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The Biodiversity of Arthropods from Northern Temperate Ancient Coastal Rainforests: Conservation Lessons from the High Canopy

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Abstract. The biodiversity crisis in global forests continues to be accelerated by habitat loss and consequent extinctions of floral and faunal species assemblages that cannot adjust to rapid, and often large scale, habitat alterations. In an effort to record arthropod diversity in northern temperate rainforests we have studied canopy arthropods in a number of Vancouver Island rainforest types since 1992. Based on these findings we summarize results to answer the following questions: (1) Does guild proportionality vary among different, geographically separated ancient rainforests? (2) Does the numerical dominance of the predator guild by spiders change across these ancient rainforests? (3) Do these ancient rainforests act as repositories for arthropod biodiversity? Answers to these questions are needed to address the issues that surround the maintenance of biological diversity (form and function) in these ancient forests and, in a broader context, rainforests throughout the world.

Key words: arthropods, biodiversity, British Columbia, temperate rain forest, conservation, canopy

Introduction

The global biodiversity crisis continues to be accelerated by habitat loss (Wilson 1988, Soulé 1991, Raven & Wilson 1992, Laurance 1997) and consequent extinctions of floral and faunal species assemblages (Lockwood 1987, Erwin 1991, Whitmore & Sayer, 1992) that cannot adjust to rapid, and often large-scale, habitat alterations (Winchester and Ring 1996a, 1996b, Stork et al. 1997, Winchester 1997a). 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 represents 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 & Ring 1996a, 1996b) and figures suggest that 49% by area of "old growth" (vs. 53% "mature" from satellite imagery) remains as of 1995 (MacKinnon & 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 the number of intact watersheds (>5000 hectares) so that only 6 of 89 remain (Winchester 1993, 1997c, Winchester & Ring 1996a, 1996b). 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 (Harding & McCullum 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 & 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 & Ring 1996a, 1996b, Behan-Pelletier & Winchester 1998, Winchester 1997a, 1997b) and tropical regions (Erwin 1983, Stork 1988, Basset 1997, 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. In this paper we summarize some of the patterns of arthropod biodiversity from three northern temperate ancient forest sites where research has focused on canopy arthropods. In particular we discuss observations on guild structure and ask the following questions: (1) Does guild proportionality vary among sites? (2) Do characteristics of the predator guild vary among sites? In addition we present evidence from the Carmanah Valley canopy suspended soil studies to support the hypothesis that ancient forest can-

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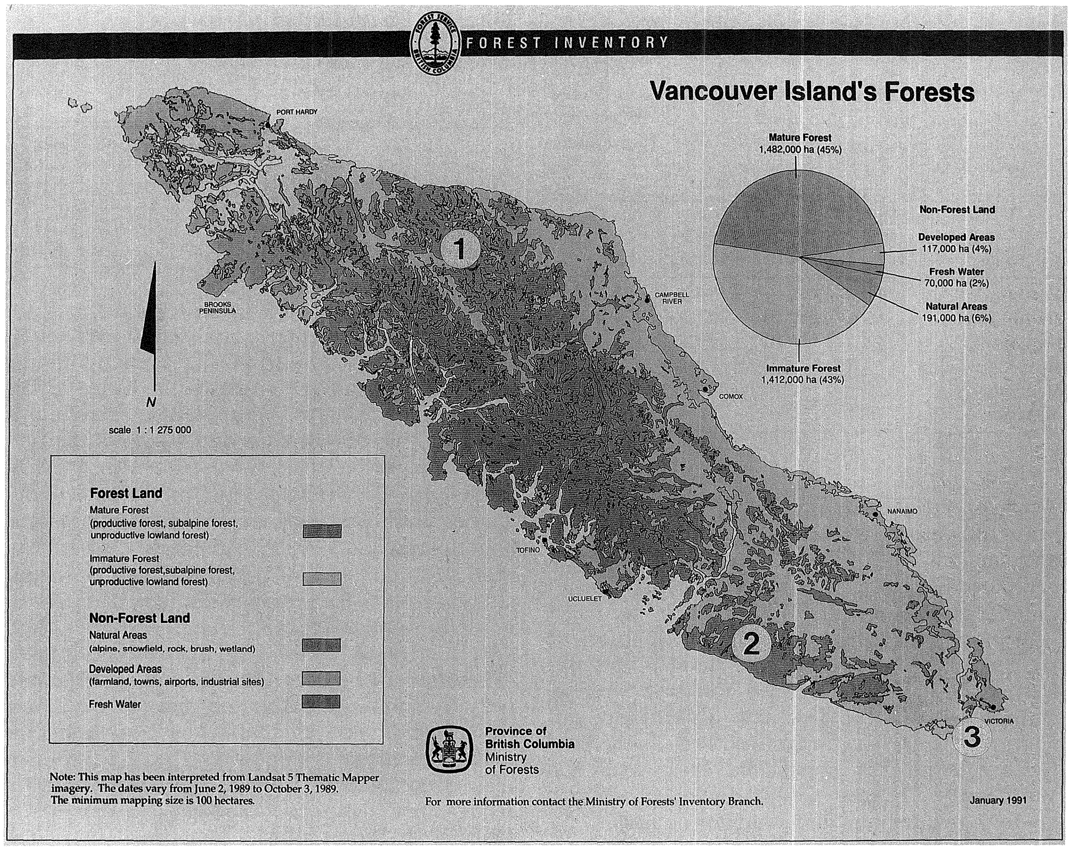

