INTRODUCTION

Recurrent outbreaks of forest insect populations have been discussed extensively in the ecological literature (Myers, 1988; Berryman, 1996), but rarely from the perspective of disturbance ecology. The reason lies, in part, in the traditional focus of quantitative animal ecologists on the species of interest (e.g., Morris, 1959) contrasted with the traditional emphasis of plant ecologists on whole communities (e.g., Tilman, 1982). Further, historical research on forest insects has been motivated largely by the practical problem of insect pest management. While yielding a rich legacy of information on the biology and ecology of a few selected insects, the modeling literature
that utilizes this information has generally tended to view disturbance as an economic disruption to be predicted and prevented (Berryman, 1991) rather than as an ecosystem process to be emulated. Emulation of natural disturbances, an approach to ecologically sustainable forest management (Bergeron and Harvey, 1997; Perera et al., 2004), has rekindled interest in insect disturbance modeling. The challenge is how to bring the rich insect population dynamics literature to bear on the subject of disturbance in forest dynamics.

In this chapter, we argue that herbivorous insects constitute a class of forest disturbance that is distinct from fire, wind-throw, or flooding in that: (1) insect outbreaks tend to be spatially synchronized and temporally periodic (periods of high impact followed by periods of low impact, over extensive areas); and (2) insect outbreaks are predictably selective and therefore result in different legacies than do abiotic disturbances. As Holling (1992) suggested, insect disturbances, because they tend to be highly selective as a result of biological relationships between the insects and their hosts (Rausher, 1983), represent an agent of “creative destruction” in the boreal forest.

We suggest that recognition of the distinct nature of disturbances caused by insect outbreaks may shed light on the analysis of other disturbances that are, by nature, aperiodic and difficult to forecast (Pickett and White, 1985). In this chapter we review the dynamics of several outbreak systems. We argue that the population density of forest insects is determined by the ecological relationships among host plants, the herbivorous insects, and their natural enemies, and that these “tritrophic” interactions1 are often lagged in space-time, and therefore tend to generate periodic, high-amplitude fluctuations, or “harmonic oscillations,”2 in population densities that are synchronized over vast areas of forest. Forest disturbance in these systems happens when periodic population oscillations are amplified to the point that insect densities have a measurable impact on the structure and/or function of dominant elements of the forest ecosystem.

Where our argument differs from that typically stated in the literature is with regard to the degree of periodicity and synchrony of oscillations in

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1 Tritrophic interaction = set of all resource-consumer interactions spanning three trophic levels: plants, herbivores, and predators
2 From physics, the term “harmonic oscillation” is used to distinguish it from the idea of a “relaxation oscillation,” which was central to the phenomenological cusp-catastrophe models developed in the 1970s to describe the process of insect outbreak occurrence (e.g., Ludwig et al., 1978; Rose and Harmsen, 1981; Hassell et al., 1999).
defoliator populations. We argue that the complexity and nonlinear nature of tritrophic interactions result in oscillations that may be imperfectly periodic. Moreover, stochastic environmental variables may further influence these dynamics and contribute to spatiotemporal patterns of disturbance that are imperfectly synchronized. So, although we agree with the idea of a well-defined outbreak return interval, we think the variation about that mean is significant and is under the control of a number of biotic and environmental variables that are worth studying.

To study these relationships, we use a comparative, process-oriented approach. In this chapter we illustrate the approach by comparing the ecologies of four species of insect defoliators (Table 1). A major challenge in insect disturbance modeling is the fact that these systems tend to be modeled in detail as single-species systems. The comparative approach to insect disturbance ecology seeks to identify meaningful similarities among systems, which helps to reduce model complexity to a bare minimum. It focuses on critical, functional ecological relationships rather than species. It is thus ideally suited to disturbance modeling, where the goal is mimicking realistic patterns of natural disturbance caused by a variety of insect species.

The chapter is organized according to Fig. 1, which illustrates a process-oriented view of the way in which insect populations cause selective forest disturbance. At the bottom of Fig. 1, insect hazard modelers will recognize the familiar terms “susceptibility” and “vulnerability” as the component factors whose product is the risk or probability of “disturbance” (defined variously as growth loss, stem mortality, or stand volume loss). Susceptibility typically refers to the probability that herbivory reaches

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**TABLE 1  Foliage Grazers**

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Latin Name</th>
<th>Acronym</th>
<th>Preferred Host</th>
<th>Secondary Hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest tent</td>
<td><em>Malacosoma disstria</em> [Hbn.] (Lasiocampidae)</td>
<td>FTC</td>
<td>Trembling aspen</td>
<td>Sugar maple, other <em>Populus</em> species, aspen</td>
</tr>
<tr>
<td>Spruce budworm</td>
<td><em>Choristoneura fumiferana</em> (Clem.) (Tortricidae)</td>
<td>SBW</td>
<td>White spruce, balsam fir</td>
<td>Black spruce, red spruce</td>
</tr>
<tr>
<td>Jack pine</td>
<td><em>Choristoneura pinus pinus</em> Freeman (Tortricidae)</td>
<td>JPBW</td>
<td>Jack pine</td>
<td>None</td>
</tr>
<tr>
<td>Western spruce</td>
<td><em>Choristoneura occidentalis</em> Freeman (Tortricidae)</td>
<td>WSBW</td>
<td>Douglas-fir</td>
<td>White fir, spruce</td>
</tr>
</tbody>
</table>
a certain intensity over a certain time frame, while vulnerability refers to the probability of tree mortality (or growth loss) at a given level of herbivory. Whereas an empirical modeler might attempt to explain observed levels of disturbance (Fig. 1, bottom) as a direct function (Fig. 1, dark-shaded area) of static spatial features in the environment (Fig. 1, top right), a process modeler would seek to understand and quantify the most important ecosystem processes (Fig. 1, middle) that determine susceptibility and vulnerability. These ecosystems processes are ultimately governed by environmental and ecological factors (Fig. 1, top) that vary both temporally (Fig. 1, top left) and spatially (Fig. 1, top right) at a variety of scales.

**FIG. 1** Overview of the common framework underlying two approaches to insect disturbance ecology: the descriptive/phenomenological/correlative approach (i.e., hazard rating/risk analysis) and the process approach (i.e., process-oriented simulation modeling).
The scope of this chapter is limited to those elements relating most directly to insect population dynamics and plant–insect interactions (Fig. 1, *light-shaded area*). We focus in particular on the creative–destructive nature of disturbance caused by the highly selective process of insect herbivory (Fig. 1, *white area*). Although we are tackling a major piece of the insect disturbance ecology puzzle, we are relying on research in other domains to help bridge the gap between insect population dynamics and insect disturbance ecology. This chapter is thus designed to complement others in this volume, as well as existing reviews that examine insect population processes (Schowalter *et al*., 1986) and forest insect disturbance (MacLean, 2004) from a more general taxonomic and ecological perspective. We do not go so far as to show quantitatively how different patterns of insect-caused disturbance can be fully explained by existing process-oriented models. Instead, our more modest objective is to convince the reader that the study of population processes is helping to solve many of the prevailing mysteries about insect-caused disturbance.

**DEFOILING INSECTS AS A DISTINCT CLASS OF FOREST DISTURBANCE**

**Insects Compared to Fire**

To understand the role of defoliating insects as a source of forest disturbance, it helps to compare the magnitude of insect disturbances to physical disturbances, such as fire. In Canadian forests, insects and fire are roughly equivalent in terms of the area disturbed. A regional scale analysis by Kurz and Apps (1999) for the period between 1920 and 1989 indicated that insects are the dominant disturbance in the East, while fire tends to dominate in the West. This distinction, however, is biased by the widespread outbreak of spruce budworm (*Choristoneura fumiferana* Clem.) in eastern Canada from 1970 to about 1990 (Hardy *et al*., 1986) and the absence, in their analysis, of the more recent outbreaks of both spruce budworm and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in British Columbia, which engulfed more than 4 million ha in 2003 (British Columbia Ministry of Forests, 2004). Over the lifetime of a forest, both sources of disturbance are significant throughout Canada.

