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Arthropod Diversity and Conservation in Old-Growth Northwest Forests¹

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SYNOPSIS. Old-growth forests of the Pacific Northwest extend along the coastal region from southern Alaska to northern California and are composed largely of conifer rather than hardwood tree species. Many of these trees achieve great age (500-1,000 yr). Natural succession that follows forest stand destruction normally takes over 100 years to reach the young mature forest stage. This succession may continue on into old-growth for centuries. The changing structural complexity of the forest over time, combined with the many different plant species that characterize succession, results in an array of arthropod habitats. It is estimated that 6,000 arthropod species may be found in such forests-over 3,400 different species are known from a single 6,400 ha site in Oregon. Our knowledge of these species is still rudimentary and much additional work is needed throughout this vast region. Many of these species play critical roles in the dynamics of forest ecosystems. They are important in nutrient cycling, as herbivores, as natural predators and parasites of other arthropod species. This faunal diversity reflects the diversity of the environment and the arthropod complex provides a sensitive barometer of the conditions of the forest. Conservation efforts for forest arthropods are limited at present and controlled largely by land-use policies. For example, an effort is being made to include arthropods in conservation efforts for the Northern Spotted Owl and arthropods will be included in the Forest Health Monitoring program now underway by the U.S. Forest Service. Evidence from other parts of the world suggest that arthropods that depend upon large pieces of dead wood may be particularly threatened by forest management practices. Much remains to be done in the conservation of forest arthropods.

INTRODUCTION

The old-growth forests of the Pacific Northwest form a distinctive biotic region that extends along the Pacific Coast from southeast Alaska to northern California. Waring and Franklin (1979) characterized these forests as unique in their size and in the longevity of the individuals of the dominant tree species, resulting in very large accumulations of biomass. The 25 dominant tree species are conifers rather than hardwoods although there are hardwood taxa found in the forests (*e.g.*, Acer L., Alnus Mill., Castanopsis (D. Don) Spach, Lithocarpus Blume, Populus L., Quercus L., and Salix L.) (Franklin and Dyrness, 1971). The large trees develop extensive canopies characterized more by their height than breadth.

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These conifer species achieve great age. Many of the oldest individuals of each species are found in these forests (e.g., Sitka spruce [Picea sitchensis (Bong.) Carr.] > 500 yr, Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] >750 yr, Alaska yellowcedar [Chamaecyparis nootkatensis (D. Don) Spach] > 1,000 yr, western red cedar [Thuja plicata Donn ex D. Don] >1,000 yr, coast redwood [Sequoia sempervirens (D. Don) Endl.] >1,250 yr) (Waring and Franklin, 1979). Other related attributes of the forests are the presence of massive amounts of coarse woody debris (CWD) as snags or on the ground (Maser and Trappe, 1984; Harmon et al., 1986; Maser et al., 1988; Harmon et al., 1990; Hz complex litter layer 1973; Lattin, 1990; and other features tural diversity of th is reflected by the found there (Lawtc) 1990; Parsons et a.

While these old ity over time and s product of sever: through succession (Lattin, 1990). Fire and diseases, are bances. The proloi a continually char ments and habitat (Southwood, 1977 Lawton, 1983). arthropods have be old-growth site, th mental Forest (HJ old-growth Doug lamette National Oregon. The HJA by the U.S. Fores consequences of 1 ulation. It was a western Coniferou International Bio 1960s, was name logical Reserve in one of the first Na funded, Long-Te Sites in 1980. Toc on the site and c tigations related Included in these many involving : lated informatior paper.

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¹ From the Symposium *The Crisis in Invertebrate Conservation* presented at the Annual Meeting of the American Society of Zoologists and the Canadian Society of Zoologists, 27-30 December 1992, at Vancouver, British Columbia.

mon et al., 1990; Harmon, 1992) and a deep, complex litter layer (Franklin and Dyrness, 1973; Lattin, 1990; Moldenke, 1990). These and other features contribute to the structural diversity of the forests—diversity that is reflected by the diversity of arthropods found there (Lawton, 1983; Asquith et al., 1990; Parsons et al., 1991).

