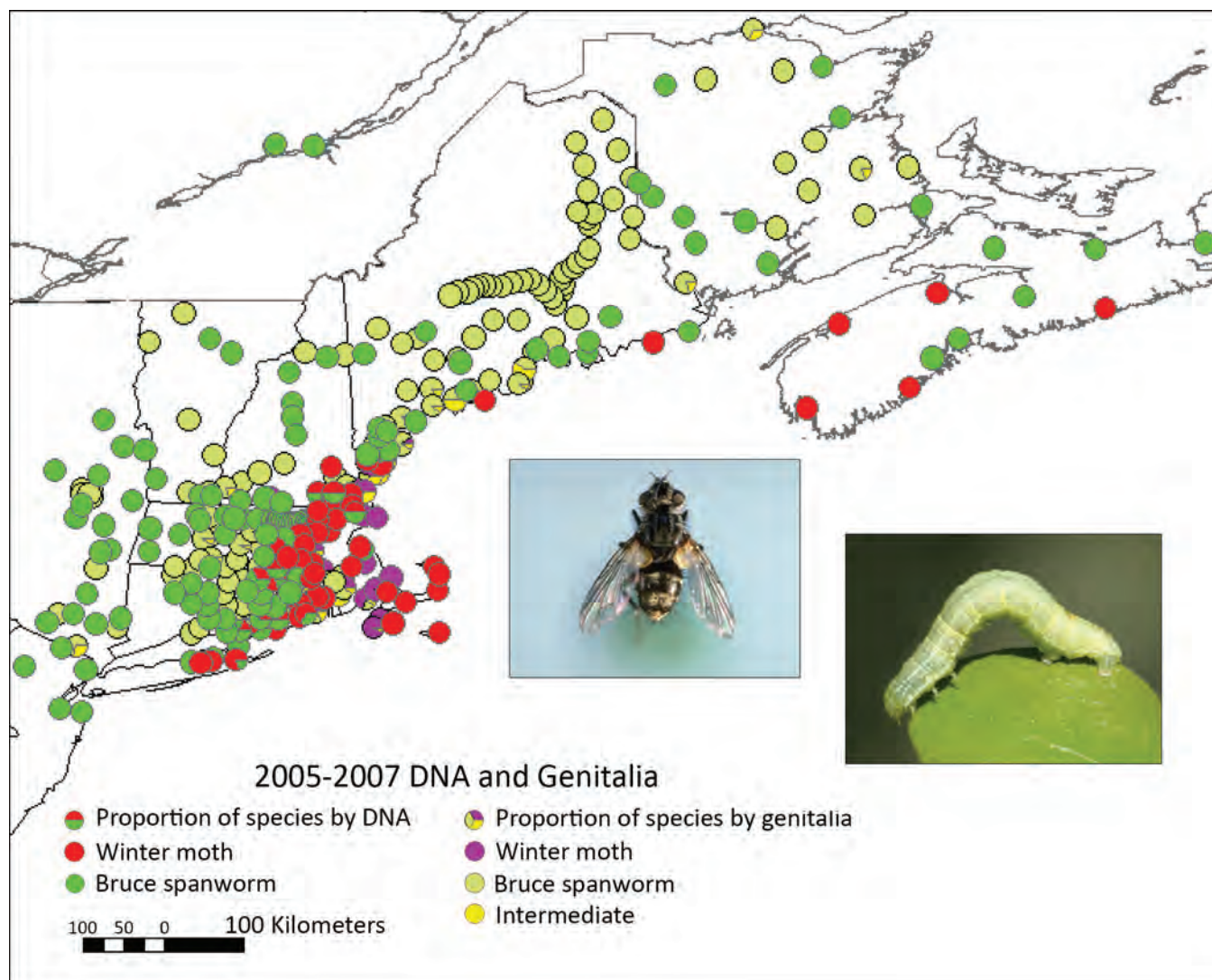


BIOLOGY, SPREAD, AND BIOLOGICAL CONTROL OF WINTER MOTH IN THE EASTERN UNITED STATES



Joseph Elkinton, George Boettner, Andrew Liebhold, and Rodger Gwiazdowski



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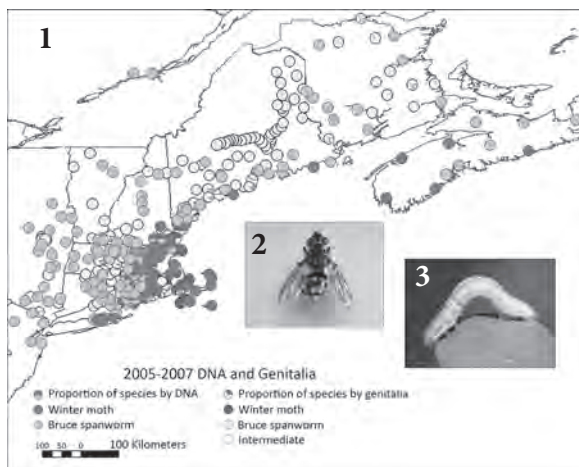


University of Massachusetts, Amherst
Department of Environmental Conservation

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Cover 1) Background map: Joe Elkinton, distribution of winter moth (*Operophtera brumata*) and Bruce spanworm (*Operophtera bruceata*) in pheromone-baited traps in northeastern North America, 2005–2007, Elkinton et al. 2010 (see page 7 for details). **2)** *Cyzenis albicans*, Nicholas Condor (see page 15 for details). **3)** Winter moth (*O. brumata* (Linnaeus), Milan Zubrik, Forest Research Institute - Slovakia, Bugwood.org. Note: 2 and 3 are not to scale.

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Biology, Spread, and Biological Control of Winter Moth in the Eastern United States

Joseph Elkinton, George Boettner, Andrew Liebhold, and Rodger Gwiazdowski

Life cycle

The winter moth (*Operophtera brumata* L.; Lepidoptera: Geometridae) is an inchworm caterpillar that hatches coincident with bud-break on its hosts and feeds on a wide range of deciduous trees. It is one of a group of geometrid species that feed in early spring and then pupate in the top layer of the soil or litter beginning in mid-May. As postulated by Feeney (1970), the early spring feeding strategy of such larvae allows them to take advantage of the high nitrogen content and low concentrations of defensive compounds, such as condensed tannins, in newly formed leaves. Winter moth larvae are pale green and are typical inchworms (Fig. 1A). They have only two pairs of prolegs at the rear of the abdomen, in contrast to other geometrids, such as fall cankerworm, *Alsophila pometaria* (Harr.) which have three prolegs. Older larvae feed in expanding leaf clusters and are capable of defoliating their hosts. When larval development is complete, they drop to the soil for pupation. They pupate inside earthen cocoons, which they