FIGURE 1. Map location of the Mt. Cain (1), Upper Carmanah Valley (2), and Rocky Point (3) canopy research sites, Vancouver Island, British Columbia, Canada.

opies act as repositories for arthropod biodiversity.

METHODS AND MATERIALS

We have been sampling selected ancient rainforests on Vancouver Island, British Columbia, Canada, since 1992 with most of our work focused on the Carmanah Valley. However, we have added four sites that encompass a range of forest types covering a wide geographic range on Vancouver Island (FIGURE 1). For the purposes of this paper we will focus on three sites; Mt. Cain, Carmanah Valley and Rocky Point (FIGURE 1).

At each site we have carried out basic arthropod inventories with a variety of sampling techniques. Data used in guild analyses were gathered using a branch clipping program. Resident microarthropods were collected from suspended soils using a hand held moss/soil corer and extracted using Tullgren funnels.

The characteristics of our northern temperate canopy sites and details of our sampling procedures can be found in: Winchester (1997a, 1997b), Carmanah Valley, and Winchester and Fagan (in press) Mt. Cain. Sampling procedures used at Rocky Point follow the protocols outlined by Winchester (1997a, 1997b) for the Carmanah Valley.

Sample Sorting and Data Analyses

Guilds

All insects were removed from each branch sample and prepared for identification. 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). The six guilds recognized in this study were: phytophages, epiphyte fauna, scavengers, predators, parasitoids, and tourists. All arthropods except the

TABLE 1. Means of percentage of arthropod individuals recorded from three samples sites (tree, time and height are pooled), arranged by guild. N scores are the number of branch samples collected from each of four tree species (AA = *Abies amabilis,* TH = *Tsuga heterophylla,* SS = *Picea sitchensis,* PM = *Pseudotsuga menziesii*).

Guild	Mt. Cain (AA)	Mt. Cain (TH)	Carmanah (SS)	Rocky Point (PM)
Predators	46.7	42.2	37.2	38.7
Phytophages	6.2	18.3	41.3	12.7
Parasitoids	3.2	0.3	11.8	4.0
Epiphyte fauna	0.0	0.0	8.3	1.2
Scavengers	9.9	12.0	1.0	10.1
Tourists	5.5	10.6	0.4	7.6

Acarina and Collembola collected from the branch-clippings were identified to family and arranged by guild. Guilds were expressed as a percentage of total individuals pooled over all sample parameters.

The predator guild is mainly composed of arachnids (Araneae) and was divided into six sub-guilds based on species foraging strategy similarities. Web builders were divided into categories of spiders with similar web characteristics, including permanent webs, daily webs and sheet webs. Hunting spiders included arboreal hunters, fast hunters and jumping hunters.

Total arachnid composition was compared for each site and arboreal spiders collected from the branch clipping samples were tabulated.

