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Population Ecology

Paradigms in Eastern Spruce Budworm (Lepidoptera: Tortricidae) Population Ecology: A Century of Debate

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Abstract

Three main hypotheses have been postulated over the past century to explain the outbreaking population dynamics of eastern spruce budworm, *Choristoneura fumiferana* (Clemens). The Silviculture Hypothesis first arose in the 1920s, with the idea that outbreaks were driven by forestry practices favoring susceptible softwood species. In the 1960s, it was proposed that populations were governed by Multiple Equilibria, with warm weather conditions releasing low-density populations from the regulatory control of natural enemies. Dispersal from outbreak foci, or "epicenters," was seen as causing widespread outbreaks that eventually collapsed following resource depletion. However, in the 1980s, following the re-analysis of data from the 1940s outbreak in New Brunswick, this interpretation was challenged. The alternative Oscillatory Hypothesis proposed that budworm population dynamics were governed by a second-order density-dependent process, with oscillations being driven by natural enemy–victim interactions. Under this hypothesis, weather and resource availability contribute to secondary fluctuations around the main oscillation, and weather and moth dispersal serve to synchronize population cycles regionally. Intensive, independent population studies during the peak and declining phases of the 1980s outbreak supported the principal tenet of the Oscillatory Hypothesis, but concluded that host plant quality played a more important role than this hypothesis proposed. More recent research on the early phase of spruce budworm cycles suggests that mate-finding and natural-enemy-driven Allee effects in low-density populations might be overcome by immigration of moths, which can facilitate the onset of outbreaks. Even more recent research has supported components of all three hypotheses attempting to explain spruce budworm dynamics. In the midst of a new rising outbreak (2006-present), we discuss the evolution of debates surrounding these hypotheses from a historic perspective, examine gaps in current knowledge, and suggest avenues for future research (e.g., intensive studies on low-density populations) to better understand and manage spruce budworm populations.

Key words: Population dynamics, density dependence, natural enemy, immigration, Allee effect

The ecological mechanisms that drive periodic oscillations in animal populations have been a subject of intrigue and debate among population ecologists for at least a century (Elton 1924, Graham 1939, Berryman 1996, Liebhold and Kamata 2000). Outbreak-prone herbivorous insects have attracted particularly intense study, because many of them have widespread and severe impacts on agricultural and forestry systems. This has included many empirical studies, of course, but herbivorous insects have also provided the foundations for theoretical debates about the mechanisms of animal population dynamics (reviewed in Berryman 2003). Such theoretical debates cry out for long-term data sets to help resolve them, and while these are unfortunately uncommon, they exist for a number of herbivorous insects.

Long-term studies tend to generate a daunting quantity of data, and surprisingly often, the concordance between long-term data and theoretical expectations is not obvious. This can result in conflicting literature and in the lengthy persistence of conflicting hypotheses about population dynamics. The eastern spruce budworm (*Choristoneura fumiferana* (Clemens), Lepidoptera: Tortricidae; henceforth, just "spruce budworm" or "budworm") exemplifies this conundrum. Despite more than 65 yr of intensive research, multiple long-term studies, and hundreds of published articles, our understanding of budworm population dynamics has seen paradigms shifting through the decades, but no broad consensus has been reached on the ecological factors that drive and modulate population oscillations (Sturtevant et al. 2015).

Spruce budworm has been a favored model system for the study of population dynamics because of its economic impact on the softwood lumber and pulp industry and the boreal forest it exploits. The magnitude and longevity of budworm outbreaks are striking compared with those of other defoliators. During an outbreak, budworm density increases by several orders of magnitude, with hundreds of larvae per branch causing severe defoliation, growth loss, and tree mortality (MacLean and Ostaff 1989, Piene and MacLean 1999). In contrast, during low-density phases, populations are nearly undetectable (Morris 1963a). Spruce budworm outbreaks have a long history in eastern Canada (defined here as Canada east of Georgian Bay [of Lake Huron], including eastern Ontario, Quebec, New Brunswick, Nova Scotia, and Newfoundland), as evidenced by dendrochronological analyses of ancient timber, far preceding the advent of broad-scale forestry practices (reviewed in Boulanger et al. 2012). This is corroborated by recent macrofossil studies in peat cores that report high quantities of spruce budworm frass dating as far back as 6,800 yr before present (Simard et al. 2006). The most recent major outbreak began in the mid-1970s, spanned a 15–20-yr period, and caused nearly 52 million ha of severe defoliation throughout the boreal forests of eastern Canada (National Forestry Database 2015). Nearly three decades have passed since the collapse of that outbreak. However, in 2006, a ~6,000-ha outbreak began to build on the north shore of the St. Lawrence River (Quebec, Canada) and, as of 2015, it has grown to nearly 6.3 million ha with no signs of slowing down (Ministère des Forêts, de la Faune et de Parcs 2015).

Spruce budworm outbreaks have been occurring in eastern Canada for centuries, with an estimated periodicity of 25–40 yr between peaks (Jardon et al. 2003). These outbreaks were documented in a combination of recent field surveys of annual defoliation and population density (Royama et al. 2005) and longer-term dendrochronology data using architectural timbers of fir and spruce (Boulanger and Arseneault 2004). There have been at least eight outbreak cycles since 1700 (including three major outbreaks during the past century) and three presumed outbreaks between 1577 and 1700 (Boulanger and Arseneault 2004). However, the underlying causes of these cycles and the main factors that modulate the rise, spread, and collapse of outbreaks have been debated for over half a century (Graham 1939, Berryman 1996, Sturtevant et al. 2015). Several basic questions are at the center of this debate: 1) What are the agent(s) and interactions that influence the rise and collapse of outbreaks, as well as suppress spruce budworm between outbreaks when populations remain almost undetectable? 2) At the regional level, do rising populations expand contagiously from "hot spots" or "epicenters" or do populations rise more or less synchronously across a landscape? 3) What does our understanding of spruce budworm dynamics tell us about how we should manage outbreaks? These questions are important because they are not unique to budworm. Instead, they have been the subject of long-standing debates about the fundamental nature of animal population dynamics (Turchin and Taylor 1992).

