Conversely, many human activities threaten the integrity of aquatic habitats in forested ecosystems and individual species within them. The most prominent of these are resource overexploitation, habitat degradation from land-based activities (primarily logging), and the introduction of exotic species. Overexploitation of fishes has been documented as human populations increase and/or greater access to water bodies is created. The giant Mekong catfish and the Asian bonytongue are both considered threatened from overfishing. Logging, both selective and clear-cut, alters water quantity, timing, physicochemical parameters, and the aquatic biota. Sedimentation increases dramatically following logging and profoundly alters the ecosystem. Exotic species can also cause major, irreversible changes, with infamous examples including the water hyacinth and Nile tilapia.

While these threats are serious and immediate, they can be overcome if appropriate, sustainable solutions are developed. This will require adequate funding, political will and the application of multidisciplinary approaches.

Further Reading

Brönmark C and Hansson L-A (1998) *The Biology of Lakes and Ponds*. Oxford, UK: Oxford University Press.

Cushing CE, Cummins KW, and Minshall GW (eds) (1995) *Ecosystems of the World*, Vol. 22, *River and Stream Ecosystems*. New York: Elsevier.

Dobson M and Frid C (1998) *Ecology of Aquatic Systems*. Harlow, UK: Longman.

Dudgeon D (1999) *Tropical Asian Streams: Zoobenthos, Ecology and Conservation*. Hong Kong: University of Hong Kong Press.

Ewel KC and Odum HT (eds) (1985) *Cypress Swamps*. Gainesville, FL: University of Florida Press.

Giller PS and Malmqvist B (1998) *The Biology of Streams and Rivers*. Oxford, UK: Oxford University Press.

Goulding M and Barthem R (1997) *The Catfish Connection: Ecology, Migration and Conservation of Amazon Giants*. New York: Columbia University Press.

Goulding M, Smith NJH, and Mahar DJ (1995) *Floods of Fortune. Ecology and Economy along the Amazon*. New York: Columbia University Press.

Junk WJ (ed.) (1997) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Berlin: Springer-Verlag.

Kalff J (2002) *Limnology*. Upper Saddle River, NJ: Prentice Hall.

Kitching RL (2000) *Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata*. Cambridge, UK: Cambridge University Press.

Lugo AE, Brown S, and Brinson M. (eds) (1990) *Ecosystems of the World*, Vol. 15, *Forested Wetlands*. New York: Elsevier.

Talling JF and Lemoalle J (1998) *Ecological Dynamics of Tropical Inland Waters*. Cambridge, UK: Cambridge University Press.

Taub FB (ed.) (1994) *Ecosystems of the World*, Vol. 23, *Lakes and Reservoirs*. New York: Elsevier.

Williams DD (1987) *The Ecology of Temporary Waters*. Caldwell, NJ: Blackburn Press.

ENTOMOLOGY

Contents

Population Dynamics of Forest Insects

S R Leather, Imperial College London, Ascot, UK

Population dynamics is the study of changes in the number of organisms in populations and the factors influencing these changes. It thus, by necessity, includes the study of the rates of loss and replacement of individuals and of those regulatory processes that can prevent excessive changes in those numbers.

A wide variety of factors can affect the population dynamics of a particular species. These can be divided roughly into two categories. First, the extrinsic or environmental influences on populations, such as temperature, weather, food supply, competitors, natural enemies, diseases, and all possible combinations of the preceding; and second, the interactions between members of the same populations, be these direct or indirect, e.g., intraspecific

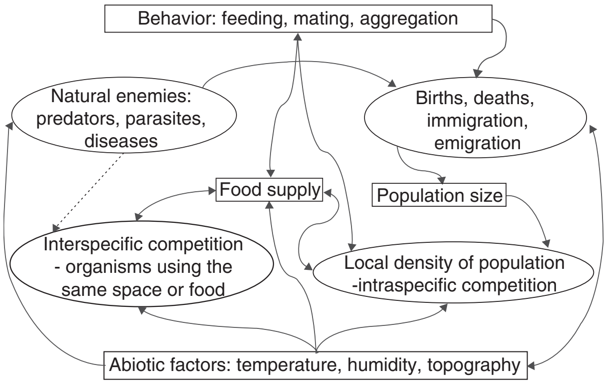

Figure 1 Factors influencing the population dynamics of a forest insect.