spin in the soil or leaf litter beneath the tree (Fig. 1B). In most locations (Northeast and Pacific Northwest in the United States and central Europe), pupation occurs in mid- to late May. The pupae remain in the soil or leaf litter until adult emergence in late autumn or early winter. In central Europe, the Pacific Northwest, and northeastern United States, adult emergence occurs in late November through early January, hence the name ‘winter moth.’ The male moths are light brown (Fig. 1C), and are active whenever

temperatures are above freezing. The female is gray with vestigial wings and, therefore, cannot fly (Fig. 1D). Females ascend the base of a nearby tree and emit a sex pheromone (Roelofs et al. 1982) that attracts males. After mating, the female deposits 150–350 eggs singly, typically under bark flaps or in crevices on the stem of the tree, where they overwinter. Eggs are green at first but, within 2–3 weeks, turn pink as embryos develop. Eggs turn dark blue just before hatching in early spring. Egg hatch can occur anytime from mid-March to mid-April in Massachusetts or to mid-May in Nova Scotia. The date of hatch depends mainly on accumulated warmth in spring, but is also affected by winter cooling (Embree 1970, Kimberling and Miller 1988, Visser and Holleman 2001, Hibbard and Elkinton 2015). Hatch typically occurs at or before bud-break of most of the host plants. Several studies indicate that synchrony with bud-break is critical to winter moth survival and a major predictor of population density change (Varley and Gradwell 1960, 1968, Embree 1965). Visser and Holleman (2001) present evidence that warmer spring temperatures in the Netherlands over the last few years have disrupted the synchrony with oak bud-break, and winter moths have shifted to other host trees. The main dispersal stage of winter moths occurs right after hatch, when larvae spin down on silken threads and blow in the wind between trees, a process known as ballooning. After settling, the larvae burrow into the swelling buds of their hosts and begin feeding. Much of the leaf damage from winter moth occurs early in spring, before buds expand.