Aspects of these questions have been addressed over the years in several reviews. There are syntheses of the ecology and dynamics of outbreak-prone *Choristoneura* species as a whole (Volney and Fleming 2007, Nealis 2015) and of the spruce budworm in its role as a disturbance agent in comparison with other outbreak pests (Cooke et al. 2007). Two book chapters have also focused on the history and contributions of various modeling approaches to our understanding of budworm dynamics (Régnière and Lysyk 1995, Sturtevant et al. 2015). The goal of our paper is to provide a synthesis of spruce budworm research and the evolution of thought behind population dynamics to a general entomology readership. We have therefore built this review around the three main hypotheses that have been developed to explain spruce budworm dynamics, and we discuss the key arguments, evidence, and knowledge gaps that seem to support or undermine each of them. These three hypotheses are the Silviculture Hypothesis, the Multiple Equilibria Hypothesis, and the Oscillatory Hypothesis (Table 1). It is worth noting that these hypotheses have not been interpreted entirely consistently in the scientific literature and that, to some extent, each hypothesis focused on particular phases of an outbreak. Despite this complexity in detail, however, each hypothesis represents a distinct interpretation of the basic nature of spruce budworm population cycles and the factors that drive long-term population trends.

As is the case for many outbreak pests, answers to questions about population dynamics have implications for forest management. Since some of the earliest studies carried out by Morris (1963a), notions of spruce budworm population dynamics have largely governed prescriptions for managing outbreaks. In this paper, we discuss three management strategies that map more or less directly onto the three hypotheses: attempts to proactively limit forest susceptibility through silviculture, attempts at population containment like those used to manage the spread of invasive pests (i.e., "early intervention strategy"; Régnière et al. 2001), or attempts to merely protect high-value trees with insecticides until outbreaks collapse naturally (i.e., "foliage protection strategy").

We conclude with a discussion of key knowledge gaps and potential directions for research that may help us better understand and manage spruce budworm outbreaks.

Life Cycle

Several articles have detailed the biology and life history traits of spruce budworm (Régnière and Nealis 2007). It is a major defoliator of boreal forests throughout Canada and the northeastern United States, preferring balsam fir, *Abies balsamea* L., white spruce, *Picea glauca* (Moench) Voss, red spruce, *Picea rubens* Sarg., and black spruce, *Picea mariana* (Mill.) B.S.P., in that order (Swaine et al. 1924). It is univoltine and larvae emerge from hibernation in the spring to feed on the new buds of host trees. Larvae develop through six instars while feeding inside protective silken webs that they construct between the needles. Pupation generally occurs in or near the webs, and male and female moths emerge in mid to late summer, depending on local temperatures, to mate and lay egg masses on host needles. Eggs hatch within 2 wk, and after one molt, second-instar larvae walk or balloon on silken threads to locate overwintering sites among scales and furrows of branches and trunks (Jaynes and Speers 1949). These larvae emerge the following spring, disperse to suitable feeding sites, molt into third instars, and begin feeding to continue the cycle.

Long-term Studies

Long-term population studies are the backbone of population dynamics research, and there have been four such studies (i.e., >10 yr) for spruce budworm in eastern Canada (Fig. 1). Morris and his team conducted the first detailed population research on budworm near Green River, in northern New Brunswick, from 1945 to 1972 (Fig. 1A–C). This period encompassed the mid-century outbreak, which peaked in 1949. The "Green River Project" was one of the

Table 1. Summary of the main hypotheses and predictions that have been developed to explain the population dynamics of spruce budworm over the past century

Hypothesis	Key agents influencing the state of population growth			Population behavior	Landscape-level population structuring	Key references
	Low density	Rising	Declining			
Silviculture Hypothesis	Low availability and high vigor of preferred host (balsam fir)	Increased balsam fir availability; age-related decline in tree resistance; diminished predator community complexity/impact	Resource collapse	Relaxed cyclical: Driven by density-dependent bottom-up or top-down interactions (underpinned by human agency)	Anthropomorphic (forestry practices): Shaped by the resulting forest structure	Swaine et al. 1924, Blais 1983, Miller and Rusnock 1993, MacKinnon and MacLean 2003, Eveleigh et al. 2007
Multiple Equilibria Hypothesis	Natural enemy control	Favorable climate (i.e., warm, dry spring weather), resource pulse (i.e., periodic pollen cone production), moth invasion	Resource collapse	Eruptive: "Boom and bust" cycles driven by density-dependent and density-independent interactions with natural agents	Contagious: Shaped by the influx of moths from "hot spots" to surrounding susceptible forests	Morris 1963a,d, Hardy et al. 1983, Régnière et al. 2013
Oscillatory Hypothesis	Natural enemy control	Population escapes natural enemy control due to decline in enemy abundance/impact	Mortality of older larvae and pupae with (sometimes) synergistic impacts of resource collapse	Cyclical: Driven by density-dependent predator–prey interactions	Spatially synchronized: Disjunct populations "evened out" by regional climatic trends and moth dispersal	Royama 1984, Williams and Liebhold 2000a, Royama et al. 2005, Régnière and Nealis 2007, 2008