An important distinction between insects and fires, however, is the way the two disturbance regimes behave on the landscape over time. In western Canada, for example, insect-caused disturbance has been somewhat periodic, while fire occurrence is not (Fig. 2). Notably, there is no negative correlation between the fire disturbance and insect disturbance in western
Canada, despite the apparent correspondence between the bi-decadal insect outbreaks of the mid-1940s, 1960s, and 1980s and periods of reduced fire disturbance (Fig. 2). The data do reveal, however, a time-lagged, positive correlation between the fire and insect outbreak time-series ($r = 0.36$ for lag = 4 y; $p = .003$), indicating that high insect disturbance tends to precede high fire disturbance by about 4 years—a result similar to that reported in Ontario with regard to spruce budworm (Fleming et al., 2002). Thus, fire and insect disturbance regimes are not entirely independent of each other. And yet, despite this interdependence, insect disturbance is distinguished by its periodicity and spatial synchrony.

**FIG. 2** Annual area disturbed by fire and insects in west central Canada (after Li et al., 2003). Spectral analysis measuring periodicity is shown in inset.
Outbreaks as Regionally Synchronized Population Oscillations

The insects listed in Table 1 are among the most damaging insect species in northern forest ecosystems. All exhibit extensive, spatially synchronized oscillations of high amplitude. It is the extent of synchrony of these cycles, and not their local destructiveness, that creates the political will to intervene as populations go through epidemic phases. Fire, in contrast, is a relatively nonsynchronous disturbance, where the need to intervene stems not from its synchrony but from its enormous destructive capacity at the local scale, and its potentially rapid rate of spread. On the temporal scale, fire occurrence tends to be uncorrelated from one year to the next, but insect outbreaks tend to last for several years because of the strong relationship between insect densities in successive generations (Royama, 1992). Thus, fire ecologists do not use the term “cycle” in its trigonometric sense but instead use the notion of a fire-return interval that is a random variable whose mean might vary according to local circumstances (Van Wagner, 1978). In the entomological literature, the term “cycle” is used liberally but most often implies oscillations that are accompanied by a fair amount of noise. Insect ecologists may interpret a cycle as a “phase-forgetting quasi-cycle” (Nisbet and Gurney, 1982) because the phase, and to a lesser degree its periodicity, is influenced readily by stochastic inputs, such as weather and migration (Royama, 1992). This phase-forgetting aspect of insect population cycles is critical because this is what makes cycles vulnerable to large-scale synchronization via weak external forces, including spatially autocorrelated but temporally random perturbations, such as those caused by minor fluctuations in seasonal climate (Moran, 1953) and interpopulation dispersal of egg-bearing adults (Barbour, 1990).

Understanding the processes that promote synchronization of cycles is important because synchronization is the critical scaling mechanism that allows insect ecologists to be more categorical than fire ecologists in their estimates of disturbance return intervals. For example, in Ontario, forest tent caterpillar (Malacosoma disstria Hübner) populations cycle every 13.0 ± 0.95 SE years (Fleming et al., 2000). If local population oscillations were not regionally synchronized, such precise generalizations would not be possible. Thus, a major topic of concern for forest entomologists is the origin of cycles and the mechanisms by which local-scale population oscillations are synchronized to form regional-scale outbreaks. For disturbance ecologists, the important point is that insect-caused disturbances are fundamentally different from physical disturbances, both in pattern and in genesis.
Foliage-Grazers versus Other Forest Insects

Most insects have little detectable impact on the forest; however, the destructive capacity of those in Table 1 is well documented. A general classification of herbivorous forest insects is illustrated in Fig. 3.

Many destructive insect species, such as bark beetles, feed on vital tissues such as the cambium and can directly kill their hosts. Some defoliators, such as the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough (Beckwith, 1978), and the hemlock loopers, *Lambdina* spp. (Rose and Lindquist, 1985), feed on all age classes of foliage (new and old) and so can completely defoliate their host tree in one or two seasons. With evergreen host species, complete defoliation usually results in death of the tree. The defoliating insect species considered in this chapter (Table 1), however, feed almost exclusively on current-year foliage of their host plant and rarely completely defoliate the tree. As such, they are more like grazers that exploit a renewable, and somewhat nonvital, host resource. The result is
less immediate stress to their host. The single deciduous tree defoliator in Table 1, the forest tent caterpillar, may seem, at first, an exception to this generalization. However, its primary host, trembling aspen (*Populus tremuloides* Michx.), can produce a second flush of foliage, even after complete defoliation, either from reserves stored in roots and stems or from photosynthesis through the bark so that defoliated trees rarely remain unfoliated throughout the season.

**THE PROCESS OF INSECT DISTURBANCE**

**Impact of Herbivory**

During an outbreak of early-season defoliators, the tree’s photosynthetic capacity is reduced. Repeated defoliation acts as a drain on the tree’s non-structural carbohydrates, leading to severe and sustained reductions in tree growth (Kulman, 1971). Repeated defoliation eventually leads to die-back of twigs, branches, roots, stems, and whole stands, as structural modules are sacrificed to reduce the demand for water and life-sustaining reserves. In the initial phase of an outbreak, however, the defoliators are actually less of a drain than one might expect because the younger, expanding tissues actually represent an early-season nutrient sink, and the photosynthetic efficiency of formerly shaded foliage of the lower crown increases following defoliation of the upper crown. Nevertheless, feeding by these insects eventually becomes less benign as the outbreak persists and the inability of the tree to renew photosynthetic material compromises vigor. For example, perennial defoliation reduces the ability of trembling aspen to produce a second flush of leaves as photosynthetic reserves (starches and storage proteins) are depleted. In the case of fir (*Abies*) and spruce (*Picea*), persistent budworm feeding leads to low recruitment of new foliage to the tree crown and increased retention of old needles (Baskerville and Kleinschmidt, 1981), which reduces the tree’s overall photosynthetic capacity because old needles are less efficient at photosynthesis than are young needles (Clark, 1961).

**Interaction with Other Agents**

Insect-caused disturbances may manifest suddenly (e.g., over a few years) or gradually (e.g., over a decade or more). The ultimate disturbance may be attributed directly to the action of the defoliator outbreak, or it may be accelerated or modified by additional stressing agents. In trembling aspen and spruce and fir, tree health declines after persistent defoliation as trees
become susceptible to other pathologies (Belyea, 1952; Churchill et al., 1964). Other biotic factors, such as competing vegetation, pathogens, and bark beetles, can also be involved in decline. These agents typically act additively and in conjunction with abiotic forces, such as wind and drought. The total impact of all these disturbance agents is mediated by site conditions (e.g., soil depth, drainage, slope, aspect, and exposure).

The interactions among various disturbance agents adds complexity to spatial and temporal patterns of tree and stand death, such that the ultimate pattern of disturbance caused by an insect outbreak may bear little resemblance to the initial pattern of defoliation. Franklin et al. (1987) suggested that forest insects are part of a “Gordian knot of intertwined causality” where tree death is governed by a complex insect-pathogen-tree-site-climate interaction. Manion and Lachance (1992) suggested that large-scale forest decline is even more complex because of multiscale spatial variation in each of these agents. Such multicausal systems are notoriously difficult to analyze (Hilborn and Stearns, 1982) because causality is hard to ascertain, and quantifying the marginal impacts of individual agents is virtually impossible. For example, while there is little doubt that spruce budworm can kill trees directly (MacLean, 1984; Nealis and Régnière, 2004a), different hazard modeling studies conducted in different parts of eastern Canada have yielded differing results regarding risk factors influencing the severity of budworm damage (MacLean and Ostaff, 1989; Archambault et al., 1990; Dupont et al., 1991; Bergeron et al., 1995; MacLean and MacKinnon, 1997; MacKinnon and MacLean, 2003). Similarly, in the case of the forest tent caterpillar on trembling aspen, although Witter et al. (1975) stated that “almost all the mortality [of trembling aspen during an outbreak in Minnesota] can be attributed to chronic, severe defoliation by the forest tent caterpillar,” it is not entirely clear to what extent herbivory alone was to blame for recent large-scale aspen declines in Alberta (Hogg et al., 2002) and Ontario (Candau et al., 2002). Any defoliator can kill its host if the host is stressed and defoliation persists for long enough.

