Chapter 9
Foliage Feeders

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9.1   Introduction

One of the most significant categories of insects that cause damage to trees are the defoliators. While many orders of insects feed on tree foliage, in this chapter we will focus on Lepidoptera, as there are so many Lepidopter larvae (caterpillars) that are known for their extensive tree damage. In this chapter we review the impact of foliage feeders on forest trees and stand composition, and the ways in which densities of these species or the defoliation they cause are monitored. We do not cover insects attacking ornamental trees in the landscape, nor do we cover insects feeding exclusively on foliage tips or buds. The species we include live and feed externally on the leaves and remove or consume leaf tissue that may or may not include leaf veins. Other species, called leaf miners, live and feed as larvae between the upper and lower surface of the leaf and produce characteristic patterns of leaf damage. Most of those species are considered pests of ornamental trees and are not included in this chapter. We provide more detail on two key species as case studies: winter moth, *Operophtera brumata* L, and spongy moth, *Lymantria dispar* L. These species are two of the most widely studied of all foliage-feeding insects attacking forest trees. Treatment of other important species such as spruce budworm, *Choristoneura fumiferana,* would produce a chapter too long for the current volume. That species, and others like it, are included in a table (Table 9.1) of the world's most forest-damaging Lepidoptera and Hymenoptera, along with key references that provide access to the most recent and important literature.

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9.2 Effects of Defoliation on Forest Trees

The general public often views defoliation in terms of aesthetics and potential economic effects. Beyond simply affecting the growth and life of the defoliated trees, defoliation has many indirect effects that have implications for future defoliator population dynamics and forest nutrient cycling, in turn affecting overall forest composition.

Defoliation that removes some or all of the leaf canopy of trees has a large impact on the ability of trees to produce carbohydrates, and most studies have shown foliage loss to be directly proportional to reductions in tree growth. While defoliation can cause tree mortality, this often occurs indirectly, as defoliation increases the susceptibility of trees to secondary insects and disease, which then are the ultimate cause of tree mortality (Kulman 1971). Outbreaks of defoliators are major events in forests worldwide and may produce landscape-wide patterns of tree mortality and result in major changes in stand tree species composition.

Even if there is no current folivore outbreak, trees may still be suffering the effects of past defoliation events. For instance, a study done in Cerro Castillo National Park by Piper, Gundale and Fajardo (2015) on *Nothofagus pumilio*, a South American deciduous tree, found that natural defoliation by *Ormiscodes amphimone* (Saturniidae) did not cause tree mortality. However, defoliated trees showed significantly stunted growth in comparison to non-defoliated trees. Contrary to previous assumptions, this growth limitation could not be explained by limitations in C and N availability. Defoliation by the larvae of the invasive winter moth (*Operophtera brumata* L.) has been shown to cause a significant reduction in radial growth and latewood production of *Quercus* trees in the same year as defoliation, as well as a reduction in earlywood production the subsequent year (Simmons et al. 2014).

Many trees produce defensive compounds in their leaves, such as phenolics or tannins, to defend themselves against free-feeding insects (Feeny 1970). On the other hand, many foliage-feeding insects are well adapted to cope with these compounds in their diet. There exists a very large literature dealing with the mode of action of tannin or phenolic compounds on insect performance, and whether or not trees respond to defoliation by producing more defensive compounds (Salminen and Karonen 2011).

When it comes to tree resistance to defoliators, there are two main types of resistance: constitutive (always present) and induced (as the result of defoliation). These effects may be either direct, wherein the plant produces either mechanical or molecular herbivore deterrents, or indirect, whereby they put up defenses, chemical or otherwise, that attract defoliator predators or parasitoids (War et al. 2012).

An important molecular mechanism plants use for defoliation resistance is the production of phenolic compounds, such as tannins, which include hydrolysable tannins, proanthocyanidins, and phlorotannins. Different kinds of tannins have greater impacts on different types of herbivores. In insects, different parts of the digestive system have different pH levels, and, as a result, differently structured tannins will react and metabolize differently in different sections of the gut, as they

are hydrolyzed or oxidized. Rather than tannins themselves, it is possible that tannin metabolites are what actually affect herbivores (Salminen and Karonen 2011).

Tannins may serve as an important factor in tree constitutive resistance. Although some herbivore species have adapted to feed on certain tannins, for non-adapted defoliators they can serve as a feeding deterrent. Tannins may also be important for induced defenses, as multiple studies have shown tannin production increases with insect damage. However, there are many other factors at play, and tannin concentration is affected by things such as environmental stress. There are so many different specific types of tannins produced by plants and so many potential interactions that most current studies are correlative rather than causative (Barbehenn and Constabel 2011). For instance, there have been disparate findings on the relationship between tannin content and amount of defoliation. A recent study on spongy moth defoliation on *Quercus ilex* found no relationship (Solla et al. 2016).

Haukioja (1991) reviewed studies on tree-induced resistance to insect defoliation. While in general insect growth rate declined with decreased food quality, there were very mixed results about the effect of induced responses. Some studies showed that foliage damage induced changes in present and future leaves that were detrimental to insects, while others showed no effect of induced resistance. To complicate matters, other studies mentioned in the review showed improved performance of insects that fed on defoliated trees. Haukioja's review made an important distinction between rapid and delayed induced resistance. The latter refers to changes in foliage chemistry that persist one or more years beyond the defoliation event, rather than those immediately following the defoliation in the same year. Only delayed induced resistance can cause the delayed density-dependent responses (see Chapter 7) that might cause forest insects to exhibit population cycles. Such effects have been proposed for autumnal moth (Haukioja 1991) and for larch budmoth (see Chapter 7; Baltensweiler and Fischlin 1988). In many cases it is not clear whether the changes in foliage chemistry involve defensive compounds or delayed effects on foliage that affect their nutrient quality.

White spruce (*Picea glauca*) trees resistant to defoliation by spruce budworm had different phenolic compounds present than non-resistant trees. Those phenolic compounds present in resistant trees were found to reduce fitness of spruce budworms (Delvas et al. 2011). However, as shown in a recent study, spruce budworm (*Choristoneura fumiferana* (Clem.)) that fed on resistant white spruce trees (*Picea glauca* (Moench) Voss) had greater fitness than those that fed on susceptible trees (Quezada-Garcia et al. 2015). Hodar et al. (2015) found that the chemical defenses in three species of pine were constitutive rather than induced. Several important herbivores are undeterred by these defenses, such as the pine processionary moth (*Thaumetopoea pityocampa*). Ultimately, as summarized by War et al. (2012), there is still much work needed to understand the biochemical response of induced resistance and how it is invoked by insect feeding.

9.3 Monitoring for Defoliation and Changes in Defoliator Population Densities

Defoliation has typically been mapped by aerial survey. For example, aerial maps of spruce budworm outbreaks have long been produced by the Canadian Forest Service (Fig. 9.1a). Annual defoliation maps of spongy moth in the eastern United States have been analyzed extensively to detect multi-annual cycles and spatial synchrony of spongy moth populations (Liebhold et al. 2004; Johnson et al. 2006b; Bjørnstad et al. 2008, 2010; Haynes et al. 2013, 2018a). Elkinton et al. (2014) used aerial survey maps of winter moth defoliation to estimate rates of spread of winter moth in the northeastern United States. More recently, imagery obtained from satellites or other forms of remote sensing has been used to map and analyze the expansion of defoliator outbreaks. Pasquarella et al. (2018) used Landsat imagery to portray the extent, severity and spread of spongy moth outbreak in the northeastern United States (Fig. 9.1b). Jepsen et al. (2009a) analyzed MODIS satellite data to relate winter moth defoliation to the timing of spring bud-burst in northern Fennoscandia. See reviews by Hall et al. (2006) and Chapter 19 for more detailed discussion of this topic.

Pheromone traps have often been used to map the spread of invasive species on the landscape. For example, Elkinton et al. (2010) used pheromone-baited traps to monitor the extent of the new invasion of winter moth in the northeastern United States (Fig. 9.2a) and its subsequent spatial spread (Elkinton et al. 2014). By far the most extensive use of pheromone traps anywhere in the world has been the Slow the Spread Program (Tobin and Blackburn 2007) to monitor the spread of spongy moth (Fig. 9.2b). Each year more than 100,000 traps are deployed along this invasion front. Pheromone traps are less frequently used to monitor changes in density of outbreak species in regions where they are native or widely established because such traps often fill to capacity even in low-density populations. Therefore, it is more
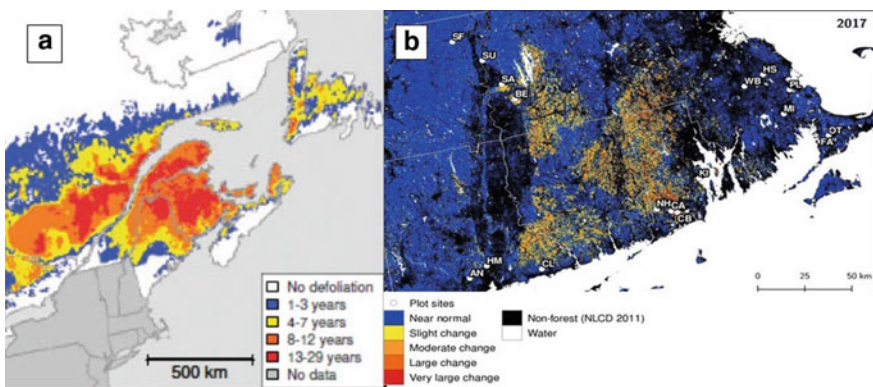
Fig. 9.1 (a) Years of defoliation by spruce budworm in eastern Canada 1954–1988 mapped by aerial survey (Williams and Birdsey 2003); (b) Defoliation by spongy moth mapped from Landsat satellite images (Pasquarella et al. 2018; Elkinton et al. 2019)
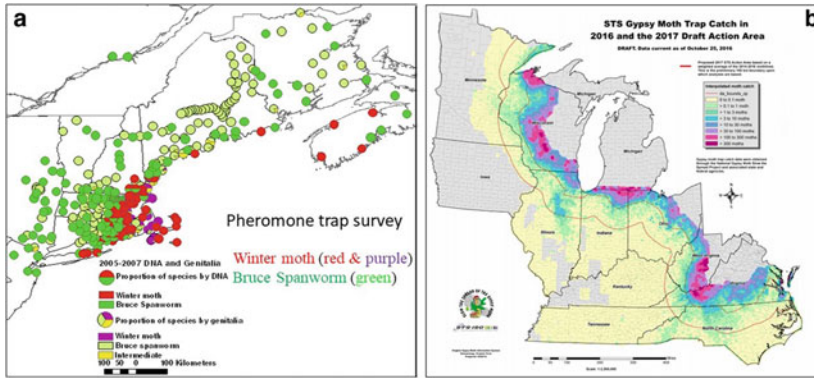
Fig. 9.2 (a) Distribution of winter moth and Bruce spanworm in pheromone-baited traps in northeastern North America in 2005–2007. Winter moths use the same pheromone compound as the native species Bruce spanworm, O*perophtera bruceata.* Identification of moths is based on male genitalia and the DNA sequence of the COI mitochondrial gene (Elkinton et al. 2010); (b) Isopleths of numbers of spongy moth males per trap captured in more than 100,000 pheromone-baited traps in 2019 from Wisconsin to North Carolina (US Forest Service Slow the Spread Annual Report 2019)

common to use sampling of other life stages, such as egg mass counts for spongy moth, to measure changes in population density. See Chapter 19 for a more thorough discussion of this topic.