first studies to use life tables to provide a detailed demographic assessment of stage-specific survival rates (Morris and Miller 1954). That period also saw the development of some of the first analytical techniques for analyzing population data (e.g., key factor analyses; Morris 1963b), and these techniques were used to infer the relative contribution to mortality and population dynamics of various factors from the life-table data. Quiring (2012) provides a more detailed description of the Green River Project. In the early 1980s, when budworm populations rose again throughout eastern North America, interest in field studies was rekindled and population studies were conducted in Ontario and Quebec (Fig. 1D), with data from multiple sites combined for analysis (Nealis and Régnière 2004b, Régnière and Nealis 2007, 2008). Population data were also collected in New Brunswick (Fig. 1E; Royama 1984, Royama et al. 2005, Eveleigh et al. 2007), until populations crashed in the early 1990s. These four relatively detailed studies are complemented by broad-scale defoliation and egg surveys carried out by provinces over the past 60 yr, as well as by tree-ring reconstructions of outbreaks from ancient spruce and fir spanning several centuries (Lynch 2012, Johns et al. 2016). Together, these studies provide most of the data on which our current understanding of spruce budworm population dynamics is based.

Silviculture Hypothesis

The first explicit attempts to explain the epidemiology of spruce budworm began in the first part of the 20th century, and argued that forest management practices played a crucial role in promoting and shaping outbreaks (this is hereafter called the Silviculture Hypothesis; Table 1). Miller and Rusnock (1993) have provided a detailed review of the early history and debate that surrounded this hypothesis. In brief, Tothill (1922) and Swaine et al. (1924) first proposed that increase in intensity of spruce budworm outbreaks was caused by forestry practices. Their observations were based on anecdotal evidence of high defoliation in large stands of mature, even-aged balsam fir stands that regenerated in locations that were subjected to intensive logging (Miller and Rusnock 1993). Population collapse was attributed to the decline of preferred hosts following wide-scale tree mortality, with the period between outbreaks reflecting the time needed for balsam fir forests to regenerate. Although this hypothesis was initially framed using anecdotal reports and some limited field data, evidence from large-scale defoliation surveys after the 1930s seemed to confirm that defoliation had increased across the three successive outbreaks of the 20th century (Brown 1970; Kettela 1983). It was suggested that forestry practices be altered to minimize forest conditions that favor defoliation by the spruce budworm (Miller and Rusnock 1993).

Critics of this interpretation contended that these data were too recent and brief (covering only three major outbreak cycles) to make long-term projections (Morris 1963a; Royama 1984). Attempts were made to support the Silviculture Hypothesis using long-term impact data derived from tree rings, which appeared to confirm an increase in extent and severity of recent outbreaks (Blais 1983). However, these data were also criticized, as dendrochronological approaches are unlikely to detect milder outbreaks and thus would lack the sensitivity needed to confidently gauge outbreak frequency and intensity centuries into the past (Régnière 1985). Finally, as time-series data on spruce budworm began to accumulate, the contention of a tight link between outbreaks and balsam fir regeneration became more dubious. Whereas budworm outbreaks occurred
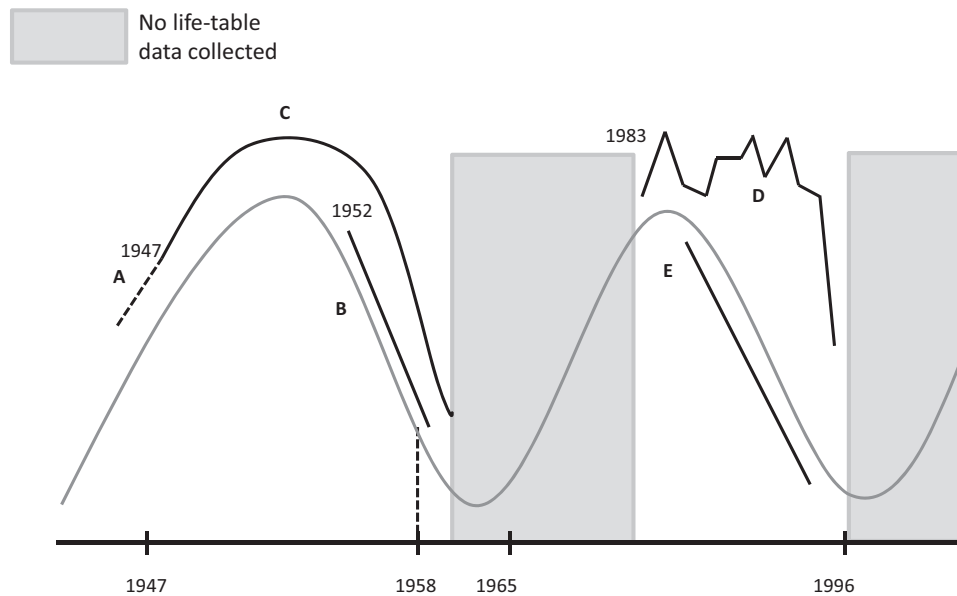
Fig. 1. General trend in spruce budworm density (light line), expressed on a log scale, and timeline of spruce budworm research (dark lines) conducted during the last two spruce budworm outbreaks. A, B, and C: Data from Green River study (Morris 1963a). A: Indirect estimates from 1945 and 1946 of eggs and pupae (this study measured only old larvae and therefore had no estimates of stage-specific mortality). B: K1 and K2 plots. C: G4 and G5 plots (Royama 1984). D: Black Sturgeon Lake (Nealis and Régnière 2004a,b). E: New Brunswick studies (Eveleigh et al. 2007, Royama et al. 2005). Black Sturgeon Lake is considerably west of all other study areas, near the Ontario-Manitoba border.

at approximately 35–40-yr intervals, forest regeneration intervals often exceed 70 yr, making it unlikely that forest maturation alone could explain spruce budworm outbreak periodicity (reviewed in Boulanger et al. 2012 and Sturtevant et al. 2015).