Suspended soils

Oribatid species composition from trap type (moss/soil cores and Malaise traps) for all sites in the Carmanah Valley were tabulated and expressed in a similarity figure.

GENERAL DISCUSSION

Canopy Guild Structure

Relative abundances of different guilds, expressed as percentage of mean number of individuals/kg dried plant material for all individuals for each study site from the branch-clipping sampling program are presented in TABLE 1. The emerging pattern of high predator loading is consistent across all sites and supports the previously published data for the Carmanah (Winchester 1997a). Predator guild proportions in our studies are higher than those reported by Moran and Southwood (1982) and Stork (1987). Numerical dominance of functional groups in this study supports the previous findings from deciduous forests by Schowalter and Crossley (1987) and coniferous forests by Schowalter (1989). The number of spider families and species richness are similar in each study site (TABLE 2) and this trend is also evident when comparing the arachnid canopy community (TABLE 3). Numerical dominance of spiders has been reported from other temperate studies (Nielsen 1975, Ohmart & Voigt 1981, Voegtlin 1982). 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). Despite similarities in spider richness between sites, spider communities are dissimilar (TABLE 4). These results agree somewhat with those reported by Halaj et al. (1998) where spider communities on different conifer species were found to be similar, but differences in community structure were noted for

TABLE 2. Comparison of the number of families, genera, species and individuals of arachnids from three coniferous rainforest types on Vancouver Island, British Columbia, Canada.

Site	Zone	Families	Genera	Species	Individuals
Mt. Cain	CWHvm2	16	62	78	1699
Carmanah	CWH	16	53	74	2179
Rocky Point	CDFmm	15	50	76	3093

TABLE 3. Comparison of the number of families, genera, species and individuals of arachnids from forest canopies of three coniferous rainforest types on Vancouver Island, British Columbia, Canada.

Site	Zone	Families	Genera	Species	Individuals
Mt. Cain	CWHvm2	10	16	25	344
Carmanah	CWH	10	12	18	313
Rocky Point	CDFmm	9	13	19	1269

TABLE 4. Percentage of arachnid individuals recorded from each of three sample sites (all factors pooled), arranged by functional group.

Sub-guild	Mt. Cain	Carmanah	Rocky Point
Web builders			
Permanent web	10.7	9.3	15.4
Daily web	16.7	1.1	2.1
Sheet web	24.3	35.7	57.3
Active hunters			
Arboreal hunter	16.1	23.6	12.3
Fast hunter	19.2	6.3	5.1
Jumping hunter	13.2	24.3	7.9

TABLE 5. Representation of canopy arachnid species from three coniferous forests on Vancouver Island, British Columbia. Total species was determined from pooling all branch clipping samples for each site. Lines represent species shared in common between all three sites.

Family	Genus/species	Rocky Point	Carmanah	Mt. Cain
Agelenidae	*Ethobuella tuonops*		●	
Amaurobiidae		●	●	
Anyphaenidae	*Anyphaena aperta*	●	●	●
Araneidae	*Araniella displicata*	●	●	●
	Cyclosa conica			●
	Zygiella sp. 1	●	●	
Clubionidae	*Clubiona* sp.		●	●
Dictynidae	*Dictyna peragrata*	●		●
	D. sp. 1			●
Linyphiidae	*Ceraticelus atriceps*		●	●
	Linyphantes sp.		●	●
	L. nr. *eureka*			●
	L. orcinus		●	
	L. pulla		●	●
	Lepthyphantes orcinus	●		
	L. pulla	●		
	Neriene digna	●		
	Pityohyphantes vancouveranus	●		
	P. sp. 1			●
	P. sp. 2	●		●
	Tachygyna ursina	●		●
	Tachygyna sp. 1	●		●
Philodromidae	*Apollophanes margareta*			●
	Philodromus mysticus			●
	P. rufus	●	●	●
	P. sp.		●	●
	P. dispar	●		
Salticidae	*Metaphidippus aeneolus*			●
	M. sp. 1	●	●	●
	M. sp. 2		●	
Tetragnathidae	*Mettellina* sp.	●		●
	Tetragnatha sp.	●	●	●
	T. versicolor		●	
Theridiidae	*Theridion montanum*			●
	T. saanichum	●	●	●
	T. sexpunctatum		●	
	T. agrifoliae	●		
Thomisidae	*Xysticus* sp.			●

