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Rethinking Insects

What Would an Ecosystem Approach Look Like?

by Timothy D. Schowalter with Jay Withgott

TWENTY-SIX YEARS AGO, Forest Service entomologists William Mattson and Norton Addy published a paper in *Science* that should have revolutionized the way land managers approached insects.

Mattson and Addy showed that low to moderate levels of herbivory do not harm most plants and contended that grazing can benefit both individual plants and plant communities. They demonstrated that caterpillars that defoliate trees in periodic outbreaks can harm trees in some years and help them in others. Outbreaks usually begin in stands that are in poor condition to begin with, they found, and can lead to healthier systems. Finally, they argued that insects can act as regulators, helping to stabilize ecosystems through time by lessening variation in primary productivity. (1)

In the quarter-century since, evidence for these assertions has grown, yet many managers have taken little notice. Approaches to insects today remain similar to the "us against them" techniques of pest control we were using back then. True, we've shifted somewhat from chemical to biological controls and recently to control by genetic engineering. But many managers and policymakers have not moved beyond a paradigm that views insects as unconditionally threatening forces.

Traditional employment patterns and discipline boundaries have helped to maintain this paradigm. Historically, biologists trained in entomology found jobs much more readily in industry or at government agencies dealing with pest control. Meanwhile, government agencies that manage forests and endangered species are loaded with biologists specializing in vertebrates and plants but are sorely lacking in entomologists. In part because of this imbalance, the entomological point of view has all too often been

Moderate levels of herbivory can benefit plants and communities and help return systems that are out of balance to a healthier state.

excluded from applied conservation biology.

So what would an ecosystem approach to the most abundant and diverse animals on Earth look like? For one thing, insects would emerge as major architects of the plant world in terms of both structure and function. We would recognize their ability to regulate plant populations and community dynamics. For example, it turns out that herbivory isn't all bad news. At the community level, outbreaks of plant-eating insects can help keep a system healthy. At the individual level, plants can rebound from being eaten, often fully compensating for their losses.

The challenge for conservation-minded managers is determining under what circumstances plants can take care of themselves versus knowing when to fall back on traditional methods of pest control.

Insects as Architects of the Landscape

First pitch begins to ooze from the bark. The needles turn yellow, then red. By the time the pine has lost its foliage, the beetles have spread to other trees, tunneling into their bark, their galleries and pathogenic fungi girdling their trunks. An infestation of southern pine beetles *(Dendroctonus frontalis)* has reached outbreak proportions. A disaster for the forest? Not necessarily.

Historically, pine beetles focused on small, dense patches of pines that occurred infrequently in open forests maintained by periodic fire. The beetles eliminated the weaker trees and reduced competition among survivors. In the process, they helped to engineer habitat conducive to the endangered red-cockaded woodpecker *(Picoides borealis)* and other species adapted to pre-settlement forest conditions. Since the beetles' pheromones only carry effectively about six meters, naturally open stands of mature pines were protected against widescale beetle outbreaks.

This is no longer the case in today's denser stands. Fire suppression in pine forests allows seedlings, especially shade-tolerant, fire-intolerant species, to grow thickly under mature pines. This turns what should be an open habitat into a dense and thicketed forest—and produces trees stressed by competition for water and nutrients. The dense forest structure allows pine beetles to hopscotch from one weakened tree to another, across entire stands.

In other words, the problem is not the beetles per se but rather the overcrowding of host plants caused by fire suppression or other factors. We have unintentionally created a forest that no longer works "ecologically." To return to historic conditions—i.e., an ecological balance between host trees and insects—we may need to weather short-term losses to achieve longer-term gains. Where fire risks are acceptable, insect outbreaks can be corrective over the long term. Defoliators and other insects reduce the density of trees and cull weak individuals. This relieves stress on the survivors and improves the overall condition of the forest. In many cases, the prime beneficiaries are non-eaten species that dominated the forest prior to the human-aided rise of fire-intolerant species.

In those cases where we cannot afford the fire risks entailed in letting an outbreak run its course, we may need to thin the understory such that we restore forest structures that are resistant to fire, insects, and disease. Similarly, we should pay attention to the scale of a distur-

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bance and whether there are opportunities for species to recolonize. When rare and/or endemic species are threatened by an outbreak, a more conservative approach may be warranted.