More recently, discussion of the Silviculture Hypothesis has shifted from emphasis on forest age structure and associated resistance (i.e., bottom-up effects) to the effect of forest composition on interactions between budworm and its natural enemies (i.e., top-down effects; Cappuccino et al. 1998). Spruce budworm is part of a remarkably complex food web involving its host, other herbivores, and a rich and multi-trophic set of natural enemies that increases in complexity with increasing budworm density (Eveleigh et al. 2007). Mixed forests (with high hardwood-to-softwood ratio) have greater parasitoid diversity (Cappuccino et al. 1998), and this may help diminish the impact of spruce budworm in mixed forest stands (MacKinnon and MacLean 2003). While this argument offers a compelling twist on the original bottom-up framing of the Silviculture Hypothesis, further analyses are required to fully understand these complex interactions. Unfortunately, few large natural forests remain in the region of budworm outbreaks, making it a challenge to test the Silviculture Hypothesis at a meaningful scale (Miller and Rusnock 1993). However, one notable exception can be found in a recent landscape-level analysis that showed that outbreaks in unmanaged forests were more synchronous, were less frequent, and had defoliated more trees than in forests managed at a fine-scale, thus lending support to the Silviculture Hypothesis (Robert et al. 2012). There is also recent evidence that stand composition influences the locations where rising budworm densities are first observed, and the rate at which high densities spread across the landscape as an outbreak mounts (Bouchard and Auger 2014). However, it is unclear by what mechanisms these effects arise or whether they drive or merely modulate outbreak dynamics.

From a management perspective, support for the Silviculture Hypothesis would primarily suggest a shift in silvicultural practices (reviewed in Miller and Rusnock 1993). For example, proactive management of stand composition could entail decreasing the percentage of even-aged, over-mature stands across the landscape in order to increase broad-scale host resistance. A corresponding increase in hardwood species composition in forests would increase natural enemy abundance and diversity and in turn diminish the impact of spruce budworm outbreaks. However, from an industrial point of view, this would involve making a serious compromise in harvesting efficiency.

Multiple Equilibria Hypothesis

Based on research from the Green River Project (summarized in a large monograph by Morris 1963a), a multiple equilibria structure became the most popular hypothesis to explain spruce budworm outbreaks (Morris 1963a, Ludwig et al. 1978, Clark et al. 1979, Holling 1988; Table 1). Also referred to as the "Double Equilibria Hypothesis," it essentially described a system characterized by two equilibria at low and high population densities (Fig. 2). Because each equilibrium was locally stable, transitions between the two required a triggering event to move the system from one basin of attraction to the other (i.e., across the dashed line in Fig. 2). The lower equilibrium (Fig. 2, left) is presumably maintained by a suite of generalist parasitoids and predators that regulate populations at low density for decades (Miller 1963; this is Holling's [1988] "predator pit"). Escape from this regulatory control is attributed to weather and synchronous production of male cones in balsam fir (Fig. 2, upper curved arrow). Weather becomes an important factor when occasional multi-year spells of warm, dry summers enhance the survival of young larvae (Wellington et al. 1950, Greenbank 1956). Broad-scale synchronously elevated male and female cone production in balsam fir provides overwintering refugia and highly nutritious food for young larvae (Greenbank 1963). Collectively or independently, these two factors boost population growth rates, enabling population levels to rise enough to escape natural enemy
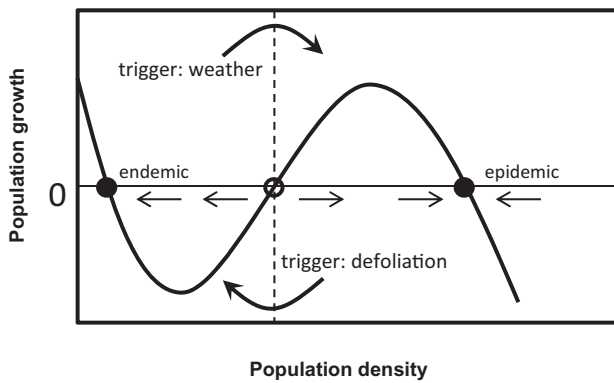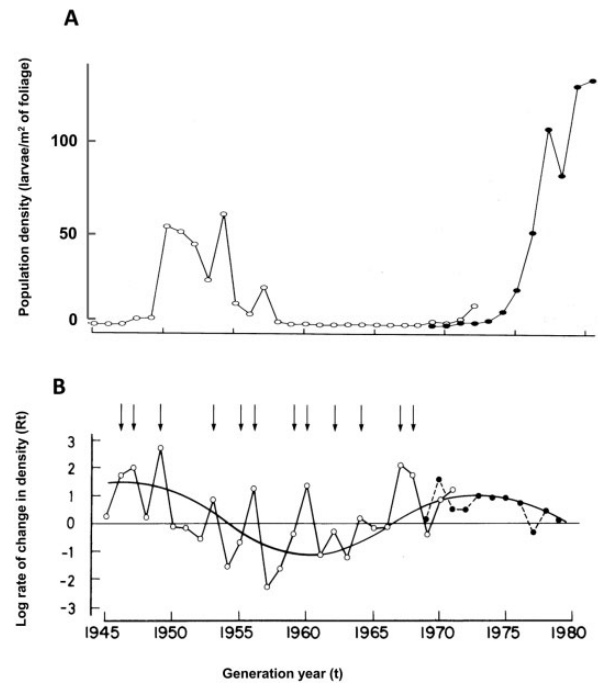
Fig. 2. Population dynamics under the Multiple Equilibria Hypothesis. Dots indicate equilibrium points: the hollow dot is an unstable equilibrium, while the others are locally stable. Straight arrows indicate expected population growth, and the dashed line divides the basins of attraction for the two equilibria. Curved arrows indicate triggers that take the system across the dashed line and thus from one equilibrium to the other.