geographically separated study sites. Spider species assemblages at our sites were not similar and only five species were shared in common across all three study sites (TABLE 5). It appears that apart from some underlying habitat characteristics common to conifer species, spider communities are influenced by other factors that may include stand structure, canopy microclimate and canopy architecture. For example, our results indicate that the sheet web builders (F. Linyphiidae) are the dominant spider group across all sites, although their percent contribution to spider community structure differs among sites. Results from our spider work need to be further analyzed, but for the purpose of this paper it should be noted that obvious differences exist among geographically separated forest types in terms of spider community structure and species assemblages.

Oribatid Conclusions

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 (Huhta & Koskenniemi 1975, Wallwork 1983) and also emphasizes the dominance of oribatid mites in coniferous soil ecosystems (Huhta & Koskenniemi 1975, Schenker 1984a, 1984b, 1986, 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

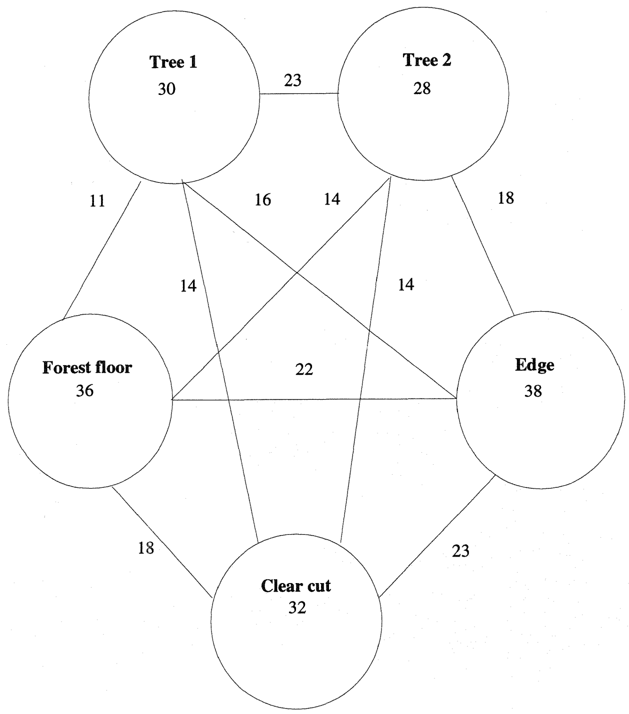

FIGURE 2. Numerical relationship between adult oribatid species from five study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time periods. Numbers along the lines represent those species in common between sites. Numbers within the circles represent species occupying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

temperate Sitka spruce forest. Details of species composition are published by Behan-Pelletier and Winchester (1998). Northern forest systems, although relatively unexplored, contain a diverse assemblage of oribatids, as demonstrated by Dwyer et al. (1997) who found 83 oribatid species from a range of microhabitats in 2 commercial balsam fir forests. Our study is the first to sample the high canopy in an ancient forest, and samples from 2 canopy sites account for 30 and 28 species respectively, of which 12 species appear to be canopy specific (FIGURE 2).

In both temperate and tropical forests oribatid mites appear to have a distinct arboreal component (Aoki 1971, 1974, Spain & Harrison 1968; Ehler & Frankie 1979, Wallwork 1983; Norton & Palacios-Vargas 1987, Wunderle 1991, 1992; Behan-Pelletier et al. 1993; Walter 1995; Winchester & Ring 1996a). Our results confirm the hypothesis that the Sitka spruce canopy contains a distinct species assemblage of oribatid mites, especially in the brachypyline families Damaeidae, Eremaeidae, Thyrisomidae, Cymbaeremaeidae and Oripodidae, and that these species are not just a random subset of the ground fauna. Our results are consistent both when viewed both from qualitative (presence/absence) and quantitative (number of individuals per species) analyses (see Winchester 1997a). Walter (1995) found similar results in a subtropical rainforest where canopy inhabiting mites did not represent an extension of the soil-dwelling fauna.

