collected on the first two and the last collecting dates. Similarly, in canopy Malaise traps mean numbers of *Eporibatula* sp. 1 and *Sphaerozetes* sp. 1 were highest in collections midway through the sampling period. In contrast, in the clear-cut Malaise traps the mean number of *Trichoribates* sp. 1 was highest on the three earliest collecting dates.

DISCUSSION

1. Diversity

The level of colonization of Malaise traps was high: 100% in the canopy, 93% in the forest floor, and 47% in the clear-cut, suggesting that oribatid mite presence in these traps is due to active rather than passive dispersal. Only 9 species from a total of 36 were not recorded from any of the Malaise traps: *Synchthonius* sp., *Nanhermannia* sp., *Gymnodamaeus* sp., *Megeremaeus montanus* Higgins and Woolley, *Tectocepheus velatus* (Michael), *Autogneta longilamellata* (Michael), *Oppiella* spp., *Quadroppia* sp., *Suctobelbella* sp. and *Pilogalumna* sp. (Winchester *et al.* in prep.). The known oribatid fauna of the Sitka spruce canopy is 34 species, 22 of which we have found in the Malaise traps. The majority of oribatid species found in the Sitka spruce canopy and in Malaise traps are members of the Brachypylina, a characteristic group of canopy oribatids irrespective of forest type (Aoki 1973). Some Brachypyline taxa known to be primarily arboreal, e.g., Licneremaeoidea, Mochlozetidae, Oripodidae, are not well represented in the Sitka spruce canopy, nor in Malaise traps; the Sitka spruce canopy fauna are dominated by Brachypyline representatives of the Peloppiidae, Oribatulidae and Ceratozetidae, as reflected in the Malaise trap fauna.

In addition to the majority of the colonizers being members of the Brachypylina, colonizing individuals are primarily adults (95-99%). The heavily sclerotized adults of oribatid mites are better equipped to deal with predators and desiccation than are the relatively unsclerotized immatures, and adults have also been shown to be the main dispersal stage (Norton 1994).

Malaise traps represent a 'newly created' environment, and we anticipated that colonizing species would be thelytokous, dominated by members of the Brachychthoniidae, Oppiidae and Tectocepheidae (Norton and Palmer 1991). Our data do not support this; for example, *Tectocepheus velatus*, common in the canopy, forest floor and clear-cut, based on high gradient extractions (Winchester *et al.*, in prep.), is absent from Malaise traps. We did not sex adult specimens but the species represented belong to sexual genera and families (Norton *et al.* 1993). A strong female bias among adult specimens in the Malaise traps can be expected, as dispersal by adult females is most likely in oribatid mites (Norton 1994).

2. Method of Colonization

We consider phoresy as the source of the oribatid fauna in the Malaise traps unlikely for the following reasons. The few oribatid mites known to have a phoretic association are endophagous, feeding on wood at particular stages of decay. Their phoretic associations are primarily with wood-burrowing insect species, especially members of the beetle family Passalidae (Norton 1980), a family not present at the Carmanah site. Of the oribatid species present in the Malaise traps, only *Maerkelotritia* sp. 1 and *Hermanniella* sp. 1 are wood burrowers or endophagous species. Other than *Paraleius* sp. 1, with its modified median tarsal claw, none of the oribatid species found in this study is modified for phoresy. Although species of *Eporibatula* and *Scheloribates* are recorded as phoretic on beetles (Norton 1980), the frequency, relative abundance and seasonality of the *Eporibatula* sp. in the Malaise traps suggests a non-phoretic colonization by most specimens.

The frequency of species with a relative abundance greater than 5% in the Malaise traps, and the frequency of species such as *Eueremaeus aysineep* and *Dendrozetes* sp. 1 in Malaise traps, otherwise recorded only from the canopy using high gradient extractions, are strong evidence for random movement contributing to colonization of new habitats by oribatid mites. Even if oribatid mites were passively dispersed by wind to Malaise traps, either individually or in association with their moss microhabitats, specimens must actively move a vertical distance of 50-70 cm to reach the Malaise trap head.

There are scant data in the literature on vertical or horizontal movement of oribatid mites (Norton 1994). Tarras-Wahlberg (1961) reported that tritonymphs of *Diapterobates humeralis* (Ceratozetidae) move upwards into shrub in peatland habitats. Murphy and Alam (1995) documented marked seasonality in occurrence of both adult and immature oribatid mites in herbage, which they relate to wet soil and absence of sunshine. Murphy and Balla (1971) recorded movement of adult *Humerobates rostrolamellatus* (Ceratozetidae) from lower parts of apple trees to the younger wood in Spring. Similar movement in old-growth Sitka spruce may explain the seasonality in occurrence of oribatid mites in Malaise traps, with relatively fewer specimens present on sampling dates in October (ie. late in the season).

Diapterobates humeralis and *H. rostrolamellatus* are widely distributed arboreal species in north temperate managed and unmanaged coniferous and deciduous forests (Andre´ 1984; Laine *et al.* 1995). They are absent from old-growth Sitka spruce, but the family Ceratozetidae is represented by undescribed species of *Sphaerozetes* and *Trichoribates*. The latter species is only known from Malaise traps at the Carmanah site, and is the main colonizer of traps in the clear-cut area. Many species of *Trichoribates* are known to be arboreal (e.g., Andre´ 1984, Norton and Palacious-Vargas 1987; Weigmann and Jung 1992). *Trichoribates trimaculatus* (Koch), is one of the dominant species recorded on moss cover of house roofs in Europe, and is considered to be an example of a colonizing species (Smrñ 1992), an ability attributed to its tolerance to changes in humidity.

CONCLUSION

Adult specimens of 1 to 15 oribatid species were collected from replicated Malaise traps in the canopy and the forest floor of an ancient Sitka spruce forest and an adjacent clear-cut area approximately every 2 weeks. The frequency of species with a relative abundance greater than 5% in the Malaise trap samples and the number of oribatid mite species present (36), primarily Brachypylina, support the hypothesis that oribatid mites use random movement as an active dispersal method to colonize canopy habitats.

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CHAPTER 4

PAPER 4

CENTINELAN EXTINCTIONS: EXTIRPATION OF NORTHERN TEMPERATE OLD-GROWTH RAINFOREST ARTHROPOD COMMUNITIES

NEVILLE N. WINCHESTER[1] AND RICHARD A. RING

Department of Biology, University of Victoria, P.O. Box 3020, Victoria, British Columbia, Canada V8W 3N5

ABSTRACT

Arthropod biodiversity is being investigated in the Carmanah Valley on Vancouver Island, British Columbia, Canada. We explore features related to the Centinelan extinction concept and ask whether or not this is applicable to northern temperate old-growth forest arthropods. Habitat loss in these forest systems is well documented and at present, of 89 old-growth forest watersheds over 5000 ha in size only 6 remain intact. Examination of identified species (1,311 to date), from the intact old-growth forest of the Carmanah Valley indicates that this structurally complex habitat acts as a reservoir of biological diversity. Thirty species of oribatid mites and 8 species of staphylinid beetles are new to science and all of these species show habitat specificity to micro-habitats found within this old-growth forest. Nowhere is this more apparent than in the moss-mats of the high-canopy, where the oribatid mite fauna is composed of 56 species, of which 15 undescribed species are canopy specific. This mite assemblage forms a major component of a discrete arboreal community. Comparisons between the high-canopy and ground sites indicate that an

additional 15 undescribed oribatid species are confined to the forest interior. No new species of oribatid mites or staphylinid beetles have been recorded in the edge or clear-cut sites. Evidence suggests microhabitats present in these old-growth forests contain an undescribed resident arthropod fauna. Without proper documentation, this faunal component is a candidate for Centinelan extinction -- extinction of species unknown before their demise and hence unrecorded.