Fig. 3. Budworm population trends at Green River (from Royama 1984). (A) Raw population density, on a linear scale. (B) Log rate of change from generation t to generation $t+1$ for the time series in (A). Hollow dots are densities of third-instar larvae; solid dots are densities of egg masses. The smooth curve in (B) is drawn by eye. Arrows indicate years of moth immigration.

control. Alternatively, growth of the forest canopy may simply dilute foraging effort by bird predators, again reducing top-down control and allowing spruce budworm populations to escape the lower equilibrium (Ludwig et al. 1978, Holling 1988). A similar phenomenon where there is a fitness increase due to the nutritional effects of male cone production occurs in the jack pine budworm, *Choristoneura pinus pinus* Freeman (Cooke et al. 2007). However, the periodicity of jack pine budworm populations appears to be variable in different parts of its range (Volney and McCullough 1994): 10-yr cycles have been documented in western Canada (Volney 1988), while the periodicity in Ontario remains obscure (Nealis et al. 2003). For a more detailed discussion of comparative ecology of the genus *Choristoneura*, see Nealis (2015). We emphasize that regardless of the specific mechanism, the Multiple Equilibria Hypothesis requires environmental pressure to push local population dynamics away from the low-density equilibrium.

Stands supporting high growth rates subsequently become sources of moths to outlying susceptible areas, which in turn escape enemy control as a result. These expanding "hot spots" or "epicenters" drive the regional spread of outbreaks (Greenbank 1957). As population density increases, it approaches the second equilibrium (Fig. 2, right), where it fluctuates around the carrying capacity of the forest, set by the capacity of trees to replace foliage lost to feeding (Fig. 3A; Morris 1963c, Clark et al. 1979). The eventual population collapse is driven by the diminishing ability of trees to replace lost foliage following repeated bouts of defoliation, coupled perhaps with periods of inclement weather (Morris 1963c, Ludwig et al. 1978). This drives populations down (Fig. 2, lower curved arrow) far enough that natural enemies can re-establish control to maintain the population at the lower equilibrium once again. The mathematics of the Multiple Equilibria Hypothesis are laid out in more detail by Ludwig et al. (1978). In between outbreaks, natural enemies maintain spruce budworm populations at low enough densities that they become rare (Clark et al. 1979). According to Clark et al.'s (1979) model, feedback between spruce budworm performance and host tree quality is faster than the response of natural enemies to changes in spruce budworm population density, as is the population response of spruce budworm compared with growth rates of trees.

This explanation of budworm dynamics had many proponents well into the 1980s (Hardy et al. 1983, Holling 1988). Although it

was not reflected in the budworm management operations of the 1950s, several researchers at the time took the implications of this model to its logical conclusion. A population control strategy would focus on controlling "hot spots" to prevent outbreaks from spreading to surrounding forests (Morris 1963a, Hardy et al. 1983). However, even as this strategy was being proposed, contemporary analyses were raising questions about the basic tenets of the Multiple Equilibria Hypothesis and, in turn, the feasibility of a "hot spot" management strategy. Three things in particular seemed problematic. First, population time-series data showed no signs of prolonged periods of fluctuation around an apparent low equilibrium. A superficial impression of such periods (Fig. 3A) is attributable to linear-scale density plots that conceal substantial population changes at low density. Replotting population data (or better, population growth rates) on a log scale show much more steadily changing populations, with no signs of prolonged stasis at either peak or trough, and no obvious long-term influence of moth dispersal events (Fig. 3B). Second, neither weather nor foliage-depletion effects seem strong or consistent enough to explain outbreaks and collapses (Royama 1984). Finally, the Multiple Equilibria Hypothesis could explain outbreaks and collapses, but not the regular periodicity of density oscillations – at least, not without the additional complication of assuming regular timing of outbreak-triggering events such as favorable weather conditions (and Royama [1981] argued that no such regularity was known). We will take up these objections as we consider the development of the third major hypothesis.

Royama's Oscillatory Hypothesis

All the crucial elements of the Multiple Equilibria Hypothesis were challenged by Royama beginning in the 1980s (Royama 1984, 1992, 2001). Instead, he proposed what is now commonly referred

to as the Oscillatory Hypothesis (Table 1). This shift in thinking was based on the detailed re-analysis of peak-to-collapse population data from the Green River Project (Morris 1963c; Fig. 3A, B). Royama rejected the idea that tree condition was the primary cause of outbreak collapse. His analysis indicated that budworm population decline occurs regardless of tree condition and is therefore caused by other agents. This view was shared more generally by ecologists who were skeptical about the importance of bottom-up effects (resources) on insect population dynamics (Hairston et al. 1960). Royama and others did not entirely dismiss the influence of foliage quality and quantity on budworm population dynamics. Resources clearly influence adult size and fecundity (Blais 1953, Delisle and Hardy 1997). However, the effects of resource quality were now interpreted as driving relatively small annual fluctuations around the main population trend, and were therefore not the cause of sustained population decline across generations (Royama 1992).

The importance of weather (a density-independent factor) in driving outbreak rise (favorable weather) or collapse (unfavorable weather) was similarly rejected. This was due to the general lack of correlation between population fluctuations in time-series data and temperature variations (Royama 1992), as well as the fact that deriving a regular population cycle from multiple equilibria with a weather trigger required that same regular timing in climate. Instead, Royama argued that regional weather patterns synchronized oscillations over broad spatial scales (the Moran effect). It is well-known that spatially correlated density-independent factors, including weather, can synchronize independently fluctuating populations over large areas (Moran 1953, Williams and Liebhold 2000a). Royama also used simulations to show that the modest impact of weather, when moderately correlated across populations, could synchronize budworm populations as well (Royama 1984, Royama et al. 2005). The role of moth dispersal in spreading population increases in an epicentric fashion was also rejected. Immigration could complement the Moran effect in synchronizing population oscillations regionally: suprisingly small rates of immigration are needed to synchronize independently oscillating populations, and they can do so over longer distances than the Moran effect typically does (Jansen 1999, Fox et al. 2011). Immigration could also contribute to small secondary fluctuations in population densities (Royama et al. 2005), but not to longer-term oscillation (Fig. 3B).