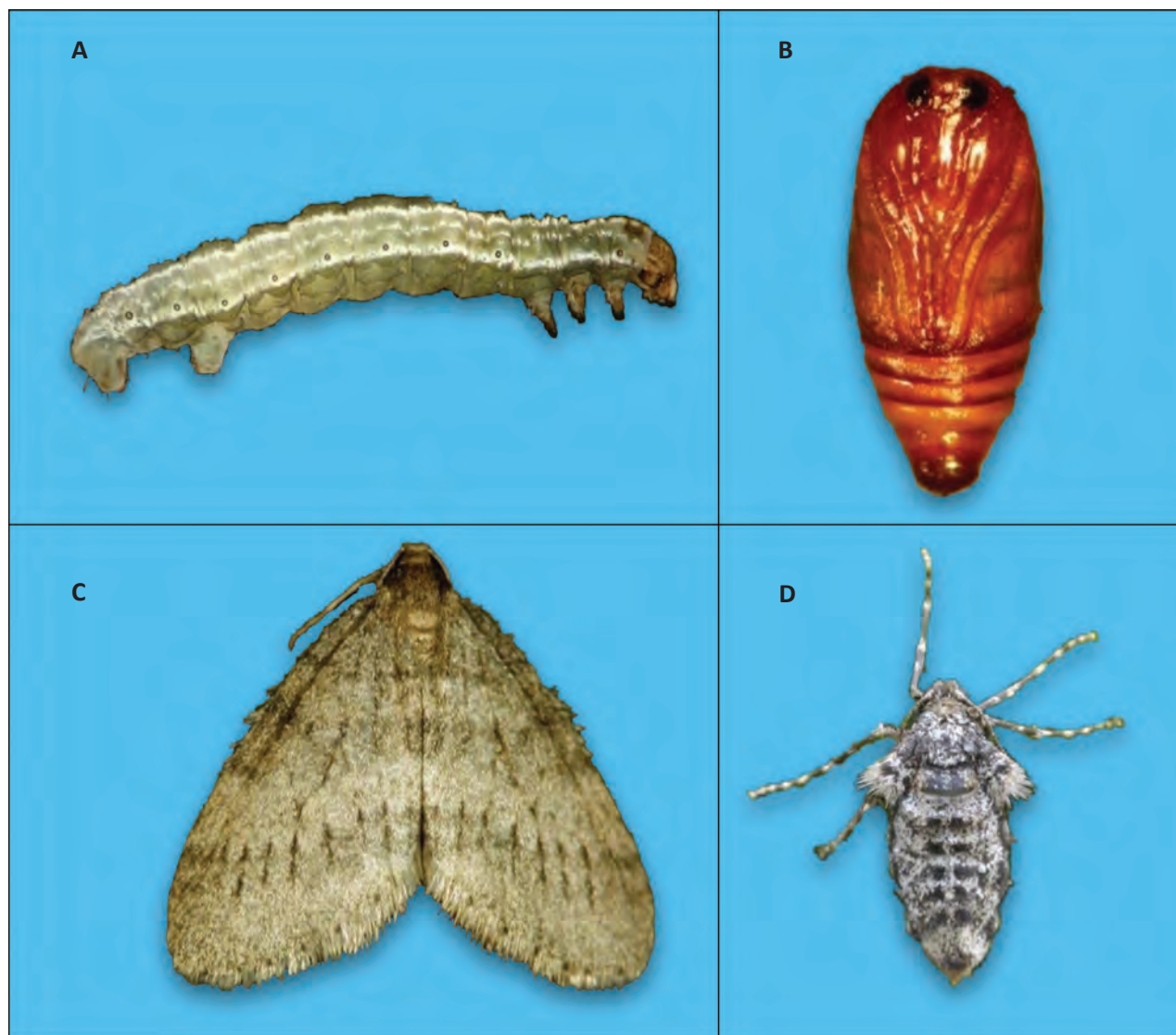


Figure 1 Winter moth (*Operophtera brumata*) life stages: **A)** larva, **B)** pupa, **C)** adult male, **D)** adult female (photo by D. Wagner, and reprinted from Elkinton and Boettner 2014).