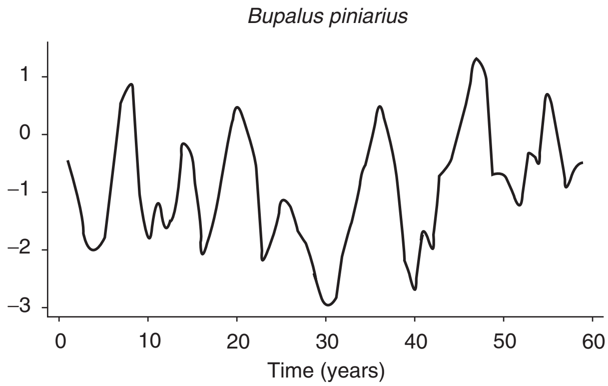

Figure 2 Populations of the pine looper moth, *Bupalus piniarius* (data from the Centre for Population Biology database).

competition, behavioral processes, and aggregation (**Figure 1**).

This article gives an overview of the main factors affecting the population dynamics of forest insects and explains how population cycles arise and are maintained.

Detecting Patterns and Identifying Processes

Perhaps the fundamental rationale behind the many published studies on population dynamics is the desire that population ecologists have for detecting and explaining patterns. The question that they are really trying to address, should they be honest, is why some species of insect are relatively scarce whilst others are extremely abundant and why some of the abundant species show cycles of abundance and relative scarcity. Cyclical fluctuations in population size are commonly seen in animal populations, with classic examples from mammals and birds, but the most dramatic examples are, without doubt, those shown by the invertebrates, and in particular, forest insects. The spectacular effects of defoliating forest Lepidoptera with their ability totally to defoliate hundreds of hectares of trees and their equally graphic population cycles have resulted in them becoming textbook examples (**Figure 2**). One of the most controversial debates of the past was whether population cycles were driven by abiotic factors or biotic interactions. At the moment the general consensus is that biotic factors, in particular density-dependent processes, are the major forces driving insect populations. The fact that the jury has voted for density-dependence does not, however, mean that the mechanisms that drive these population cycles are either fully understood or agreed upon.

As forest insects are of general and economic interest and generally occur in long-lived environments, there has been a tendency for field data to be collected over many years. The resulting time series (**Figure 2**) are often analyzed using sophisticated mathematical techniques. For example, autocorrelation analysis is used to describe the effects of a lagged population density and can also provide an indication of the periodicity of the time series. Partial autocorrelation, on the other hand, can provide an indication of the respective roles of direct and delayed density-dependent processes within a population. Whichever analysis is undertaken, the usual outcome is that the majority of forest insects, in particular the Lepidoptera, show periodic cyclical dynamics oscillating around a 6–11-year period, with delayed density-dependent effects being the most common driving variable. Although these mathematical and statistical approaches to exploring long-term data series are useful in providing an overview of the ecological processes and revealing hidden patterns, the mechanisms that drive the patterns are what most ecologists are really interested in discovering.

Although abiotic factors such as weather, plant stress, and site factors have all been implicated as contributing to, if not driving, the oscillatory behavior of forest insects, it is generally agreed that biotic factors, in particular natural enemies and the insect's host plants, are the major factors causing the population cycles. Weather and other abiotic factors undoubtedly play a major supporting role in modifying the peaks and troughs of the populations, if not in their timing and frequency.

Top-down versus Bottom-up

During the latter part of the twentieth century the acrimonious nature of debate over the factors enabling the regulation of herbivorous insect populations derived from the peculiar and partisan views of the importance of the host plant versus the natural enemies of the herbivore, i.e., whether the population was driven from the bottom up by the effects of the plant or from the top down by the impact of the natural enemies. These positions were at one time deeply entrenched and I remember as a postgraduate student being deeply sceptical about the relevance of natural enemies in agroecosystems and crop protection, despite the undoubted success of some biological control operations. Ecologists tended to study only one part of the system and ignore the other as being largely irrelevant – the emphasis was on ditrophic rather than on multitrophic interactions. Fortunately, most ecologists now agree that there is room for both top-down and bottom-up forces to act together to influence the populations of insect herbivores. There is, however, still much debate as to which is the most important and whether the relative importance of one over the other is fixed in a particular system or varies according to environmental conditions.