Having rejected the Multiple Equilibrium Hypothesis, Royama suggested instead that the primary oscillation arises from attack by natural enemies on late-instar larvae and pupae (the survival of which is most closely correlated with population change; Royama 1984). The action of parasitoids (and perhaps other enemies) can be modeled as generating second-order density dependence, in which population growth rates depend on current population density, and also on the previous year's population density. The latter dependence incorporates the effect of enemy attack (Royama 1981). Thus, the second-order model represents a situation in which spruce budworm populations temporarily escape regulation from top-down control by the gradual decline in natural enemies as larvae become increasingly rare. This escape allows spruce budworm populations to rebound. However, unlike other situations in which ecologists discuss release from top-down control (e.g., invasions, host shifts, predator extinctions), enemy escape in this case arises as an intrinsic part of the enemy–victim dynamics, and so no external trigger is needed either for the initiation or the collapse of an outbreak.

One of the challenges the Oscillatory Hypothesis has to contend with is the long period that separates budworm outbreaks (i.e., 35–40 yr) and the persistence of outbreaks once they manifest themselves (10 yr or more). Such long periods may seem surprising for a

univoltine organism in which dynamics are merely captured by second-order density dependence (i.e., with a time lag of only one generation). However, Royama (1977) showed that simple second-order density-dependent models could generate persistent oscillations of arbitrarily long periods given appropriate strengths of density-dependent feedback from the current and previous generations. More intuitively, Royama (1984) attributed the length of the budworm cycles to the relatively weak response of the parasitoid community to increasing spruce budworm density. For instance, high densities of hyperparasitoids (i.e., parasitoids of other parasitoids) can have a significant impact on the primary parasitoids that attack budworm (Eveleigh et al. 2007), hindering their ability to respond rapidly to increasing budworm populations (Royama 1992, 1997). Moreover, many of the key natural enemies in the budworm food web (Eveleigh et al. 2007) are bivoltine or multivoltine generalists, and they may face bottleneck effects associated with the availability of alternate lepidopteran hosts in spring and/or fall, when budworm larvae are not available. If such alternate hosts are rare, it matters little to parasitoid population growth how many budworm hosts are available (at least over times scales >1 yr; Royama 1997).

From a management standpoint, the Oscillatory Hypothesis undercuts the idea that outbreaks might be contained by a population control strategy that targets "hot spots." Under this hypothesis, apparent hot spots are merely artifacts of areas with particularly favorable conditions for budworm population growth, and, thus, where budworm density rises a little faster than elsewhere. They have little bearing on the overarching population cycles, and treating them would be pointless, as moths from surrounding rising populations would simply repopulate the treated area. This line of argument has been the primary basis for the foliage protection strategy. Foliage protection is essentially a stop-gap measure to limit tree mortality and growth loss by killing larvae with insecticide early in their development (fourth to fifth instar; Carter and Lavigne 1987), before severe defoliation occurs. The decision to treat a particular area would depend on the value of the stand and the likelihood of mortality or growth loss if it is left untreated, and not on the expectation of any broad impact on budworm population dynamics. Foliage protection has been the dominant strategy used to control spruce budworm for as long as management strategies have been implemented (Webb et al. 1961).

Recent Advances

Although many of the main conclusions of the Oscillatory Hypothesis have been upheld through subsequent study, recent work suggests some modifications. Intensive, independent population studies during the peak and declining phases of the outbreaks in Ontario, Quebec, and New Brunswick in the 1980s and 1990s supported the principal tenet of the Oscillatory Hypothesis. Mortality caused by natural enemies was indeed the main cause of the cycling of population density (Royama 1997, Régnière and Nealis 2007). However, at least in the Ontario study, declines in foliage quantity and quality as a result of larval feeding played an important additional role. While Royama argued for the exclusivity of natural enemies in driving population cycles, life-table work by Nealis and Régnière (2004a) and Régnière and Nealis (2007, 2008) suggested that resource limitation could also be important to population decline. In particular, reduced foliage availability associated with severe defoliation diminished early-instar larval survival, thereby temporarily decreasing outbreak severity (Nealis and Régnière 2004b, Régnière and Nealis 2008). However, as the trees recover,
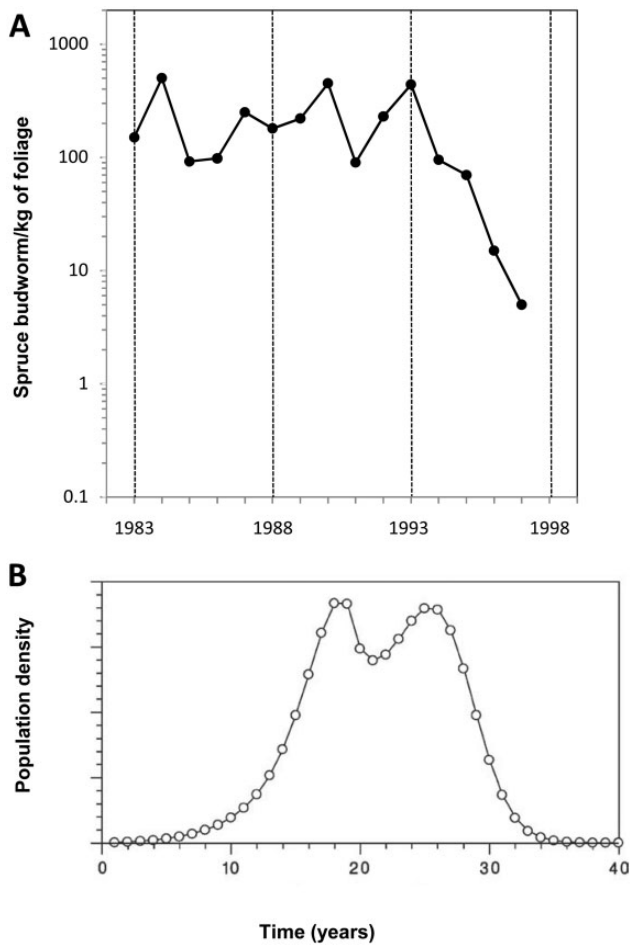
Fig. 4. Idealized representation of spruce budworm outbreak dynamics as a second-order density-dependent process (from Régnière and Nealis 2007). (A) Field estimates of budworm density during peak and early decline; note the strong dips in 1985 and 1991, with subsequent recovery. (B) Simulated outbreak cycle, incorporating defoliation effects but with no stochastic perturbation. The dip during the peak is the result of incorporating defoliation.