Geographic range

The native range of winter moth covers most of Eurasia, including all of Europe and much of Russia, including the Russian Far East (Troubridge & Fitzpatrick 1993). In North America, winter moths were accidentally introduced to Nova Scotia in the 1930s (Hawboldt and Cuming 1950), to Oregon in the 1950s (Kimberling et al. 1986) and the Vancouver area of British Columbia around 1970 (Gillespie et al. 1978). In the northeastern United States, winter moth defoliation was first noted in Massachusetts starting in the late 1990s, and the cause was definitively identified as winter moth by 2003. In all of these introductions, casual observers initially mistook the infestation for that of native geometrid defoliators, such as the fall cankerworm (*A. pometaria*

Harr). Elkinton et al. (2010) completed a survey for winter moths with pheromone-baited traps in the northeastern United States and adjacent areas of Canada (Fig. 2) showing that winter moth occurs from Long Island, New York, through southeast Connecticut, most of Rhode Island, eastern Massachusetts and coastal areas of New Hampshire and Maine.

The coastal nature of the winter moth infestation very closely matched the geographical extent of zone 5b and warmer in the USDA plant cold-hardiness zone map based on minimum winter temperatures (Cathey 1990) (Fig. 3A). Recent updates of the USDA plant cold-hardiness map (Fig. 3B) indicate that zone 5b now extends into more interior regions of Maine and New Hampshire, and that these areas may now be suitable