Insect population biologists working in forest ecosystems could perhaps be excused for espousing the top-down view, as it is well known that forest Lepidoptera are attacked by a large number of natural enemies, in particular Hymenopteran and Dipteran parasitoids. Parasitoids are distinguished from parasites in that their host usually dies as a result of their attack and that some parasitoids also directly predate their hosts as well as laying their eggs inside or next to them. Parasitoids do have an important role in the population dynamics of forest insects and, in many cases, as in small ermine moths, appear to be the major cause of the cyclical crashes in population seen in these insects.

The role of predators is less well supported. There is good evidence that predators have an effect on the population dynamics of forest insects, e.g., outbreaks of the pine beauty moth, *Panolis flammea*, in northern Scotland are associated with a lack of generalist predators such as carabid beetles and spiders; other forest Lepidoptera, notably the Douglas-fir tussock moth and the spruce budworm in North America, are subject to substantial predation by these agents. Evidence for the action of predators as a causal mechanism for cyclical population fluctuations is in shorter supply. The predation of pine sawfly cocoons by small mammals (*Sorex* spp.) has been postulated to influence the cyclical population dynamics of Diprionid sawflies in northern Europe and predators are claimed to be the driving mechanism causing the oscillatory behavior of southern pine beetle populations in the USA.

An important natural enemy complex that may be responsible for the maintenance of population cycles in forest insects are the insect pathogens: viruses, bacteria, protozoa, and fungi. For example, nuclear polyhedrosis viruses (NPVs) and the granulosis viruses have dramatic physical effects on forest Lepidoptera and Hymenoptera and appear to be responsible for sudden population crashes in these organisms. In addition, they have been used worldwide in attempts to control forest insect pests. Until recently, however, it was difficult to prove that they had a major role to play in the induction of population cycles. New developments supported by simulation modeling indicate that if pathogens act at the same time as resource competition then population cycles are more likely to be generated.

All of the preceding are so-called 'top-down agents.' What about those operating from the bottom up? It may appear that the plant can have little influence on the generation of population cycles. It seems intuitively obvious that plants are inherently more or less susceptible/suitable to attack by a particular herbivore species. Plant breeders have used this knowledge for a long time when seeking to breed insect- and disease-resistant crop plants as part of pest management systems. There are, however, ways in which the host plant can influence the development of population cycles in forest insects. First, even if the nutritional quality of the host plant remained unchanged, the build-up of the herbivore population on the host plant can result in competition for resources, either through depletion of the food source or by the increase in the number of larvae feeding on a finite host plant. Second, the physiological state of trees (and other plants) is not static, and their susceptibility/suitability as food plants both within and between years can be changed. Insect feeding, for example, can in some cases induce rapid changes in plant physiology and biochemistry (rapid induced responses). The biochemistry of the leaves can change detrimentally for the insect and leave the equivalent of a nasty taste in the insect's mouth, resulting in its either ceasing feeding altogether or moving to a new leaf or site on the same leaf. Although this phenomenon has been demonstrated on many occasions, it is not likely to influence cyclical population behavior. A more likely candidate is the so-called delayed induced responses where attacked trees become more resistant or less palatable to the insect herbivores the following year. The effect is mediated through the mother, in that the changes in food quality and an increase in the degree of larval crowding cause reductions in growth and developmental rates, resulting in smaller, less fecund adults. A reduction in the fitness of individual adults can markedly affect the population dynamics. In other words, the population cycles are driven by long time lags by the action of density-dependent factors, i.e., larval quality is impaired by insect-induced changes to the host plant, the insect population decreases, and the quality of the host plant slowly improves or returns to normal, at which point individuals within the insect population become fitter (faster-growing, larger and more fecund) and the cycle starts anew.

