

Arthropod Diversity In Northwest Old-Growth Forests

John D. Lattin

Old-growth coniferous forests of the Pacific Northwest are a paradox: they are characterized by long-term persistence and stability but at the same time are the product of two or more centuries of change. Jerry F. Franklin, a professor of ecosystem analysis at the University of Washington's College of Forest Resources, refers to these forests as Douglas-fir / western hemlock forests, but they are not pure stands, and typically contain an assortment of other tree, shrub, and forb species. The precise assemblage varies with the moisture gradient, soil type, site aspect, and disturbance history. The result is a mosaic of diverse plant and animal communities, an ecosystem that is complex in structure, organization, and function.

Arthropods are an integral part of this system—from the deep litter-soil layer and the extensive deposits of coarse woody debris to the tree canopy 70 meters above the ground. On the H. J. Andrews Experimental Forest (a 6,400 hectare, Long-Term Ecological Research site on the west slope of the Oregon Cascade Mountains), we have found more than 3,400 species.

To date, all primary habitats of the forest have been sampled: high elevation meadows (about 1,500 meters), rocky ridges, streams, springs, and

disturbed areas. We estimate that only about half of the arthropod species present on the site have been collected. By way of comparison, there are 143 vertebrate species and 460 vascular plant species on the site. Currently, the arthropods represent about 85 percent of all the species found in these three categories. Few arthropods appear to be found exclusively on the old-growth portions of the H. J. Andrews Forest, but many species occur there in greatest abundance, and we still have much to learn about their distribution.

If you examine biological diversity along a succession of communities whose later states include the old-growth forests, you see an increase in plant species richness through time, from bare ground, through the forb and shrub stage, to the time when young trees emerge above the surrounding vegetation and arthropod richness responds accordingly. Below ground the story is similar, but species richness develops more slowly because it takes much longer for the litter layer to develop. When the trees become large enough and the canopy closes (between 20 and 40 years), plant diversity declines because much of the understory is shaded out—and arthropod diversity generally declines as



Recent clearcuts of Douglas fir interior forest. The area shown is in the western foothills of the Oregon Cascade Mountains. Photograph by Spencer B. Beebe.

measuring the well-being of managed and highly perturbed systems, especially as we begin the next-century task of ecosystem restoration.

As the indicators of ecosystem health, little things will have special importance. Signs of ecosystem stress may first be observed in populations of microorganisms in lake and stream bottoms and soils. Species may disappear, and, after these structural changes occur, nutrient cycling through the system could be modified.

It may be difficult to convince a large public that invertebrates are getting too little attention on the growing conservation agenda. Charis-

matic mega vertebrates will probably still drive much of the public's interest. Some might argue that myriad invertebrates will be conserved where spotted owls are protected. But as conservationists move towards a more whole systems / whole earth approach, to the extent that invertebrates can be shown to help point the way toward priority ecosystems and ecosystem health, the brave voices of the Xerces Society will be heard worldwide.

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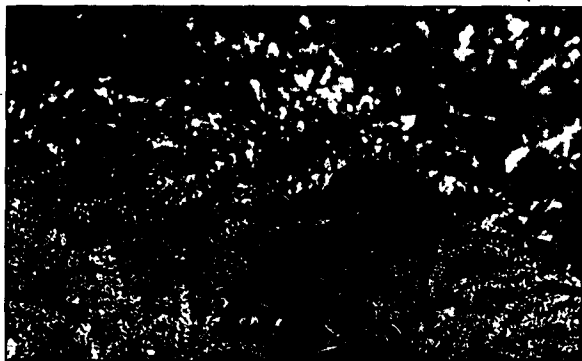
well. But in the litter layer beneath the trees, which is still developing, arthropod diversity continues to increase. When the stand approaches early old-growth (between 150 and 200 years), natural thinning occurs and openings appear, allowing further development of the understory. This adds to the structural complexity of the forest, and, in turn, arthropod diversity increases.