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[1] Corresponding author

INTRODUCTION

The ongoing global biodiversity crisis continues to be fueled by habitat loss (Wilson 1988, 1989, 1992; Soule´ 1991; Colwell & Coddington, 1994) and subsequent extinctions of floral and faunal species assemblages that cannot adjust to rapid and often large scale habitat alterations. Rates of extinctions are difficult to measure and often are confounded by the absence of species inventory information which is particularly prevalent in 'hyperdiverse' groups (eg. insects, mites, nematodes, fungi and micro-organisms). The silent hemorrhaging of biological diversity was termed 'Centinelan Extinctions' by Wilson (1992) to designate extinctions of species unknown before their demise and hence unrecorded. With increased human disturbance across virtually all natural landscapes the focus to record and preserve biological diversity has been centered in the tropics, which are being rapidly lost contain over half of the world's species (Erwin 1988, Jansen 1988, Myers 1988, Wilson 1988). Tropical biotopes most at risk are the species-rich forests. However it is a global reality that forests throughout the world are being compromised by human-induced perturbations. In temperate zones the largest remaining tracts of intact old-growth coniferous forests occur in the Pacific Northwest of North America (Franklin 1988).

Historically very little research concerning the maintenance and conservation of biodiversity has been done on the primeval old-growth forests of the Pacific Northwest (Winchester & Ring, 1996). In British Columbia these forests are thought to contain much of the biodiversity of the province (Bunnell 1990, Fenger & Harcombe 1989). They often have diffuse boundaries with other ecosystems, and this temporal and spatial mosaic creates a dynamic and complex set of habitats that are utilized by a variety of species. The species associated with these old-growth forests are a heterogeneous group, and nowhere is this more evident than in the arthropods. Arthropods play a primary role in the function of natural ecosystems, may regulate nutrient cycling (Mattson & Addy 1975, O'Neill

1976), and are now frequently mentioned as important components of diversity that need to be identified (May 1986, Wilson 1988, di Castri *et.al.* 1992, Samways 1994).

The diversity of arthropods and ecological concepts surrounding them presents several difficulties for researchers. Nowhere is this more obvious than with species estimates which on a global basis vary from 5-80 million (Wilson 1988, Erwin 1988, Stork 1988). Most of this biota is unknown and composed primarily of arthropods. The most species-rich category, the insects remain largely undescribed. In Canada, approximately half of the estimated 66,000 insect species have been described (Danks 1993). In British Columbia there may be as many as 40,000 arthropod species (Cannings 1992), many of which are undescribed (Winchester and Ring, 1996). Given the importance of arthropods in terrestrial ecosystems the objective of this paper is to present evidence from our ongoing study to address whether or not the Centinelan extinction concept is applicable to the coastal old-growth forests of Vancouver Island. We use two taxonomic groups, the staphylinid beetles and the oribatid mites to address the following questions:

— Are coastal old-growth forests within intact watersheds on Vancouver Island becoming rare?

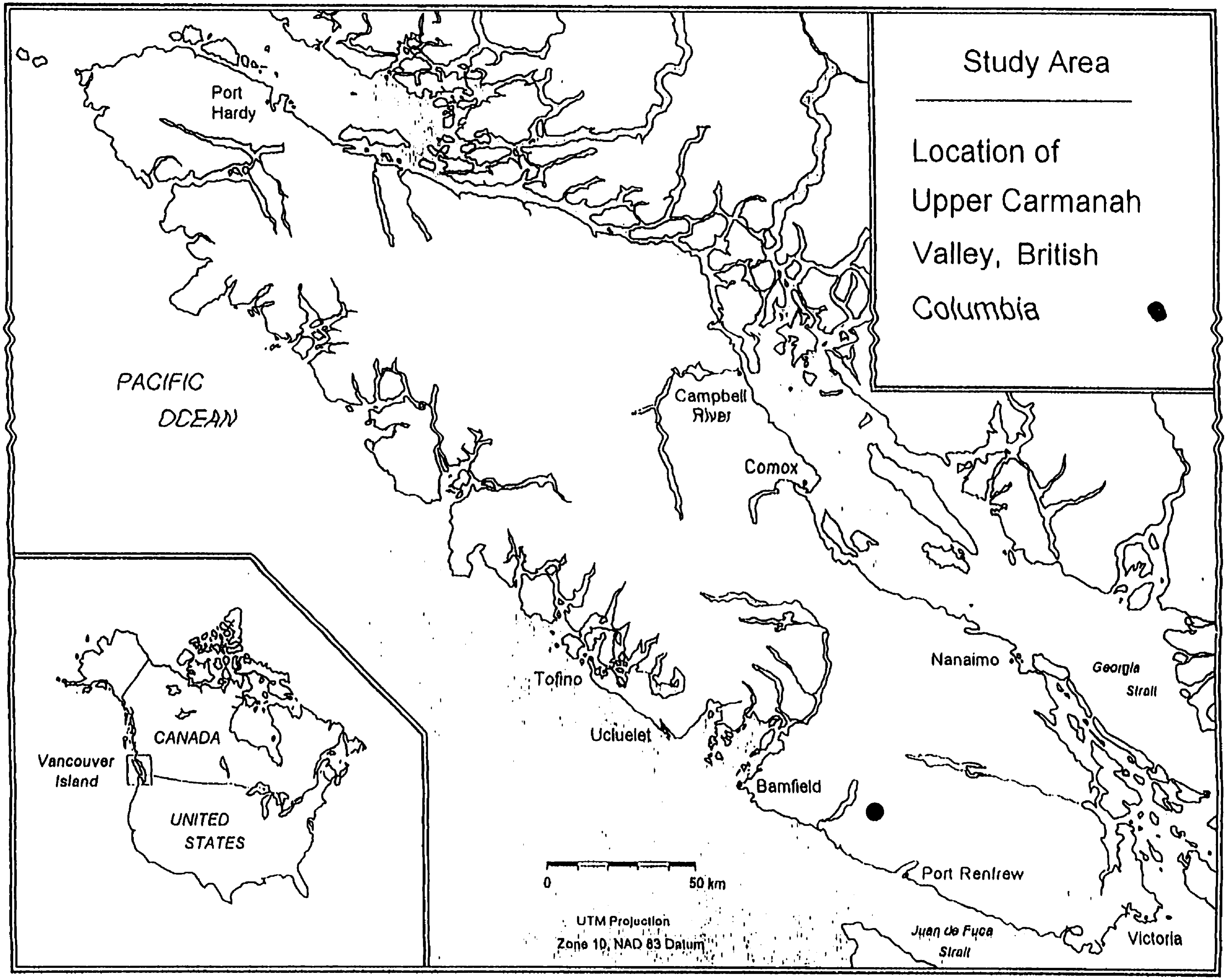
— Are we dealing with an unrecorded fauna that contains new species?

— If new species are present do they exhibit habitat specificity?

METHODS and MATERIALS

Study area — The study area is located in the Upper Carmanah Valley drainage (48° 44'N; 124° 37'W) on the south-west coast of Vancouver Island, British Columbia, Canada (Figure 1). This typical U-shaped coastal valley, approximately 6,731 ha in extent, is situated between the villages of Port Renfrew and Bamfield. The entire valley lies within the Coastal Western Hemlock Biogeoclimatic Zone with the exception of two high-elevation areas (Meidinger and Pojar, 1991). A maritime climate prevails, with wet,

Figure 1. Map location of the Upper Carmanah Valley canopy research site, Vancouver Island, British Columbia, Canada.



Map by Andrew A. Bryant Services

humid cool summers and mild winters with little snow. Precipitation can vary, but the mean annual precipitation is in excess of 2000mm.

The sample area in the Upper Carmanah Valley drainage includes four study sites: ancient forest canopy, ancient forest floor (both undisturbed ancient forest sites contain trees that are approximately 700 years old), transition zone (edge between ancient forest and clear-cut) and clear-cut. All study sites are located adjacent to each other along an approximately 4 km transect.

Vegetation plot surveys supported the observation that there was no observable gradients (moisture and nutrient regimes) among or between the ground study sites before harvesting. Vegetation at the Upper Carmanah Valley is dominated by undisturbed ancient forest with dominant trees in excess of 700 years of age. Ancient trees commonly exceed 60 meters in height and 135 cm dbh. The dominant conifers in the Carmanah drainage are western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.),Sitka spruce (*Picea sitchensis* (Bong) Carr.), Pacific silver fir (*Abies amabilis* (Dougl.) Forb.), and western red cedar (*Thuja plicata* D.Don), accounting for 30, 25, 25 and 10% total cover, respectively. Ground shrubs are dominated by salmonberry (*Rubus spectabilis* Pursh), Devil's club (*Oplopanax horridus* (Smith) Miq.), Alaskan blueberry (*Vaccinum alaskaense* Howell) and false azalea (*Menziezia ferruginea* Sm.).

