

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

NEVILLE N. WINCHESTER¹ AND RICHARD A. RING

Department of Biology, University of Victoria, P.O. Box 1700,
Victoria, British Columbia, Canada V8W 2Y2

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 for 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 forest 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 the Centinelan extinction concept—extinction of species unknown before their demise and hence unrecorded.

INTRODUCTION

The ongoing global biodiversity crisis continues to be fueled by habitat loss (Wilson 1988, 1989, 1992, Soulé 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 extinction are difficult to measure and often confounded by the absence of species inventory information which is particularly prevalent in 'hyperdiverse' groups such as 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 concordant with the observation that these areas contain over half of the world's species (Erwin 1988, Janzen 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 in press). 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 elements of biodiversity associated with these old-growth forests form 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 present several difficulties for researchers. Nowhere is this more obvious than with species estimates which on a global basis vary from 5 to 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

¹ Corresponding author.

arthropod species (Cannings 1992), many of which are undescribed (Winchester and Ring in press). 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?

MATERIALS AND METHODS

Study area—The study area is located in the Upper Carmanah Valley drainage (48° 44'N; 124° 37'W) on the Southwest 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 & Pojar 1991). The dominant conifers in the Carmanah drainage are Sitka spruce (*Picea sitchensis* (Bong.) Carr), western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.), western red-cedar (*Thuja plicata* D. Don) and Pacific silver fir (*Abies amabilis* (Dougl.) Forb.).

The 1991 field program centered in the Upper Carmanah Valley included one canopy and three ground sites: old-growth canopy, old-growth forest interior (both old-growth sites are characterized by trees greater than 300 years of age); transition zone (edge between old-growth and clear-cut) and clear-cut (approx. four hectares, harvested in 1985).

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 2:1 mechanical advantage pulley system. Strapped into a harness and attached to a series of permanent climbing lines, we are able to sample 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 meters 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), randomly placed along a 100m linear transect, were run 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 run at each ground sample site. Pans (23 × 15 × 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 × 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 × 5 cm) 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 undeter-