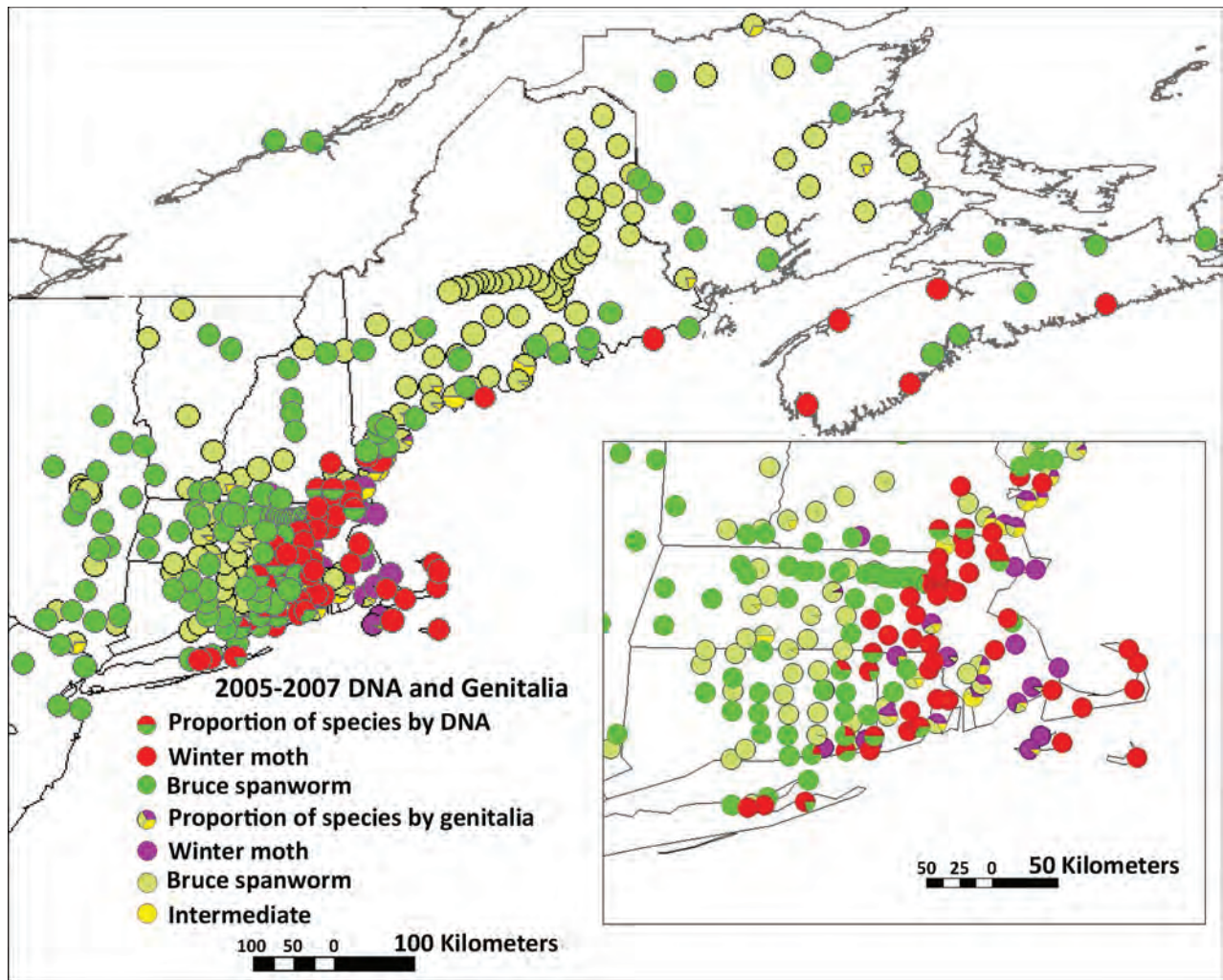


Figure 2 Distribution of winter moth (*Operophtera brumata*.) and Bruce spanworm (*Operophtera bruceata*) in pheromone-baited traps in northeastern North America, 2005–2007. Unfortunately, winter moths (*O. brumata*) use the same pheromone compound as the native species Bruce spanworm (*O. bruceata*). Adult males of the two species are difficult to distinguish, especially the battered specimens we recover from pheromone traps. Identification of moths is based on male genitalia and the DNA sequence of the COI mitochondrial gene (reprinted from Elkinton et al. 2010).

habitat for winter moth, as a consequence of climate change. Indeed, in 2012 and 2013, coastal regions of Maine experienced winter moth outbreaks for the first time (Fig. 4), although winter moths were documented in these locations in the 2006 pheromone-trap survey (Fig. 2). Earlier surveys by the Canadian Forest Service in New Brunswick show that winter moth extended all along the coast of that province in the 1960s (Embre 1991).

Winter moth spread

Elkinton et al. (2014) analyzed historical defoliation maps (Fig. 5A) that documented the spread of winter

moth in eastern Massachusetts and Rhode Island between 2004 and 2011. Outbreaks were first noted in areas north and south of Boston, as illustrated by the defoliation in 2004. Over the next few years, defoliation spread across southeastern Massachusetts, including Cape Cod, and into Rhode Island at a rate of 8.3 km per year (Elkinton et al. 2014). At the same time, winter moth was spreading across central Massachusetts, as documented by pheromone-baited traps deployed along an east-west highway (Fig. 5B). Between 2005 and 2011, winter moth spread west at a rate of about 7.4 km per year, over a combined distance of about 44 km (Fig. 5B), or (Elkinton et al. 2014), into the western half of the state. During this same period, however, virtually no