This watershed represents an intact ancient forest that has evolved since the Wisconsin glaciation. In 1985 the clear-cut site (approx. 4 hectares) was harvested and is the only area in the entire Carmanah watershed to be logged.

Canopy access — The old-growth canopy site was composed of five Sitka spruce trees that were randomly chosen to be incorporated into a fixed access system. Access to the Sitka spruce canopy is by means of a 2:1 mechanical advantage pulley system. Strapped into a harness and attached to a series of permanent climbing lines, we are able to sample the five adjacent Sitka spruce trees. Four wooden platforms strapped onto the branches and trunk of the main tree give us consistent heights at 31 to 67 metres from which to sample. A series of burma bridges enables us to access the four other trees, complete with platforms.

Survey design — Owing to the diverse nature of arthropods and their varied habits no single survey method or sampling technique can be used for a complete study. A variety of techniques must be employed and those that are most easily used, and the relevant taxa that can be collected by each method, have been summarized in Winchester and Scudder (1993) and the Biological Survey of Canada (1994). The sampling methodologies used in the 1991 portion of this study are listed below.

Malaise traps — Five Malaise traps (Townes 1962), were randomly placed along a linear transect at each of the three ground sites. A single Malaise trap was placed in each of the five Sitka spruce trees that were incorporated into the fixed-access system. Arthropods were collected into 70% ethyl alcohol to which 6 drops of ethylene glycol had been added. Traps were cleared at two-week intervals from May - October. A total of 245 trap samples were collected and arthropods from each trap were sorted and enumerated.

Pan traps — Five pan/window traps were placed at each ground sample site. Pans (23 X 15 X 5 cm) were buried with rims flush at ground level. They were randomly placed along a 50 m linear transect. A clear glass window (0.5 by 0.5 m) was placed above each pan trap. A saturated salt solution was used as a preservative with a few drops of detergent added as a wetting agent. A total of 120 trap samples were collected. All arthropods were washed in water, sorted and stored in 75% ethyl alcohol.

Moss cores — A hand-held moss/soil corer (Approx. 3 cm X 5cm) was used to collect 5 moss/soil cores at random from each of the four sample sites once a month from May - October. A total of 120 cores were collected. In the laboratory the arthropods were extracted from each core using Tullgren funnels for 48 hours. Samples were preserved in 75% ethyl alcohol. Volume displacement and dry weight were recorded for each core sample.

Data analysis — All samples were sorted to family. Species level identifications were completed for all of the staphylinid beetles and most of the oribatid mites. Numerical relationships between the staphylinid species and four study sites were calculated using all trap data that was pooled over all collection times. Numerical relationships between the oribatid species and four study sites were calculated using all moss core samples that were pooled over all collection times.

RESULTS

Taxonomic composition — Approximately 612,396 arthropods representing an undetermined number of species were collected during the 1991 sample season (Table 1). The numerically dominant arthropod groups, are Diptera, Collembola, Hymenoptera, Thysanoptera and Acarina. When total number of individuals are partitioned among sites, the transition zone (edge between old-growth and clear-cut) is most numerous in orders that are highly mobile (eg. Diptera, Hymenoptera) and in aquatic orders represented by the Ephemeroptera, Plecoptera and Trichoptera. The forest floor site has the next highest abundances for many groups and is particularly abundant in Collembola, Coleoptera and Pscoptera. The canopy site is somewhat depauperate in most taxonomic groups, although the Acarina are extremely numerous. The most altered site, the clear-cut, shows a high number of mobile taxa such as Diptera, Hymenoptera and Lepidoptera. However, groups such as the Thysanoptera seem to exhibit 'ecological release' and rapidly accumulate numbers that are several orders of magnitude greater than any other sample sites.

To date, 150,000 individuals from a variety of taxonomic groups have been sent to 90 systematists for identification. Identifications are continuing, and to date, 1,311 species have been identified and a conservative total of 65 species (5.0% of identified species) are confirmed as new to science. Species identifications are lacking for many

Table 1. Summary of the arthropods collected from all traps in the Upper Carmanah Valley during 1991.

Taxon	Site				# of specimens
	Can	FF	TZ	CC	
Acarina	5,171	4,259	5,206	4,548	19,184
Araneae	629	783	765	733	2,910
Chilopoda	1	25	8	2	36
Coleoptera	883	3,102	7,598	2,198	13,781
Collembola	2,425	18,367	16,709	10,536	48,037
Diplopoda	0	51	57	10	118
Diptera	8,401	58,236	230,186	146,068	442,891
Ephemeroptera	0	3	201	17	221
Hemiptera	24	10	159	538	731
Homoptera	358	361	2,017	4,878	7,614
Hymenoptera	955	4,915	24,744	15,727	46,341
Isopoda	0	18	0	4	22
Lepidoptera	354	222	682	876	2,134
Lumbriculida	1	50	27	7	85
Microcoryphia	1	58	87	21	167
Neuroptera	23	33	42	98	196
Orthoptera	1	61	43	93	198
Plecoptera	18	57	2,607	120	2,802
Phalangida	15	76	62	10	163
Pseudoscorpionida	4	34	40	45	123
Pscoptera	353	786	1,466	112	2,717
Stylomorpha	1	21	6	11	39
Thysanoptera	24	33	1,112	20,068	21,237
Trichoptera	17	8	437	117	579
Other	3	31	15	20	69
Totals	19,662	91,600	294,276	206,857	612,395

Abbreviations: Can = Canopy, FF = Forest Floor, TZ = Transition Zone, CC = Clear-cut groups (eg.) Braconidae, Proctotrupidae which have been sorted to genera and morphospecies. This indicates the poor state of taxonomy in these groups and the inability to indicate with certainty the existence of new species.

The most complete information on identifications and habitat associations is for the Staphylinidae (Figure 2) and the Oribatida (Figure 3). Numerical relationships between staphylinid species and study sites indicate that the transition zone has the greatest number of species (49) while the canopy has the least number of species (6). The forest interior and transition zone had the most species in common (20) while the number of species shared in common between the forest interior and clear-cut is low (7). Percent similarity is lowest between the canopy and all ground sites (range 6% - 15%). The clear-cut site shows lower similarity to the forest interior (18%) and higher similarity to the transition zone (31%). The highest similarity (62%) exists between the forest interior and transition zone. Of the 8 new species recorded, all exhibit strict habitat associations with the forest floor interior, but one of these species also occurs in the canopy. Numerical relationships of the oribatid mite fauna indicate that the canopy has the highest number of species (56) followed by the forest floor (48). Total number of species present in the transition zone (34) is similar to the clear-cut zone (35). Canopy percent similarity is lowest between the forest floor (18%) and highest between the clear-cut (41%). Overall, percent similarity is generally high between any of the other ground pairwise site comparisons (range 42% - 88%). Of the 30 confirmed new species, 15 were specific to the forest floor and the other 15 were specific to the canopy site.

DISCUSSION

Habitat changes that occur through logging of old-growth forests have been well documented, but the effect that this type of habitat alteration has on arthropods has only been addressed to a limited extent (McLeod 1980, Chandler 1987, 1991, Niemela *et al* (1988,1993, Schowalter 1989, Chandler & Peck 1992). Between 200,000 and 250,000

Figure 2. Numerical relationship between staphylinid species from four study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time intervals. Numbers along the lines represent those species in common between the sites. Percents represent percent similarity between the sites. Numbers within the circles represent the number of species occupying a given site and numbers in brackets represent the presence of new species.