Defoliators Cause Selective Disturbance

A distinctive aspect of disturbances caused by insects is their highly selective nature. Selectivity arises from three sources: insect host plant preferences, insect population dynamics, and host tolerance to herbivory (Fig. 1).

All insects have, to a greater or lesser extent, host plant preferences. During an insect outbreak, nonhost plant species are often left undamaged.
With reduced interspecific competition, these undamaged nonhosts are left free to grow and to play an important role in stand-level succession and ecosystem-level maintenance of biodiversity. Even in so-called “stand-replacing” insect-caused disturbances, not all hosts are completely removed. Residual, surviving host trees and even dead trees and snags continue to have a significant impact on stand dynamics.

At the level of the individual insect, host plant preferences can manifest differently in the different life stages. Sometimes these stage-specific preferences reinforce one another, as when adults lay eggs in close proximity to the food source preferred by the larvae. But this is not always the case. The different life stages of spruce budworm, for example, show varying degrees of preference for black spruce (*Picea mariana* (P. Mill.) BSP). Spruce budworm moths find black spruce highly acceptable as a host on which to oviposit, and hatchlings find many suitable sites on the tree to use as overwintering sites. Young feeding larvae, however, will disperse actively in large numbers from black spruce in springtime as the late-flushing characteristic of black spruce renders the buds too difficult for early-season feeders, such as budworm, to establish feeding shelters. Once budburst has occurred, not only is black spruce an adequately nutritious host for spruce budworm larvae, but larvae actually perform better later in the season on black spruce than on either white spruce (*Picea glauca* (Moench) Voss) or balsam fir (*Abies balsamea* (L.) Mill.) (Nealis and Régnière, 2004a). In this case, preference is a function of relative phenology of host and insect, and this could vary across a landscape. Thus, generalizing host plant preferences can be misleading without specific knowledge of the mechanisms that govern this process.

Insects being relatively small organisms, the preferences discussed so far are manifest at very small spatial scales. However, the act of dispersing to fulfill a preference, when carried out by many individuals in a population, leads to enormous potential for richly textured patterns of herbivory and disturbance at larger scales. As fine-scale, subpopulation processes, insect aggregation, congregation, and dispersion are major sources of spatial variability in the selective process leading to disturbance. To the extent that preferred resources are clumped, insect aggregation can lead to consistently higher rates of immigration into some patches over others and thus link small- and large-scale patterns. Hardy *et al*. (1983) observed that spruce budworm “epicenters” tend to occur in old white spruce stands located in river valleys in the subboreal mixed-wood forest region of Quebec. Moth congregation and aggregation could play a critical role in the formation of these epicenters. What is interesting from a disturbance
ecology perspective is that although outbreak epicenters may indicate a preferred habitat type for ovipositing moths, these are not the areas where outbreaks tend to last the longest or cause the most damage. The areas of greatest disturbance are those where outbreaks tend to linger the longest, and in spruce budworm these areas are located typically outside the epicenters (Gray et al., 2000). A reasonable conjecture is that the points that are first to show signs of damage are those that are first to begin exporting moths in large numbers (Nealis and Régnière, 2004b). This would be consistent with key elements of the epicentric theory of spruce budworm outbreak spread (Greenbank et al., 1980) while at the same time maintaining consistency with Royama’s (1984) noneruptive theory of budworm outbreak cycles. In other words, if these so-called epicenters are also the initial points of outbreak collapse, then they may not function as mere sources of outbreaks. If they are also a source of predators, then they may be acting as relay points in what is a loosely coupled network of oscillating predator and prey populations (Régnière and Lysyk, 1995).

Overview of Insect Population Dynamics

When insect preferences for a particular species, size class, or condition of host plant are met, the result is increased rates of survival and reproduction on that host. Over time, this can lead to an increase in insect density and disturbance. For example, survival of jack pine budworm (Choristoneura pinus pinus Freeman) larvae is much higher on host trees that produce pollen cones than on those that do not (Nealis and Lomic, 1994). Consequently, disturbance tends to be more severe in stands with a high proportion of flowering trees (Nealis et al., 2003).

While it is conceptually useful to distinguish between sub–population-level aggregative processes and population-level reproductive processes, that distinction is often blurred by the fact that preferred host plants tend to both boost population growth rates and foster aggregations, either through active recruitment or passive arrestment of individuals simultaneously. Three points arise. First, host plant preferences have a strong influence on the spatial pattern of disturbance because they are operating through two synergistic mechanisms, insect aggregation and population growth. The blurring that results from the strong interplay between individual-level host preferences, population dynamics, and host distributions is precisely the reason that the species-level insect–plant association is such a durable ecological concept. Second, different systems will exhibit different patterns of selective disturbance, depending on whether the aggregative
or reproductive processes dominate. With bark beetles, where the aggregative process is key to overcoming strong plant defenses, disturbance tends to be locally patchy and aperiodic (see Chapter 16). With the defoliators discussed here, where the reproductive process often dominates over the aggregation processes, disturbance tends to be diffuse and periodic (see Chapter 17). Third, to the extent that preferred resources are clumped, so too will population growth be higher in some patches than others, and so therefore will be the pattern of disturbance.

Once insect populations have increased to a very dense state, the positive synergy between population growth and insect dispersal can become negative, as insects switch from aggregative to diffusive behavior, and as populations switch from a phase of unlimited exponential growth to a phase of resource-limited growth. The spillover effect that results from density-dependent dispersal often leads to seemingly paradoxical patterns of disturbance. For example, during a jack pine budworm outbreak, although stands with many pollen-producing trees are far more prone to recruitment of budworms, even the trees not producing pollen cones will be defoliated, as there is often spillover from the flowering trees. Similarly, spruce budworm oviposit in the upper canopy of large trees but spill over in large numbers onto smaller size classes of suppressed trees as they disperse there in springtime upon emerging, or in midsummer in search of food. That subdominant and understory balsam fir tend to be killed first in a spruce budworm outbreak indicates the preference of moths to oviposit in tall trees, the preference of larvae to avoid overcrowding (or starvation), and the frequency with which understory fir are found occupying canopy gaps in mature coniferous stands. As a result, during outbreaks, spruce budworm can sometimes act in the manner of a silvicultural “thinning from below.”

The same spillover phenomenon has been reported in western spruce budworm (*Choristoneura occidentalis* Freeman; Fellin, 1976) and Douglas-fir tussock moth (*Harris et al.*, 1985), where, in shelterwood and partial cuts of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), the absence of an intercepting subcanopy led to the movement of young larvae in large numbers from canopy trees to regenerating trees, ultimately killing them. These are cases where modified silvicultural practices stimulated, rather than emulated, natural disturbance. They are noteworthy because many defoliating insects tend to perform better in thinned forests (Bauce, 1996; Dobesberger, 1998) and in sunny, exposed, edge-dominated habitats (*Moore et al.*, 1988; Roland and Kaupp, 1995; Fortin and Mauffette, 2001).
Host Tolerance
Some host plants are more tolerant of herbivory than others because of their ability to cope with reduced foliage or their ability to recover lost foliage (Haukioja and Koricheva, 2000). These responses vary as functions of numerous factors, such as tree architecture, site condition, competition, and health status or vigor (reviewed in Tiffin, 2000). A tree’s internal programs for resource acquisition and allocation are also important because they determine the tree’s ability to re-establish apical dominance, to alter production of short and long shoots or leaf-level photosynthetic activity, to use stored reserves, or to shed and re-grow fine roots. Differences in this capacity can be manifest at any level, from individual (e.g., large vs. small crown) to species (e.g., white spruce vs. fir), and can be associated with a range of compensatory growth responses, such as epicormic shoot production, rootlet regrowth or enhanced flowering and seed production in conifers, or suckering in trembling aspen. Variability in tolerance to herbivory introduces spatial variability and patchiness in a tree’s vulnerability to a given level of herbivory. Even if insect densities were uniform in space (i.e., no host preferences, no dynamics), impact would vary locally.