9.4 Case Study 1: Winter Moth

9.4.1 Biology and Host Range

The winter moth, *Operophtera brumata* L, is a geometrid species that is native to Europe, where it is one of the most common Lepidoptera feeding on a wide range of tree species. These include oaks (*Quercus*), maples (*Acer*), birches (*Betula*) and many others (Wint 1983). It is an occasional orchard pest, because it performs extremely well on apple (*Malus*). It is also especially damaging to blueberry (*Vaccinium*) crops, because the larvae feed inside the buds, where they are inaccessible to most pesticides and destroy developing berries before the buds open. In Europe, outbreaks of winter moth have occurred on Sitka spruce (*Picea sitchensis)* (Stoakley 1985; Watt and Mcfarlane 1991), on heather (*Calluna vulgaris*) in Scotland (Kerslake et al. 1996), and on mountain birch (*Betula pubescens czereapanovii*) in Fennoscandia (Jepsen et al. 2008).

Winter moth gets its name from the fact that adults typically emerge in November or December. The females attract males with a pheromone (Roelofs et al. 1982) and, after mating, lay eggs singly on the bark of host trees and overwinter in this stage. Winter moth larvae typically hatch at or before budbreak of their host trees

and then bore into the expanding buds, so much of the damage occurs before leaf expansion. Classic work by Feeny (1970) proposed that winter moth is one of a suite of early spring-feeding Lepidoptera larvae that are relatively intolerant to accumulated tannins in oak foliage. Even though there may be many larvae per bud in outbreak populations, defoliation of oak and maple in New England, at least, rarely approaches 100%, presumably because the larvae finish feeding and pupate before defoliation is complete. Given that pupation occurs before the end of May, Pepi et al. (2016) showed that winter moth larvae disperse from partially defoliated oak leaves, possibly in response to tannins or other compounds induced by defoliation. Although the typical damage caused by winter moth results in only partially defoliated leaves, this can cause lasting damage to the tree, especially when defoliation persists year after year, as it did in Nova Scotia in the 1950s (Embree 1965, 1967) and Massachusetts after 2004 (Elkinton et al. 2014). Simmons et al. (2014) showed that defoliation by winter moth caused significant decline in tree growth in red oak (*Quercus rubra* L.) in Massachusetts, as measured by growth rings in increment cores of tree stems. Embree (1967) reported that repeated defoliation by winter moth resulted in as much as 40% tree mortality in red oak stands in Nova Scotia.

9.4.2   Geographical Range

Winter moth occurs in every European country, as well as Iran and Tunisia. Early reports included the Russian Far East and Japan, but the Japanese population was redescribed as *Operophtera brunnea* (Nakajima 1991). Recent collections from the Russian Far East suggest that those populations also are closely related to *O. brunnea* (Andersen et al. unpublished). Winter moth has been introduced to four distinct locations in North America: Nova Scotia in the 1930s (Hawboldt and Cuming 1950), Oregon in the 1950s (Kimberling et al. 1986), the region around Vancouver, British Columbia in the 1970s (Gillespie et al. 1978) and in the northeastern United States in the 1990s (Elkinton et al. 2010). Recent studies of winter moth DNA (microsatellites) from these populations by Andersen et al. (2021a) indicate that all four populations represent separate introductions from different European sources. The same techniques show that European populations of winter moth arose from distinct eastern and western forested glacial refugia that existed at the height of the last Ice Age 20,000 years ago (Andersen et al. 2017). Molecular analyses also have shown that in North America winter moth readily hybridizes with a native congener Bruce spanworm, *O. bruceata*, (Elkinton et al. 2010; Havill et al. 2017), that hybridization occurs in all regions where winter moth is known to have invaded (Andersen et al. 2019a), and that, at least in the northeastern United States, the hybrid zone appears to be stable in nature, existing under a tension hybrid zone model (Andersen et al. 2022).

9.4.3 Early Ecological Studies

Winter moth is one of the most famous of all forest insects, due in large part to the classic work by Varley and Gradwell (1960, 1963, 1968, 1970) and Varley et al. (1973), who collected annual life table data on this species on four oak trees near Oxford University in England during the 1950s and 1960s. They introduced important methodology for collecting annual data on density and mortality of different life stages and how to analyze the data to detect the presence of density-dependent factors regulating density and the causes of year-to-year changes in density. Based on these studies, they concluded that winter moth densities were typically regulated at low density by a community of predators that preyed upon winter moth pupae in the leaf litter beneath the infested trees. Subsequent research suggested that pupal predation was caused mainly by staphylinid and carabid beetles (Frank 1967). Other sources of mortality, including overwintering mortality and larval mortality combined, were not density-dependent, but experienced large year-to-year variation in impact and were thus responsible for the observed changes in population density. Varley and Gradwell used the term 'key factor' to describe such mortality factors.

Varley and Gradwell (1960, 1968) believed that the main cause of overwintering mortality was the periodic failure of winter moth hatch to adequately synchronize with budburst of their principal host trees, mainly oaks (*Quercus*). These ideas have been supported by research in North America (Embree 1965) and by Jepsen et al. (2009b), who studied outbreaks of winter moth in northern Fennoscandia.

9.4.4 Pathogens

Like most outbreak species of forest Lepidoptera, winter moth larvae are killed by a nuclear polyhedrosis virus (NPV) (Wigley 1976; Raymond et al. 2002; Raymond and Hails 2007). This virus has been recovered from winter moth in North America (Burand et al. 2011; Broadley et al. 2017), but it rarely, if ever, causes a major epizootic resulting in the collapse of outbreak populations. The virus is thus different from those that occur in other forest Lepidoptera such as spongy moth, *Lymantria dispar,* (Campbell and Podgwaite 1971) or forest tent caterpillar, *Malacosoma disstria* (Cooper et al. 2003), whose outbreaks are typically terminated by these agents. Broadley et al. (2017) showed that the NPV of winter moth was closely related to, but distinct from, an NPV recovered from Bruce spanworm (*O. bruceata*), the North American congener of winter moth. These two NPV's were not cross-infective in the other species, discounting an earlier suggestion (Murdoch et al. 1985) that declines of winter moth in Nova Scotia in the 1950s might have been partially caused by infection of winter moth populations with viruses derived from Bruce spanworm.

Microsporidia are another pathogen that have been recovered from winter moth in Europe (Canning 1960; Canning et al. 1983) and were recorded by Varley et al. (1973). Broadley (2018) showed that microsporidia in North America (Donahue et al.

2019) were a major source of mortality in the rare outbreak populations of the North American congener of winter moth, Bruce spanworm, *O. bruceata*. They have not been recovered from winter moth in North America (Broadley 2018).

9.4.5 Biological Control in North America

Winter moth invaded Nova Scotia in Canada sometime before 1930 and soon caused widespread defoliation of oak forests in that region (Hawboldt and Cuming 1950). Beginning in 1954, Embree and colleagues undertook what would become one of the most famous biological control successes in forest entomology of all time (Embree 1966; Murdoch et al. 1985; Roland and Embree 1995; Kenis et al. 2017). Embree and his colleagues introduced several parasitoid species from Europe, two of which, the tachinid *Cyzenis albicans* and the ichneumonid *Agrypon flaveolatum*, began to cause high levels of mortality in winter moth populations after 4–5 years (Fig. 9.3a). By 1962, winter moth densities had declined to non-pest status, where they have remained ever since (Fig. 9.3a). Hassell (1980) presented a simulation model of *C. albicans* impact on winter moth that appears to explain why in Nova Scotia it was effective at suppressing winter moth populations, whereas it seemed to play a minor role in the population studied by Varley and Gradwell in England. The model was built on his earlier life table studies of *C. albicans* in England (Hassell 1968, 1969a, 1969b).

Similar biological control efforts were undertaken in the 1970s following an introduction of winter moth to Southwest British Columbia in Canada. Winter moth densities there soon declined following the onset of high levels of parasitism, mainly by the tachinid *C. albicans* (Roland 1986; Roland and Embree 1995). Yet another successful biological control effort was initiated by Elkinton et al. (2018, 2021)
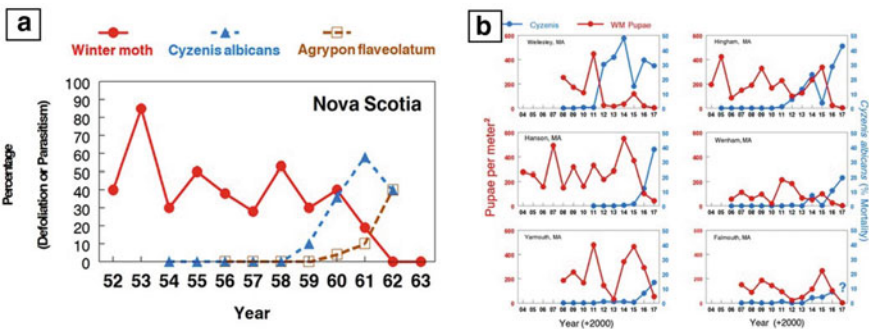
Fig. 9.3 (a) Defoliation by winter moth and percent parasitism by *C. albicans* and *Agrypon flaveolatum* in Nova Scotia in the 1950s following parasitoid release in 1954 (adapted from Embree 1965); (b) Density of winter moth pupae and percent parasitism by *C. albicans* at six widely spaced release sites in Massachusetts (Elkinton et al. 2018)

(Fig. 9.3b) against an outbreak of winter moth that appeared in the northeastern United States in the late 1990s (Fig. 9.1a) Elkinton et al. (2010). This effort was based solely on the release of the tachinid *C. albicans,* because *Agrypon flaveolatum,* the other parasitoid released in Canada, was deemed too much of a generalist and also of uncertain taxonomy. Over 14 years Elkinton and his colleagues established the fly at 41 release sites in New England and observed a substantial decline in winter moth densities (Fig. 9.3b) (Elkinton et al. 2018, 2021).

9.4.6 Population Ecology in North America

Roland (1990b) analyzed the decline of winter moth densities associated with the onset of parasitism by *C. albicans* in Nova Scotia and in British Columbia. He concluded that the decline was caused mainly by predation rather than parasitism and that the presence of *C. albicans* enhanced predation rates on winter moth pupae. He proposed several possible mechanisms for this phenomenon, which included reductions of winter moth densities to levels below which predators were saturated and caused inversely density-dependent mortality, or that parasitized pupae provided a food resource available in the spring months following the emergence of un-parasitized pupae in November and December. He further provided evidence that pupal predators caused density-dependent mortality that regulated the low-density populations of winter moth following the population decline induced by the presence of *C. albicans* (Roland 1994, 1995). Broadley et al. (2022) analyzed data from the recent biological control success in the northeast United States and confirmed Roland's findings that low-density populations of winter moth following the onset of high parasitism by *C. albicans* were regulated by density-dependent predation by a suite of pupal predators. Broadley et al. (2019) also discovered a parasitoid, *Pimpla aequalis* that consisted of two cryptic species causing density-dependent mortality of winter moth pupae. Broadley et al. (2022) found no evidence in support of Roland's findings that the presence of *C. albicans* enhanced predation on winter moth pupae.

Other research on winter moth population ecology in North America includes the life table studies of outbreak populations of winter moth in stands of red oak, *Qurecus rubra*, in Nova Scotia prior to the establishment of parasitoids (Embree 1965). Embree found that the main cause of population change in outbreak populations was synchrony of winter moth hatch with budburst, confirming similar conclusions reached by Varley et al. (1973) in England. In years where spring occurred phenologically early, hatch was well synchronized with budburst, yielding high larval survival. In contrast, in years where springtime warming came later, synchrony was poor and larval survival low. Embree's research was followed up by MacPhee et al. (1988), who studied the lower-density populations of winter moth that existed on apple trees in Nova Scotia over the decade that followed the population decline induced by *C. albicans* in the early 1960s. He found that both *C. albicans* and *A. flaveolatum* caused parasitism in the range of 10 to 20%, far lower than the values observed by Embree in high-density populations in the early 1960s. These findings

reinforce the idea that *C. albicans* has its biggest impact on high-density populations of winter moth. A principal reason is that this species is attracted to defoliated trees and oviposits tiny (micro-type) eggs on partially eaten leaves (Hassell 1968, 1980; Roland 1990a; Roland et al. 1995). Winter moth becomes parasitized by *C. albicans* only when the larva consumes the egg. These eggs then hatch, and the larval fly migrates to the salivary glands of the winter moth larva, where it stays until the moth stops feeding and drops to the ground to pupate. After this, the larval fly completes development, kills the winter moth pupa and forms a puparium inside the pupal cadaver.