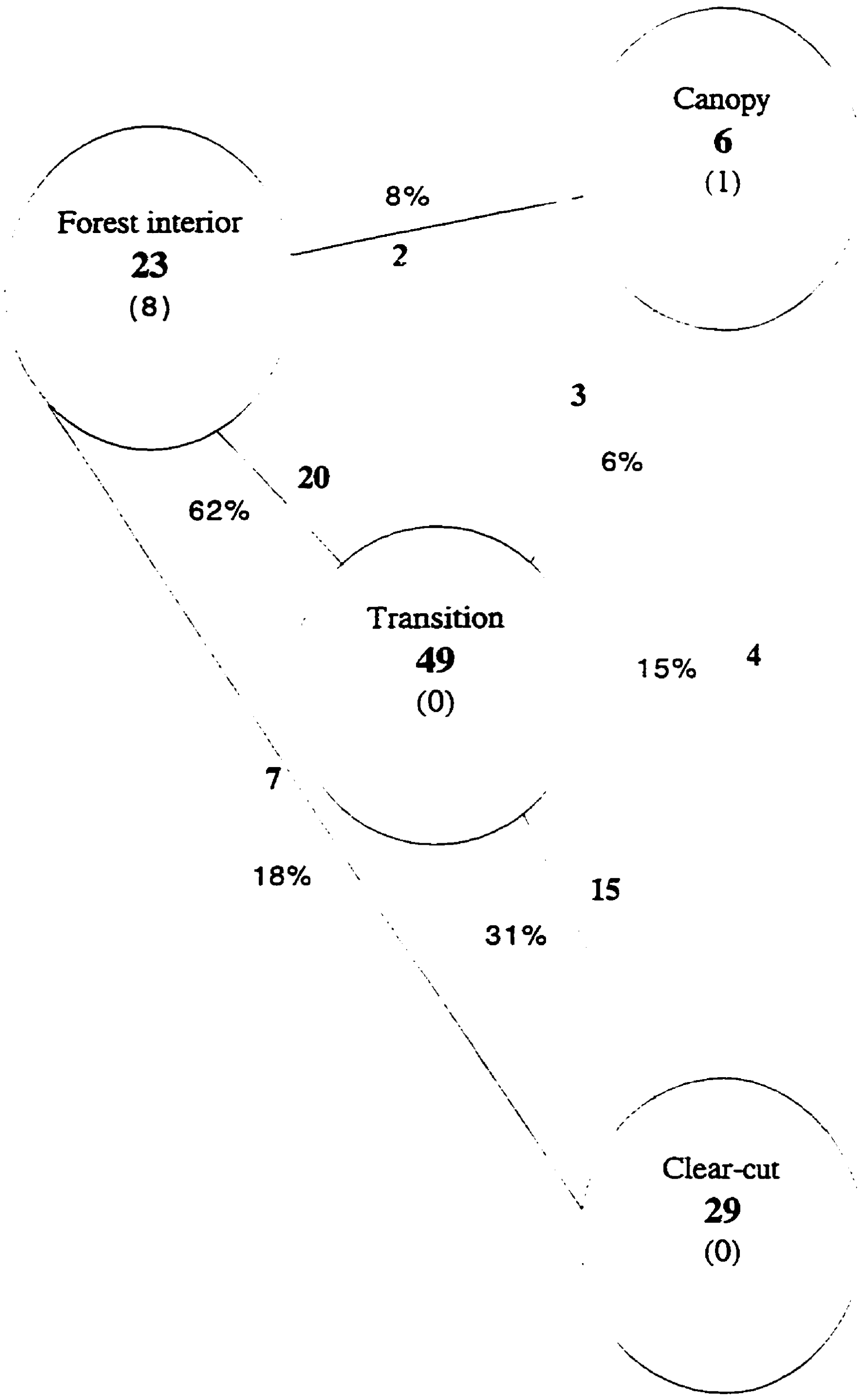
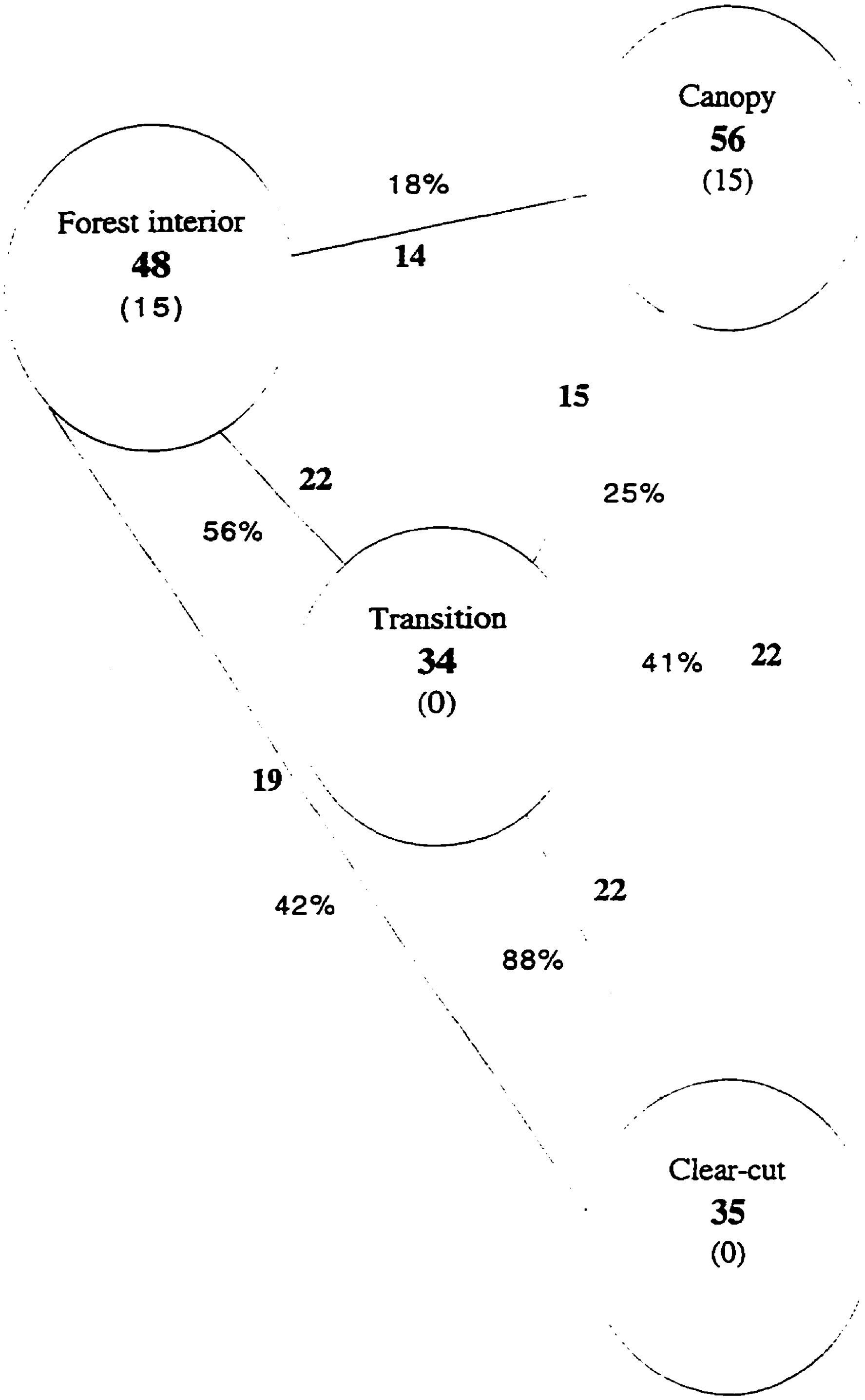

Canopy
6
(1)
Forest interior
23
(8)
8%
2
3
6%
20
62%
Transition
49
(0)
15%
4
7
18%
15
31%
Clear-cut
29
(0)

Figure 3. Numerical relationship between oribatid species from four study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time intervals. Numbers along the lines represent those species in common between the sites. Percents represent percent similarity between the sites. Numbers within the circles represent the number of species occupying a given site and numbers in brackets represent the presence of new species.