Modeling Herbivore Impact: Empirical versus Process Approach
There are many examples of herbivore impact studies reaching different conclusions under ecological circumstances that vary only slightly. One case in point concerns the spruce budworm in eastern Canada, where two correlative impact studies in the province of Quebec (Dupont et al., 1991; Bergeron et al., 1995) reached different conclusions, despite a fairly similar range of ecological circumstances. Dupont et al. (1991) emphasized local factors acting within stands and concluded that site conditions (hydrology, geology, soil moisture, and texture) were critical factors influencing tree death during an outbreak. In contrast, Bergeron et al. (1995) concluded that forest conditions (stand age and species composition) were more important and that the spatial context of stand composition in the surrounding forest matrix was significant. A third study from New Brunswick suggests both studies may be partially correct, and that the differing results could be a product of differing sampling schemes and ecological contexts, possibly emphasizing different aspects of susceptibility and vulnerability (MacLean and MacKinnon, 1997). Specifically, they argue that because outbreak intensity varies among regions, the risk factors that emerge as significant in any spatial analysis also tend to vary.
Rather than dwell on the failures of the correlative approach to insect disturbance modeling, we wish to highlight its close relationship with process modeling, showing how the two approaches can be pursued synergistically within a common framework (Fig. 1). The correlative approach, or empirical hazard modeling, is conceptually simple and more direct than the process approach in that it seeks to explain spatial variation in disturbance risk as a function of spatial variation in forest landscape characteristics. The problem is that hazard models are static, descriptive models and therefore limited in their predictive capacity, especially under conditions of system change. Because they downplay the importance of the dynamic temporal processes that mediate insect population growth and forest structure, hazard models that work well during one outbreak will tend to perform less well in subsequent outbreaks, where forest conditions and population growth processes may differ.

Process studies can help resolve unexpected differences between impact studies, and they may suggest more appropriate hypotheses worth testing. For example, where Bergeron et al. (1995) showed that conifer stands are less vulnerable to budworm disturbance when embedded in mixed-species forests, Su et al. (1996) showed that hardwoods located within the focal stand produce the same effect, only locally. They hypothesized that this was a result of the effects of forest composition on the budworm natural enemy community—a result that is now supported by more recent process studies showing that the natural enemy complex indeed varies as a function of forest attributes both within the focal stand and in the surrounding forest matrix (Cappuccino et al., 1998; Quayle et al., 2003).

Patterns of Disturbance

Spatial Patterns
Although some defoliators tend to be more destructive than others, all species exhibit substantial spatial and temporal variability in the extent of damage they cause. The extent and degree of disturbance during a defoliator outbreak depend largely on the intensity and duration of defoliation over the landscape. When herbivory is intense and prolonged, stand death and stand-replacement can occur. What is more common, under regimes of more moderate or brief herbivory, are milder disturbances, such as the formation of small canopy gaps, patches of accelerated self-thinning among suppressed stems, or a brief increase in light, nutrient, and water availability, and loss of productivity.
For herbivore population fluctuations to reach outbreak status, it is typically necessary that the size, density, and quality of preferred hosts exceed some level. For an outbreak to be extensive, the preferred hosts need to be distributed extensively, although not necessarily contiguously (Roland, 1993). When and where preferred hosts are less available, the herbivore must deal with suboptimal conditions, and this can influence the dynamics of local populations. Thus, the interplay between population dynamics processes and host plant preferences can be a source of both spatial and temporal variability in the pattern of disturbance.

**Temporal Patterns**

Boreal forest ecosystems are often dominated by relatively few tree species and, because of their genesis from previous disturbances, tend to be correlated over large spatial scales. In such homogeneous forest types, even a relatively specialist feeder, such as the jack pine budworm, can find sufficiently extensive, favorable habitats to support an increase in its density, leading to a significant disturbance at the landscape scale. Because of the relative homogeneity of northern forests, insect-caused disturbances can affect multiple regions simultaneously.

One of the most obvious results of forestry of the past century has been conversion of the forest toward more homogeneous or bimodal age classes dominated by a few tree species. Furthermore, the tree species favored have been those which tend to be shade intolerant, fast-growing, ruderal species: balsam fir over white spruce, jack pine (*Pinus banksiana* Lamb.) over white pine (*Pinus strobus* L.), poplar (*Populus* spp.) over everything. One of the urgent objectives of disturbance ecology is to determine whether these anthropogenic patterns have resulted in new patterns of natural disturbances, and whether this threatens the stability and sustainability of forest ecosystems.

Herein lies a major limitation in the correlative, historical approach to risk analysis: disturbance patterns of the past will not be a strong indicator of the future if environmental conditions have changed substantially. In contrast, process-oriented studies, because they model mechanisms, have greater predictive value.

**POPULATION DYNAMICS OF FOLIAGE-GRAZERS**

We have argued that insect defoliators constitute a distinct class of forest disturbance because they are selective and because they tend to exhibit cyclic and synchronized outbreaks. Next we discuss the nature of the mechanisms
that generate cycles and synchronize these cycles across the landscape. We propose a template of intermediate complexity that could be used to structure a process-oriented insect disturbance model. We develop this template by comparing and contrasting the dynamics of the forest tent caterpillar and three of the Canadian conifer-feeding budworms, all cyclic defoliators.

Case Studies

**Forest Tent Caterpillar, Malacosoma disstria (Hübner)**

Forest tent caterpillar outbreaks in Ontario, Canada, are remarkably cyclic, with a periodicity of $13.0 \pm 0.95$ years SE during the 20th century (Fleming et al., 2000). Longer-term reconstructions by Baird (1917) for all of central Canada suggest that outbreaks in the 19th century followed much the same pattern. While Baird found no reason to suspect any regional differences in outbreak periodicity, Hildahl and Reeks (1960), studying outbreak patterns in western Canada from 1920 onwards, were at odds with Sippell (1962) in Ontario as to whether forest tent caterpillar outbreaks were cyclic. Thus, the degree of cyclicity or synchrony in forest tent caterpillar outbreaks may vary by region. Such regional variability was confirmed by Cooke and Lorenzetti (2006), who reported a 9-year outbreak cycle in the aspen-dominated Abitibi region of northwestern Quebec and a 14-year cycle in the maple-dominated Appalachian region of southern Quebec, during the interval 1938–2002. They also noted that outbreak cycles in Quebec covered, on average, only $37\% \pm 13\%$ SE of the insects’ potential outbreak range.

A similar but less variable result is revealed in data from Ontario (Fig. 4). Of the six forest tent caterpillar cycles occurring during the period 1929–2003 (Fig. 4, *top panel*), the most extensive outbreak (cycle II) spanned 65% of the insects’ outbreak range; the least extensive (cycle III) spanned only 22% of that range (Fig. 4, *bottom panels*). On average, individual outbreak cycles span only $43\% \pm 7\%$ SE of the insects’ outbreak range. Thus, despite the regularity of the cycle, it appears that there are always significant areas where populations do not get high enough to cause detectable damage. In fact, there are only two very small areas (near Dryden, northwest region, and Sudbury, northeast region) where all six outbreak cycles have occurred.