9.4.7 Recent European Studies

In recent years, European research has focused mainly on the outbreaks of winter moth in northern Fennoscandia (Tenow et al. 2007; Jepsen et al. 2008). Winter moth outbreaks occur approximately every 10 years in the mountain birch (*Betula pubescens czereapanovii*) forests of that region in synchrony with, but lagging 2–3 years behind, those of another well-studied geometrid, the autumnal moth, *Epirrita autumnata* (Tenow et al. 2007). Jepsen et al. (2008) showed that outbreak populations of winter moth in this region were moving to higher altitudes in response to climate change (Fig. 9.4a) and were moving into forests formerly occupied only by autumnal moth. Consecutive outbreaks of both species are threatening widespread mortality of the mountain birch forests. Vindstad et al. (2022) documented the more recent spread of winter moth into willow (*Salix*) stands in the subarctic tundra of northeastern Fennoscandia.

Jepsen et al. (2009a, 2009b) used multitemporal remotely-sensed data of leaf-out and defoliation to show that favorable synchrony of winter moth hatch with budbreak fueled the synchronous outbreak of winter moths during the increase phase of the population cycle. The spatial synchrony was reduced during the peak and declining phase of the outbreak. Analyses by Tenow et al. (2013) indicated that waves of defoliation by winter moth spread from east to west across Europe approximately every 10 years. However, subsequent analyses challenged that conclusion (Jepsen et al. 2016), and no underlying mechanism for such a phenomenon has been proposed, especially since weather systems at that latitude move from west to east and winter moth females are incapable of flight.

Vindstad et al. (2013) reported the complex of larval parasitoids attacking winter moth and autumnal moth in Norway and compared it to the complex from other sites in Western Europe. These parasitoids included a total of 18 species, including five ichneumonids, three braconids, nine tachinids and one eulophid. The majority of these species occur in winter moth in northern Fennoscandia, with the exception of the tachinids, such as *C. albicans,* which do not occur there, despite being very common elsewhere (Vindstad et al. 2013). Recent studies by Schott et al. (2010) of winter moth mortality caused by these other larval parasitoid species often showed levels of mortality exceeding 50% in northern Norway. However, they do not appear
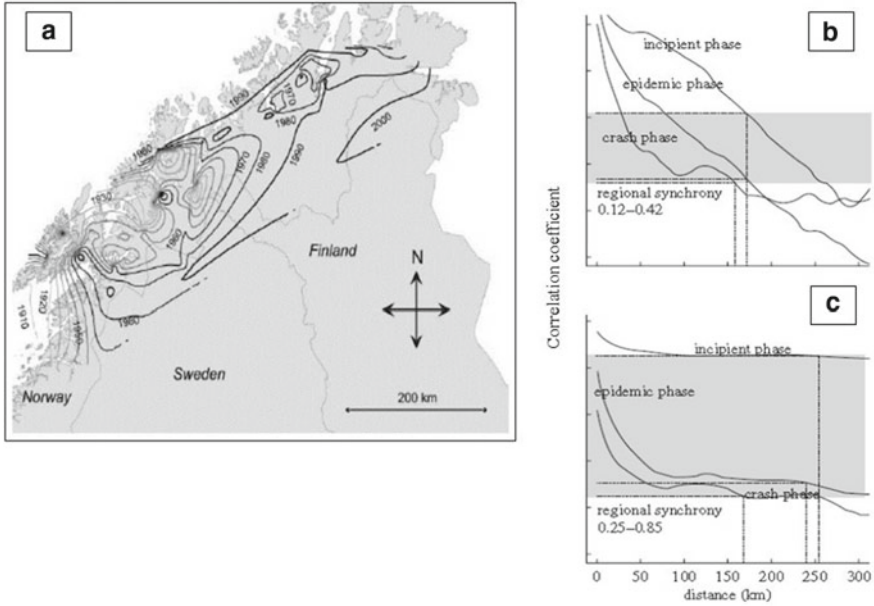
Fig. 9.4 (a) Contours connecting years of first outbreaks of winter moth in northern Fennoscandia abetted by climate change (Jepsen et al. 2008); (b) Spatial synchrony of winter moth outbreaks and; (c) spring bud-burst phenology in mountain birch forests in the incipient, epidemic and crash phases of the winter moth outbreak (Jepsen et al. 2009b)

to be responsible for the decline of outbreak populations. In contrast, Klemola et al. (2010) concluded from manipulative experiments that larval parasitoids are responsible for the decline of outbreak populations of the autumnal moth in northern Finland. Meanwhile, Schott et al. (2013) reported that outbreaks of winter moth in northern Norway are not caused by the release of winter moth populations from regulation at low density by invertebrate predation. It is evident that, despite all this research, the role of natural enemies in the dynamics of winter moth in northern Fennoscandia remains unresolved.

Other recent research has used modern molecular techniques to analyze the expansion of the winter moth's range across Europe and the European origins of winter moth in North America. Gwiazdowski et al. (2013) sequenced the CO1 barcoding gene in a world-wide study of winter moth males collected using pheromone traps and found that nearly all the sampled individuals in the four North American populations shared a single haplotype. However, this haplotype was also found in winter moths collected from 10 of the 11 sampled European countries. This study was thus unable to determine the European origins of winter moth in North America. The lack of genetic diversity revealed by Gwiazdowski et al. (2013) was surprising given the fact that female winter moths are flightless, and thus strong biogeographic patterns might be expected. In a follow-up study, Andersen et al. (2017) examined gene regions called

"microsatellites" that have greater sensitivity than the CO1 barcode gene for examining the genetic structure of populations. They showed that one possible explanation for the lack of genetic diversity in Europe found by Gwiazdowski et al. (2013) is that winter moth populations in central and western Europe (Fig. 9.5) represent a blend of populations from eastern Europe and the Iberian peninsula. They argue that this pattern arose as a result of widely separated forest refugia on the Iberian peninsula and in southeastern Europe during the last glacial maximum (Fig. 9.5).

Subsequent analyses of moths collected in the Mediterranean region have identified two additional glacial refugia: one in southern Italy and another in North Africa (Andersen et al. 2019b). A follow-up analysis showed that winter moth invaded northern Scandinavia via the United Kingdom instead of alternate routes via Denmark or eastern Europe (Andersen et al. 2021b). More recently, these microsatellite markers have been used to reexamine the geographic origins of the invasive winter moth populations in North America (Andersen et al. 2021a). These analyses show
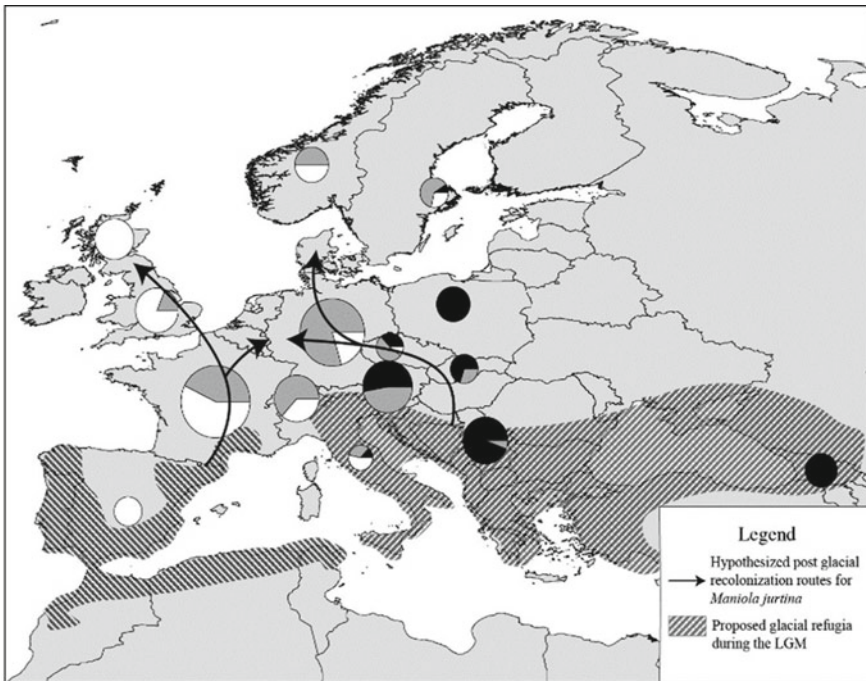
Fig. 9.5 Genetic diversity of winter moth in Europe with populations that utilized glacial refugia of the forests in southern Europe on the Iberian peninsula at the height of the last glacial maximum about 20 thousand years ago shown in white, eastern Europe shown in black, and populations that are admixed shown in grey. The populations into northern Europe represent a merger of these two populations following the retreat of the ice sheet (adapted from Andersen et al. 2017). The hash-marked lines represent the likely locations of glacial refugia during the last glacial maximum, and the arrows represent the likely post-glacial recolonization route of winter moth similar to that of another European Lepidoptera, the meadow brown, *Maniola jurtina* (adapted from Schmitt 2007)

that each one of the four North American populations of winter moth (Nova Scotia, New England, British Columbia and Oregon) are all quite distinct from one another and probably represent separate introductions (Andersen et al. 2021a). In addition, the populations from Nova Scotia, British Columbia, and New England all appear to be introduced from western Europe (likely France or Germany), while the population in Oregon appears to be introduced from somewhere in the British Isles.

Other European studies have focused on the effects of climate change on the timing of winter moth hatch in spring. Winter moth larvae have been hatching earlier and earlier as spring temperatures have become warmer over the last several decades. Although winter moth is rarely a significant defoliator in central Europe, it is an important source of food for nesting birds in the spring. Migratory birds have timed their arrival based on solar cues and in recent years have arrived too late after winter moth larvae have finished feeding and dropped to the forest floor to pupate (Visser et al. 1998). Visser and Holleman (2001) showed that warmer springs have caused winter moths to desynchronize with budbreak of oaks (*Quercus* spp.), their principal host tree, and shift to other tree species that break bud earlier. They also showed that egg hatch in spring is influenced by factors more complex than predicted by growing-degree-day models that are widely used to predict hatch of most insects in the spring. Hatch times in their model were also influenced by the number of winter days below freezing. Hibbard and Elkinton (2015) applied this model with some success to egg hatch data in North America. Salis et al. (2016) proposed a revised model, wherein developmental rate of winter moth eggs as a function of temperature increased with egg age or egg development (see also Gray, 2018). Elkinton is currently attempting to fit versions of these models for egg hatch and bud-break to data from North America. Van Dis et al. (2021) have provided detailed information on the effects of temperature on embryonic development of winter moth eggs.

9.5 Case Study 2: Spongy Moth

9.5.1 Biology

Spongy moth, *Lymantria dispar* L. (formerly called gypsy moth) is another major defoliator, mainly of deciduous trees, that is native to both Europe and Asia. Three subspecies have been described (Pogue and Schaefer 2007): European spongy moth (*Lymantria dispar dispar*), Asian spongy moth (*Lymantria dispar asiatica*), and Japanese spongy moth (*Lymantria dispar japonica*). Although spongy moth females have wings and the Asian subspecies tend to be capable of flight, most populations of the European subspecies *L. dispar dispar* do not fly (Keena et al. 2008). Spongy moth females mate in mid-summer and lay egg masses that contain from 100–1000 eggs on the stems of trees, rocks or other objects and cover them with their tawny brown body hairs. Larvae hatch in spring coincident with host tree budburst and develop through five (males) or six (females) larval instars until late June or early July, depending on

latitude. Late-instar larvae in low-density populations seek daytime resting locations under bark flaps or on the forest floor, presumably as a defense against day active predators and parasitoids (Lance et al. 1987). Pupation typically occurs in these resting locations. Adults emerge in mid-summer. There is one generation per year.