In Sequoia and Kings Canyon National Parks in California, scientists and managers decided to allow a recent outbreak of the Douglas fir tussock moth to run its course over two years. Early indications are that this experiment in progressive management has reduced the density of invasive white fir growing in the understory beneath the pines and sequoias. Although the abundance of fir snags and litter temporarily increases the likelihood of fire, the decomposition of this material should eventually help return the forest to its historic condition.

In addition to thinning, insects can also shape forest landscapes in a variety of other ways, sometimes more subtle, but no less profound. For example, the outcomes of insect attacks may vary with environmental conditions. In western North American forests, insects can retard or advance succession, depending on moisture levels. In moist situations, where fire is rare and fire-intolerant species crowd pines, mountain pine beetles *(Dendroctonus ponderosae)* advance succession by killing pines and making room for shade-tolerant, fire-intolerant firs. But in dry conditions, fir engraver beetles *(Scolytus ventralis)* and other insects focus their diet on water-stressed firs. These dead firs provide fuel for the next fire, creating positive feedback that favors pine dominance. It seems reasonable to suppose that landscape-level changes in canopy cover that are driven by insects may even influence regional climate; this now stands as a promising area for future research.

Insects also can help drive patterns of plant distribution. They limit the distribution of some shrubs and herbs to habitats in which the plants can escape or tolerate insects. In tropical forests, seed-feeding insects limit the distribution of tree species and affect the rate at which these species can recolonize openings (2). Shea and colleagues found that germination of several legume species in Western Australia was increased by ants moving seeds to nests where they were protected from fire (3).

Regardless of their effects on particular species, insects can invigorate plant communities. Opened canopies let in more light and allow more rain to reach the forest floor. Fewer leaves on the trees and fewer trees in the forest can significantly increase soil water content and streamflow, often for years following tree mortality (4,5). This dynamic may alleviate the water stress that triggered the insect outbreak in the first place.

Insect outbreaks also produce very large amounts of nutrient-rich material—insect frass, molts, bodies, and partially eaten foliage—that falls as litter. Along with the nutrients that leach from damaged leaves, these all stimulate decomposition in the soil.

The species that stage outbreaks showcase how insects can wield powerful influence on the ecosystems of which they're a part. Rather than combat them as pests, we can view their population swings as indicators of changing conditions in the environment and can seek to address the underlying causes.

Because they usually result from unnatural environmental conditions, outbreaks demonstrate how our own management practices may sometimes be to blame. In addition to fire suppression, monocultures tend to aid and abet the irruption of pests. The southern pine beetle, for instance, has benefited from our replacement of longleaf *(Pinus palustris)* and shortleaf *(P. echinata)* pine with faster-growing loblolly *(P. taeda)* stands. As many farmers are finding in their fields, monocultures are more susceptible

Further Reading:

Coleman, D.C. and P. Hendrix (eds.). 2000. Invertebrates as Webmasters in Ecosystems. CABI Publishing, Wallingford, Oxon, U.K.

Ecosystem Services Provided by Insects

Because insects provide vital ecological services, they are crucial to recovery and restoration of degraded ecosystems. Understanding the ways insects can alter ecosystem conditions can help land managers better predict the results of their own action (or inaction). Consider five major ways in which insects influence their environments:

Decomposers. Insects stimulate and accelerate breakdown of organic materials by fungi, bacteria, and other organisms, enhancing soil fertility and plant growth. Burrowing soil insects mix organic and inorganic material, increasing soil porosity and water-holding capacity. Ants and termites move deeply buried soil to the surface and concentrate organic matter in their nests, which can occupy up to 30 percent of soil volume to depths of 3-4 meters, over up to 10 percent of landscape surface area.

Herbivores. Insects eat plants, sometimes causing substantial damage and influencing which plants grow where. However, the effects of herbivory can be complex and difficult to predict. Growing evidence shows that plants can compensate for being eaten. Some pests decried by farmers and foresters may improve the health and long-term productivity of the plants they attack.

Food Source. We generally pay more attention to vertebrates that eat insects than to the insects themselves. For example, major freshwater fisheries, especially those of salmonids, are supported largely or entirely by aquatic insects. The effects of management practices that maintain high insect numbers and diversity will extend up the food chain, supporting large or healthy populations of vertebrates.