The spatial variation in cycle synchrony is an empirical fact which requires explanation. Many environmental factors, both stochastic and deterministic, could modulate cycle amplitude and vary sufficiently in space and time to effectively reduce observed levels of cycle synchrony. Cooke and Roland (2003), for example, discussed how fluctuations in winter
FIG. 4  Periodicity and extent of six cycles of forest tent caterpillar outbreaks in Ontario. The number of years of defoliation during the full period 1929–2003 (gradient) is overlain by the extent of defoliation during each cycle (dark grey, surface area measured as percentage of full extent).
temperature may play a complex role in both synchronizing and then desynchronizing forest tent caterpillar cycles in western Canada. We argue that process-oriented studies that explicitly address variable patterns of synchrony are needed to prevent uncritical acceptance or rejection of synchronization theory. Understanding how real-world population oscillations may be synchronized is key to understanding how large-scale insect disturbance occurs.

**Jack Pine Budworm, Choristoneura pinus pinus Freeman**

Analyses of jack pine budworm defoliation records in the Great Lakes region of North America indicate that outbreaks of this species recur at vaguely periodic intervals (Fleming *et al.*, 2000; McCullough, 2000). However, as with forest tent caterpillar, the degree of cyclicity and the estimates of periodicity vary among regions, such that it would be a drastic oversimplification to suggest that outbreaks are strictly cyclic. Although a 10-year cycle appears defensible in western Canada (Volney, 1988), outbreak periodicity in the pine barrens of Wisconsin varies geographically, with 10-year cycles in the northeast, 5- to 6-year cycles in the drier central region, and very weakly periodic 14-year cycles in the southwest (Volney and McCullough, 1994). The recent patterns in Ontario seem equally vague (Nealis *et al.*, 2003).

As with the forest tent caterpillar, there are always large subregions where expected cycles fail to materialize. Outbreaks in Ontario, for example, never expand to cover the entire range of the insect over the course of a decadal cycle (see Fig. 1 in McCullough, 2000) despite the presence of preferred host plants, favorable climate, and plenty of neighboring infestations that could act as sources of dispersing moths.

**Spruce Budworm, Choristoneura fumiferana (Clem.)**

Candau *et al.* (1998) found differences of 32, 45, and 36 years between the peaks of two successive outbreak cycles of spruce budworm in western, central, and eastern Ontario, respectively. With data from only two cycles, one cannot estimate interval means and variances. The estimate of low-frequency, approximately 30-year periodicity nevertheless agrees with similar short-term analyses of defoliation data from Quebec (Hardy *et al.*, 1986; Gray *et al.*, 2000) and of population data from New Brunswick (Royama, 1984)—all from the 20th century.

Longer-term tree ring studies of white spruce from Quebec, initiated by Blais (1983) and extended spatially by Jardon *et al.* (2003) and Boulanger
and Arseneault (2004), confirm that spruce budworm outbreaks tend to occur every 32.0 ± 5.1 years SE although the six reconstructed cycles that are thought to have occurred since 1800 have varied substantially (see Chapter 17). A similar result has been reported from nearby New Brunswick (Royama, 1984).

Tree ring data from northern British Columbia indicate that spruce budworm outbreaks in the far west of its range are occurring at roughly 26-year intervals (Burleigh et al., 2002). Thus, there is substantial long-term evidence for a low-frequency cycle in spruce budworm outbreaks over a wide geographic range of conditions. Spruce budworm cycles are not as regular as those of forest tent caterpillar, but neither is the forest tent caterpillar perfectly periodic.

It has been argued that the low-frequency outbreak cycle (approximately 30–40 years) of *C. fumiferana* in eastern North America is the result of the naturally short lifespan of the average balsam fir stand (approximately 60–80 years), which could be shortened to approximately 40 to 60 years in the presence of budworm (Ludwig et al., 1978; Clark et al., 1979; Hassell et al., 1999). However, as discussed below, this argument clearly does not stand up for western spruce budworm (*C. occidentalis*). Although outbreaks of this species recur every 22 years, Douglas-fir forests are renewed on a much longer time frame (some individual trees may live up to 700 years). So, while *C. fumiferana* outbreaks in the east often result in significant forest disturbance, it does not follow that the low-frequency population cycle is dictated by the disturbance cycle. It may simply be that, for this particular system, the two processes are close enough to one another in frequency that they are often correlated without being causally linked.

**Western Spruce Budworm, *Choristoneura occidentalis* Freeman**

It is noteworthy that tree ring reconstructions of outbreaks of two other western North American budworms indicate highly periodic, low-frequency cycles. The 2-year cycle budworm (*C. biennis* Freeman), feeding on white spruce and subalpine fir (*Abies lasiocarpa* Nutt.) in northcentral British Columbia, appears to have an outbreak every 32 years, or 16 generations (Zhang and Alfaro, 2002; 2003). The western spruce budworm, *C. occidentalis*, on Douglas-fir in southern British Columbia appears to have an outbreak every 22 years (Alfaro et al., 1982). In New Mexico, approximately 15 outbreak cycles of *C. occidentalis* have occurred in the past 400 years (Swetnam and Lynch, 1993). In Colorado, approximately 32 outbreak cycles have occurred in the past 700 years (Ryerson et al., 2003). As a group it thus appears that the North American fir–feeding bud-
worms do outbreak periodically, with a return interval that is much longer than a decade.

Many of the defoliated trees on which the Colorado *C. occidentalis* outbreak reconstructions are based exhibited top-kill, while relatively few were thought to have died as a result of defoliation (Ryerson et al., 2003). These outbreaks are thus thought to be less disturbing to the forest than are outbreaks of the spruce budworm in the eastern spruce–fir forest.

This is strong evidence that not all defoliator population cycles translate into severe forest disturbances. Indeed, the cyclic western spruce budworm and the Douglas-fir forest may represent a resilient “equilibrium state”—even more resilient than the spruce budworm–fir forest ecosystem. This resilience implies that some process other than forest destruction must cause the primary western spruce budworm cycle. This may well be the case in other folivore-dominated forest systems, including spruce budworm (Royama, 1992).

**Summary**

Our goal was to show that much of the theoretical population dynamics literature on population cyclicity and spatial synchronization is highly relevant to disturbance modeling. At the same time, we also wanted to show that defoliator outbreaks are imperfectly cyclic and imperfectly synchronous.

If defoliator outbreaks were perfectly periodic and synchronized, and if the frequency of oscillation were fixed in time and in space, then, from a disturbance ecology perspective, there would be little need to model population processes; a simple mathematical description of the phase characteristics would be adequate. But as we have shown, there is systematic variability in systems behavior (e.g., trends in outbreak cycle amplitude, and areas where outbreak cycles do not emerge), suggesting that additional variables are at play. If these can be identified, then our ability to predict disturbance will increase. The key questions are the following:

1. How are cycles generated?
2. How are cycles synchronized?
3. What factors serve to modulate cycle amplitude and synchrony?

Volumes have been written on these complex questions, so a quick and lasting synthesis is simply not possible. But we believe it may be possible to make some gains in disturbance ecology by working with simpler, semi-mechanistic, data-rich models, as we outline next.
A Tritrophic Model of Cycle Induction

The specific reasons put forward for animal population cycles are many. Among forest insects, some of the most common biological mechanisms discussed are the following:

1. Predator–prey interactions (Nicholson and Bailey, 1935)
2. Host–disease interactions (Anderson and May, 1980)
3. Induction of host plant defenses or changes in plant nutritional quality (Denno and McClure, 1983; Haukioja, 1991)
4. Intrinsic changes in individual traits (Wellington, 1964; Chitty, 1967)
5. Changes in population allele frequencies (Campbell, 1966; Stenseth, 1981)
6. Induction of maternal effects (Ginzburg and Taneyhill, 1994)

The common consensus is that harmonic cycles in density of insect populations are the result of delayed, negative feedbacks between the insect and its environment (Berryman, 1978; 2002). Negative feedback results from the finite capacity of populations to grow in a limited environment. The delay is inherent in the relationship between the density of the population and the impact of that density on the environment when the negative effects of resource depletion or increased predation are experienced by future generations (i.e., the effect of present-day population densities is delayed until the future).