While these old forests have great stability over time and space, the forests are the product of several centuries of change through succession following disturbance (Lattin, 1990). Fire and wind, besides insects and diseases, are the main natural disturbances. The prolonged succession results in a continually changing mosaic of environments and habitats available to arthropods (Southwood, 1977; Southwood et al., 1979; Lawton, 1983). Over 3,400 species of arthropods have been documented from one old-growth site, the H. J. Andrews Experimental Forest (HJA). This site is a 6,400 ha old-growth Douglas-fir forest in the Willamette National Forest east of Eugene, Oregon. The HJA was established in 1948 by the U.S. Forest Service to examine the consequences of long-term habitat manipulation. It was a major component of the western Coniferous Forest Biome during the International Biological Programme in the 1960s, was named an Experimental Ecological Reserve in the 1970s, and became one of the first National Science Foundation funded, Long-Term Ecological Research Sites in 1980. Today, over 50 scientists work on the site and conduct a variety of investigations related to forest ecosystems. Included in these and past investigations are many involving arthropods. This accumulated information provides the basis for this paper.

ARTHROPODS OF OLD-GROWTH FORESTS

Insects were first collected in the Pacific Northwest between 1834 and 1836 by Dr. John Kirk Townsend, an ornithologist from Philadelphia (Hatch, 1949). Remarkably, he collected specimens of a typical oldgrowth forest insect, the beetle, *Omus dejeani*, described by the French coleopterist, Louis Reiche, in 1838. This is a flightless, nocturnal tiger beetle. A second species of *Omus*, collected during the same period

also was described by Reiche. These were the first insects to be recorded in the scientific literature from the Pacific Northwest (Hatch, 1949).

Other collectors came to the region in the vears that followed. M. H. Hatch (1949) provided an interesting account of the history of entomology in the Pacific Northwest. One collector/sportsman was Lord Walsingham from England who traveled through Oregon and California in 1871 and 1872 collecting moths while on a hunting expedition. This trip resulted in a slim volume on the plume moths of California and Oregon, complete with colored plates of most species (Walsingham, 1880). At the time, European specialists wrote most of the scientific literature based upon these early collections. As the area became populated and institutions established, there was a gradual accumulation of knowledge on the arthropods of the region. The number of species involved, and the relatively few scientists present, made progress slow. Even today, the problem of numbers of species and the shortage of specialists continues. There are still many taxa largely unstudied and unknown (Stanton and Lattin, 1989). By way of example, the collection of the Systematic Entomology Laboratory, Department of Entomology, Oregon State University, was initiated over 100 years ago. Today, the collection contains over 2,500,000 specimens with heavy emphasis on the Pacific Northwest. It contains thousands of unstudied specimens because there are no specialists for many groups.

Our knowledge of insects in forest ecosystems grew in several ways. As interest in these productive forests increased, there was increased interest in the arthropods of the forests, chiefly insects. Emphasis was on those species that were considered pests for one reason or another. Eventually this knowledge was synthesized by Keen (1952) and, more recently, by Furniss and Carolin (1977). The latter volume contains a vast amount of information on western forest insects, including many that occur beyond the region considered here. Central to the acquisition of such information were the Canadian and United States governmentbased forest services. Other major sources

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of information were the many taxonomic revisions of major taxa found in forests (e.g., wood boring beetles, sawflies, loopers, and spiders). These studies provided the backdrop to studies focussing upon arthropods found in old-growth forests in western North America. Without the previous work of literally hundreds of individuals, studies on old-growth forests would have been extremely difficult or impossible.

The international biological programme

The International Biological Programme (IBP), started in the 1960s, increased interest in ecosystem structure and function. One sub-unit of the IBP in North America was the Western Coniferous Biome. Within this group, attention was given to the structure and function of coniferous forests, including old-growth forests along the Pacific Coast. Many reports and publications resulted from these efforts, including some on arthropods (e.g., Deyrup, 1975; Mispagel and Rose, 1978). As investigations proceeded, the recognition of the role arthropods play in such ecosystems increased. Initial emphasis was more on functional group than on the species composition. As taxonomic and biological information increased, the role of some species in the systems became clarified. The variety of studies carried out provided vast numbers of specimens of many taxa that accumulated at different localities. One such site was the H. J. Andrews Experimental Forest in western Oregon.