Canopy
56
(15)
18%
Forest interior
48
(15)
14
15
22
25%
56%
Transition
34
(0)
41%
22
19
22
42%
88%
Clear-cut
35
(0)

hectares, principally comprised of older forests, are harvested each year by the forest industry in British Columbia (MacKinnon 1993). Nowhere is this habitat loss more apparent than on Vancouver Island where only 6 of 89 watersheds greater than 5000 hectares remain intact (Winchester 1993). We submit that the first assumption (habitat scarcity) needed to satisfy the Centinelan extinction definition has been met — coastal old-growth forests within intact watersheds on Vancouver Island are becoming rare.

Taxonomic and habitat knowledge for terrestrial arthropods from these forests is at best sketchy and what information is available is usually difficult to interpret because of the number of independent sources and the rather diffuse nature of the pertinent data. The pattern of biodiversity in the terrestrial arthropod component of Pacific Northwest forests is largely unstudied. The complex mix of taxonomic groups in our study and different patterns of representation across habitat gradients is characteristic of terrestrial arthropods. Determination of the species richness component in this study is restricted by the inability to identify specimens to species. Given the fact that only a small percentage of the total number of specimens in this study have been identified to species, it is likely that the number of new species recorded represents a conservative estimate. Even at this early taxonomic stage we are dealing with a largely unexplored fauna that contains new species and therefore we have met the second assumption needed for Centinelan extinction.

The new species of staphylinid beetles and oribatid mites recorded in this study are restricted to habitats that are associated with old-growth forests. Two important habitat components that occur on the ground are first, a supply of over-mature large diameter, fallen logs which are allowed to decay under natural conditions in the shade of the forest canopy, and secondly, the maintenance of deep layers of undisturbed forest floor litter which have not been eradicated by the extreme conditions of clear-cuts and the subsequent exposure to desiccation and erosion (Campbell & Winchester 1994). Forest litter and decaying logs are rich in a large variety of species of fungi, many of which also serve as hosts for species of beetles and other arthropods. This habitat specificity is well documented for the staphylinid beetles; examples include *Pseudohaida rothi* which represents the first record for Canada (Campbell & Winchester 1994) and *Trigonodemus fasciatus* which is endemic to British Columbia (Scudder 1994). Eight new species of Omaliinae staphylinid beetles appear to rely on old-growth forests as a source area to maintain reproductively viable subpopulations (Campbell & Winchester 1994). The forest interior oribatid fauna is not as species rich as the canopy. However this forest interior habitat contains 15 new species that were not recorded in any of the other sample sites. This habitat association shown for these new species may be due to a variety of abiotic factors that affect microclimate conditions. Even though taxonomic information is not complete these trends are also apparent in some of the other groups such as the mycetophilids (fungus gnats), where a large number of new species have been recorded. The majority of these species are associated with habitats found only in the old-growth forest interior. Similar results have been found by Økland (1994) in Norway where semi-natural (i.e. the oldest) forests are more sustaining for mycetophilids.

Perhaps the most interesting habitat and least explored habitat in old-growth forests is the canopy. In the Sitka spruce canopy a key habitat feature, are the 4-28 cm deep moss mats which support a well developed soil layer. These mats are primarily composed of three moss species, *Isothecium myosuroides* Brid., *Antitrichia curtipendula* (Hedw.) Brid., *Dicranum fuscescens* Sm., which are also abundant on the forest floor. Soil microarthropods dominate this canopy soil/litter habitat, a fact which has not been well documented in these forests but has been noted in other canopy studies (Nadkarni & Longino 1990, Paoletti *et al.* 1990). From the oribatid mites that have been processed to date there is strong evidence that we are dealing with a distinct arboreal fauna. A high number of species with low percent similarity to ground sites is consistent with the findings of Behan-Pelletier *et al.* (1993). The discovery of several new oribatid species is not surprising (see Behan-Pelletier 1993) given the scope of this study, and fifteen undescribed species appear confined to habitats found only in the old-growth forest canopy. For example, *Dendrozetes* represents the first record for this genus in North America and this new species has modifications for an arboreal existence (Behan-Pelletier personal communication). *Parapirnodus*, *Paraleius*, and *Anachipteria* are genera that are known to be arboreal (Behan-Pelletier personal communication) and in this study each are represented by an undescribed, strictly arboreal species. Similarly, new species with unique habitat associations have been recorded in northern Venezuela (Behan-Pelletier *et al.* 1993); in Peru (Wunderle 1991) and in Australia (Walter *et al.* 1994). The microhabitats associated with the canopy of the ancient Sitka spruce trees are not replicated in any second growth forest canopies that we have surveyed to date and it is unlikely that these habitat features will develop in second growth forests that are in an 80-120 year rotation. We suggest that there are enough differences in canopy microhabitat conditions to promote the development of taxonomically discrete species assemblages that will be lost if these canopy habitats are not retained or allowed to develop in second growth forests. Given the striking old-growth habitat associations of the new species recorded in this study, there is strong supporting evidence to satisfy the third assumption applicable to Centinelan extinctions: that of habitat specificity.

Although the analysis of our data is in a preliminary state we present evidence from two groups, the oribatid mites and the staphylinid beetles that indicates that we are dealing with many new species that are old-growth dependent. Forest conversion affects arthropod diversity by altering key patterns of natural processes that are inseparably linked to habitat diversity. The summarizing of these key patterns and documentation of changes due to disturbances should identify ecological roles of arthropods that are at the heart of the biodiversity challenge. However, before this goal can be reached it is clear that proper documentation of the arthropod fauna at these sites must occur in order to prevent Centinelan extinctions.

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SUMMARY and CONCLUSIONS

Canopies of natural forests in temperate (Winchester 1997c; Winchester and Ring 1996 a, b; Schowalter 1989) and tropical regions (Stork 1988; Erwin 1983), contain largely undescribed and little understood assemblages of arthropods that have greatly expanded estimates of the total number of insect/arthropod species (Winchester 1997c). In my studies with emphasis on the canopy, in the northern temperate coastal rainforest of the Carmanah Valley on the southwest coast of Vancouver Island, British Columbia, I have recorded an estimated 10,000 arthropod species, of which approximately 500 are undescribed. In order to document, or even begin to understand, this biodiversity, I contend that efforts must not focus on single species but on species assemblages (Franklin 1993; Kremen *et al.* 1993) and that larger scale approaches (Kitching 1994), at the landscape level for example, are the only way to conserve the overwhelming numbers of species that exist in these systems.

Soule´ (1991) admirably outlined the challenge of conserving biodiversity and noted that human interference, which can be placed into six classes, is largely responsible for the accelerating rate of loss of many species. Of these six proximal causes, habitat loss, over exploitation and habitat fragmentation are the three main factors that exert the heaviest pressures on the arthropod fauna of the ancient forests on the west coast of Vancouver Island. Of the original 89 coastal watersheds over 5000 ha in size, the Carmanah Valley represents one of only six that have not been harvested during the last 60 years. Harvesting techniques that are generally referred to as clear-cutting alter habitat diversity and structure on a landscape scale to such a degree that arthropods associated with ancient forests experience direct habitat loss (Winchester 1997c; Winchester and Ring 1996a; Winchester 1993).

When the fragmentation of ancient forests is equated with rapid habitat alterations on the spatial scale of watersheds greater than 5000 hectares, this decreases the spatial and structural heterogeneity of the forest. Consequences for insects may vary but fragmentation-induced changes documented from a variety of forests indicate that changes in community structure, species richness and abundance occur in many taxa (Schowalter *et al.* 1980; Southwood *et al.* 1982; Saunders *et al.* 1991; Didham *et al.* 1996; Recher *et al.* 1996a; Winchester and Ring 1996b). The inclusion of movement (i.e. dispersal ability) as a landscape component associated with arthropods (see Didham *et al.* 1996; Straw and Ludlow 1994; Doak *et al.* 1992; Recher *et al.* 1991.) may have important implications for ecological processes that occur in ancient forests where fragmentation as a result of harvesting occurs. At present the framework for understanding these concepts and their application to ancient forests is largely undeveloped. The recent development of landscape linkages and so called "wildlife corridors" has given the false impression that we have information that allows us to link suitable areas that are surrounded by altered habitats. The basic components of landscapes and the ability to disperse successfully within these components are still largely unknown for most species.