All the biological mechanisms listed above are, in theory, capable of generating cycle-inducing feedback. In practice, modern insect ecologists tend to focus on a subset of these: the so-called “top-down” effect of natural enemies (1 and 2) and the “bottom-up” effect of the host plants (3). The ensemble, referred to as a tritrophic interaction, is a marvelously complex ecological phenomenon, despite its conceptual simplicity.

The tritrophic model is a good conceptual aid but is too abstract to use for analytically understanding how disturbances arise in particular systems as a result of specific biological processes. A more concrete model, presented here in strictly graphical form, shows how our concept can be implemented and used to describe the dynamics of many defoliator species.

Model Formulation

Fig. 5 represents the cyclic behavior of a general tritrophic interaction as it might be expected to manifest in the systems considered here. The dark gray line represents herbivore population densities over a population cycle. The black line represents natural enemy populations. These natural enemies could be predators, parasites, or pathogens. Both curves are jagged,
rather than smooth, to represent the imposition of stochastic environmental influences (highly variable weather, generalist predators, and other density-independent effects). The shaded regions around these curves represent an envelope, or range, of possible population trajectories. The top edge of the light gray region indicates the expected herbivore population trajectory in a favorable environment; the bottom edge of this region is the expected trajectory in an unfavorable environment. The dark gray region applies similarly to natural enemy populations.

When the trajectory of the natural enemy population (black line) intersects that of the herbivore population (dark gray line), a herbivore decline is inevitable. The decline results from the effects of both host plants and natural enemies, with natural enemies being the more proximal and fast-acting of the two agents. Note also how stochastic factors may help in bringing about decline, or in propping up a peak, while having no role in

3 In effect, there are two ways to interpret these regions: as a probability field or as an environmental range. Under the first interpretation, the population cycle, as a stochastic process, may follow any path within an infinite ensemble of theoretical possibilities within the envelope. Under the second, cycle amplitude may be considered a variable parameter that changes (slowly in time, or predictably in space) according to varying ecological circumstances. The second interpretation is the one emphasized here.
causing the cycle—that is, the stochastic elements may affect the timing and amplitude, but not the nature, of the pattern.

When natural enemy population growth is favored over herbivore population growth (black trajectory near the top of dark gray region and the dark gray trajectory near the bottom of light gray region), a natural enemy–induced population collapse at point A (left portion of the medium gray zone of intersection) is likely. This would occur, for example, in forest types that are not rich in primary host plants but are rich in host plants for other species of herbivores on which these natural enemies can feed.

In contrast, where herbivore population growth is favored over natural enemy population growth (black line low, dark gray line high), herbivory lingers on long enough that there are some destruction of the host plant resource, some reduction in carrying capacity, and a decline in herbivore populations not attributable to natural enemies. In such a case, natural enemies will not appear to cause a population collapse until point B, at the right of the medium gray zone of intersection. Because this decline is retarded, the system suffers significant disturbance.

**Model Behavior**

As forest and natural enemy communities may vary, so may the shape of the regions and the behavior of the model. In this way the model can be made to fit a variety of systems. According to the scheme depicted in Fig. 5, the forest tent caterpillar, being more strongly limited by fast-acting natural enemies than are the budworms, exhibits a higher-frequency primary oscillation (Fig. 5A). The budworms, as a group, exhibit a lower-frequency primary oscillation because of the relative inefficiency of natural enemies and the relative importance of host plants.

The western spruce budworm, being the most oscillatory budworm system with the highest degree of synchrony and the lowest amount of severe disturbance, exhibits the least distinct pattern of host plant responsiveness (Fig. 5D). It is like the forest tent caterpillar in that any host plant effects (i.e., ill effects of resource depletion) are manifest at the same spatial scale over which natural enemies operate (e.g., within stands); hence, a cycle that is regular in periodicity.

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4 Eastern spruce budworm outbreaks (in the 20th century) may have been more extensive than those of western spruce budworm (but not after adjustment for size of host range); however, tree ring studies indicate stronger periodicity and greater synchrony in western spruce budworm (especially when desynchronizing effects of terrain-related dispersal barriers and microclimatic variability in western North America are discounted).
In contrast, the spruce budworm (Fig. 5B) is a system where resource depletion has little impact early in the cycle (as larvae continually space themselves out and adjust their fecundity according to food availability) but a large impact later in the cycle (as damage accumulates, tree death becomes widespread, environmental carrying capacity drops, and moths emigrate en masse). At this late stage, a population collapse is inevitable and natural enemies will finally begin to take over.

The jack pine budworm is different still from the other two budworms in that larvae depend so heavily on pollen cones, which fluctuate periodically in availability. When pollen cone production is shut down by previous defoliation, local populations begin to decline as the impact of natural enemies is accentuated (Nealis, 1991). When flowering resumes, after defoliation has abated, local populations can rebound; however, the degree of rebound depends on natural enemies. The result is a scale-dependent multifrequential oscillation (wiggly region in Fig 5C). Jack pine budworm outbreaks are usually observed in areas where production of pollen cones is intense and natural enemies are lacking. Either of the two mechanisms is sufficient to bring about population decline, but reduction of pollen cone production, being a highly localized process, initiates the decline and natural enemies follow (Nealis et al., 2003).

As in jack pine budworm, host plant–associated feedback in the spruce budworm system counteracts the cycle-inducing effect of negative feedback from natural enemies, with the result that oscillations are actually multifrequential rather than unifrequential. The difference is that the higher-frequency “sawtooth” oscillations are not as prominent a feature of spruce budworm outbreaks, and went largely unnoticed until a study by Royama (1984) was published.

Although all coniferous hosts probably reduce their rates of pollen cone production in response to budworm defoliation, it is in the jack pine system where this has a measurable impact on budworm spatial dynamics. Here, the reduction in pollen cone production leads to a spatially shifting mosaic of local-scale population eruptions that are nested within the landscape-scale outbreak cycle. For example, during the 1980s outbreaks of jack pine budworm in Ontario, population eruptions tended to last about 2 years at the stem level (approximately 10^9 m), about 4 years at the stand level (approximately 10^2 m), about 5 years at the regional level (approximately 10^5 m), and about 7 years at the inter-regional (provincial) level (approximately 10^6 m) (McCullough, 2000; Nealis et al., 2003). In contrast, the high-frequency fluctuations in spruce budworm tend to be spatially correlated across whole regions (Royama, 1984). Indeed, this is the
main reason that spruce budworm outbreak cycles are thought to be synchronized across whole regions (Royama et al., 2005).

**Model Summary**

All four insect–forest systems can be interpreted within the context of the same tritrophic regulatory structure. What differs is the strength and nature of host plant feedback relative to the cycle-inducing effect of delayed feedback caused by natural enemies. Host plant feedback is relatively weak in the forest tent caterpillar system, hence the strongly periodic, natural enemy–related pattern of outbreaks. What differs among the individual budworm systems is the rate at which the cumulative effects of host damage are expressed and, therefore, the spatial scale over which damage and disturbance occur. The important point is that the tritrophic model accommodates both top-down (natural enemies) and bottom-up (host plant) forces explicitly; the functional relationships are the same but their speeds are different.