THE H. J. ANDREWS ARTHROPOD COLLECTION

This collection had its origins in the International Biological Programme of the 1960s. The H. J. Andrews Experimental Forest was established by the U.S. Forest Service in 1948 and when the IBP was organized, the site became an important part of the Western Coniferous Biome program. Some of the forest ecosystem research at that time involved arthropods and the specimens from that era formed the basis for the present collection (Mispagel and Rose, 1978).

I joined the H. J. Andrews Research Group in 1976 and began to organize and build the collections with the cooperation of over 100 individuals. As the arthropod work expanded, many additional specimens were added (Lewis and Maser, 1981; Anderson et al., 1982; Lightfoot, 1986). Emphasis was placed on aquatic taxa, the insects associated with different plant species, and extensive collections from the litter and soil habitats (Moldenke and Fichter, 1988; Lattin and Moldenke, 1990; McIver et al., 1990; Moldenke and Lattin, 1990a, b). Canopy studies were conducted 70 m overhead and resulted in a surprising number of species (Voegtlin, 1982; Moldenke et al., 1987; Schowalter, 1989, 1990; Schowalter et al., 1986). There were studies of the fauna of early successional trees as well (Schowalter et al., 1986). The role of arthropods in the long-term decomposition of wood received special attention and many species resulted from these studies (Deyrup, 1975; Carpenter et al., 1988; Moldenke and Fichter, 1988; Schowalter et al., 1992). After a number of draft editions, the annotated list of over 3,400 species from the Andrews Forest was published (Parsons et al., 1991). This document, combined with many other papers and reports, forms the basis for our present knowledge. We owe a debt of gratitude to the many people who contributed to that volume.

During the completion of the annotated list of arthropods for the H. J. Andrews Forest, many interesting details emerged. A few of these are cited below.

- Although they are considered quite mesic forests, a small, but distinct xeric arthropod fauna is present. More common are warm-dry adapted species found chiefly to the south, less common are the colddry adapted species whose distribution is northern. Monitoring the populations of warm-dry species should be of value in detecting response to Global Climate Change (Table 1).
- A rich and diverse litter/soil arthropod fauna, regularly containing 250 species per m². This fauna plays an important role in nutrient cycling (Moldenke, 1990).
- A very distinct fauna of flightless species, chiefly beetles but including some of the true bugs. These are species of low vagility and certain to be impacted by forest fragmentation (Lattin, 1990) (Table 1).

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- A small but dis enous species est. This contra non-indigenou 1).
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- A substantial number of arthropods associated with the abundant coarse woody debris (Schowalter *et al.*, 1992). New (1984), Warren and Key (1991), and Peterken (1992) indicated that some elements of this fauna are entirely dependent upon adequate amounts of large, old wood and are likely targets for conservation (Table 1).
- A small but distinct number of non-indigenous species (56 of 3,400) on the forest. This contrasts to 41 of 480 species of non-indigenous plants on the site (Table 1).
- While these old-growth forests may appear rather homogeneous from a distance, they contain a mosaic of habitats. Approximately half of the species of butterflies known to occur in Oregon are found on the H.J.A. For the true bugs (Hemiptera: Heteroptera), 206 species out of 659 are found there and 134 genera of the 260 found in the state.

Conservation of Arthropods of Old-Growth Forests

Our knowledge of arthropod diversity in old-growth forests is limited even though we know such information is highly desirable and essential if we are to develop conservation strategies. So few detailed studies have been made at different localities that we are forced to extrapolate from the very few sites where we have some knowledge. Additional studies are urgently needed while some undisturbed forests remain (Morrison, 1988; Lattin and Moldenke, 1992).

The Problem

Much of our specific knowledge about the arthropods of old-growth forests comes from the information gathered on the H. J. Andrews Experimental Forest in western Oregon (Mispagel and Rose, 1978; Asquith *et al.*, 1990; McIver *et al.*, 1990; Lattin and Moldenke, 1990; Moldenke and Lattin, 1990 *a*, *b*; Parsons *et al.*, 1991) where perhaps 50–60 per cent of the fauna is known. There is, of course, a considerable literature on taxa found in forests (*e.g.*, Prentice, 1962; Furniss and Carolin, 1977; Danks, 1979; Bright, 1987; Danks and Foottit, 1989) but

most such information is not site-specific enough to know whether it applies to oldgrowth forests. Since it is unrealistic to assume that there will be massive efforts to acquire such information for all taxa, it seems more reasonable to identify representatives of key groups that belong to different functional guilds or occur in habitats unique to these forests (e.g., coarse woody debris) for study, collection, and sampling (Goldsmith, 1991). Some of the important terrestrial functional groups include: pollinators, foliage feeders, xylophages, litter and fungal comminutors, root feeders, predators, and parasitoids. There are appropriate aquatic counter groups. Some examples of proposed efforts follow:

Arthropod diversity and forest health

A national program has been established to monitor the health of forests under the direction of the United States Forest Service and in cooperation with the Environmental Protection Agency. The goals of the Forest Health Monitoring Program are "to detect changes and trends in forest conditions and to report and interpret these changes at a multistate level." Fourteen states have or are developing forest health monitoring programs. A plan for Oregon is being developed while that for California is nearing completion. This nation-wide program is superimposed upon the EPA-EMAP grid established several years ago. Approximately 4,500 of the 12,600 plots established are considered forested. While pest species will receive special attention, we feel that the inclusion of representatives of different functional groups will provide valuable information about the health of forested ecosystems. At the same time, more widespread knowledge about the distribution and abundance of forest arthropods will result, making conservation efforts more effective. We are developing sampling protocols to deal with selected taxa found in forested ecosystems (Table 2). The numbers of species and individuals of each species are high for arthropods. These very numbers create logistical problems when large-scale sampling efforts occur. Still, the fine resolution provided by these numbers makes the effort worthwhile.

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TABLE 1. Examples of old-growth forest arthropods.

Warm xeric insects Hemiptera: Heteroptera Berytidae: Acanthophysa echinata Uhler Lygaeidae: Malezonotus obrieni Ashlock Thylochromus nitidulus Barber Miridae: Macrotylus essigi Ban Duzee Macrotylus multipunctatus Van Duzee Cold xeric insects Hemiptera: Heteroptera Scutelleridae: Vanduzeeina borealis californica Van Duzee Tingidae: Acalypta lillianus Torre-Bueno Flightless insects Orthoptera Acrididae: Boonacris alticola Rehn and Randall Gryllacrididae: Pristoceutophilus spp. Tropidischia xanthostoma (Scudder) Hemiptera: Heteroptera Lygaeidae: Plinthisus longisetosus Barber Tingidae: Acalypta saundersi (Downes) Coleoptera Carabidae: Cychrus tuberculatus Harris Metrius contractus Eschscholtz Promecognathus laevissimus Dejean Zacotus matthewsi LeConte Cicindelidae: Omus dejeani Reiche Curculionidae: Lobosoma horridum Mannerheim Mecoptera Boreidae: Boreus sp. Diptera Tipulidae: Chionea sp. Coarse woody debris arthropods Isopoda Ligidiidae: Ligidium gracile Dang Insecta Isoptera Hodotermitidae: Zootermopsis angusticollis (Hagen) Coleoptera Buprestidae: Buprestis aurulenta Linnaeus Cerambycidae: Leptura obliterata Haldeman Lucanidae: Playcerus oregonensis Westwood Platypodidae: Platypus wilsoni Swaine Scolytidae: Dendroctonus pseutotsugae Hopkins Trogositidae: Ostoma ferruginea (Linnaeus) Hymenoptera

Formidicae: Camponotus spp. Siricidae: Urocerus albicornis (Fabricius) Diptera

Xylophagidae: Xylophagus cinctus DeGeer

Non-indigenous insects

Hemiptera: Heteroptera

Lygaeidae: Megalonotus sabulicolus (Thomson) Stygnocoris sabulosus (Schilling) Miridae: Megaloceroea recticornis (Geoffroy) Stenotus binotatus (Fabricius) Coleoptera Curculionidae: Otion Otion Siton Scarabaeidae: Aphoe

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The National Park Inventory and mor

While not direc National Park Serv tory and monitor Patterson, 1992). to a 1988 Manage "assemble baselin ing the natural res ship and will mo to detect or prediwill generate infoi tebrate conservaincluded in such o see that indeed th

TABLE 2. Exa

Organism

Acarina Oribatid mites

Diplopoda Millipedes Collembola Springtails

Insecta Hemiptera: Heter Seed bugs (Lyg:

Plant bugs (Mi

Coleoptera Ground beetles

Bark beetles (S

Hymenoptera Sawflies (Sym1 Lepidoptera Caterpillars

Adults

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TABLE 1. Continued.