FOREST INVENTORY

Vancouver Island's Forests

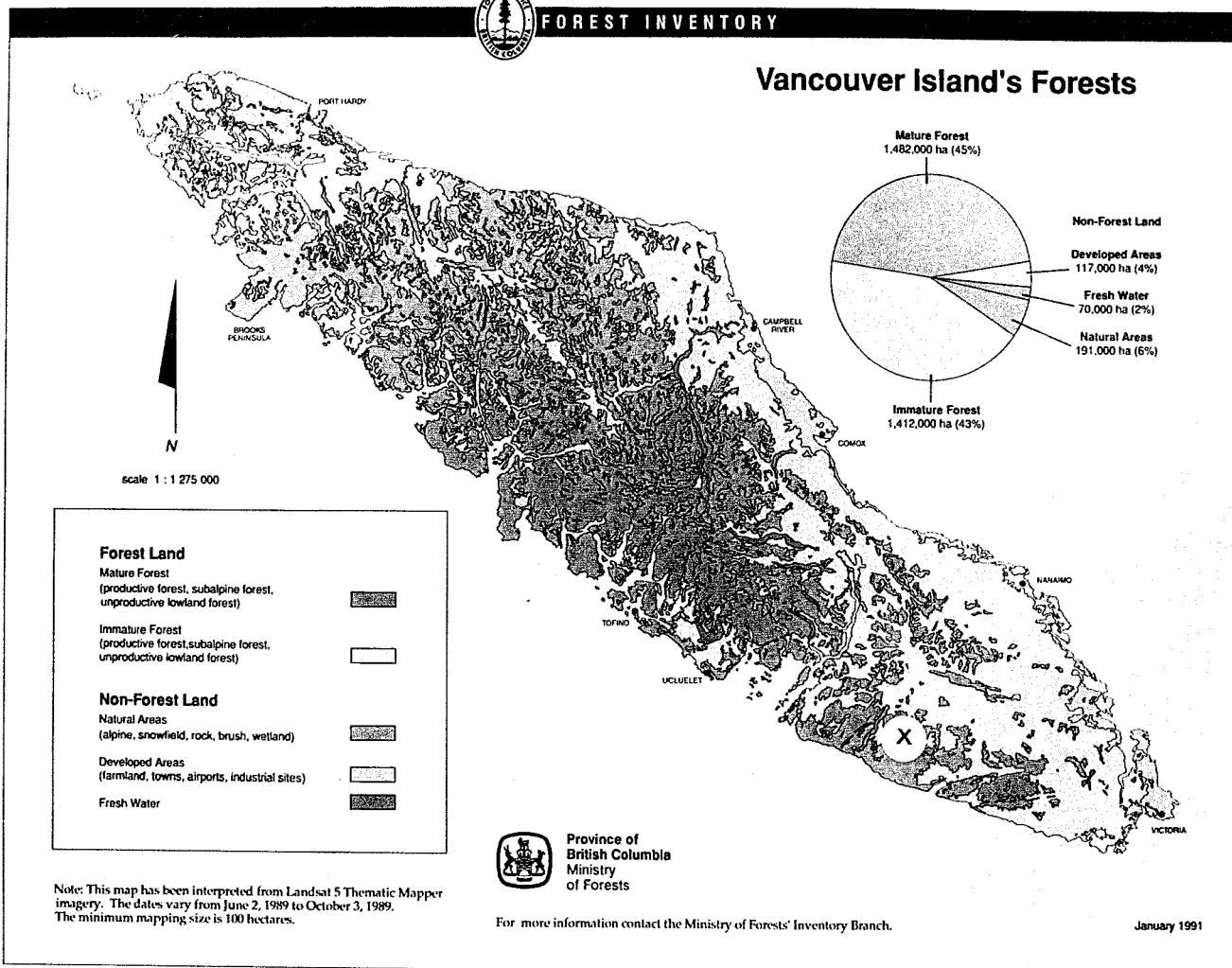


FIGURE 1. Map location of the Upper Carmanah Valley canopy research site on Vancouver Island, British Columbia, Canada.

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	13,782
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
Psocoptera	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	91,601	294,276	206,857	612,396

Abbreviations: Can = Canopy, FF = Forest Floor, TZ = Transition Zone, CC = Clear-cut.

mined 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 individuals are partitioned among sites, the transition zone (edge between old-growth and clear-cut) is most numerous in orders that are highly mobile (e.g. 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 Psocoptera. The canopy site is somewhat depauperate in most taxonomic groups, although the Acarina are extremely abundant. 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 groups (e.g. Braconidae and Proctotrupidae have been sorted to genera and morpho-species). 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 are for the Staphylinidae (FIGURE 2) and the Oribatidae (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 have 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 asso-

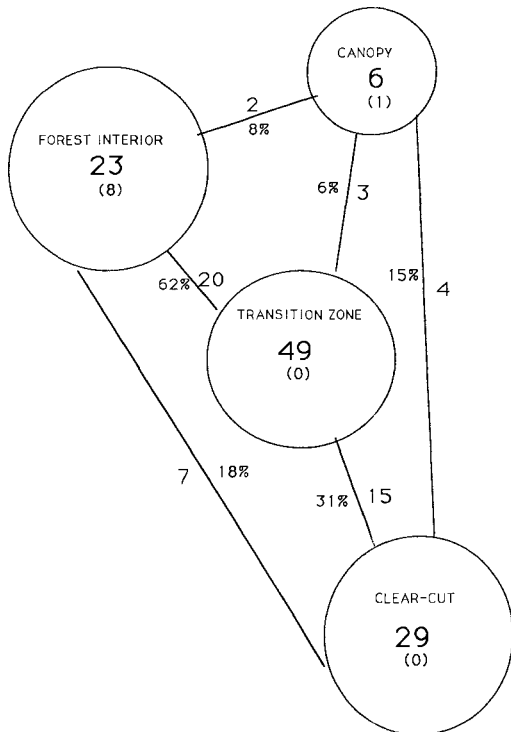


FIGURE 2. Numerical relationship between staphylinid species from four study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time intervals. Numbers along the lines represent those species in common between the sites. Numbers within the circles represent the number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