In all these systems, the amplitude of population oscillations is expected to vary randomly as a function of stochastic forces. Some cycles will be amplified to the level of evident disturbances; others will result in undetectable levels of defoliation, but cycles nonetheless. The nature of these stochastic forces will vary among cycles in time and space. Sometimes the modulating force will be more weather-related, other times more predation-related. Sometimes it will be a spell of consecutive years of favorable conditions; sometimes it will involve a single catastrophic event. A key challenge for insect ecologists is to identify in each system which stochastic elements are critical agents and how they influence other functional processes within the system.

**Spatial Implementation**

The collective dynamics of environments that are patchily structured in terms of forest and natural enemy communities can be represented by using a spatial mosaic of the various types. For example, we know that balsam fir is more like jack pine than white spruce in the low proportion of carbohydrate reserves held in storage. Fir declines more quickly in quality as a host (Nealis and Régnière, 2004a) and is more vulnerable to mortality (MacLean, 1980; Blais and Archambault, 1982). In the same way that jack pine is intolerant of and reproductively adapted to fire disturbance, balsam fir appears to be intolerant of and reproductively adapted to spruce budworm disturbance (Morin, 1994). Thus, we expect budworm disturbance dynamics to differ in spruce versus fir forests. This difference is not illus-
trated in Fig. 5 because in central Canada spruce and fir stands are often sufficiently intermingled that the distinctly different dynamic processes are not free to scale up from the stand level to the landscape level.

Fig. 5B can thus be considered as the average behavior of spruce budworm over a complex landscape in central Canada. In practice, the model would need to be parameterized for all the different stand types one encounters in the forest landscape, hence the need for spatially structured population models operating on realistic landscapes. For this purpose we expect that comparative studies in spruce-dominated western Canada versus fir-dominated eastern Canada to be particularly informative.

Spatial Synchronization

We have shown that periodic insect outbreaks are the result of local insect populations cycling in response to changes in both their resource and in the impacts of their natural enemies. A key question is how these local-scale oscillations are synchronized to form large-scale outbreaks. This is an area of intensive research, so a complete synthesis would be premature. However, a brief review is necessary to explain how such tiny organisms can inflict such widespread ecological disturbance. Three principal mechanisms could, in theory, account for cycle synchronization:

1. Spatially autocorrelated random perturbations, which act as a phase-locking mechanism (Moran, 1953)
2. Spatially autocorrelated nonrandom shocks, which act as a period-forcing mechanism (Berryman, 1981)
3. Interpopulation migration, which acts as both a frequency-homogenization and phase-locking mechanism (Barbour, 1990)

The literature has generally done a poor job discussing the various theories of cycle synchronization (but see Royama, 1997). Even now there is insufficient evidence with which to decide which of these mechanisms is most important. We cannot dismiss the possibility that all three processes are operating, perhaps at multiple spatial scales. The challenge for insect ecologists is to develop mature, inclusive hypotheses by looking at specific systems and using long-term data and formal analytical methods with well-designed, system-specific process models. This approach, for example, has led to a much clearer understanding of how spruce budworm population cycles are synchronized by multiple mechanisms (1 and 3) acting on a single life stage—the egg-carrying adult female moth (Royama et al., 2005).
**Synchronizing Mechanisms**

Catastrophic shocks, periodic or otherwise, are “regional” in scale. Thus, only mechanisms 1 and 3 are capable of what is termed “global” synchronization: the ability to synchronize locally induced cycles across the entire range of a continentally distributed insect.

From a biological perspective, dispersal and spatially autocorrelated weather perturbations appear to be very different mechanisms. Mathematically, however, they operate in similar ways—with one resultant difference. The similarity is this: because the phase of a population oscillation is determined largely by the sum history of stochastic perturbations, any set of oscillators can be readily brought into phase with one another by ensuring they have a shared history of stochastic perturbation. As Bjornstad *et al.* (2002) put it: “cyclic systems yearn to align themselves.” To understand the argument it is necessary to understand how delayed negative feedback is capable of generating oscillatory dynamics, and how stochastic perturbations imposed on this regulatory loop are incorporated into the system state, such that the system state at any point in time is largely determined by the sum history of perturbations. While the periodicity of oscillations is determined by the nature of the feedback loop, the phase of those oscillations is free to be determined by the accumulated history of perturbations, which eventually overwhelm any influence of initial conditions.

What Moran (1953) understood was that independently fluctuating populations at two locations will be quickly brought into a common phase when random perturbations, such as those caused by fluctuations in a climatic factor, are correlated between the two locations. The higher the correlation of these perturbations, the faster and more complete will be the synchronization of the phases of these populations.

What Barbour (1990) understood was that dispersal of moths could act not only as a source of correlated perturbation but also as a dynamic homogenization mechanism, whereby ecologically dissimilar populations regulated by different sets of factors could effectively be blended to form a single meta-population regulated by a common superset of factors. With sufficient dispersal rates between them, the dynamic similarity of populations is guaranteed, and any differences in periodicity or phasing will diminish to zero through time.

The main difference between Barbour’s and Moran’s proposed mechanisms of synchronization is that dispersal is a robust mechanism, whereas correlated perturbation is not. To be more precise, Moran’s effect is constrained by the requirement that the oscillating populations be governed by a generating process that is homogeneous in its parameters (i.e., identical...
periodicity), whereas Barbour’s is not. What this implies is that in real, heterogeneous landscapes, where predator and prey communities surely vary spatially in their composition, only the dispersal mechanism is robust enough to ensure landscape-wide spatially synchronized population oscillations.

**Synchrony versus Synchronization**

If the synchronizing forces of dispersal and correlated perturbation are strong and universal, then why is it rare to see systems that fluctuate in perfect synchrony? While dispersal and correlated perturbations may tend to pull systems toward a synchronized state, in real, natural systems, multiple uncorrelated perturbations are at play, so that precise and universal synchronization is by no means guaranteed. This would not be obvious from a reading of the ecological literature, which often refers to the pattern of population synchrony and rarely to the process of synchronization. The literature is so replete with examples of synchronized oscillatory systems that one might be tempted to conclude that all systems behaved this way. In fact, even the best-synchronized oscillatory systems, such as larch budmoth (*Zeiraphera diniana*) in Europe, do not exhibit synchrony over their full range (Bjornstad *et al.*, 2002). As we have shown with North American foliores, synchrony occasionally breaks down in time, in space, or under particular ecological circumstances.

The important message for disturbance ecologists is that synchronization is a critical scaling process that makes insect outbreaks very different from abiotic disturbance processes, both in pattern and in cause. Synchrony varies naturally, and can be made to vary artificially, by altering parameters such as insect dispersal rates, landscape connectivity, and homogeneity in regulatory processes. Once again, the insight is gained from the study of the processes that create the phenomenon, rather than analysis of the patterns the phenomenon creates.

**Amplitude Modulation, Outbreak Trends, and Environmental Change**

A mechanistic theory of insect-caused forest disturbance should be able to address the observation that outbreaks of several major periodic defoliators have increased in severity, extent, duration, or synchrony during the 20th century. Among these are spruce budworm (Blais, 1983), jack pine budworm (Volney, 1988), western spruce budworm (Swetnam and Lynch, 1993), and forest tent caterpillar (Roland, 1993).
The two theories most commonly invoked to explain the apparent dynamical changes in these insect outbreaks are:

1. Large-scale forest clearing, often with recolonization by pioneering tree species, is altering forest structure and species composition (Jackson et al., 2000; Carleton, 2000) in a way that may favor pioneering herbivores (Blais, 1983; Swetnam and Lynch, 1993) and disfavor their natural enemies (Roland, 1993).

2. A reduction in the frequency, duration, extent, and distribution of wildfires, caused by either climate change (Bergeron and Leduc, 1998; Carcaillét et al., 2001) or large-scale fire suppression (Swetnam and Lynch, 1993; Carleton, 2000), has created an older, more homogeneous forest, which may be more susceptible and more vulnerable to insect attack (Blais, 1983; Volney, 1988).