Coleoptera	Co	leo	pter	ra
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Curculionidae: Otiorhynchus ovatus (Linnaeus) Otiorhynchus sulcatus (Fabricius) Sitona lineatus (Linnaeus) Scarabaeidae: Aphodius fossor Linnaeus

The National Park Service: Inventory and monitoring plan

While not directed at forests alone, the National Park Service is initiating an inventory and monitoring program (Rugh and Patterson, 1992). This effort is in response to a 1988 Management Policy directive to "assemble baseline inventory data describing the natural resources under its stewardship and will monitor those resources ... to detect or predict changes." These efforts will generate information of value to invertebrate conservation provided they are included in such efforts. We are working to see that indeed they are included. Stolhgren (1992) has reviewed the state of inventories in southwestern U.S. National Parks and included both aquatic and terrestrial invertebrates. The present level of knowledge about the invertebrates was quite low. We initiated a similar idea with Acadia National Park a few years ago and it now appears it may become a reality.

Northern spotted owl conservation

There have been extensive investigations on the northern spotted owl as an indicator of old-growth forests. The threatened status of the bird throughout much of its range has resulted in the proposal to establish Habitat

Organism	Functional role	Sampling method
Acarina		
Oribatid mites	fungal, litter feeders, predators	high-gradient extractors
Diplopoda		
Millipedes	litter communitors	pit-fall traps
Collembola		
Springtails	litter/soil organic matter feeders	Berlese funnels, high-gradient extractors
Insecta		
Hemiptera: Heteroptera		
Seed bugs (Lygaeidae)	seed feeders on ground	pit-fall traps
Plant bugs (Miridae)	foliage feeders, predators	beating foliage
Coleoptera	•	
Ground beetles (Carabidae)	Predators, seed feeders	pit-fall traps
Bark beetles (Scolytidae)	xylophagous	pheromone, intercept traps
Hymenoptera		• •
Sawflies (Symphyta)	foliage feeders	malaise traps
Lepidoptera		
Caterpillars	foliage feeders	beating, branch clipping
Adults	nectar feeders	blacklight traps

TABLE 2. Examples of arthropod taxa for monitoring with functional roles and sampling methods.

Conservation Areas (HCAs) for its conservation. We have provided information on potentially sensitive arthropod species likely to benefit from the establishment of these HCAs (Lattin and Moldenke, 1992) (Table 3). As mentioned several times, these recommendations represented extrapolation from information from the H. J. Andrews Experimental Forest. We will feel more comfortable when sources from other localities are available.

The Ministry of Forestry, British Columbia

We supplied information to the Ministry of Forestry, Province of British Columbia on selected species of arthropods that are likely to be of conservation value (Lattin and Moldenke, 1992) (Table 3). This was in response to a request for information that could be considered in decisions about the types of forests for inclusion in a series of old-growth reserves. Naturally, field work will be required to even determine the presence of such species on the proposed reserve. This request is similar to others which we have received to extrapolate our site-specific information to other localities.

Conservation of Pacific Yew (Taxus brevifolia)

I am completing a monograph on the arthropods associated with Taxus throughout the world, including the Pacific Yew, Taxus brevifolia. The great interest in Taxus species as a source of taxol, a cancer drug, has vaulted this obscure understory tree into international prominence. Virtually nothing was known about arthropods on any species of Taxus except on those species widely used as ornamentals, chiefly Taxus baccata and T. cuspidata. Conservation efforts for Taxus brevifolia naturally will benefit the few associated arthropods found on it. The threat to the tree, and perhaps to its arthropod fauna, is likely to be greatest from non-indigenous arthropod species moving into natural stands from cultivars. The establishment of yew plantations for the production of foliage and stems for taxol production may create populations of arthropods able to move out into undisturbed forested ecosystems as well. Thus,

the location of such plantations should be selected with care.