populations generally rebound. There could be several such "dips" and subsequent recovery from the highest outbreak level (Fig. 4A), but these are not associated with much variation in mortality due to parasitism (Régnière and Nealis 2007). Instead, complete population collapse occurs only when budworm density drops sufficiently low that natural enemies can regain control. In addition, fecundity is inversely related to defoliation, being highest at the beginning and at the end of outbreaks when defoliation is lowest (Régnière and Nealis 2007). These findings suggest two important roles for bottom-up factors: first, in explaining the "secondary fluctuations" around the outbreak peak that Royama (1984) attributed primarily to weather and moth immigration, and second, in eventually triggering collapse by reducing budworm density to a level at which natural enemies can exert control once again. Régnière and Nealis (2007) adapted Royama's (1984) second-order density-dependent population models to incorporate these effects of defoliation and found that they could indeed predict population cycles with dips and recoveries (Fig. 4B). This body of work reintroduced the importance of host plant quality in shaping—but not actually driving—the outbreak ecology of spruce budworm.

Several researchers have also revisited the importance of weather and moth dispersal in the regional synchronization of budworm populations. In a novel approach connecting population ecology theory to landscape ecology, Williams and Liebhold (2000a) examined empirical evidence for spatial synchrony across the budworm's outbreak range, over a 40-yr period, and found that synchrony decreased with distance and approached zero at a distance of ∼2,000 km. They then used spatially explicit simulations to investigate whether Moran effects and dispersal (singly or in combination) could explain the observed synchrony. In their model, patches were linked by dispersal and were under the influence of "disturbances" (abiotic effects that could include weather) that were either purely local, purely regional, or spatially autocorrelated. They were successful in reproducing the actual spatial pattern in synchrony when 1) populations exchanged dispersers over substantial distances (∼500 km), and 2) the Moran effect was driven by disturbance with spatial autocorrelation out to ∼800 km. Both parameter choices are reasonable: budworm females can disperse over hundreds of kilometers (and very few dispersers are needed to synchronize populations; Jansen 1999), and major weather patterns are autocorrelated over similar distances. Williams and Liebhold (2000a) concluded that the regional synchrony of budworm outbreaks probably results from dispersal acting in concert with spatially autocorrelated Moran effects arising from weather.

Other models have focused on the potential influence of climate change on the distribution and duration of outbreaks (reviewed in Fleming and Volney 1995). These temporal models predict the response of plants and insects over large spatial scales using life-table data collected from individuals in detailed field studies. Important and startling predictions can emerge, such as the possibility that climate change may disrupt the phenological "matching" of budworm with its parasitoids, and thus allow it to escape from natural-enemy regulation (Fleming and Volney 1995). However, the scaling-up of models built from fine-scale data to the coarser spatial scales typical of climate models and regional studies can affect model dynamics in ways that sometimes drastically change model predictions (Fleming et al. 1999, 2002). This realization brought to the forefront the importance of considering the spatial scale in studies of population dynamics (Williams and Liebhold 2000b).

More recent models have predicted that a warmer climate will increase the duration (Gray 2008, 2013) and severity (Régnière et al. 2012, Gray 2013) of budworm outbreaks at northern latitudes (although this conclusion may be host-dependent; see Fierravanti et al. 2015). In fact, the current outbreak began north of the 49th parallel, where historically the impact of spruce budworm was relatively mild (Pureswaran et al. 2015). Warmer temperatures can alter the phenology of host trees, spruce budworm, and natural enemies, and potentially change disturbance regimes, resulting in important changes in nutrient cycling that, in the long term, can alter forest composition and ecosystem functioning (Fleming and Volney 1995, Pureswaran et al. 2015). At more southerly latitudes, the duration and severity of outbreaks may decline (Gray 2013). However, more work (with careful attention being paid to spatial scale) will be necessary to predict future outbreak dynamics with any level of confidence.