The Sitka spruce canopy of the Carmanah Valley contains distinct species assemblages that form a discrete arboreal community (Winchester and Ring 1996a). An informative perspective on these canopy arthropods can be gained by placing them in guilds defined in terms of feeding habits (Root 1967, 1973; Moran and Southwood 1982) and it is these models that allow us to extend our understanding beyond single species approaches and look at the organization of ecosystem functioning. I also submit that many studies use common diversity measures (e.g. Shannon index) to answer questions about functional processes and as Didham *et al.* (1997), noted these inferences are at best weak. Viewing components of guilds (i.e. species richness or abundances) using diversity indices (e.g. Shannon index) could be misleading since proportional abundances and their weighting are at best contentious (Hurlburt 1971), and different species assemblages could, and often do, give values that are not significantly different even when the species composition is markedly dissimilar (e.g. see Klein 1989). A more interesting pursuit would be to explore the possibility (using guilds to quantify functional groups) that common factors shape canopy communities across a wide geographic range (Winchester 1997c). An understanding of these factors may provide us with predictive information that could be used as a tool to examine patterns in community structure (Longino 1994) and provide models to answer process-driven biodiversity (e.g. see Colwell and Coddington 1994) and conservation questions. I suggest that species abundance distributions provide a better characterization of ancient forest habitats and in the context of biodiversity, simple diversity indices are inappropriate to answer meaningful questions concerned with habitat change and its impact on biodiversity (Kempton 1979; Simberloff *et al.* 1987; Soberon and Llorente 1993; Williams *et al.* 1993; Tokeshi 1993; Pettersson 1997, Winchester 1997c). If biodiversity has a special meaning and forms the cornerstone of a 'new' conservation ethic then meaningful measurements need to be developed that allow us to expand our views beyond a narrowly defined ecological community (Pielou 1993).

From my work I find that numerically dominant groups are composed of individuals from the phytophagous (all living plant-feeders and facultative plant-feeders) and predator/parasitoid guilds. The remarkable feature of my guild analysis is the similarity (measured as percentage of total individuals for Sitka spruce) in overall composition when comparisons to previous studies are made (e.g. Moran and Southwood 1982; Stork 1987), and numerical dominance of functional groups in this study supports previous findings from coniferous forests by Schowalter and Crossley (1987) and Schowalter (1989, 1995). The phytophagous guild is composed of a small number of species (eg. Lepidoptera, 13 species) which contain a large number of individuals, a feature that is in agreement with Stork (1988). This appears typical of canopy species in the plant-feeding guild and may relate to the reduced number of food options (mainly developing vegetative buds and female cones). The predator guild contains substantially more species each containing fewer individuals than the phytophagous guild (eg. Arachnida, 38 species). Numerical dominance of spiders has been reported from other temperate studies (Renault and Miller

1972b; Nielsen 1975; Ohmart and Voigt 1981; Voegtlin 1982; Bigot and Kabakibi 1987; Basset 1991a; Pettersson *et al.* 1995; Pettersson 1996) and is further supported by observations that I have made in 4 other canopy studies on Vancouver Island. The maintenance of high predator loading in a structurally and functionally diverse ecosystem such as the Carmanah Valley supports previous findings by Karieva (1983), Risch (1981) Schowalter (1986, 1989), Pettersson *et al.* (1995), and Pettersson (1996, 1997). The parasitoid guild is represented by a large number of species (eg. F. Braconidae, 118 species) with low numbers of individuals. The main prey components of the parasitoids are species from the Lepidoptera and Aphididae. Species accumulation of parasitoids is not driven by taxonomic richness in the phytophagous guild but is structured by the host-stage that is attacked. From the branch clippings, I have reared several parasitoid species that attack the egg or larva or pupa of a variety of lepidopteran species. This variety of available host stages may contribute to an increase in parasitoid species that inhabit the canopy. Conspicuous by their absence in the canopy are Formicidae, with only 4 winged individuals collected during the entire study. Ants can exert considerable impact on other insects in arboreal habitats (Stork 1987; Majer 1993), although percentage contributions in temperate forests are generally low (Southwood *et al.* 1982; Bassett 1991a; Basset and Arthington 1992; Basset *et al.* 1992). The paucity of tourists is related to the transitory nature of these arthropods and the fact that branch clipping does not adequately sample this faunal component. Basset (1991a) noted that interception traps collected many more vagile arthropods, whereas restricted canopy fogging yielded more sedentary, apterous and juvenile specimens. This point is supported by my work using canopy Malaise traps which in 1991 collected 14,000 individuals, most of which are tourists (Winchester 1997a).

Where differences in proportional representation of insects in guilds between trees are evident, accumulations of single species in the phytophagous guild (usually aphids) occur. The accumulation of single species such as the aphid *Euceraphis punctipennis* (Zetterstedt) has been recorded by Southwood *et al.* (1982) and I found variation in guild proportionality between trees arising primarily from accumulation of aphid taxa such as *Cinara*. The species composition in each Sitka spruce tree that I examined was virtually identical, confirming the observation by Moran and Southwood (1982) that the major guilds in the arboreal community are shaped by habitat characteristics of the tree which provide a stable resource (Southwood 1961, 1978). This serves to impose a proportional consistence and, therefore, tree species play a role in structuring species profiles (Kitching and Zalucki 1996; Recher *et al.* 1996a). Thus mature Sitka spruce present a habitat template that may dictate the guild composition of species but not individuals. Individuals in the phytophagous and predator guilds exhibit non-uniformity between trees which may be the result of a myriad of factors that are coupled with the physical characteristics of the tree. Factors may include plant chemistry (Southwood *et al.* 1982), plant architecture (Lawton 1978, 1983, 1986; Morse *et al.* 1985), and plant health. Trees may act as individuals; in the sense that there are differences in guild proportionality and these differences are most evident in the phytophagous guild.

The high incidence of a predator/parasitoid complement in this study is in agreement with the results of previous studies (Schowalter 1985, 1989, 1995), and is an indication that herbivory in mature, structurally-complex forests occurs at a lower intensity than in planted second-growth areas where forest simplification and age-specific patterns of herbivory has resulted in examples of insect outbreaks (i.e. accelerated accumulation in the phytophagous guild; see Schowalter 1986, 1990, 1995; Karban 1987). Change in guild structure has a direct bearing on ecosystem processes by modifying higher-order interactions between insects and other taxa (see Didham *et al.* 1996). Therefore, I suggest that biodiversity in second-growth sites is altered and, in many important ways different from that of old-growth forests. The general guild pattern of the arboreal community is related to characteristics of the tree and, as Southwood (1961) noted, the magnitude of the populations of particular species is influenced by a variety of factors. Perhaps tree canopies can be considered as ecological islands, separate from adjacent ground habitats.

There are not necessarily differences in species composition among trees, yet differences in density and dispersal ability may, on closer inspection, lead to differences in ecosystem function. Details of life histories and phenologies of species can be correlated with seasonal trends and should afford opportunities to document periods of dispersal and impact on canopy processes.

For example, one of the most interesting habitats in the Sitka spruce canopy is that provided by the 4 to 28 cm deep moss mats that are underlaid by a well developed soil layer. Acari and Collembola dominate the canopy soil litter habitat, and our study is the first to demonstrate that the high canopy of an ancient Sitka spruce forest contains a resident oribatid fauna; samples from 2 sites yielded 30 and 28 species of which, 12 species appear to be canopy specific. When compared with other forest ground sites the resident arboreal soil litter mites have minimal dispersal capabilities, a feature also noted for forest-dwelling staphylinid beetles (Campbell and Winchester 1994). Acari, composed primarily of oribatids had the highest relative abundance in all sites over all time intervals and highest relative frequency was most pronounced in the canopy sites at all sampling times. This finding is consistent with other faunal studies in mature forests (Cornaby *et al.* 1975; Huhta and Koskenniemi 1975; Behan *et al.* 1978; Norton 1980; Wallwork 1983) and also emphasizes the dominance of oribatid mites in coniferous soil ecosystems (Huhta and Koskenniemi 1975; Schenker 1984a,b, 1986; Dwyer *et al.* 1997). The range of microhabitats available for colonization by oribatids is impressive (Wallwork 1983) and the importance of epiphytic cover as a determinant of species composition has been discussed (Andre´ 1984). I suggest that the ancient forest canopy provides microhabitats that are sufficiently different from the ground, thereby providing a habitat template to facilitate the evolution of arboreal specific oribatid species assemblages. Our results confirm this hypothesis and oribatids, mainly Brachyphlina, (e.g., Oppiidae, Peloppiidae, Ermaeidae, Cymbaeremaeidae) show arboreal specificity and are not just a random subset of the ground fauna. This result is supported by observations on temperate forest oribatids by

Gjelstrup (1979), Wallwork (1983), Winchester and Ring (1996a), and is consistent both when viewed from a qualitative (presence/absence) or a quantitative (number of individuals per species) analysis and supports the observations on arboreal specificity made by Travé (1963), Spain and Harrison (1968), Spain (1969), Aoki (1971, 1973), Norton and Palacios-Vargas (1987), Paoletti *et al.* (1990), Wunderle (1991), Behan-Pelletier *et al.* (1993).