David Voegtlin (now with the Illinois Natural History Survey) recovered more than 500 species of arthropods from the canopy of three old-growth Douglas-fir trees whose ages were estimated to be about 450 years. Many of these species are found not only in the canopy, but elsewhere in the forest. On the ground, the litter layer becomes deep and complex as the forest matures. The diversity of arthropods in the litter layer approaches the greatest number to be found anywhere in the Northern Hemisphere—sometimes reaching 250 species per square meter. Andrew Moldenke and

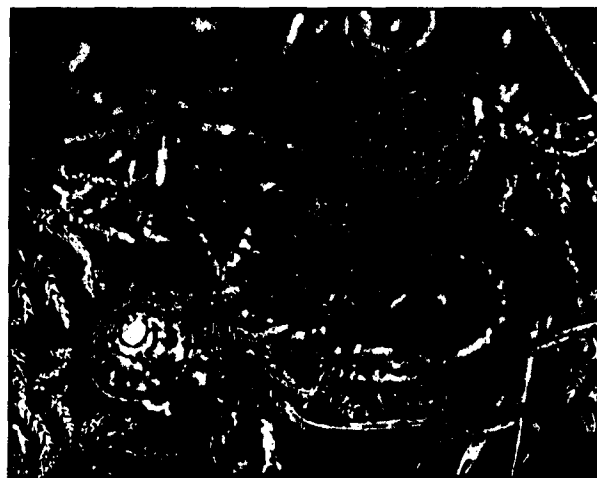
Becky Fichter of Oregon State University have reported densities of oribatid mites as high as 120,000 per square meter in the H. J. Andrews Forest. More than 90 genera have been collected there. (See page 11 of this issue.)

Once the forest matures, its persistence is determined largely by the disturbances to which it is subjected. According to Franklin, fire is the primary natural disturbance, wind a secondary factor. While smaller understory wildfires are not uncommon in these forests, only catastrophic stand-replacement fires, which occur approximately every 400 years, reset the system and re-initiate secondary succession. Because not all of the old forest burns, the resulting landscape is a mosaic of different-aged stands. This intricate environment is reflected by the arthropod diversity, perhaps as great as 8,000 species.

The long persistence of some old-growth forest stands and the habitats they contain have given rise to an interesting faunal component, flightless



A snail-feeding ground beetle of the genus Scaphinotus. Photographed in the H. J. Andrews Experimental Forest by Trygve Steen.



Cychrus tuberculatus, a flightless ground beetle, is a typical inhabitant of the mature forest. It is a specialized predator of terrestrial molluscs. Photographed in the H. J. Andrews Experimental Forest by Andrew Moldenke.

arthropod species. Some of these species probably predate the dominance of the present old-growth forests, and may extend back five million years. The dynamic aspects of succession, even over the long term, require that arthropods have some degree of mobility, but the persistence and stability of the climax stage allows accumulation of arthropod species whose ability to disperse is limited. In an article in the September 1989 issue of *Scientific American*, Xerces Society President E.O. Wilson pointed out that the persistence of an environment may allow development of diversity through species accumulation. However, such assemblages are not necessarily stable and robust enough to resist various types of disturbance.

We have found insect species in old-growth forests of the Pacific North-

west and other habitats whose ability to fly has been lost through wing reduction or wing loss; more such species certainly exist. Loss of flight in insects is often associated with habitats that have remained stable through time. The region that contains the old-growth forests appears to be an area of such stability, and the arthropod fauna reflects this in the number of flightless species present. Further, many normally wingless arthropod groups (spiders, mites, millipedes, and springtails, for example) are richly represented in these forests, especially in the litter-soil layer.

An example of an arthropod group encountered in the forest is the true bug family Tingidae (lacebugs), whose members are plant feeders and who often show bizarre body shapes. The family contains some flightless

species. The genus *Acalypta* contains moss-feeding species found throughout the Northern Hemisphere; three occur in the H. J. Andrews Forest.