Resolving the Enigma of Low-density Populations

All the hypotheses we have discussed have specific explanations of how spruce budworm populations escape the control of natural enemies at the onset of an outbreak. However, herein lies the major data gap for budworm population ecology. Due in part to the

difficulty of studying low-density populations, there are almost no field data covering the key transition from low-density to rising populations, and no experiments testing the predictions derived from each hypothesis. Recent work has sought to address this gap, leading to some reconsideration of previously rejected elements of the Multiple Equilibria Hypothesis. A key prediction of the Oscillatory Hypothesis is that natural enemy populations should gradually decline following the collapse of spruce budworm populations. Consequently, the rise of the next spruce budworm outbreak should be preceded by a reduction in mortality caused by parasitism. From 1992 through 2015, Régnière and his team at the Canadian Forest Service in Quebec City deployed "sentinel" budworm larvae in areas with little or no natural budworm and recorded juvenile mortality associated with parasitoids (Régnière and Martel 2015, see also Fidgen et al. 2000). Surprisingly, even as we face a new rising outbreak, budworm populations appear to still experience extremely high mortality due to attack by generalist parasitoids.

Another prediction of the Oscillatory Hypothesis that has come into question is that moth dispersal plays a negligible role in the spread of populations. There is no doubt that moth behavior and meteorological conditions can combine to effect movement of substantial numbers of individuals over hundreds of kilometers (Sturtevant et al. 2013), but the question is whether or how often this has any impact on local population dynamics. Régnière et al. (2013) showed that at low population density, males have difficulty locating females despite the powerful pheromone signals used by females to attract them (Sanders 1984). Budworm mating success is therefore density-dependent (Fig. 5), and population growth would be hindered at very low density (Régnière et al. 2013). Such mate-finding Allee effects (Robinet et al. 2008, Robinet and Liebhold 2009, Rhainds et al. 2015) need not lead to local population extinction, but could significantly reduce population growth rates and hamper their escape from parasitoid pressure. Mass influx of male moths from high-density source stands could counteract local mate-finding Allee effects by providing mates for females that might otherwise go unmated (Régnière et al. 2013). This recent experimental work suggests the need for further study of low and rising populations.
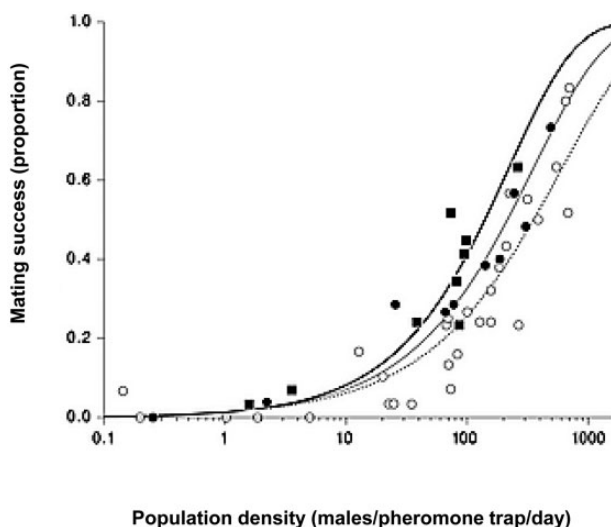

Fig. 5. Relationship between male moth density and female mating success (from Régnière et al. 2013). Hollow dots and dotted line, solid dots and thin line, and solid squares and thick line represent early, mid, and late season trapping periods, respectively, during the 2009 mating season.

The reemphasis on dispersal has also led researchers to revisit the question of whether the population control strategy prescribed under the Multiple Equilibria Hypothesis might yet be helpful for managing spruce budworm. A sizeable research program in Atlantic Canada is currently testing an early intervention strategy that focuses on the control of hotspots to reduce production of dispersers (Régnière et al. 2001, Régnière and Martel 2015). In its operation, this strategy resembles containment strategies used to manage invasive pests in the United States (e.g., the Slow the Spread program for gypsy moth; Tobin and Blackburn 2007). Regardless of the outcome, this work is likely to shed further light on spruce budworm population dynamics.

In conclusion, we have identified three key questions that have underpinned debates around spruce budworm population dynamics. As made evident in our review, progress has especially been made on aspects surrounding the peak and declining phases of outbreaks. In summary, control by natural enemies and, to a lesser extent, declines in resource availability appear to be responsible for the collapse of outbreaks. Control by natural enemies is the primary agent keeping populations at low levels between outbreaks. In general, the argument of the Oscillatory Hypothesis for strong, lagged, density-dependent regulation of populations has been largely upheld. There is strong evidence for spatial synchronization of populations across a landscape, driven by the joint action of weather and moth dispersal (Williams and Liebhold 2000a, Royama et al. 2005). These population features strongly support the foliage protection strategy being the most effective means of managing the impact of spruce budworm. However, recent insights from studies on low-density and rising populations suggest that some degree of population control in "hot spots" or "epicenters" may also be possible.

Although significant progress has been made toward understanding spruce budworm population dynamics, there remains much for us to learn. Recent research has supported components of each of the three hypotheses, but none of them is supported in all its details. This can be attributed to the complex dynamics of spruce budworm populations that incorporate elements from each of those hypotheses rather than exactly fitting any single hypothesis. Spruce budworm researchers appear to have revisited various past paradigms of budworm population ecology and, in doing so, have renewed the debate around how we should manage outbreaks. Such debates are common in population ecology and are not often easily or quickly resolved (Turchin and Taylor 1992). However, periodic syntheses of the debate and evidence are invaluable to ongoing discussions. As suggested in another recent review, a modern synthesis of spruce budworm dynamics is likely to require consideration of reciprocal feedbacks between host trees and spruce budworm and spruce budworm and its natural enemies, the role of moth dispersal, and how these interactions change at different spatial scales, especially in the context of a changing climate (Sturtevant et al. 2015). There are still many data gaps, particularly in the low-density to rising phase of outbreaks, and these need to be filled before we can be certain of the key processes driving and shaping the dynamics of budworm outbreaks. To quote one of the pioneers of spruce budworm population research, Frank Morris (1963a), "[...] applied control, like natural control, cannot be discussed until we understand the dynamics of endemic budworm populations and, particularly, the exact mechanism of population release."

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