Of course, correlation does not imply causation, especially when it comes to shared trends in relatively short time-series. Thus, it is still a matter of some debate whether or not there is a causal link between environmental change and the increasing severity of outbreaks in any one of these systems.

That the evidence is equivocal is illustrated most clearly in the tree ring studies of western spruce budworm on Douglas-fir conducted by Swetnam and Lynch (1993) in New Mexico versus those of Ryerson et al. (2003) in Colorado. The New Mexico data prompted Swetnam and Lynch (1993) to speculate that the increased extent and severity of *C. occidentalis* outbreaks was a result of increased availability of susceptible hosts—echoing the argument made by Blais (1983) about increasing frequency and severity of *C. fumiferana* outbreaks in eastern Canada. However, the Colorado data of Ryerson et al. (2003) exhibited no such trend, despite a similar land use history. The parsimonious conclusion is that the western spruce budworm cycle is a highly stochastic process governed by random variables (such as weather and capricious, high-order interactions among members of the budworm community food web) that vary both spatially and temporally.

In summary, all four of these pests depend on disturbance-loving tree species (trembling aspen, balsam fir, jack pine, Douglas-fir) that are becoming more common across significant parts of the landscape. Yet there is little evidence of a consistent trend in population densities toward greater synchrony or cycle amplitude with increasing host plant abundance. Where such “trends” are reported, they often span as few as two to four population cycles, which is clearly insufficient for what we know, from process-oriented ecological studies, to be a highly stochastic process. This should not be con-
strued as outright dismissal of the forest composition/land use hypothesis. Rather, what it indicates is healthy skepticism given limited data and limited opportunities to apply a meaningful test.

Proponents of this hypothesis often find it necessary to assume that the mechanism by which forest structure influences insect dynamics consists of a relaxation oscillation—that is, a periodically eruptive cusp-catastrophe event (Ludwig et al., 1978; Hassell et al., 1999). We wish to close by pointing out that this is not the case, that there are other more realistic mechanisms by which a trend toward more homogeneous host plant distributions could result in more extensive insect outbreaks. In the case of the spruce budworm/spruce-fir system, one scenario might operate as follows: 1) selective removal of white spruce from mixed coniferous stands leads to conversion toward fir-dominated stands; 2) reduced fire frequency increases the rate of retention of mature and “overmature” fir stands; 3) increased extent of a more vulnerable host leads to greater levels of defoliation and tree mortality earlier on in the budworm population cycle (Blais, 1958; MacLean, 1980); 4) increased levels of damage lead to higher rates of dispersal out of damaged stands (Royama, 1984); 5) decreased distances between acceptable host stands increase the survival rate, and realized fecundity, of dispersing moths; 6) increased rates of interpopulation migration lead to stronger synchronization of population oscillations (Barbour, 1990); 7) stronger density-dependence of dispersal leads to higher amplitude oscillation in population density (Royama, 1980); and 8) delayed density-dependent insect mortality factors act with increasing strength, further increasing the amplitude of harmonic oscillations (Royama, 1992). Over time, feedbacks between these various processes reinforce one another: increased cycle amplitude leads to increased damage, increased rates of dispersal, increased cycle synchrony, stronger collapse of budworm populations, stronger rebound of populations, and so on.

Although this scenario may seem complex, it is logical. And, as we have shown, several (though not all) of its presumptions and predictions are supported by data. To what extent the scenario may account for the apparent “increase in the frequency, extent and severity of [spruce budworm] outbreaks” reported by Blais (1983) we cannot say; however, it is consistent with his earlier (Blais, 1968) interpretation that the “extent of recent [spruce budworm] attacks was the result of a fortuitous synchronization of a number of independent outbreaks.” What we can say for certain is that process-oriented theoretical and empirical studies of spruce budworm dynamics are necessary, and they are starting to reveal much about how disturbance arises and plays out across the landscape and through time.
As to the role of enviroclimatic change in modulating disturbance probabilities, time alone will not tell. In addition to large-scale, long-term monitoring, measurement and manipulative experiments are required to elucidate the independent roles of various environmental factors such as forest landscape structure and climate. These findings then need to be integrated in the form of process-based simulation models capable of predicting when and where disturbance is likely to occur. Once these models have been validated, we will be better able to emulate and manage for insect disturbances, which will bring us one step closer to the path of forest sustainability.

CONCLUSION

Defoliating insects constitute a special class of forest disturbance because the impact of outbreaks is selective, extensive, periodic, and spatially synchronized, albeit imperfectly. We have shown that in four systems, and maybe more, the ecological relationships between the defoliating insect, its resource, and its natural enemies are critical processes governing insect-caused disturbance. We know that the periodicity of outbreaks is caused by temporal lags in the interactions between herbivores, their host plants, and their natural enemies. But because these multiple processes act at multiple spatial scales, population fluctuations are loosely periodic rather than strictly cyclic. Stochastic influences such as weather further modify the detail of these patterns.

Population oscillations in different areas are synchronized through interpopulation migration and through the action of mild, spatially autocorrelated random perturbations, such as large-scale weather patterns. Departures from synchronous cyclicity are not well understood; however, we do know that this is an important determinant of the duration of outbreaks and of the amount of disturbance caused. Investigation of the causes of this variation requires focus on the common processes mentioned above through comparative analysis.

Understanding the causes of periodic fluctuations in insect populations helps in modeling insect-caused disturbance. But our imperfect knowledge of what modulates the amplitude of oscillations and the degree of synchrony identifies a gap that remains to be closed. Spatial analysis of outbreak patterns and impacts is revealing that the most severe budworm and forest tent caterpillar outbreaks tend to occur where local populations do not decline in synchrony with the collapse of surrounding populations or where the outbreak return interval is shorter than expected, and consequently trees do not have enough of a respite between individual outbreak cycles. We propose
that this variability can best be understood by examining the dynamics of biotic interactions tempered by the influence of stochastic perturbations. Because the disturbance caused by insect outbreaks is itself a biotic interaction, casting insect population dynamics in terms of disturbance dynamics is a mutually beneficial context.

The other major requirement for closing the gap between insect population dynamics and insect-caused disturbance is a concerted effort to quantify the impacts of defoliators on tangible host plant parameters, such as foliage volumes, photosynthetic rates, carbohydrate levels, and growth rates. Because insects are highly selective, the variable pattern of tissue loss caused by insects leads to highly complex patterns of disturbance.

We suggest that the best way to simulate (and manage) insect-caused disturbance is through process-oriented modeling for at least four reasons:

1. The traditional, correlative approach to insect disturbance modeling (hazard modeling) is fast reaching its limit of effectiveness.
2. Major gains in predicting disturbance will come through a more careful consideration of the way local biotic processes are integrated across a variable forest mosaic to scale up to the landscape level.
3. Multivariate environmental change will continue to erode the capacity of the historical approach (using the past to forecast the future) to predict disturbance, and this at a time when the accuracy of inventory projection is becoming increasingly necessary to achieve sustainability.
4. Understanding what determines insect numbers will improve the usefulness of insect biodiversity studies that seek to explain spatial patterns of species abundance as a function of forest characteristics and land management practices.

We also suggest that the deepest insights in insect disturbance ecology are likely to come from model systems that have been studied for long periods of time, and where much of the basic biology has been worked out. The virtue of the detailed information gained to date is our current ability to design process-oriented research in a tightly structured, comparative framework, combining and interpreting results from a broad array of highly comparable process studies. This ensures a synthesis that applies to more than one forest–insect ecosystem. This is perhaps the most exciting aspect of process-based insect disturbance ecology: the possibility of having spatially explicit, multi-system models that can be used to examine broad questions about ecosystem resilience under multivariate eniviroclimatic regime change.
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REFERENCES


Clark, J. (1961). *Photosynthesis and Respiration in White Spruce and Balsam Fir*. State University of New York, College of Forestry, Syracuse, NY.


REFERENCES


REFERENCES