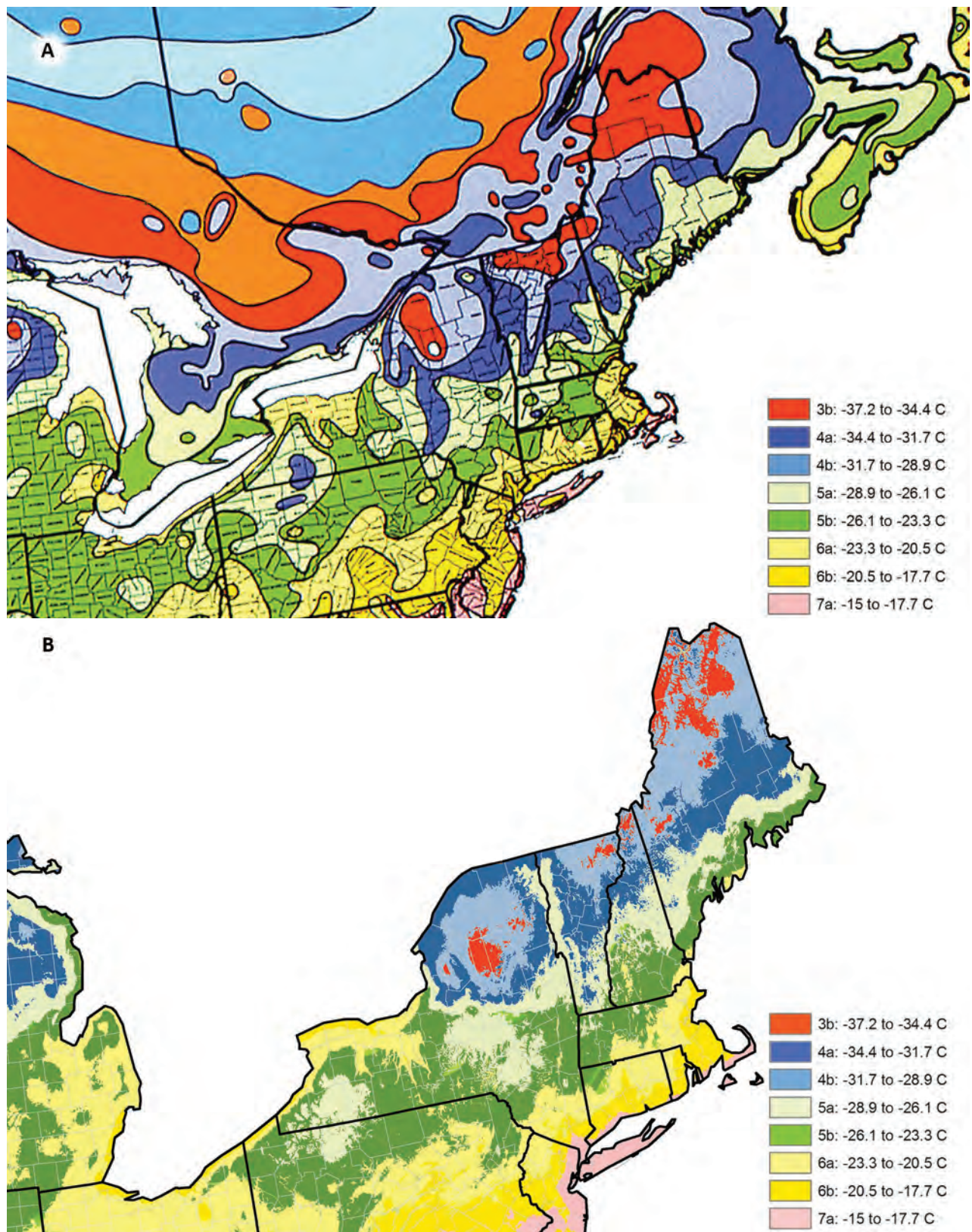


Figure 3 **A)** Plant cold hardiness zone map for northeastern North America (adapted from Cathey 1990, reprinted from Elkinton et al 2010) for the period 1974–1986. **B)** More recent USDA cold hardiness map for the period 1976–2005. Zones are based on average absolute minimum winter temperature. Note: Zone 6a, which occurred in eastern Massachusetts and Nova Scotia in 1990 (**3A**), has now moved northward and inland encompassing coastal Maine and New Hampshire (**3B**)