9.5.2 Introduction to North America

European spongy moths (*L. dispar dispar*) were introduced into North America in 1868 or 1869 by Leopold Trouvelot for the purpose of various experiments. The insect escaped from his home in a suburb of Boston, Massachusetts and began to spread across the landscape. Trouvelot tried to notify local officials of the potential problem resulting from his accident, but his efforts were ignored until widespread defoliation in his neighborhood became apparent in the late 1880s. The Massachusetts state legislature allocated funds to eradicate spongy moth by mechanical removal of egg masses and applications of primitive pesticides such as lead arsenate (Spear 2005). This effort failed and spongy moth continued to spread, albeit quite slowly, since the females of the European strain of the species do not fly. Indeed, 140 years later, spongy moths are still spreading south and west in North America as shown in Fig. 9.2a and only occupy about 1/3 of their potential range (Figs. 9.6 and 9.7).
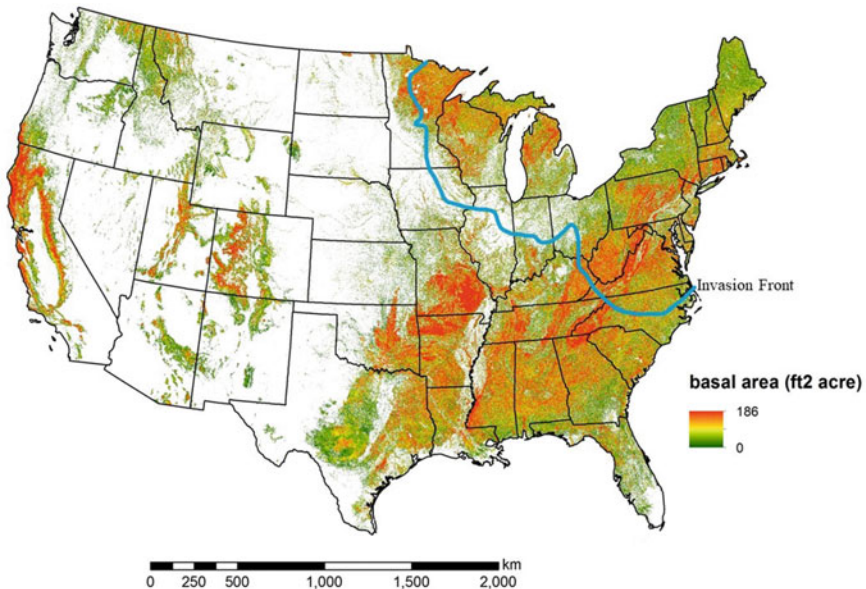
Fig. 9.6 Forest types susceptible to spongy moth invasion. Orange represents highly susceptible forest, green low susceptibility (Morin et al. 2005). Blue line indicates the current invasion front of spongy moth in N. America (see Fig. 9.2b)
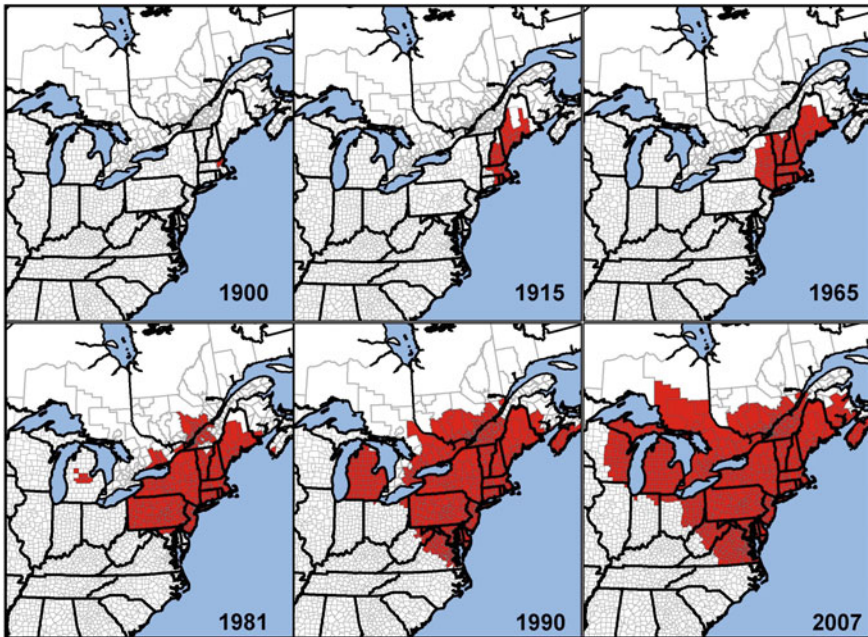
Fig. 9.7 Spread of spongy moths in northeastern North America after 1900 (Figure from Leibhold et al. 2007)

9.5.3   Host Preferences

Like winter moths, spongy moths feed on a wide range of host tree species, but perform best on oaks (*Quercus* spp), aspen (*Populus*), and birches (*Betula*) (Liebhold et al. 1995; Davidson et al. 1999). They will feed on many conifers and indeed on most tree species, especially if preferred hosts are unavailable or already defoliated. A handful of species are avoided altogether, even in stands that are otherwise completely defoliated. These species include ash (*Fraxinus spp),* silver maple *(Acer saccharinum)* and tulip poplar (*Liriodendron tulipifera*).

9.5.4   Impact on Forests and Trees

Defoliation is more frequent in forest stands that are dominated by tree species preferred by spongy moths, as described above, than in stands dominated by other tree species. In eastern North America, oaks (*Quercus*) dominate the forests in southern New England, the mid-Atlantic states and the Midwest. Aspen (*Populus*) dominated forests are often defoliated in the region around the Great Lakes (Fig. 9.6). These

forests are most frequently defoliated by spongy moth and experience the greatest tree mortality (Campbell and Sloan 1977; Davidson et al. 1999).

Most hardwood trees defoliated > 50% by spongy moths will re-foliate in midsummer. However, those that fail to re-foliate at that time, or fail to re-foliate the following spring, will be killed, due to insufficient carbohydrate reserves (Kulman 1971). Defoliated trees become susceptible to attack by secondary organisms, such as the two lined chestnut borer, *Agrilus bilineatus,* or the shoestring fungus, *Armillaria* spp., and these agents are often the main causes of tree death (Campbell and Sloan 1977; Wargo 1977). Repeated defoliations in consecutive years can lead to levels of tree mortality exceeding 50% (Kegg 1973; Campbell and Sloan 1977). Other studies show less mortality following defoliation (Brown et al. 1979; Gansner et al. 1993). Campbell and Sloan (1977) analyzed the impact of spongy moth on stands from 1911 to 1931 in New England and reported that defoliation occurred most frequently on oak-dominated stands and that oaks were the most likely to die. Dominant trees survived better than ones that were subdominant or suppressed. Non-favored host trees, such as white pine and red maple, were more likely to die after one defoliation than oak trees. Morin and Liebhold (2016) analyzed the impact of spongy moth defoliation on changes in the tree species composition data collected by the USDA Forest Service between 1975 and 2010. They found that most of the stands with repeated defoliation in the northeastern USA were oak-dominated, and the effect of defoliation was to hasten the process of replacement of overstory oaks with other species such as maple (*Acer*), which are less preferred by spongy moth. Even though the volume or basal area of oak was increasing across this region due to tree growth, mortality of the younger age classes of oaks contributed to the overall decline of oaks and replacement by other species.

9.5.5   Spread of Spongy Moth

The enormous spatial detail evident in the spongy moth pheromone trap catch data (Fig. 9.2a) across the landscape, and the long time period over which spread has been monitored, have allowed investigators to study the rate of spread of spongy moths and make important contributions to the theory of spread of invasive organisms. Liebhold et al. (1992) compared historical rates of spongy moth spread (1900–1989) with predictions made using the spread model of Skellam (1951). The Skellam model consists of two components: exponential population growth defined by the parameter '*r*' and diffusion analogous to molecular diffusion defined by the parameter *D*. The model predicts that the rate of spread *V* of an invasion front is constant: $V = 2\sqrt{rD}$. Liebhold et al. (1992) estimated both parameters from earlier studies of spongy moth population growth and diffusion based on dispersal of first-instar larvae that spin down on threads from tree canopies and are blown in the wind. Experimental studies of that process (Mason and McManus 1981) suggest that most such larvae spread only a few hundred meters, but a few of them spread several kilometers. The Skellam model based on these parameters predicted that spongy moth dispersal would

be about 2 km/year. The spongy moth spread prior to 1966 varied between 2 and 10 km/year compared to 20.78 km/year after 1996. Liebhold et al. (1992) concluded that the discrepancy between predicted and observed spread was due to accidental human movement of spongy moth life stages which form isolated populations ahead of the advancing population front and thereby accelerate spread.

Analyses of spongy moth spread were greatly enhanced by implementation of regional grids of pheromone traps (Fig. 9.2a, 9.8a). Analyses of such data from the central Appalachians (Sharov et al. 1995, 1996, 1997) indicated a rate of spread that varied yearly and ranged from 17 to 30 km/year. These data show that clumps of small populations of spongy moths arise many kilometers in front of the infested zone (Figs. 9.2a, 9.8a), and their growth and coalescence contribute significantly to the rate of spread. These data suggest that spread of spongy moth is an excellent example of stratified dispersal (Hengeveld 1989), consisting of a short-range process governed by larval dispersal and a longer-range process governed by human transport of spongy moth egg masses. The latter process has long been understood to be a central feature of the spongy moth system. Spongy moths lay the overwintering egg masses in midsummer on backyard objects, such as lawn furniture, that are readily transported in succeeding months elsewhere in the United States. As a result, new infestations arise many kilometers from the generally infested area or indeed anywhere else in North America. Models of stratified dispersal (Shigesada and Kawasaki 1997) were fit to the spongy moth system (Sharov and Liebhold 1998a). These analyses form the theoretical basis of the spongy moth Slow the Spread Program (Sharov et al. 1997, 1998, 2002a; Sharov and Liebhold 1998a, 1998b; Tobin and Blackburn 2007) discussed below. Suppression of these incipient populations, arising ahead of the invasion front, slows the spread.
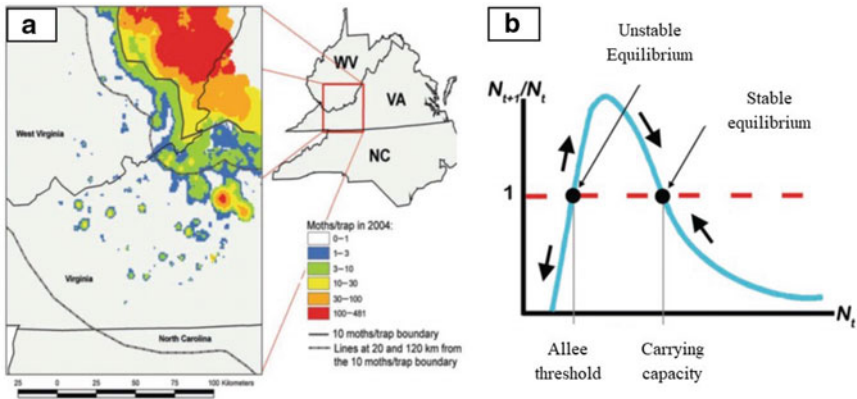
Fig. 9.8 (a) Leading edge of spongy moth infestation arising ahead of the invasion front, resulting in stratified spread and; (b) Allee effect showing population growth as a function of density. Below the horizontal dashed line populations decline; above the line they increase (from Liebhold et al. 2007)

Understanding the survival and expansion of incipient populations thus became a key feature of managing spongy moth. Such populations are governed by Allee effects (Fig. 9.8b), which express the survival or growth of populations as a function of population densities. At the very low densities characteristic of newly founded populations, survival or population growth of many species increases with population density. At higher densities, in virtually all populations survival or growth rates decline to an equilibrium that represents either the carrying capacity, or else a lower-density equilibrium maintained by natural enemies. Allee effects refer to the positive density dependence at lower densities, and they can be weak or strong (Taylor and Hastings 2005). If they are strong, then at very low densities there exists what is called the Allee threshold (Fig. 9.8b). At densities above the threshold, populations steadily increase. When populations are below the threshold, however, densities typically decline to extinction. In other words, the low-density Allee threshold is an unstable equilibrium. There are several possible causes of low-density Allee effects in spongy moth populations, including predation (see below), but probably the most common cause at the very lowest densities characteristic of incipient populations is failure to locate mates. The implication of this is that many incipient populations of spongy moth will decline to extinction on their own accord. Indeed, data suggest that this frequently occurs (Liebhold et al. 2016). Eradication of such populations with pesticides or indeed mating disruption (Sharov et al. 2002b) is entirely feasible because even if the treatment fails to kill all the spongy moths it will surely vastly lower their densities and thus hasten their natural tendency to decline to extinction.