The classic example of this phenomenon is the larch bud moth, *Zeiraphera diniana*, the larvae of which defoliate *Larix decidua* and *Pinus cembrae* in the European Alps. Outbreaks of the larch bud moth occur at regular 9-year intervals in the Engadine valley. The cycles are hypothesized to be caused by host-induced changes in the quality of the larvae. When defoliated by the moth larvae, the raw fiber content of the new larch needles increases considerably; this has a strong negative effect on larval survival and female fecundity. It can take several years for the raw fiber content to return to normal and this in itself constitutes a delayed negative-feedback mechanism which in theory could be sufficient to generate regular population cycles. Mathematical modeling and many years of observation appear to support this hypothesis. Gypsy moth, western tent moth, and autumnal moth populations also show similar responses to the quality of their host plant in that host-mediated maternal effects affect the quality of their offspring and may generate cyclical population dynamics. There is, however, some debate as to the generality of these results and evidence of whether the maternal carry-over effects can generate the cycles on their own is equivocal.

Multitrophic Interactions

The situation becomes more complex when the top-down forces meet those operating from the bottom up: the tritrophic or multitrophic interactions, between the predators, parasites, and other natural enemies, the herbivores and their host plants. This can be expressed in a number of ways, but perhaps one of the best known is the sublethal plant defenses paradox. The paradox resides in the fact that the host plant gains more by being partially resistant to the insect herbivore than by being immune. To possess total immunity against an insect herbivore requires a large investment in defenses, be this through antibiosis, antixenosis, or architectural attributes such as spines, thick cuticles, and resin flow. Any resources invested in defense are of course not available for growth and reproduction and this imposes a fitness cost. If, on the other hand, the plant reduces its investment in defenses, it has more reproductive currency to spend. By being partially resistant (i.e., partially susceptible), however, the insect herbivore is able to consume it, thus reducing reserves available for growth and reproduction. On the face of it this is potentially reducing the fitness of the plant. If there was a simple trade-off between the plant's investment in defenses (carbon-based) and the amount likely to be eaten by the herbivore (nitrogen-based), there would be no paradox. Put simply, the insect herbivore requires x amount of nitrogen to complete development and any reduction in plant nutritional quality implies that the insect needs to eat more plant to obtain the required amount of nitrogen to complete its development. As the insect is not killed or repelled by the plant, it remains on the plant and continues to feed until it reaches adulthood or its own reproductive threshold. Hence the paradox. By being less suitable as a food source, the plant appears to be encouraging the insect to eat more of it. This does not appear to be the best form of defense. Bear in mind, however, that the general effect of sublethal plant defenses is either to slow down the growth of the insect or, for example as in the case of rapidly induced defenses, to cause the insect to change feeding site more often. These effects have the same net outcome. The insect herbivore becomes more vulnerable to its natural enemies. In the case of reduced insect growth rates, it remains in a vulnerable (less developed) stage for longer and thus has more chance of encountering a predator or parasitoid. In the case of the rapid-induced defense scenario, where the leaf becomes less palatable, the insect moves from one feeding site to another more often and spends more time exposed on the leaf (caterpillars often feed in bouts, coming out from sites within the inner parts of the plant foliage to feed, and then returning to the relative safety of the area near the main stem). The overall result is more journeys back and forth and thus more chance of encountering a predator or parasitoid. In addition, by changing feeding sites more often, the insect makes more holes in the leaves and this acts as a 'supercue' for vision-dependent predators such as birds.

Yet another effect of sublethal plant defenses is that the insect herbivore, feeding as it does on a suboptimal diet, is more likely to become stressed and more susceptible to infection by pathogens, e.g., fungal and viral diseases, although in some cases it is possible that the insect is able to sequester plant chemicals that inhibit virus infection.

Population Cycles

So how do these top-down and bottom-up forces interact with the insect herbivore to produce the population cycles seen in so many forest Lepidoptera? Populations that cycle are characterized by highs (peaks) and lows (troughs) in abundance. As foresters usually first become aware of defoliating insects when they outbreak, it is appropriate to start our consideration on a peak, when the population is at its maximum.