Importation of raw logs

The decline in the availability of logs for mills in the west has increased the interest in importing raw logs from other countries. It has not stopped the export of raw logs from our region, however. Over the past two years, there has been intense interest in bringing in raw logs from Siberia, New Zealand, and Chile (Anonymous, 1991, 1992). The present lack of adequate quarantine regulations for large-scale log importations has intensified the efforts to bring in such material. Only now are comprehensive regulations under public review that will provide some protection against the unintentional introduction of insects and pathogens. The risks are very high. This has been documented extensively for the Siberian logs (Anon., 1991), less so for New Zealand logs (Anon., 1992) and is presently underway for Chilean log importation. While this is not *directly* related to conservation, one has only to look at Hawaii to see what impact nonindigenous species have had upon the local biota of all types. One should examine, too, the forests of northeastern North America to see the damage that has occurred from only a few diseases and insects, a forest changed forever. In spite of statements to the contrary, the large-scale importation of raw logs without absolute certainty of pestfree logs poses an enormous risk to the forests of the west and to the native arthropods living in them.

THE FUTURE

Many activities will influence the successful conservation of arthropods in oldgrowth forests, not the least of which will be the achievement of a balance between forest harvest and conservation. This balance is a highly politicized topic that became an issue in the 1992 presidential campaign. A "forest summit" is planned for 1993 to try to resolve the conflicts. A major goal is to agree upon a level of sustainable harvest. Such action will create the template for any effort in forest arthropod conservation (Southwood, 1977; New, 1984; Wilcove *et al.*, 1986; Warren and Key, 1991; Peterken, T _____0

Diplopoda Xestodermidae: Harpaphe haydeni.

Insecta Orthoptera Acrididae: Boonacris altico. Gryllacrididae: Pristoceutophilu. Pristoceutophilu Pristoceutophilu Tropidischia xa.

Hemiptera: Heteror Enicocephalidae: Boreostolus am

> Lygaeidae: Plinthisus longi Thylochromus

Miridae: Phytocoris nobi Pithanus maer

Polymerus cast. Scutelleridae:

Vanduzeeina b Tingidae: Acalypta lillian Acalypta sauna

Coleoptera Carabidae: Cychrus tuberc Metrius contra Promecognath. Zacotus matth

Cicindelidae: Omus dejeani

Curculionidae: Lobosoma hor

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OLD-GROWTH FOREST ARTHROPOD CONSERVATION

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TABLE 3. Examples of old-growth arthropods of conservation value.

Organism	References
Diplopoda	
Xestodermidae: Harpaphe haydeniana haydeniana (Wood)	1
Insecta	
Orthoptera	
Acrididae: Boonacris alticola Rehn and Randall	1, 2, 3
Gryllacrididae: Pristoceutophilus celatus (Scudder) Pristoceutophilus cercalis Caudell Pristoceutophilus sargentae Gurney Tropidischia xanthostoma (Scudder)	1, 2, 3 1, 2, 3 1, 2, 3 1, 2, 3 1, 2, 3
Hemiptera: Heteroptera	
Enicocephalidae: Boreostolus americanus Wygodzinsky and Stys	1, 2
Lygaeidae: Plinthisus longisetosus Barber Thylochromus nitidulus Barber	1, 2 1, 2
Miridae: Phytocoris nobilis Stonedahl Pithanus maerkeli (Herrich-Schaeffer) Polymerus castilleja Schwartz	1, 2 1, 2 1, 2
Scutelleridae: Vanduzeeina borealis californica Van Duzee	1, 2
Tingidae: Acalypta lillianus Torre-Bueno Acalypta saundersi (Downes)	1, 2 1, 2
Coleoptera	
Carabidae: Cychrus tuberculatus Harris Metrius contractus Eschscholtz Promecognathus laevissimus DeJean Zacotus matthewsi LeConte	1, 2 1, 2 1, 2 1, 2 1, 2
Cicindelidae: Omus dejeani Reiche	1, 2
Curculionidae: Lobosoma horridum Mannerheim	1, 2

For other details see references, viz., 1: Parsons et al., 1991; 2: Lattin and Moldenke, 1992; 3: Lightfoot, 1986.

1992; Pimentel et al., 1992), especially on public land.

Effective arthropod conservation in oldgrowth forest will require better knowledge of (1) the fauna, (2) species distribution throughout the region, (3) habitat requirements, (4) ecological functions of at least the key taxa, (5) the community structure and dynamics of the fauna, (6) the impact of different disturbance regimes upon the special habitats and the associated fauna, (7) appropriate and adequate sampling and monitoring protocols, (8) and an adequate systematic knowledge base of the appropriate taxa in order to allow intelligent decisions to be made (Wilson, 1985, 1989).

ACKNOWLEDGMENTS

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