Subsequent analyses of spongy moth spread have shown that the rate of spongy moth spread declines with the strength of Allee effects (Tobin et al. 2007, 2009), which varies in time and space across the landscape. The strength is measured by the intercept of the plot shown in Fig. 9.8b with the vertical axis; it is strongest when the intercept with the vertical axis (below the figure) is most negative. For example, Tobin (2007) reported that there were strong Allee effects and, as a result, slower spread in parts of the Midwest compared to Great Lakes or Appalachian regions.

An exciting recent finding (Tobin et al. 2014) is that spongy moth populations in North Carolina have stopped spreading, and indeed have retreated northward in recent years. Tobin et al. (2014) suggest that in that region spongy moths have exceeded temperature maximums that inhibit optimal growth and further spread to southern states, and the northward retreat may be due to climate change. These findings imply that spongy moths may never occupy southern regions of the Midwest with highly susceptible oak forests (Fig. 9.6).

9.5.6   History of Spongy Moth Control

Efforts to control spongy moth in Massachusetts began in 1890, with a large program funded by the state legislature. The program focused on an attempt to mechanically destroy spongy moth egg masses, which are present on the trunks of trees from August through April each year. In addition, there was a large effort to spray the larvae with

pesticides, mainly with lead and copper arsenate. There was little or no appreciation in those days of the environmental danger posed by these toxins. Furthermore, they were largely ineffective and failed to stem the spread of the population.

In 1905, the US Department of Agriculture launched what became the most extensive worldwide effort for biological control of an invasive forest insect ever conducted. Twelve species of parasitoids became established of the 34 species that were released over several decades. Fuester et al. (2014) provide the most recent of several reviews of this effort. These included the egg parasitoid *Ooencyrtus kuvanae* (Howard) [Hymenoptera Encyrtidae]; three tachinid [Diptera] species: *Compsilura concinnata* (Meigen), *Parasetigena silvestris* (Robineau-Desvoidy), and *Blepharipa pratensis* (Meigen); a braconid *Cotesia melanoscelus* (Ratzeburg) and an ichneumonid *Phobocampe disparis* (Viereck) which attack the larval stage of spongy moth. Pupal parasitoids established were two hymenopterans: the chalcid *Brachymeria intermedia* (Ness) (Chalcidae) and the ichneumonid *Pimpla disparis* (Viereck). Of these, *O. kuvanae* and *P. disparis* were introduced from Japan, the other species from Europe. *Compsilura concinnata* was introduced to North America in 1906 and has gained some notoriety because Boettner et al. (2000) showed that it has become the dominant source of mortality on several native species of giant silk moths (Saturniidae) and is probably responsible for the decline of these species since the nineteenth century. On the other hand, Elkinton et al. (2006) showed that the same parasitoid was probably responsible for the extirpation of the invasive brown tail moth, *Euproctis chrysorrhea*, over much of its invasive range in the northeastern United States.

Unfortunately, these parasitoids did not prevent spongy moth outbreaks. Williams et al. (1992) published the only long-term data on parasitism by these species and concluded that none of them regulated spongy moth density. The results of this study confirmed the conclusions drawn by earlier investigators: that parasitoids played a limited or equivocal role in the population dynamics of spongy moth in North America (Campbell 1975; Reardon 1976; Elkinton and Liebhold 1990). In addition to parasitoids, biological control introductions included predatory beetles, such as *Calosoma sychophanta* (Weseloh 1985) and pathogens such as *Entomophaga maimaiga* from Japan (Fuester et al. 2014). That pathogen was initially collected and released in 1910 and 1911 in the Boston area but was not established (Speare and Colley 1912). The recent invasion of spongy moth populations by *E. maimaiga* in North America that began in 1989 (see below) was evidently an accidental or inadvertent introduction (Hajek 2007). *Entomophaga maimaiga* was recently established in Bulgaria from where it has spread to other European countries and has become quite common (Hajek et al. 2020). But with the notable possible exception of *E. maimaiga* after 1989, none of these introductions prevented spongy moth outbreaks.

Following World War II, the pesticide DDT became widely available. It was cheaper and more effective than any previous pesticide. In the succeeding decades, widespread aerial application of DDT was made against spongy moth. Applying pesticide by air allowed application at a landscape level, something that was never feasible or affordable from the ground. Entomologists in those days were convinced that DDT was a new tool that would solve most insect problems. By the 1960s, however, the environmental costs of DDT and related compounds were evident and

were popularized by the famous book *Silent Spring* by Rachel Carson. DDT and its breakdown products persist indefinitely in the environment and accumulate in the fatty tissue of many animals. It was particularly damaging to birds, especially those at the end of long food chains, such as eagles and ospreys. DDT and other chlorinated hydrocarbon insecticides were banned in the late 1960s and 1970s. The Environmental Protection Agency was established, and laws were passed to require safety testing of all pesticides. Nevertheless, populations of birds such as eagles and ospreys took many decades to recover, a process that goes on to this day.

Meanwhile, new pesticides were developed and used against spongy moth. In the early 1980s aerial applications of carbaryl were very popular. Carbaryl gave way to diflubenzuron, an insect growth regulator. By the end of the decade the bacterial insecticide *Bacillus thuringiensis* (Bt.) became popular. Its advantage was that it affected only foliage-eating insects, and not the adult stages of their insect natural enemies. Other bacterial insecticides such as spinosad were added to the mix in subsequent decades. Thus, in the modern era, we now have much safer pesticides that affect a more narrow spectrum of target and nontarget insects. In the northeastern states large scale aerial application of pesticides largely ceased after 1990 (Fig. 9.9b), coincident with the arrival of a new fungal pathogen of spongy moth, *E. maimaiga* (see below). It appears likely that the days of aerial application of any pesticides against spongy moth in New England are finished. We now know that the spongy moth outbreaks will subside on their own, and the forests will recover, even if there is significant tree mortality. Even the modern pesticides with a narrow spectrum will kill many nontarget insects and aerial applications are too expensive to justify for the governmental agencies charged with carrying them out. Applications to individual shade trees, however, are another matter. Homeowners place high value on these trees which provide beauty and shade to their yards. If a shade tree dies, it is expensive to remove. Homeowners are thus willing to spend significant funds to protect their trees, and many tree care professionals are available to help them to do that. The small scale of such applications presumably has a limited impact on non-target species at the landscape scale.

The federal effort against spongy moth in recent years has focused on the "Slow the Spread" project (Tobin and Blackburn 2007) (Fig. 9.2a). This involves annually deploying 80,000 to 100,000 traps baited with spongy moth pheromone each year in a grid along a front that extends from Minnesota to North Carolina. The objective of this effort is to identify incipient populations arising ahead of the invasion front that facilitate spread, as described above. Efforts are thus made to suppress them and slow the overall rate of spread of spongy moth. While this effort is expensive, cost–benefit analyses have shown that it is justified (Sharov and Liebhold 1998c). To suppress isolated populations, the program mostly relies on aerial applications of pheromones in small slow-release dispensers such that spongy moth males in treated areas are unable to locate females. Consequently, many females go unmated (Sharov et al. 2002b). This approach is called mating-disruption or the confusion technique (Carde and Minks 1995). It has been widely applied against agricultural pests such as pink bollworm, *Pectinophora gossypiella,* on cotton, but this is one of the only applications that has been widely applied against a forest insect. Another
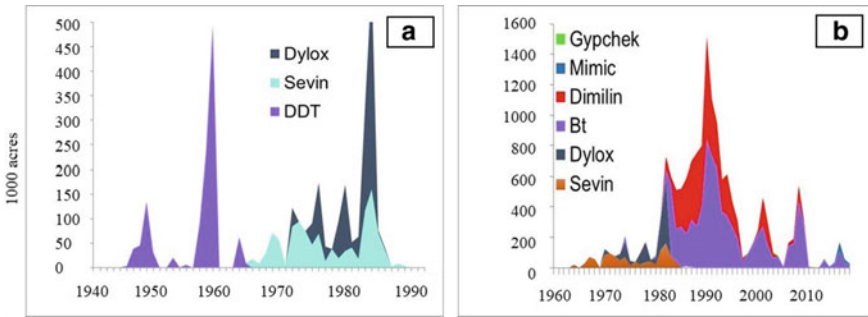
Fig. 9.9 (a) Aerial application from 1945 to 1985 of DDT, carbaryl (Sevin®) and Dylox in the northeastern United States and; (b) other more recently developed pesticides, including LdNPV (Gypchek), Mimic, diflubenzuron (Dimilin®)and Bacillus thuringiensis (Bt) after 1960 (figure courtesy of A. Liebhold)

more widely used eradication technique involves application of microbial pesticides such as *Bacillus thuringiensis* (*Bt*) (Hajek and Tobin 2010).

A parallel effort is used to detect and eradicate isolated populations of spongy moth that arise far from the invasion front in the western and southern United States, where spongy moth egg masses are transported inadvertently by homeowners arriving from the infested region in the east. Again, the strategy is to annually deploy networks of thousands of traps that are used to detect newly-founded populations. Following detection, these populations are eradicated, mostly using aerial applications of the microbial pesticide *Bacillus thuringiensis.* Of particular concern are populations of Asian spongy moths arriving on ships from East Asia, where the flying female spongy moths are attracted to lights associated with various ports in Asia and thus often deposit egg masses in large numbers on ships in the ports. Asian spongy moths represent a major threat to North America, because, once established, they can spread across the continent very rapidly, and they attack different tree species, including conifers (Baranchikov and Sukachev 1989). Thus, a major effort has been made to locate spongy moth egg masses on cargo and ships arriving from East Asian ports and prohibit imports of contaminated cargo. Recent theoretical studies show that eradication of incipient populations is far more feasible than originally thought (Liebhold et al. 2016).

9.5.7 Population Ecology of Spongy Moth

Robert Campbell, of the US Forest Service, in the 1960s and 1970s, led the first comprehensive research aimed at understanding the population ecology of spongy moth in North America. Campbell and Sloan (1978a) suggested that predation by small mammals, in particular the white-footed mouse, *Peromyscus leucopis,* feeding on the late larval and pupal stages, was the key to maintaining populations at low

density in the years between outbreaks. Predation by birds, in contrast, was much less important. Many bird species feed to some extent on spongy moth caterpillars, but many are also deterred by the hairs on the integument.