Acalypta lillianis, apparently a relict of colder times, is found in mosses growing on the cool, high, rocky ridges. While the only specimen collected from the forest is flightless, winged individuals of this species are known to occur elsewhere. The second species, *A. mera*, is found at lower elevations in mosses growing on the ground in more open sites. It is usually flightless, but about five percent of the individuals of both sexes are fully winged and able to disperse should the necessity arise. The third species, *Acalypta saundersi*, has been found only in the flightless state. It appears to occur in mosses in truly mature forests, its wing reduction seemingly a response to habitat stability. A group of species of *Acalypta* that closely resembles *saundersi* and that are also flightless are found in other areas of long-term stability—the Ozark and Great Smoky Mountains in the United States, the Mexican Plateau, parts of Europe, and parts of eastern Asia, including Japan. No fully winged individuals of these species have ever been collected.

Other insect orders found in this forest have flightless species, such as those found among the Hemiptera (true bugs). The beetles are well represented: 824 species collected to date, and some of these are flightless. Snails and slugs are common inhabitants of forests, and a group of flightless ground beetles (Carabidae), including *Cychrus tuberculatus* and several species of *Scaphinotus*, are specialized

predators of these terrestrial molluscs. Besides beetles, other orders of insects contain flightless species found in the forest, and we will certainly discover more.

The old-growth forests of the Pacific Northwest, with trees of enormous height and mass, diverse shrubs and forbs, and large accumulations of coarse, woody debris, provide many habitats. The highly varied and deep litter and soils supply resources for a diverse and characteristic fauna. Meadows, openings, ridges, streams, and springs add to the variety. The number of arthropod species conservatively represents more than three-quarters of all species of higher life forms (plants, invertebrates, and vertebrates) found there. Persistence of the later successional stage has provided habitats not found in earlier stages, whose durations are usually brief. What we see today in the fauna is, in part, the product of long-term stability, even though the persistent components of the habitats are themselves the product of change. In the midst of the controversy swirling around old-growth forests of the Pacific Northwest, it is important to remember that there is more to the forest than the trees.

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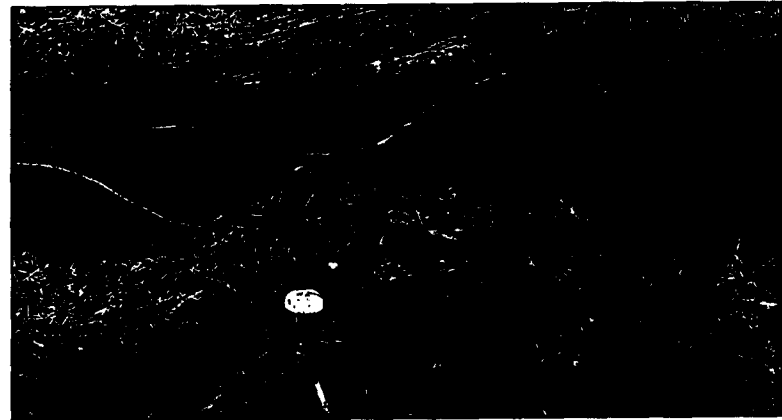
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One Hundred Twenty Thousand Little Legs

Andrew Moldenke

Nowhere are the critical roles of insects and other invertebrates easier to understand, yet more poorly investigated, than in forest soil. Proper growth of forest trees depends on receiving appropriate nutrient levels and water from the roots. The metabolic activity of fungi and bacteria liberate nutrients through litter decomposition and chemical transformations of the soil. Experiments have shown that insects and other microarthropods control these rates.

No one has ever counted the number of kinds of bacteria and fungi under a single tree in the forest; no ecologist knows just how many chemical transformation processes are necessary for the full recycling of nutrients. We do know, however, that in undisturbed forests there are 200 to 250 species of invertebrates per square meter of forest soil in the Pacific Northwest—probably literally thousands of kinds in all the microhabitats of a square mile of forest. There are 100,000 to



*Dead logs are crucial for forest health. The final step in nutrient recycling is uptake of nutrients by mycorrhizal fungi, which pass nutrients to the trees in exchange for photosynthetic sugar pumped to the roots. Here the mycorrhizal fungus *Russula emetica* is attached to the roots of western hemlock. Photograph © 1990 by Gary Braasch.*