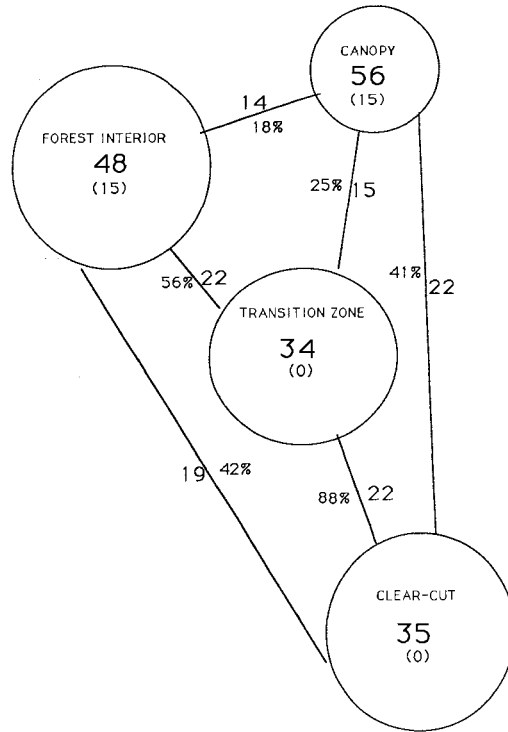


FIGURE 3. Numerical relationship between oribatid species from four study sites in the Upper Carmanah Valley. Data are pooled from all trap collections over all time intervals. Numbers along the lines represent those species in common between the sites. Numbers within the circles represent the number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

ciations 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 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 ha remain intact (Winchester 1993). We suggest that our first assumption (habitat scarcity) needed to satisfy the Centinela 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. Exploring 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 appear to be dealing with a largely unexplored fauna that contains new species and therefore we have met the second assumption needed to address the Centinelan extinction definition.

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 overmature, 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* Hatch which represents the first record for Canada (Campbell & Winchester 1994) and *Trigonodemus fasciatus* Leetch 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. Despite lack of complete information 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 (Winchester unpublished data). The majority of these species are associated with habitats found only in the old-growth forest interior. Similar results have been found by Okland (1994)

in Norway where semi-natural (i.e., the oldest) forests are more sustaining for mycetophilids.

Perhaps the most interesting habit in old-growth forests is the canopy. In the Sitka spruce canopy a key habitat feature is provided by the 4–28 cm deep moss mats which support a well developed soil layer. These mats are primarily composed of three moss species, *Isoetecium myosuroides* Brid., *Antitrichia curtispindula* (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 1992) and in Australia (Walter *et al.* 1994). The microhabitats associated with the canopy of the ancient Sitka spruce trees is 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 taxonomic determinations for most of our specimens are not complete we present evidence from two groups, the oribatid mites and the staphylinid beetles that indicates that we are dealing with a 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 in these forests must occur in order to prevent Centinela extinctions.

ACKNOWLEDGEMENTS

This project was made possible by financial support from FRDA research grants from B.C. Ministry of Forests, Research Branch. Acknowledgement is made to A. Mackinnon and B. Nyberg of that Branch for their continued support.

We are indebted to the following taxonomic experts for identifications: their contributions are invaluable and form the essence for understanding arthropod biodiversity in these old-growth forests: V. Behan-Pelletier, Y. Bousquet, D.E. Bright, J.M. Campbell, B.E. Cooper, A. Davies, B. Footitt, G.A.P. Gibson, H. Goulet, K.G.A. Hamilton, J. Huber, E.E. Lindquist, L. Masner, J.H. Redner, M.H. Sharkey, A. Smetana, D.M. Wood, H.C.W. Walther (Agriculture Canada, Ottawa, Canada); A.T. Finnamore (Provincial Museum of Alberta, Edmonton, Canada), E.L. Mockford (Illinois State University, Normal, IL, USA); G.B. Wiggins (Royal Ontario Museum, Toronto, Canada); G.E. Ball, A.P. Nimmo, D. Pollock, D. Shpeley (University of Alberta, Edmonton, Canada); R.S. Anderson, F. Brodo, F. Rafi (Canadian Museum of Nature, Ottawa, Canada); R.G. Bennett (Ministry of Forests, Victoria, Canada); R.A. Cannings, R. West (Royal British Columbia Museum, Victoria, Canada); D. Buckle (Saskatoon, Canada); R. Duncan, L.M. Humble (Pacific Forest Centre, Victoria, Canada); S.J. Peck (Carleton University, Ottawa, Canada); J.F. Burger, D.S. Chandler (University of New Hampshire, Durham, USA); A. Fjellberg (Tromsø University, Norway); E.I. Coher (Long Island University, New York, USA); S.A. Marshall (University of Guelph, Canada); V.R. Vickery (McGill University, Ste-Anne-de-Bellevue, Canada); R.M. Shelley (North Carolina State Museum of Natural Science, North Carolina, USA); J. Turgeon (FPMI, Sault Ste. Marie, Canada); J.D. Oswald (National Museum of Natural History, Washington, USA); the late G. Eickwort (Cornell University, Ithaca, NY, USA).