Elkinton et al. (1996) presented results of research initiated in the 1980s at two sites in Massachusetts that confirmed the importance of small mammal predation on low-density spongy moth populations. They showed that spongy moth populations would rise when populations of white-footed mice declined. Furthermore, they showed that mouse populations fluctuate with the acorn crops, their major overwintering food source. As is true with many tree species, acorn crops vary enormously from year to year. A variety of weather conditions, such as a late spring frost or mid-summer drought, can nearly eliminate the acorn crop. They also showed that when acorn crops failed, as in the autumn of 1992 (Fig. 9.10), mouse populations had declined dramatically by the following summer, and spongy moth populations therefore increased (Fig. 9.10). All of this occurred at low spongy moth density, when they were in a non-outbreak phase (egg mass densities < 100/ha).

Somewhere above one hundred egg masses per acre, a density threshold is reached, beyond which predation by mice or other small mammals, such as shrews, declines with increasing spongy moth density. Unlike spongy moth parasitoids, changes in the density of vertebrate predators such as mice or birds are fairly constrained. Birds defend territories and so do mice. Thus, the population densities of mice rarely increase beyond about 100 mice per ha. Spongy moths, in contrast, can increase from 1 to 100 to 10,000 egg masses per ha, which is characteristic of outbreak populations. At these higher densities, mice or birds can feed all day on spongy moth and never make a dent in the population, whereas, at lower spongy moth densities, the mice may consume most of the spongy moth pupae in the forest. Therefore, as spongy moth density increases, there is decline in the percent mortality caused by mice and other generalist predators. Thus, vertebrate predators play almost no role in regulating outbreak populations. With many caterpillar species, parasitoids can regulate density and prevent outbreaks because their numbers can increase along with their hosts. Unfortunately, introduced and native parasitoids that attack spongy moth in North America do not do this effectively. Their numbers are constrained for reasons that are poorly understood, and they never cause very high levels of parasitism. So, once spongy moth densities reach a threshold in the vicinity of 100 egg masses per acre, the spongy moth population will grow inexorably over the next one or two years into an outbreak phase that results in widespread defoliation.

Outbreak populations become limited only by the availability of green foliage. Few spongy moth larvae actually starve in outbreak populations, but many fail to get sufficient food resources. As a consequence, the adults that arise from such populations are smaller and the females might lay 100 eggs per mass, instead of 600 (Campbell and Sloan 1978a). More importantly, there is a virus disease called nuclear polyhedrosis virus (*LdNPV*) that causes epidemics in these outbreak populations and may kill 99% of larvae before they reach the pupal stage (Campbell and Podgwaite 1971). Such viruses are common in outbreak populations of many insect species. Virus diseases reach epidemic proportions in outbreak populations because high caterpillar densities increase disease transmission. When the caterpillar dies from
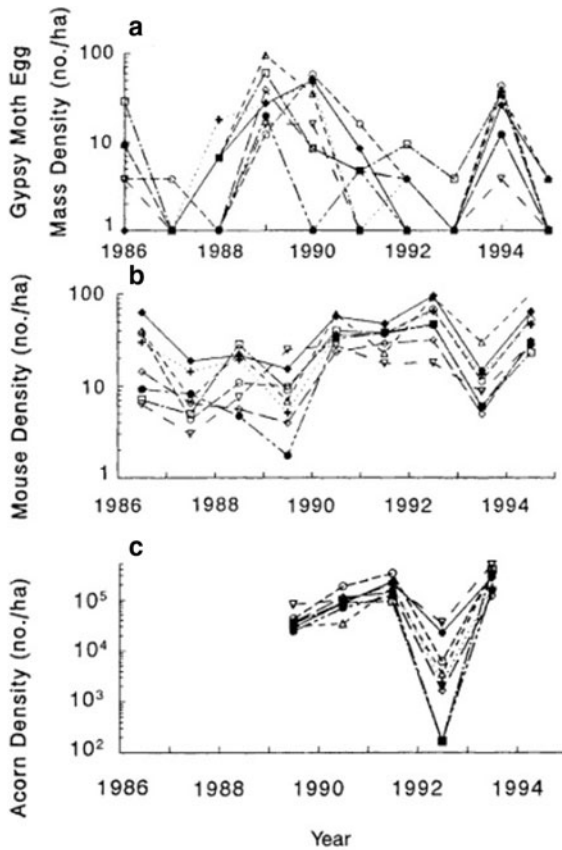
Fig. 9.10 Yearly estimates of (a) spongy moth egg masses per ha; (b) densities of white-footed mice and; (c) acorn crops at eight different plots near the Quabbin reservoir in central Massachusetts (Elkinton et al. 1996)

LdNPV, the virus causes the caterpillar cadaver to liquefy and spread virus particles over the leaf surface. Transmission occurs when a healthy caterpillar consumes virus particles released by these liquefied cadavers. Mortality from *LdNPV* starts in the early larval stages but grows exponentially in the late larval stage and peaks just before the caterpillars form pupae (Campbell and Podgwaite 1971; Murray et al. 1989). It is this epidemic that brings an end to spongy moth outbreaks and causes the populations to retreat back to low density. Therefore, outbreaks will typically last for 1 to 3 years before this population collapse happens. In the years following collapse of the outbreak, predation by small mammals resumes as the dominant force of mortality that maintains spongy moth at low density (Campbell and Sloan 1978b).

Campbell and Sloan (1978b) believed that spongy moth was a multi-equilibrium system (see Chapter 5) with a low-density equilibrium maintained by predators, mainly mice, and a high-density equilibrium wherein foliage supply and the resulting

decline in fecundity, coupled with epizootics of *LdNPV*, limited further expansion of spongy moth densities and ultimately caused the collapse of outbreak populations. While it is very clear that there is indeed an upper limit to spongy moth densities, and that *LdNPV* plays a major role in the collapse of outbreaks, evidence for the low-density equilibrium remains undemonstrated. Campbell believed that predation rates by small mammals increased with spongy moth density at the lowest spongy moth densities but lacked supporting evidence. Unlike parasitoids, densities of small mammal predators do not increase in response to increased spongy moth density. Mouse densities are governed in large part by acorn crops, their principal overwintering food source. In contrast, spongy moth pupae and late instar larvae represent an extremely ephemeral food resource for mice at a time of year when they have many other things to feed on. Predation rates, if they are to increase with spongy moth density, must, in response, entail a change in foraging behavior of the predator (a Type III functional response) (Holling 1959) to increasing density of prey. In field experiments, Elkinton et al. (2004) showed that mice exhibited a Type II functional response, wherein rates of predation decline steadily as densities increase from the lowest spongy moth densities. This implies that mice cannot serve to regulate spongy moth populations at low density. This type of predation may contribute to the Allee effect in low-density spongy moth populations, as discussed above.

Dwyer et al. (2004) developed a model of spongy moth populations that combined the effects of *LdNPV* and small mammal predators. The model predicted regular outbreaks of spongy moths with an approximate 10-year periodicity. Fundamentally, this was a pathogen-driven model analogous to earlier models (e.g. Anderson and May 1981), but the addition of predators added an unstable low-density equilibrium to the system. Even a minor amount of stochasticity, however, resulted in quasi-periodic oscillations (Fig. 9.11B) that matched those of spongy moth defoliation data in New Hampshire (Fig. 9.11A) characterized by chaotic dynamics (May 1975) that make them susceptible to dynamical change with small environmental perturbations or small changes in model parameter values (Fig. 9.11C). Subsequent analyses of spongy moth defoliation data confirmed the existence of such periodicities in the spongy moth system (Bjørnstad 2000).

The Dwyer et al. (2004) model was elaborated by Bjørnstad et al. (2010) and applied to defoliation data. The revised model replaced the Type III functional response of predation with a Type II functional response, which made a low-density equilibrium caused by predators impossible. Indeed, there exists no evidence to support such an equilibrium. These analyses suggested the existence of a dominant 10-year cycle with a subdominant four-year cycle (Johnson et al. 2006a; Haynes et al. 2009a). Allstadt et al. (2013) analyzed 86 years of defoliation data, the longest available for/in North America, and concluded that population cycles appeared or disappeared four times over the duration of the spongy moth infestation in North America (Fig. 9.12B).
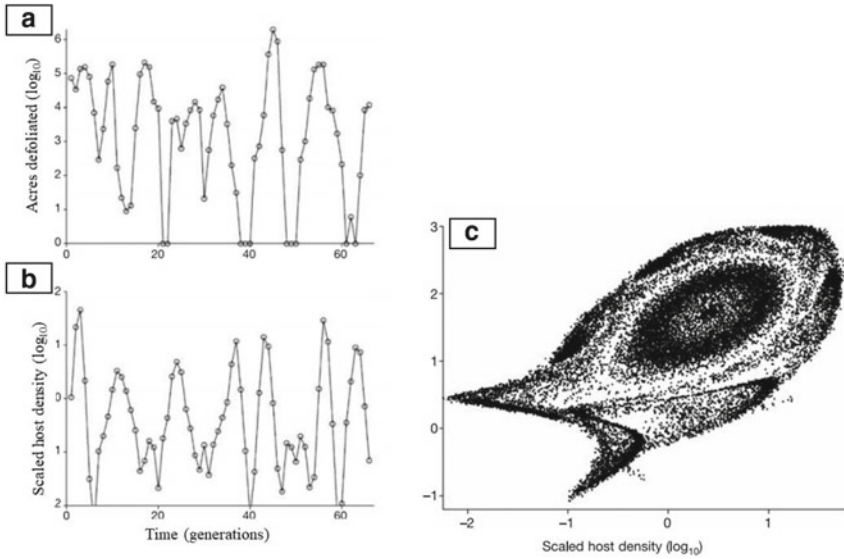
Fig. 9.11 (a) Time series of spongy moth population model of Dwyer et al. (2004) showing quasi-periodic dynamics similar to those exhibited by; (b) spongy moth defoliation in New Hampshire and; (c) a phase plot of model with stochasticity
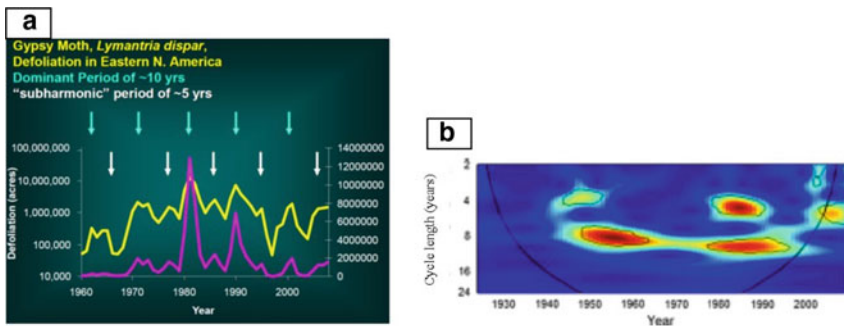
Fig. 9.12 (a) Spongy moth population dynamics model of Bjornstad et al. (2008, 2010) versus defoliation data (figure courtesy of A. Liebhold) and; (b) wavelet analysis by Allstad et al. (2013) showing changes in periodicity of spongy moth defoliation in N. America over 86 years. Vertical axis shows cycle period in years; orange/yellow colors indicate statistically significant periodicities. Only patterns above the curved black line in this figure are statistically significant

Another conspicuous feature of the spongy moth population system is that populations fluctuate in synchrony with one another across the landscape (Williams and Liebhold 1995a, 1995b; Peltonen et al. 2002; Liebhold et al. 2004; Johnson et al. 2006a, 2006b; Bjørnstad et al. 2008; Haynes et al. 2013; Allstadt et al. 2015). This phenomenon is nearly ubiquitous with most forest insects (Liebhold and Kamata

2000). Dispersal from one population to another can synchronize adjacent populations, but for spongy moth, and most other forest insects, this occurs over far too short a distance to account for the regional synchronies observed (Peltonen et al. 2002). Instead, the standard explanation for this phenomenon involves the Moran (1953) effect. Moran was a statistician who studied the famous snowshoe hare-lynx predator prey oscillation in Canada. He showed that model time series of such populations in different locations would come into synchrony with one another, provided they were influenced by a common random factor, such as synchronous weather. The shared weather conditions are not responsible for the oscillation, but they do explain why snowshoe hares or forest insects typically oscillate in synchrony with one another across much of northern Canada. The synchrony breaks down at greater distances because weather conditions become uncorrelated at these distances. Bjørnstad et al. (1999) developed statistical methods to detect such synchrony and how it declines with distance between two or more populations (see Fig. 9.4b, c). Moran's model assumed that the dynamics of spatially separated populations were all governed by the same density-dependent processes. In fact, these dynamics undoubtedly vary somewhat in space. Peltonen et al. (2002) showed that populations with similar but distinct dynamical parameters still exhibited spatial synchrony, as Moran described, but the synchrony declined with distance more sharply than the synchronizing weather conditions. Haynes et al. (2009b) utilized the model of Bjørnstad et al. (2010) and analyzed data on the spatial synchrony of spongy moths, white-footed mice, and acorn crops in the northeastern United States. All three are synchronized out to a distance of approximately 1000 km. They concluded that synchrony of acorn crops was the main cause of spongy moth and mouse synchrony, as opposed to the independent regional stochasticity (i.e. weather conditions) directly affecting each of the latter two species. The synchrony of all three is evident on a small spatial scale (ca 10 km) in Fig. 9.10.