I consider the oribatids of the canopy moss mats to be inhabitants of islands in the sense that they are isolated from their ground counterparts and have a distinct fauna that is characterized by two ecological groups of species; group 1, those specific to arboreal habitats which have low dispersal capabilities, and group 2, those species that occur in the arboreal environment but are not specific to that habitat and have high dispersal capabilities. Regardless of site and group designation, approximately 26% of the species recorded contain 74% of the individuals, suggesting that each site is characterized by an assemblage of euryecious species (i.e., group 1, wandering forms) that are numerically dominant and common to all sample sites and a set of stenoecious species (group 2, i.e., strictly arboreal) which are specific to each sample site. Species placed in group 1 have several genera in common with the truly arboreal forms that have been given separate group status as an ecological life-form by Aoki (1971) and include *Megeremaeus*, *Dendrozetes*, *Liacarus*, *Scapheremaeus* and *Achipteria*. Group 2 species include several genera reported by Aoki (1971) and include: *Hermannia gibba* (C.L. Koch), *Tectocepheus velatus* (Micheal), *Ceratoppia*, and *Eupterotegaeus*.

Observed differences in the mean number of species present across study sites and time suggest that these differences, which led to observed increased patchiness in the ground sites, especially the clear cut site, can be viewed in terms of macroscale influences which apply to microscale patterns. This suggests that in times of microhabitat stress (e.g., desiccation of the moss mats) that wandering early colonizing species in the clearcut site such as, *Scheloribates* sp. 1, *Achipteria nr. oregonensis* Ewing, *H. gibba* and *T. velatus* become patchy as they disperse to suitable microhabitats (eg. forest interior). These results further support the observations which indicated that oribatids (eg. *Trichoribates* sp. 1, and *Ceratoppia* sp. 1) actively disperse by random movement and this is an important mode of colonization. Oribatid presence was not as patchy in the canopy site as in the ground sites, an observation attributable to the resident, non-dispersing oribatids and supported by the observations in paper 3. Specialized canopy dwellers are also supported by the Q statistical results which indicate that the canopy has comparable diversity values to the most diverse ground site (edge) and agree with observations by Aoki (1971, 1973, 1974; Norton and Palacios-Vargas 1987; Wunderle 1991).

In summary, the microhabitats associated with the canopy of the ancient Sitka spruce trees contain a rich assemblage of oribatid mites that inhabit suspended moss/soil mats. I have demonstrated that the number of oribatid species in the canopy is comparable with that of ground sites, and that these habitats act as a reservoir for a distinct arboreal oribatid assemblage. Differentiation into a separate arboreal fauna has been demonstrated in other forest types (Niedbala 1969; Travé 1963; Nadkarni and Longino 1990; Wunderle 1992) but until now, distinct species assemblages in ancient coniferous forests canopies have not been well documented (Winchester and Ring 1996a). Oribatid mites can be used as a surrogate for other soil microarthropods, and I predict that arboreal specificity will also be pronounced in groups such as Collembola, Diplura, Protura and gamasid mites. The results of this study support previous conclusions by Winchester and Ring (1996a) and Winchester (1997a,b) that arboreal habitats act as reservoirs for arthropod biodiversity and habitat features important for long-term residency in the canopy are only found in intact coastal ancient rainforests.

The implications of island biogeography for fragmented habitats (Wilcove *et al.* 1986; Hudson 1991) coupled with habitat-specific arthropods with poor dispersal capabilities suggest that fragmentation and isolation can only further erode biodiversity. Soil microarthropods inhabiting the high Sitka spruce canopy have different dispersal abilities, and I suggest that oribatid mites use random movement as an active dispersal method to colonize canopy habitats.

Twenty two species of oribatids recorded from Malaise traps suggest that presence in these traps is due to active rather than passive dispersal. The majority of oribatid species found in the Sitka spruce canopy and in Malaise traps are members of the Brachypylina, a characteristic of the canopy oribatid fauna irrespective of forest type (Aoki 1973). In addition to the majority of colonizers being members of the Brachypylina, colonizing specimens are primarily adults (95-99%). The heavily sclerotized adults of oribatid mites are better equipped to deal with predators than the relatively unsclerotized immatures, and are the dispersal stage (Norton 1994).

Malaise traps represent a 'newly created' environment, and I anticipated that colonizing species will be thelytokous, dominated by members of the Brachychthoniidae, Oppiidae and Tectocepheidae (Norton and Palmer 1991). My data do not support this; for example, based on high gradient extractions, *Tectocepheus velatus* was common in the canopy, forest floor and clear-cut but was absent from Malaise traps. I did not sex adult specimens, but the species represented belong to sexual genera and families (Norton *et al.* 1993). A strong female bias among adult specimens in the Malaise traps could be expected, as higher dispersal in adult females is probable in oribatid mites (Norton 1994).

I consider phoresy as the source of the oribatid fauna in the Malaise traps unlikely for the following reasons. The few oribatid mites found in a phoretic association are endophagous, feeding on wood at particular stages of decay. Their phoretic associations are primarily with wood-burrowing insect species, especially members of the beetle family Passalidae (Norton 1980), a family not represented at the Carmanah site. Of the oribatid species present in the Malaise traps, only *Maerkelotritia* sp. 1 and *Hermanniella* sp. 1 are wood burrowers or endophagous species. Other than *Paraleius* sp. 1, with its modified median tarsal claw, none of the oribatid species found in this study is modified for phoresy. Although species of *Eporibatula* and *Scheloribates* are recorded as phoretic on beetles (Norton 1980), the frequency, relative abundance and seasonality of the *Eporibatula* sp. in the Malaise traps suggest a non-phoretic colonization by most specimens.

The frequency of species with a relative abundance greater than 5% in the malaise traps, and the frequency of species such as *Eueremaeus aysineep*, and *Dendrozetes* sp. 1 in malaise traps, otherwise recorded only from the canopy using high gradient extractions, are strong evidence for random movement contributing to colonization of new habitats by oribatid mites. Even if oribatid mites were passively dispersed by wind to malaise traps, either individually or in association with their moss microhabitats, specimens must actively move a vertical distance of 50-70 cm to reach the malaise trap head.

In conclusion, adult specimens of 1 to 15 oribatid species were captured in replicated malaise traps in canopy and forest floor of ancient Sitka spruce forest and an adjacent clear-cut area every 2 weeks. The frequency of species with a relative abundance greater than 5% in the malaise traps and the number of oribatid mite species (36) represented, primarily Brachypylina, support the hypothesis that oribatid mites use random movement as an active dispersal method to colonize canopy habitats.