We also thank D. Blades, A. Braybrooks, B. Lund, N. Prockiw, A. Thompson and a host of volunteers for assistance with sorting and prepa-

ration of specimens; and, finally, K. Jordan and S. Hughes for providing technical expertise in the arboreal aspects of this project.

LITERATURE CITED

- BEHAN-PELLETIER V.M. 1993. Diversity of soil arthropods in Canada: Systematic and ecological problems. Pp. 11–50 in G.E. Ball and H.V. Danks, eds., Systematics and entomology: Diversity, distribution, adaptation, and application. Mem. Ent. Soc. of Canada.
- BEHAN-PELLETIER V.M., M.G. PAOLETTI, B. BISSETT AND B.R. STINNER. 1993. Oribatid mites of forest habitats in northern Venezuela. Tropical Zoology, Special Issue 1: Pp 39–54.
- BIOLOGICAL SURVEY OF CANADA. 1994. Terrestrial arthropod biodiversity: planning a study of recommended sampling techniques. Supplement to the Bull. Ent. Soc. Canada, 26: 1–33.
- BUNNELL F.L. 1990. Forestry wildlife: w(h)ither the future? Pp. 163–176 in A.F. Pearson and D.A. Challenger, eds., Proc. Symp. on Forests—Wild and Managed: Differences and Consequences. Students for Forestry Awareness, U.B.C., Vancouver, B.C.
- CAMPBELL J.M. AND N.N. WINCHESTER. 1994. First record of *Pseudohaida rothi* Hatch (Coleoptera: Staphylinidae: Omaliinae) from Canada, J. Entomol. Soc. Brit. Columbia 90:83.
- CANNINGS S. 1992. Arthropods—where diversity is really at. Pp. 43–58 in L.R. Ramsey, ed., Methodology for Monitoring Wildlife Diversity in B.C. Forests, B.C. Environment, Wildlife Branch, Victoria.
- CHANDLER D.S. 1987. Species richness and abundance of Pselaphidae (Coleoptera) in old-growth and 40-year-old forests in New Hampshire. Can. J. Zool. 65: 608–615.
- . 1991. Comparison of some slime-mold and fungus feeding beetles (Coleoptera) in old-growth and 40-year-old forest in New Hampshire. Coleopt. Bull. 45: 239–256.
- CHANDLER D.S. AND S.B. PECK. 1992. Diversity and seasonality of Leiodid beetles (Coleoptera: Leiodidae) in an old-growth and a 40-year-old forest in New Hampshire. Env. Entomol. 21: 1283–1293.
- COLWELL R.K. AND J.A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Trans. R. Soc. Lond. 345: 101–118.
- DANKS H.V. 1993. Patterns of diversity in the Canadian insect fauna. Pp. 51–74 in G.E. BALL AND H.V. DANKS, eds., Systematics and entomology: diversity, distribution, adaptation, and application. Mem. Ent. Soc. Can. 165.
- DI CASTRI F., J.R. VERNHES, AND T. YOUNES 1992. Inventorying and monitoring of biodiversity. A proposal for an international network. Biol. Intl. Special Issue November 27: 1–27.
- ERWIN T.L. 1988. The tropical forest canopy: the heart of biotic diversity. Pp. 123–129 in E.O. WILSON, ed., Biodiversity. National Academy Press, Washington, D.C.
- FENGER M. AND A. HARCMBE. 1989. A discussion