In 1989, a dramatic change occurred to spongy moth populations with the accidental introduction of a fungal pathogen of spongy moth, *Entomophaga maimaiga*, from Japan (Andreadis and Weseloh 1990; Hajek et al. 1990b). That year, the fungus caused extensive mortality in both high and low-density populations throughout southern New England. The following year, the infection spread over the rest of New England and halfway across Pennsylvania (Elkinton et al. 1991). The rapid spread was due to the fact that spongy moth cadavers killed by the fungus produce conidia that are blown in the wind across the landscape. Subsequent research showed the fungus depends on rainy conditions in May and June for successful transmission to healthy larvae, and, indeed, 1989 was an especially rainy year. Beginning in 1991, spongy moth researchers worked to spread *E. maimaiga* to Michigan (Smitley et al. 1995) and to Virginia (Hajek et al. 1996), but the fungus spread rapidly on its own, so that by about 1996 all of the areas infested by spongy moth in the northeastern United States were infested with the fungus (Hajek 1997, 1999). The fungus caused a major change in status of spongy moth as a serious forest pest in New England states. Spongy moth populations in that region declined to low density where they

have mostly remained for the last 35 years (Fig. 9.13). In contrast, spongy moth populations in areas further south, such as Pennsylvania, have continued to have periodic outbreaks despite the presence of the fungus (Morin and Liebhold 2016). Laboratory tests demonstrated that the fungus does best in cooler conditions (Hajek et al. 1990a). Temperatures in May and June in the mid-Atlantic states are much warmer than in New England.

Studies of the interaction of spongy moth fungal and viral pathogens demonstrated that *E. maimaiga* develops more quickly and outcompetes *LdNPV* when both pathogens affect the same larva (Malakar 1997; Malakar et al. 1999). The same is true for infections of *E. maimaiga* and parasitoid larvae in spongy moth larvae. Hajek et al. (2015) (Fig. 9.14a) demonstrated that *E. maimaiga* has now become the dominant mortality factor in both low and high-density populations of spongy moth. However, Liebhold et al. (2013) demonstrated that *LdNPV* still causes comparable levels of density-dependent mortality in outbreak populations in the presence of *E. maimaiga* as it had before the fungal pathogen was introduced in 1989 (Fig. 9.14b).
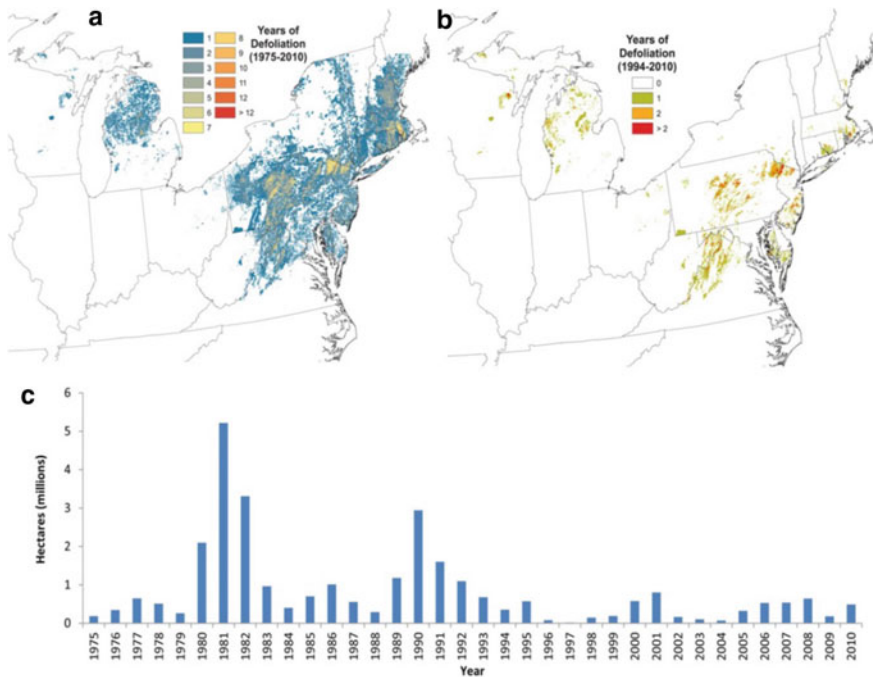
Fig. 9.13 (a) Spongy moth defoliation before and; (b) after the introduction of *Entomophaga maimaiga* in 1989 in the northeast United States (Morin and Liebhold 2016); (c) The annual hectares defoliated by spongy moth 1975–2010 in the United States

Various studies indicate that rainfall in May and June are critical to transmission of *E. maimaiga* (Hajek et al. 1990a; Hajek 1999; Reilly et al. 2014). A recent outbreak of spongy moth in New England (Fig. 9.1b; Pasquarella et al. 2018), the first widespread one since 1981, was likely caused or facilitated by three consecutive years of drought conditions in May and June beginning in 2014. Thus, rainfall has likely become a critical feature in promoting or suppressing spongy moth outbreaks. Most of the time series analyses of spongy moth defoliation data described above were applied to data collected prior to widespread establishment of *E. maimaiga,* so perhaps it is still too early to tell how it will affect the overall dynamics of spongy moth. For example, the disappearance of the population cycles after 1996 described by Allstadt et al. (2013) might be due to this major new source of mortality. Unlike the viral pathogen *LdNPV*, which only causes major epizootics in outbreak populations of spongy moth, *E. maimaiga* causes high levels of mortality in both low- and high-density populations (Hajek 1999; Fig. 9.14c). As such, it may play a significant role in preventing the onset of outbreaks in contrast to *LdNPV*. Even so, *E. maimaiga* is weakly density dependent because transmission depends on conidia that spread from nearby high-density populations (Bittner et al. 2017; Elkinton et al. 2019). Thus, *E. maimaiga* might contribute to the development of a low-density equilibrium, whose existence has not yet been demonstrated in spongy moth populations. Kyle et al. (2020) developed a population model of the impact of *E. maimaiga* on spongy moth population dynamics. Recent analyses by Liebhold et al. (2022) demonstrate that *E. maimaiga* has reduced the intensity of spongy moth outbreaks but not necessarily their frequency. Further studies and longer population time series are needed to resolve its role in low-density population dynamics of spongy moth.
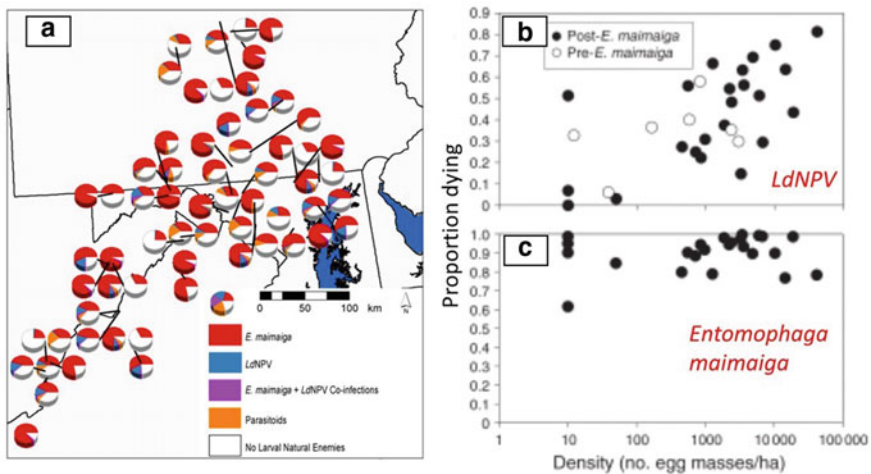
Fig. 9.14 (a) Proportions of spongy moth larvae dying from *E maimaiga, LdNPV* and parasitoids in Pennsylvania, Maryland and West Virginia (Hajek et al. 2015); (b) Mortality of spongy moth larvae in Pennsylvania from *LdNPV* and; (c) from *E maimaiga* vs. egg mass density before and after the introduction of *E maimaiga.* (Liebhold et al. 2013)

As described above, spongy moth has been exhaustively researched both from a population dynamic and from a management perspective. The extensive data on spongy moth defoliation and pheromone trap catch is almost certainly the most extensive such data for any species and has allowed researchers to make significant contributions to the general theory of population spread and eradication of invasive species. Analysis of spongy moth population data has made important contributions to the general theory of population cycles, Allee effects, and spatial synchrony of population fluctuations.

In Table 9.1, we list what we believe are the most important or damaging foliage-feeding forest insects in the world. We list the geographical range, the host tree species, and key references that give readers access to the literature on these species. We do not include the two species we have already discussed at length: winter moth, *Operophtera brumata* and spongy moth, *Lymantria dispar*.