Dispersal Agents. Insects disperse seeds, transmit viruses, carry fungal spores, and even transport other invertebrates from place to place, guiding their spatial distribution. Ants are important seed dispersers for many species; some plants produce specialized nutritive bodies attached to seeds to attract ants. Seeds brought to ant nests may escape predation by rodents or may germinate among rich nutrient concentrations.

Pollinators. Pollinators can be a limiting resource for plants. Their movements help to determine the distribution of a plant's progeny. Such dependencies are magnified when species-specificity is tight. Because pollinators often don't fly between distant habitat fragments, ecologists should consider plant-pollinator relationships when restoring native plant communities.

A WINDOW ON UNDER-GROUND ECOSTYSTEMS

"Each time you take a step in a mature Oregon forest, your foot is being supported on the backs of 16,000 invertebrates."

- Andrew Moldenke

We often select habitat-specific plants, large vertebrates, and top predators as indicator species to judge the well-being of ecosystems. But sometimes a bottom-up approach using insects may be easier, cheaper, and more effective.

Soil arthropods can provide a remarkable view into one of the least known ecosystems—the one beneath our feet. Dr. Andrew Moldenke of Oregon State University is looking at the potential for using arthropods as "biological probes."

In natural forest communities there are more than 200 species of arthropod per square yard of soil, and usually more than 200,000 individuals. However, in forest land converted to row-crop agriculture in Oregon, the soil supports only a few dozen species—if you are lucky—and less than 30,000 individuals.

Simple surveys of soil invertebrate numbers and diversity can provide a rough estimate of soil quality. You do not have to be or hire a trained entomologist to do this type of work. With something as simple as a margarine container filled with soapy liquid, you can capture crawling insects, or you can filter insects from leaf litter with an inverted funnel, a jar of alcohol, and a lamp.

Even for whole forest stands, monitoring can be as simple as shaking out insects from samples of leaves. With such methods, you can get a pretty good idea of the health of the soil and plants of interest—as well as counts of any "pests," natural enemies of the pests, and introduced biocontrol agents. Likewise, you can test how different treatments or land practices are affecting a system.

For the trained expert, arthropod surveys can be better predictors of soil quality than standard chemical tests, which do not reflect important factors such as compaction and nutrient cycling. For example, soil arthropods can reveal history cryptic to the human eye. Moldenke has found that on Oregon sites clearcut 40 years ago, soil invertebrate populations reveal which areas were burned for site preparation and which were not—despite the fact that the two areas appear identical. Burned sites bear a legacy of reduced arthropod abundance and diversity for many decades, giving us a hint of potential future uses for these "biological probes."

For more information: *www.orst.edu/dept/entomology/moldenka*

to catastrophic spread of insects than are mixed stands. In farm and forest alike, traditional modes of management involving monocultures and fire suppression encourage insects to become nuisances. The pests that plague us are all too often of our own making.

Being Eaten Isn't All Bad

While plant communities may sometimes benefit from herbivory, research is showing that even on the level of the individual, plants often can compensate for being partially eaten. Massive outbreaks like those discussed above are the exception. Most cases of insects feeding on plants are chronic and moderate. Insect herbivory levels in nature are generally low, usually <20 percent of annual primary productivity in temperate forests and grasslands. Such levels appear not to harm most plants as long as they have adequate nutrition to compensate by inducing chemical defenses or putting on new growth. Some studies suggest herbivory levels as high as 40-50 percent make little or no difference to plant growth and survival (6). Under moderate herbivory, therefore, we would be wise not to invest money and time in battling insect "pests" with costly controls.

Not all herbivory occurs at moderate levels, however. Some insect outbreaks may strip plants of 100 percent of their yearly output. Insects also can vector plant diseases that greatly increase plant injury and mortality. This is the level of destruct-ion that gives farmers nightmares and keeps managers concerned about spruce budworm awake at night. However, even in cases of massive defoliation, there are often silver linings that managers routinely overlook.