The herbivore population is at its peak, and the trees are likely to be showing marked signs of defoliation, either totally stripped or at least half their foliage removed. The nutritional quality of the plants for the insect is at its lowest, either because of a scarcity of foliage and/or because of induced defenses. Interspecific competition between the insects is markedly higher than before and the caterpillars are small and stressed. Their growth rates will be low and this will make them susceptible to natural enemies. Natural enemy populations are now increasing rapidly and parasitism and disease rates are now extremely high. Any caterpillars that survive to pupate will be small and, if they survive the winter, will produce even smaller and less fecund adults than before. The herbivore population now begins to decline steeply. The natural enemy populations are now at their highest levels and competing amongst themselves. The nutritional quality of the trees is still very low, although consumption of the foliage is lower than before as there are now fewer caterpillars. The caterpillars, although likely to be growing and developing slightly faster than the season before, are now greatly outnumbered by their natural enemies. The herbivore population crashes and they virtually disappear from the forest. The following season caterpillar numbers are extremely low indeed. New foliage will be available and the nutritional quality will be improving. Food is thus in relatively plentiful supply. Most of the natural enemies will fail to find suitable hosts or prey as the herbivore population is so low.

The natural enemy populations now crash. The following year, the few emerging herbivore adults are able to exploit an underutilized food resource and pick egg-laying sites likely to maximize offspring fitness. The emerging caterpillars thus find themselves with a plentiful and relatively defenseless source of nutrition. Their environment is relatively competition-free and consequently they are able to grow and develop rapidly, attaining relatively large sizes and hence, after pupation, producing large and fecund adults. Natural enemy populations are almost nonexistent and, as the herbivores are likely to be widely dispersed and uncommon, predation, parasitism, and disease are also likely to be very low. The herbivore population will thus start to increase. However, as the herbivore population increases, the nutritional quality of the host plant begins to decrease, first perhaps by the induction of plant resistance but also by depletion of the resource as more and more foliage is removed by the feeding caterpillars. Interspecific competition is also likely to influence the quality of the herbivore. As a result the larvae will be smaller and less well defended, and will grow and develop more slowly. After pupation, the emerging adults will be smaller and less fecund. The effects of the levels of natural enemies (predation, parasitism, and disease) will also be more marked. The herbivore population, although composed of poorer-quality individuals, will continue to increase, but at a slower rate and the herbivore population reaches its peak as the combined effects of natural enemies, host quality, and insect quality have their greatest effect and then the cycle starts again.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Bark Beetles; Defoliators; Foliage Feeders in Temperate and Boreal Forests; Sapsuckers. **Health and Protection**: Integrated Pest Management Principles. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Bonsall MB, Godfray HCJ, Briggs CJ, and Hassell MP (1999) Does host self regulation increase the likelihood of insect–pathogen population cycles?. *American Naturalist* 128: 228–235.

Dempster J and McLean IFG (eds) (2000) Insect Populations in Theory and Practice. Dordrecht, The Netherlands: Kluwer Academic.

Dwyer G, Dushoff J, Elkinton JS, and Levin SA (2000) Pathogen-driven outbreaks in forest defoliators revisited: building models from experimental data. *American Naturalist* 156: 105–120.

Ginzburg LR and Taneyhill DE (1994) Population cycles of forest Lepidoptera: a maternal effect hypothesis. *Journal of Animal Ecology* 63: 79–92.

Hanski I (1987) Pine sawfly population dynamics – patterns, processes, problems. *Oikos* 50: 327–335.

Haukioja E (1991) Induction of defenses in trees. *Annual Review of Entomology* 36: 25–42.

Herms DA and Mattson WJ (1992) The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67: 283–335.

Hunter MD, Varley GC, and Gradwell GR (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences USA* 94: 9176–9181.

Mason RR, Jennings DT, Paul HG, and Wickman BE (1997) Patterns of spider (Araneae) abundance during an outbreak of western spruce budworm (Lepidoptera: Tortricidae). *Environmental Entomology* 26: 507–518.

Myers JH (1990) Population cycles of western tent caterpillars: experimental introductions and synchrony of fluctuations. *Ecology* 71: 986–995.