Table 9.1 Major foliage-feeding insects: species, geographic range, hosts, and key references focusing on population ecology and impacts on forests excluding winter moth and spongy moth

Common name	Geographic range/Principal host trees	Key references
Lepidoptera		
Family: Erebidae		
Lymantria monacha Nun moth	Range: Europe, temperate Palearctic to Japan Hosts: *Picea abies*, *Pinus sylvestris*	(Bejer 1986; Skuhravý 1987; Maksimov 1999; Keena 2003; Platek 2007; Vanhanen et al. 2007; Sukovata 2010; Ilyinykh 2011; Lee et al. 2015; Nakládal and Brinkeová 2015; Faelt-Nardmann et al. 2018a, 2018b, 2018c; Hentschel et al. 2018; Melin et al. 2020)
Euproctis chrysorrhoea Brown-tail moth	Range: mid and southern Europe into western Asia and northern Africa Invasive range: Northeast United States into Canada (1890s); reports in China, Japan, New Guinea Host trees: Polyphagous, fruit orchards, ornamental trees, most hardwoods incl. *Quercus*	(Blair 1979; Purrini 1979; Schaefer 1986; Kelly et al. 1988; Sterling and Speight 1989; Cory et al. 2000; Elkinton et al. 2006, 2008; Frago et al. 2010, 2011; Moraal and Jagers op Akkerhuis 2011; Elkinton and Boettner 2012; Frago et al. 2012; Klapwijk et al. 2013; Marques et al. 2014); Boyd et al. 2021
Orgyia pseudotsugata Douglas fir tussock moth	Range: western N. America into British Columbia Host trees: *Pseudotsuga, Abies, P. menziesii, Abies grandis, A. concolor, A. lasiocarpa*	(Beckwith 1976; Mason 1976, 1978, 1996; Dahlsten et al. 1977; Berryman 1978; Brookes et al. 1978; Torgersen and Ryan 1981; Mason et al. 1983, 1993; Wickman et al. 1986; Alfaro et al. 1987; Mason and Torgersen 1987; Shepherd et al. 1988; Swetnam et al. 1995; Negrón et al. 2014)
Leucoma salicis Satin moth	Range: Eurasia south of the Polar circle up to northeast Siberia Host trees: *Salix, Populus*	(Burgess 1921; Burgess and Crossman 1927; Brown 1931; Doucette 1954; Wagner and Leonard 1979, 1980; Humphreys 1996)

(continued)

Table 9.1 (continued)

Common name	Geographic range/Principal host trees	Key references
Family: Tortricidae		
Choristoneura fumiferana Spruce budworm, eastern spruce budworm	Range: Eastern US and Canada	(Royama 1984; Crawford and Jennings 1989; Campbell 1993; Régnière and Lysyk 1995; Nealis 2003; Belle-Isle and Kneeshaw 2007; Venier and Holmes 2010; Sonia et al. 2011; Boulanger et al. 2012; Chang et al. 2012; Rhainds et al. 2012; Régnière et al. 2013; MacLean 2016; Pureswaran et al. 2016; Fuentealba et al. 2017; Royama et al. 2017; Bouchard et al. 2018a, 2018b; Drever et al. 2018; Goodbody et al. 2018; Rahimzadeh-Bajgiran et al. 2018; Legault and James 2018; Pureswaran et al. 2019; Regniere et al. 2019a, 2019b; Regniere and Nealis 2019; Lumley et al. 2020); Bhattarai et al. 2021; Berguet et al. 2021; Donovan et al. 2021; Germain et al. 2021; Maclean et al. 2019; Regniere et al. 2021; Nealis and Regniere 2021; Rhainds et al. 2022
	Host trees: *Abies balsamea, Picea glauca, P. mariana*	
Choristoneura freeman Western spruce budworm	Range: Western N. America (Western Canada into PNW United States)	(McKnight 1974; Torgersen and Campbell 1982; Campbell et al. 1983; Anderson et al. 1987; Swetnam and Lynch 1989; Alfaro and Maclauchlan 1992; Campbell 1993; Clancy et al. 1993; Swetnam and Lynch 1993; Volney 1994; Shepherd et al. 1995; Williams and Liebhold 1995a, 1995b; Chen et al. 2001, 2002; Hummel and Agee 2003; Clancy et al. 2004; Campbell et al. 2006; Maclauchlan et al. 2006; Alfaro et al. 2014; Flower et al. 2014a, 2014b; Gilligan and Brown 2014; Nealis and Régnière 2014; Axelson et al. 2015; Meigs et al. 2015; Flower 2016; Nealis and Régnière 2016; Senf et al. 2017; Vane et al. 2017; Régnière and Nealis 2018; Santiago 2022)
	Host trees: *Pseudotsuga menziesi, Abies grandis, A. concolor,* etc	

Table 9.1 (continued)

Common name	Geographic range/Principal host trees	Key references
Choristoneura pinus Jack pine budworm	Range: NE US and throughout Canada Host trees: *Pinus banksiana*	(Clancy et al. 1980; Volney and McCullough 1994; Nealis 1995; McCullough 2000; Radeloff et al. 2000; Mamet et al. 2015; Robson et al. 2015; Fahrner et al. 2016; Cadogan et al. 2018)
Tortrix viridana Green oak moth	Range: Europe, Northern Africa, western Asia Host trees: *Quercus*	(Carlisle et al. 1966; Witrowski 1975; Horstmann 1977; Du Merle 1983; Hunter 1998; Simchuk et al. 1999; Ivashov et al. 2001; Mannai et al. 2010; Ghirardo et al. 2012; Schroeder and Degen 2012; Klapwijk et al. 2013; Schroeder et al. 2015; Nedorezov 2019)
Zeiraphera griseana Larch budmoth, larch tortrix	Range: Europe, China, Korea, Japan, Russia, N. America Host trees: *Larix*	(Baltensweiler et al. 1977; Baltensweiler 1993a, 1993b; Björnstad et al. 2002; Peltonen et al. 2002; Dormont et al. 2006; Esper et al. 2007; Kress et al. 2009; Iyengar et al. 2016; Hartl-Meier et al. 2017; Saulnier et al. 2017); Büntgen et al. 2020; Liebhold et al. 2020; Rozenberg et al. 2020; Din 2021
Family: Lasiocampidae		
Malacosoma disstria Forest tent caterpillar	Range: Throughout North America Host trees: *Quercus, Liquidambar, Nyssa, Populus, Acer saccharum*	(Daniel and Myers 1995; Parry 1995; Parry et al. 1997; Rothman and Roland 1998; Cooke and Roland 2000; Parry et al. 2001; Cooke and Roland 2003; Parry et al. 2003; Wood et al. 2009; Trudeau et al. 2010; Wood et al. 2010; Charbonneau et al. 2012; Cooke et al. 2012; Moulinier et al. 2013; Hughes et al. 2015; Uelmen et al. 2016; Schowalter 2017; Haynes et al. 2018b; Lait and Hebert 2018; Plenzich and Despland 2018; Robert et al. 2020; Cooke et al 2022

(continued)

Table 9.1 (continued)

Common name	Geographic range/Principal host trees	Key references
Dendrolimus superans Siberian silk moth	Range: Kazakhstan, Mongolia, China, Russia, Korea, Japan Host trees: *Larix, Picea, Pinus*	(Maeto 1991; Li et al. 2002; Kharuk et al. 2004, 2018; Kovacs et al. 2005; Kirichenko et al. 2009; Jeger et al. 2018)
Family: Geometridae		
Operophtera bruceata Bruce spanworm	Range: Southern Canada, northern USA, Alaska, Greenland Host trees: *Acer saccharum, Fagus, Populus*	(Brown 1962; Eidt et al. 1966; Ives and Cunningham 1980; Ives 1984; Troubridge and Fitzpatrick 1993; Elkinton et al. 2010; Gwiazdowski et al. 2013; Broadley et al. 2017; Havill et al. 2017; Andersen et al. 2022)
Epirrita autumnata Autumnal moth	Range: Palearctic region and Middle East Host trees: *Betula*	(Ayres and MacLean 1987; Tenow and Nilssen 1990; Ruohomäki and Haukioja 1992; Tammaru et al. 1996; Ruohomäki et al. 2000; Tammaru et al. 2001; Tanhuanpaa et al. 2001; Klemola et al. 2004; Nilssen et al. 2007; Ruuhola et al. 2007; Tenow et al. 2007; Jepsen et al. 2008; Klemola et al. 2008; Ruuhola et al. 2008; Klemola et al. 2009; Ammunét et al. 2010; Jepsen et al. 2011; Myers and Cory 2013; Klemola et al. 2014)
Alsophila pometaria Fall cankerworm	Range: across N. America, south to Colorado Host trees: *Ulmus, Fraxinus, Acer*	(Smith 1958; Kegg 1967; Appleby et al. 1975; Mitter and Futuyma 1977; Schneider 1980; Mitter et al. 1987; Walter et al. 2016)
Ennomos subsignaria Elm spanworm	Range: Eastern N. America spanning south to Texas and north to Alberta Host trees: *Ulmus, Malus, Betula, Acer, Quercus*	(Ciesla 1964a, 1964b; Fedde 1965; Kaya and Anderson 1974; Anderson and Kaya 1976; Fry et al. 2008, 2009; Ryall 2010)

(continued)

Table 9.1 (continued)

Common name	Geographic range/Principal host trees	Key references
Lambdina fiscellaria Hemlock looper	N. America (Pacific to Atlantic coast) south from Canada to Pennsylvania, Wisconsin and CA	(Alfaro et al. 1999; MacLean and Ebert 1999; Hébert et al. 2001; Pelletier and Piché 2003; Butt et al. 2010; Iqbal et al. 2011; Rochefort et al. 2011; Legault et al. 2012; Delisle et al. 2013, 2016; Seehausen et al. 2015; Wilson et al. 2016; Oswald et al. 2017; Sabbahi et al. 2018)
	Host trees: *Tsuga, Abies balsamea, Picea, Quercus*, other hardwoods	
Family: Notodontidae		
Heterocampa guttivitta Saddled prominent	Range: Central and eastern N. America	(Fiske and Burgess 1910; Fisher 1970; Allen 1972, 1973; Ticehurst and Allen 1973; Martinat and Allen 1987)
	Host trees: *Malus, Betula, Cornus, Corylus, Acer, Quercus, Rhus, Juglans*	
Syntypistis punctatella Beech caterpillar	Japan	(Kamata 2000, 2002)
	Host trees: *Fagus*	
Family: Coleophoridae		
Coleophora laricella Larch casebearer	Range: Central and northern Europe	(Ryan 1983, 1986, 1997; Habermann 2000; Ward and Aukema 2019; Ward et al. 2019, 2020a, 2020b)
	Introduced: N. America (nineteenth century)	
	Host trees: *Larix decidua*; in invasive range: *L. occidentalis, L. laricina*	
Family: Thaumetopoeidae		

(continued)

Table 9.1 (continued)

Common name	Geographic range/Principal host trees	Key references
Thaumetopoea pityocampa Pine processionary caterpillar	Range: Central Asia, N. Africa, southern Europe Host trees: *Pinus, Cedrus*	(Battisti 1988; Hódar et al. 2003, 2015; Pérez-Contreras et al. 2003; Carus 2004, 2010; Battisti et al. 2005, 2006; Stastny et al. 2006; Arnaldo et al. 2010; Ronnås et al. 2010; Seixas Arnaldo et al. 2011; Jacquet et al. 2012; Van Dyck 2012; Tamburini et al. 2013; Cayuela et al. 2014; Li et al. 2015; Castagneyrol et al. 2016; Salman et al. 2016; Pimentel et al. 2017; Atvis et al. 2018; Camerero et al. 2022; Georgiev et al. 2022; Martin et al. 2022; Mirchev et al. 2021
Hymenoptera		
Family: Diprionidae		
Neodiprion sertifer European Pine sawfly	Range: Native: Europe Introduced: N. America (1925) Host trees: *Pinus, P. sylvestris, P. resinosa, P. banksiana, P. mugo*	(Austara et al. 1987; Pschorn-Walcher 1987; Kouki et al. 1998; Larsson et al. 2000; Lyytikäinen-Saarenmaa et al. 2001; Gur'yanova 2006; Kollberg et al. 2013, 2014; Bellone et al. 2017; Kosunen et al. 2016; Klapwijk and Björkman 2018; Chorbadjian et al. 2019)
Diprion similis Introduced pine sawfly	Range: central & northern Europe, Siberia, China Introduced (1914): eastern USA & Canada Host trees: *Pinus, P. strobus*	(Weber 1977; Drooz et al. 1985)
Gilpinia hercyniae European spruce sawfly	Range: Quebec, New Brunswick, NE USA Host trees: *Picea*	(Balch 1939; Dowden 1939; Neilson and Morris 1964; Wong 1972; Schopf 1989; Williams et al. 2003)
Family: Pamphiliidae		
Acantholyda erythrocephala Red-headed pine sawfly	Range: Native: Europe Introduced (1925): N. America Host trees: (Introduced range): *Pinus strobus, P. sylvestris, P. Resinosa*	(Asaro and Allen 2001; Kenis and Kloosterman 2001; Mayfield et al. 2007)

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