Herbivory can induce changes in a plant's physiology, spurring growth and stimulating nutrients to redistribute themselves toward leaves, buds, and flowers. Results from aquatic systems and later from grasslands led researchers in the 1980s to propose the "herbivore optimization hypothesis" and to model "optimum grazing intensities" to pinpoint levels of herbivory that would maximize plant growth. (7) In grasslands, dead matter accumulates and limits light penetration and photosynthesis, effectively smothering new shoots and depressing growth. But

The more an individual tree is defoliated by the tussock moth, the more it may compensate afterwards.

moderate grazing by insects and other animals can prevent this inhibition and spur productivity. Some research even suggests that certain plants respond favorably to the saliva of grasshoppers and grazing mammals. (8)

We now are beginning to see similar patterns in forests. Red oak *(Quercus rubra)* seedlings, for instance, greatly increase their growth following defoliation, at both low and high soil nitrogen levels (though they maintain fast growth longer with high nitrogen concentrations) (9). Experimental needle removal from Scots pine *(Pinus sylvestris)* showed that while 100 percent defoliation depressed growth, 50 percent did not (10). With Douglas fir *(Pseudotsuga menziesii)*, the more an individual tree is defoliated by the tussock moth, the more it compensates afterwards; those trees most eaten increase their growth the most later (11).

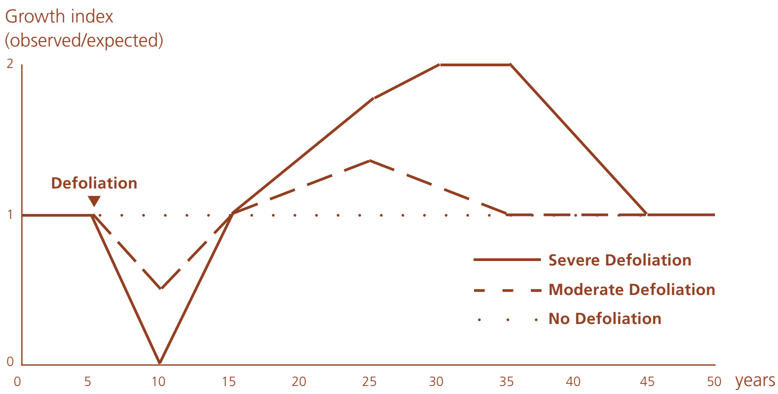
The key here is patience. Researchers waited three to four years after outbreaks to detect this pattern. In some long-term monitoring, compensation has been documented to extend for decades after defoliation. Wood production in western U.S. pine forests, for instance, reached or exceeded pre-attack levels 10-15 years following mountain pine beetle outbreaks (12).

Herbivory may also alleviate drought stress by reducing a tree's demand for water, some studies suggest. Under some conditions, defoliated plants may, in fact, survive drought better than uneaten plants. Herbivory can also alter competitive interactions between plant species. Insects that reduce the biomass of a dominant plant species may sometimes permit the persistence of plant species that otherwise would be replaced. Callaway and colleagues reported that plant-eating insects used in biological control can increase the competitive ability of their invasive host by stimulating compensatory growth (13).

Allies for Management

To the extent that herbivory benefits plants and communities when they are in poor condition and helps return systems that are out of balance to a healthier state, insects can be thought of as

▼ Over the long term, trees compensate for defoliation after an initial reduction in growth.



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a stabilizing force. Herbivory is only one way in which insects play a regulatory role in ecosystems. By acquiring and releasing nutrients, feeding larger animals, pollinating flowers and dispersing seeds, damaging or killing some plants, and promoting growth of others, their actions help shape the environments around them and help keep systems functioning smoothly.

The manager who views insects as ecologically important regulators will come to look more carefully at the need for human intervention in any particular situation and to assess whether self-regulating factors are already present in the system in question. In many cases, working with insects rather than against them may produce new solutions for maximizing yield of commodities while achieving conservation goals and ensuring healthier ecosystems.

We should point out, however, that non-native species complicate the picture. We might expect native insects to act as regulators of native systems, since they have likely evolved together for many hundreds, thousands, or millions of years. Exotic species introductions, however, create novel species combinations and greatly hasten the speed at which systems change. An invasive insect on a native plant—or a native insect on an invasive plant—cannot be expected to serve as a reliable regulator. In such cases, more traditional pest control methods may be called for. However, it will be wise whenever possible to research whether mechanisms of compensation exist before launching into new and costly programs of pest control.

nocultures, fire suppression, replacement of native species with exotics, chemical overuse—that can weaken systems to the point they are susceptible to insect outbreaks. And we are finding that when systems are so weakened, it may sometimes benefit the system to let outbreaks run their course. By doing so, we can use the insects' natural role as regulators as a powerful tool for our management ends.❧

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Note:
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