Price PW, Bouton CE, Gross P, *et al.* (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural

enemies. *Annual Review of Ecology and Systematics* 11: 41–65.
Solomon M (1969) *Population Dynamics*. London: Edward Arnold.
Speight MR, Hunter MD, and Watt AD (1999) *Ecology of Insects: Concepts and Applications*. Oxford, UK: Blackwell Science.
Turchin P, Taylor AD, and Reeve JD (1999) Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285: 1068–1071.
Watt AD, Leather SR, Hunter MD, and Kidd NAC (1990) *Population Dynamics of Forest Insects*. Andover, UK: Intercept.

Foliage Feeders in Temperate and Boreal Forests

D Parry, State University of New York, Syracuse, NY, USA
D G McCullough, Michigan State University, East Lansing, MI, USA

Introduction

Insect consumers of tree foliage comprise one of the most abundant and diverse feeding guilds in forest ecosystems. Known as folivores, this guild is integral to the structure and functioning of forests. Folivores influence vital ecosystem processes in forests, including nutrient turnover, competition among plants, and stand structure. In addition, these insects are critical sources of food for many invertebrate and vertebrate predators. In this article, we will address foliage-feeding insects that affect trees in temperate and boreal forests. In these ecosystems, an estimated 10–30% of the total leaf area is annually removed by leaf-chewing forest insects. In some forest types, defoliating insects strongly influence productivity and the long-term dynamics of the ecosystem. Foliage-feeding insect species have little effect on tree health in most years. During outbreaks of some insect defoliators, however, the entire canopy can be consumed, sometimes for several years in succession. While outbreaks may cause significant economic harm by accelerating tree mortality, reducing productivity and increasing fire risk, they may also play an important long-term role in maintaining healthy forests.

Diversity

In this section, we focus on folivores with chewing mouthparts, which represent the vast majority of insects feeding on the leaves of hardwood trees (deciduous angiosperms) and the needles of conifers (gymnosperms). The forest defoliator guild is comprised of insects from several different orders. The greatest diversity of species is found within the order Lepidoptera. Nearly all larval Lepidoptera are herbivorous whereas the adults may imbibe fluids such as nectar or, as in many economically important species, may not feed at all. The sawflies (Symphyta), a relatively primitive group of Hymenoptera, are also important foliage feeders. Like the Lepidoptera, larval sawflies are herbivorous while adults generally do not feed. In addition to sawflies, leaf-cutting ants (family Formicidae) are another group of Hymenoptera that feed on foliage. While not important or diverse in temperate regions, leaf-cutter ants are the dominant herbivore in many tropical forests. Among the beetles (order Coleoptera), the diversity of leaf-feeders is richest in the large families Chrysomelidae and Curculionidae. Both adults and larvae in these families feed on foliage. Several other insect orders also contain species that can function as forest defoliators. These include grasshoppers, crickets, and walking-sticks from the order Orthoptera, and several families of flies (order Diptera). Other guilds of tree-feeding insects, such as sap-feeders and shoot borers, can also cause defoliation but will be described in other articles (*see* **Entomology**: Defoliators; Sapsuckers).

Feeding Ecology

Folivores with chewing mouthparts can be partitioned based on their general feeding type. Three types are generally recognized: free-feeding, shelter-feeding, and leaf-mining. Insects that free-feed consume leaf tissue openly. Species utilizing this type of feeding may consume all parts of the leaf (many caterpillars, sawflies, and orthopterans) or may avoid veins and other structural tissue (shot-hole, window-feeding, or skeletonizing). Skeletonizing is characteristic of chrysomelid beetles as well as some caterpillars and sawflies. Because free-feeding species are exposed to predators as they forage, many have adaptations, that may reduce their risk of mortality from these natural enemies. These include high mobility, nocturnal feeding, cryptic coloration, sequestration of toxins, physical defenses such as urticating or stinging hairs, or stereotyped defensive behaviors like regurgitation, head flicking, or dropping immediately to the ground upon sensing danger.

Another common feeding strategy is shelter-feeding. Shelter-feeding species may enclose and feed on foliage within a silk structure, or may use silk to roll leaves or to tie leaves or needles together. Enclosures