This "suspended" moss/soil in our study is located between 30 and 66 m in the canopy, and is discontinuous with the ground, although the numerically dominant moss cover in both habitats is composed of the same species. We consider the oribatid inhabitants of these canopy moss mats to be inhabitants of islands, in the sense that these mats are isolated from their ground counterparts. Canopy moss mats 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 & Winchester 1998), analogous to the "strictly arboreal" ecological life-form (Aoki 1971); and group 2, those species that occur in the arboreal but are not specific to that habitat, have high dispersal capabilities, and can move between soil and arboreal habitats (Behan-Pelletier & Winchester 1998), analogous to "wandering forms" of Aoki (1971). Species from the Sitka spruce canopy in group 1 represent many genera considered strictly arboreal by Aoki (1971), including *Megeremaeus, Dendrozetes, Liacarus, Scapheremaeus,* and *Achipteria.* Similarly, several genera considered to contain "wandering" species are included in our Group 2, including *Hermannia, Tectocepheus, Ceratoppia,* and *Eupterotegaeus* (see Behan-Pelletier & Winchester 1998).

Another way of considering how species are distributed across the forest gradient is in terms of "isovalent" species assemblages (Wallwork 1983). Ecological flexibility is exhibited by those species that are not constrained by microhabitat conditions. These species are active in terms of their dispersal ability (Behan-Pelletier & Winchester 1998), often occurring in large numbers across all habitat gradients. This high ecological valence (sensu Wallwork 1983) is typified by *Trichoribates* (Behan-Pelletier & Winchester 1998) which is found in all study sites and by *Sphaerozetes* sp. which comprises 20% of all the oribatid individuals sampled.

We have begun making comparisons of the oribatid fauna associated with canopy microhabitats (e.g., suspended soils, lichen accumulations) at our other canopy sites. Preliminary results suggest that parallel trends in oribatid distribution across geographically separated forest ecosystems occur. For example, several species are new to science and a number of species are specific to the arboreal zone (e.g., Fagan & Winchester 1999). These results clearly indicate that in ancient forests of Vancouver Island, several species of the canopy arthropod community exhibit arboreal specificity, and species overlap between the different study sites is low.

Conclusions

Based on the avenues of investigation we are currently pursuing with our canopy research, conservation measures concerned with the retention of biodiversity in the ancient forest of Vancouver Island should take the following points into account:

1. Arboreal habitats act as reservoirs for arthropod biodiversity.
2. Microhabitat features important for long term residency of some species within the canopy are only found in intact coastal ancient rainforests.
3. We conclude that species assemblages will be lost if these canopy habitats are not retained or are not allowed to develop over time, in second growth forests.
4. Oribatid mites can be used as representatives for other soil microarthropods, and we predict that arboreal specificity in the Sitka spruce canopy will also be pronounced in groups such as Collembola, Diplura, Protura and gammasid 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 this suspended moss/soil habitat.
5. The resident canopy arthropod fauna in this study is dominated by individuals of the predator guild. We infer from this guild structure that predator loading in these mature, structurally-complex forests is an important factor that has a direct influence on herbivores and, through a series of checks and balances has a direct effect on damage caused by herbivore accumulations.
6. The predator community is dominated by the arachnid fauna, but this fauna, both in terms of species richness and functional groups, is not similar across the different forest types on Vancouver Island.

Future Directions for Canopy Research

Although many countries including Canada, signed the Rio Convention on Biological Diversity in 1992 and the ecological, economic and social importance of sustaining forest ecosystems has been clearly outlined in several document (e.g., Canadian Biodiversity Strategy, 1995), current policy has not fostered the development of sustainable forestry that is inseparably coupled with the maintenance of biodiversity both in form and function, in our global forests. We still operate under the assumption that silvicultural practices and managed second growth forests somehow mimic the natural dynamics of ancient forests. Clearly this is not measured by empirical data. In order to meet the stated goals of sustainable forest management and retention of biodiversity, an extensive plan of ecological research that includes arthropods is needed to catalogue species assemblages and address dynamic processes such as the dispersal of organisms as well as the effects of fragmentation in ancient forests. These are the future challenges for policy makers, for managers, and for the canopy research community.

Acknowledgments

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Finally, we acknowledge the many people and institutions involved in canopy work and look forward to sharing in the excitement of exploring the rainforest canopies of the world.

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