Habitat changes that occur through logging of ancient forests have been well documented, but the effect that this type of habitat alteration has on arthropods has been addressed only to a limited extent (McLeod 1980; Chandler 1987, 1991; Niemela *et al.*1988, 1993; Schowalter 1989; Chandler & Peck 1992; Pettersson *et al.* 1995; Pettersson 1996, 1997) and I am aware of no studies that have looked at impacts of forest conversion on dispersal. Arthropod dispersal can affect the resident canopy fauna by adding significant "pulses" of individuals from adjacent habitats (i.e.tourist guild inputs). For example, of the 27 species of Trichoptera (adults) recorded from the Carmanah project, several species were collected in the canopy (Winchester 1997c) where species specific emergence patterns were apparent and this raises the question about how changes in habitat effect this rapid input of biomass into the canopy. Does the input of this resource into the canopy relax competition among prey items for predators such as the arachnids which comprise a major portion (over 80%) of the predator guild?

The pattern of biodiversity in the terrestrial arthropod component of Pacific Northwest forests remains largely unstudied. Given the fact that only a small percentage of the total number of specimens in this study have been identified to species it is likely that the number of new species recorded represents a conservative estimate. For example, the new species of staphylinid beetles and oribatid mites recorded in this thesis are restricted to habitats that are associated with ancient forests. Two important habitat components that occur on the ground are first, a supply of over-mature, fallen logs which are allowed to decay under natural conditions in the shade of the forest canopy, and second, the maintenance of deep layers of undisturbed forest floor litter which have not been eradicated by the extreme conditions of clear-cuts and the subsequent exposure to desiccation and erosion (Campbell and Winchester 1994). This habitat specificity is well documented for the staphylinid beetles; examples include *Pseudohaida rothi* which represents the first record for Canada (Campbell and Winchester 1994) and *Trigonodemus fasciatus* which is endemic to British Columbia (Scudder 1994). Eight new species of Omaliinae staphylinid beetles appear to rely on old-growth forests as a source area to maintain reproductively viable subpopulations (Campbell and Winchester 1994).

Even though taxonomic information is not complete these trends are also apparent in many other groups such as the mycetophilids (fungus gnats), where a large number of new species have been recorded (eg. *Anacliliea vallis* Coher and *A. winchesteri* Coher, Coher 1995) . Similar results have been found by Økland (1994) in Norway where semi-natural (i.e. the oldest) forests are more sustaining for Mycetophilidae. Most other dipteran groups contain several undescribed species that have restricted to habitats contained in ancient forests (eg. *Miniliomosina n. sp.,* F. Sphaeroceridae, Marshall, in prep.).

Microhabitats associated with the canopy of the ancient Sitka spruce trees are not replicated in any second growth forest canopies that I have surveyed to date and it is unlikely that these habitat features will develop in second growth forests that are in an 80-

120 year rotation. I suggest that there are enough differences in canopy microhabitat conditions to promote the development of taxonomically discrete species assemblages that will be lost if these canopy habitats are not retained or allowed to develop in second growth forests.

Given the striking ancient forest habitat associations of the new species recorded in this study, I suggest that many ancient forest arthropods are candidates for Centinelan extinctions: extinction of species unknown before their demise and hence unrecorded (Winchester and Ring 1996a). Forest conversion affects arthropod diversity by altering key patterns of natural processes that are inseparably linked to habitat diversity. The summarizing of these key patterns and documentation of changes due to disturbances should identify ecological roles of arthropods that are at the heart of the biodiversity challenge. However, before this goal can be reached it is clear that proper documentation of the arthropod fauna at these sites must occur in order to prevent Centinelan extinctions.

The importance of describing species assemblages and the inclusion of dynamic processes such as dispersal into the framework of how we think about arthropods in old-growth forests is a challenge that lies ahead of the entomological research community. Recognizing these components should assist efforts in addressing the issues that surround the maintenance of biological diversity (form and function) in these ancient forests.

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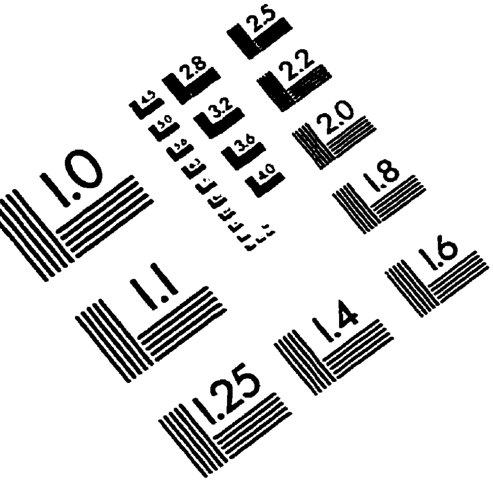
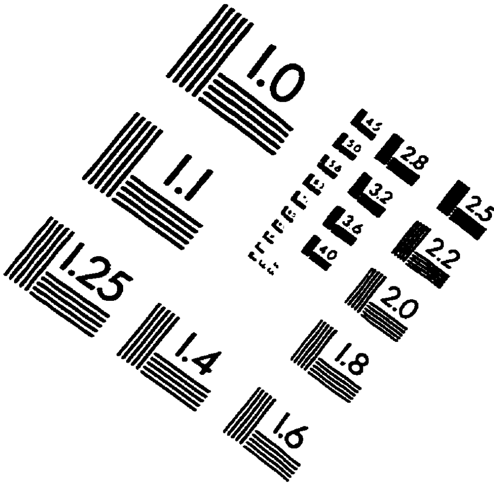
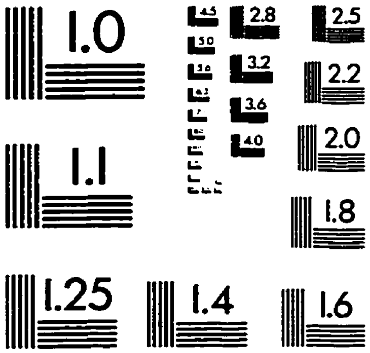
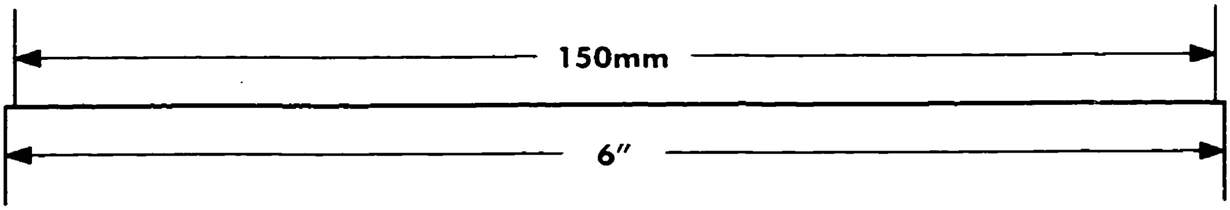
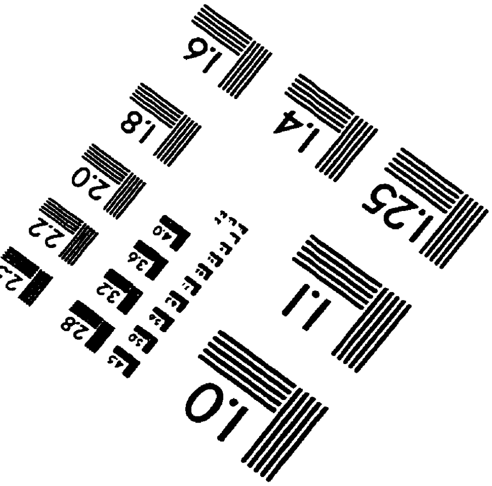
IMAGE EVALUATION TEST TARGET (QA-3)

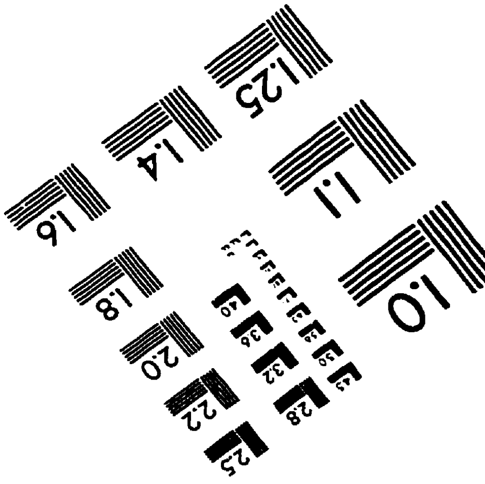












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Phone: 716/482-0300
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