- paper on old-growth forests, biodiversity, and wildlife in British Columbia. Prepared by the Wildlife Branch, B.C. Min. Environment, for the invitational workshop "Towards an Old-Growth Strategy", Nov. 3-5, Parksville, B.C.
- FRANKLIN J.F. 1988. Structural and functional diversity in temperate forests. Pp. 166-175 in E.O. WILSON, ed., *Biodiversity*. National Academy Press, Washington, D.C.
- JANZEN D.H. 1988. Tropical dry forests: The most endangered major tropical ecosystem. Pp. 130-137 in E.O. Wilson, ed., *Biodiversity* National Academy Press, Washington, D.C.
- MACKINNON A. 1993. British Columbia's old-growth forests. *Bioline* 11 (No. 2): 1-9.
- MAY R.M. 1986. The search for patterns in the balance of nature: advances and retreats. *Ecology* 67: 1115-1126.
- MATTSON W.J. AND N.D. ADDY. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515-522.
- MCLEOD J.M. 1980. Forests, disturbances, and insects. *Can. Ent.* 112: 1185-1192.
- MEIDINGER D. AND J. POJAR 1991. *Ecosystems of British Columbia*. B.C. Min. of Forests, Victoria, B.C..
- MYERS N. 1988. Tropical forests and their species: Going going . . . ? Pp. 28-35 in E.O. WILSON, ed., *Biodiversity*. National Academy Press, Washington, D.C.
- NADKARNI N.M. AND J.T. LONGINO. 1990. Invertebrates in canopy and ground organic matter in a Neotropical montane forest, Costa Rica. *Biotropica* 22(3): 286-289.
- NIEMELA J., Y. HAILA, E. HALME, T. LAHTI, T. PAJUNEN AND P. PUNTILA. 1988. The disturbance of carabid beetles in fragments of old coniferous taiga and an adjacent managed forest. *Ann. Zool. Fenn.* 25: 107-119.
- NIEMELA J., D. LANGOR AND J.R. SPENCE. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Cons. Biol.* 7: 551-561.
- OKLAND B. 1994. Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. *Biodiversity and Conservation* 3: 68-85.
- O'NEILL R.V. 1976. Ecosystem perturbation and heterotrophic regulation. *Ecology* 57: 1244-1253.
- PAOLETTI M.G., B.R. STINNER, D. STINNER, D. BENZING, AND R. TAYLOR. 1990. Diversity of soil fauna in the canopy of Neotropical rain forest. *J. of Tropical Ecology* 7: 135-145.
- SAMWAYS M.J. 1994. *Insect Conservation Biology*. Chapman and Hall, London, UK.
- SCHOWALTER T.D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. *Can. J. For. Res.* 19: 318-322.
- SCUDDER G.G.E. 1994. An annotated systematic list of the potentially rare and endangered freshwater and terrestrial invertebrates in British Columbia. *J. Entomol. Soc. Brit. Columbia, Occasional paper* 2.
- SOULÉ M.E. 1991. Conservation: tactics for a constant crisis. *Science* 253: 744-750.
- STORK N.E. 1988. Insect diversity: facts, fiction and speculation. *Biol. J. Linnean Soc.* 35: 321-337.
- TOWNES H. 1962. Design for a Malaise trap. *Proc. Entomol. Soc. Wash.* 64: 253-262.
- WALTER D.E., D.J. O'DOWD AND V. BARNES. 1994. The forgotten arthropods: foliar mites in the forest canopy. *Mem Queensland Museum* (in press).
- WILSON E.O. 1988. The current state of biological diversity. Pp. 3-18 in E.O. WILSON, ed., *Biodiversity*. National Academy Press, Washington, D.C.
- 1989. Threats to biodiversity. *Scientific American*: 109-116.
- 1992. *The Diversity of Life*. Harvard University Press, Cambridge, Mass., USA.
- WINCHESTER N.N., 1993. Coastal Sitka spruce canopies: conservation of biodiversity. *Bioline* 11 (No. 2): 9-14.
- WINCHESTER N.N., AND G.G.E. SCUDDER. 1993. Methodology for sampling terrestrial arthropods in British Columbia. Resource Inventory Committee, B.C. Ministry of Environment, Lands and Parks.
- WINCHESTER N.N., AND R.A. RING. 1995. Arthropod diversity of a coastal Sitka spruce forest on Vancouver Island, British Columbia, Canada. *Northwest Science* (in press).
- WUNDERLE I. 1992. Die baum- und bodenbewohnenden Oribatiden (Acari) im Tieflandregenwald von Panguana, Peru. *Amazoniana*, Vol. X11 (1). Pp. 119-142.