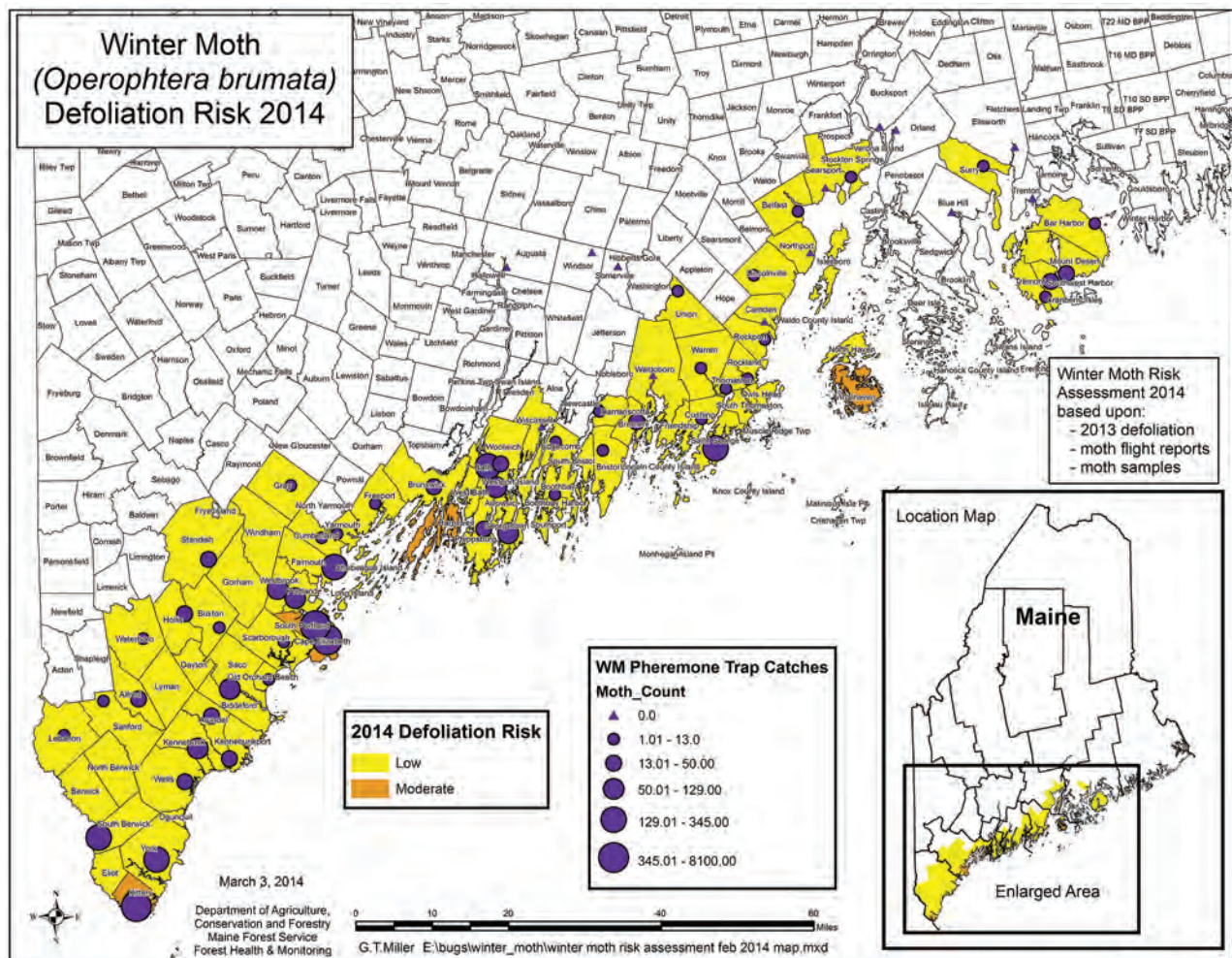


Figure 4 Winter moth (*Operophtera brumata*) outbreak areas estimated for 2014 in coastal Maine, based primarily on males captured in pheromone-baited traps, and on defoliation in 2013. (Figure courtesy of Maine State Forest Service.)

defoliation occurred in central Massachusetts, at least as recorded by aerial survey (Fig. 5A). The implication is that cold winter temperatures, or whatever factors limit the distribution of winter moth to coastal areas of Maine and New Brunswick, may prevent winter moth populations from reaching defoliating levels in central Massachusetts. On the other hand, it is clear from our analysis of winter moth spread and from the cold hardiness maps (Figs. 3A, B) that most of the eastern United States will be excellent habitat for winter moth outbreaks, and that winter moth is well on his way to spreading over the entire region. So, winter moth will soon be a defoliator of significant concern in most of the eastern United States.

Taxonomy

The genus *Operophtera* occurs in both North America and Eurasia, with the largest number of species occurring in the Far East. A revision of the North American species of *Operophtera* has been completed by Troubridge and Fitzpatrick (1993). In North America there are two native species: *O. danbyi* (Hulst) on the West Coast, and Bruce spanworm (*O. bruceata* [Hulst]), which is transcontinental in the northern United States and Canada. *Operophtera bruceata* has been divided into two subspecies, *O. bruceata bruceata*, which occurs across the continent except for the far-west and *O. bruceata occidentalis*, the western Bruce spanworm, which occurs from Alaska to California, west of the Cascades and Sierra Nevada mountains. Gwiazdowski et al. (2013) collected specimens throughout this range

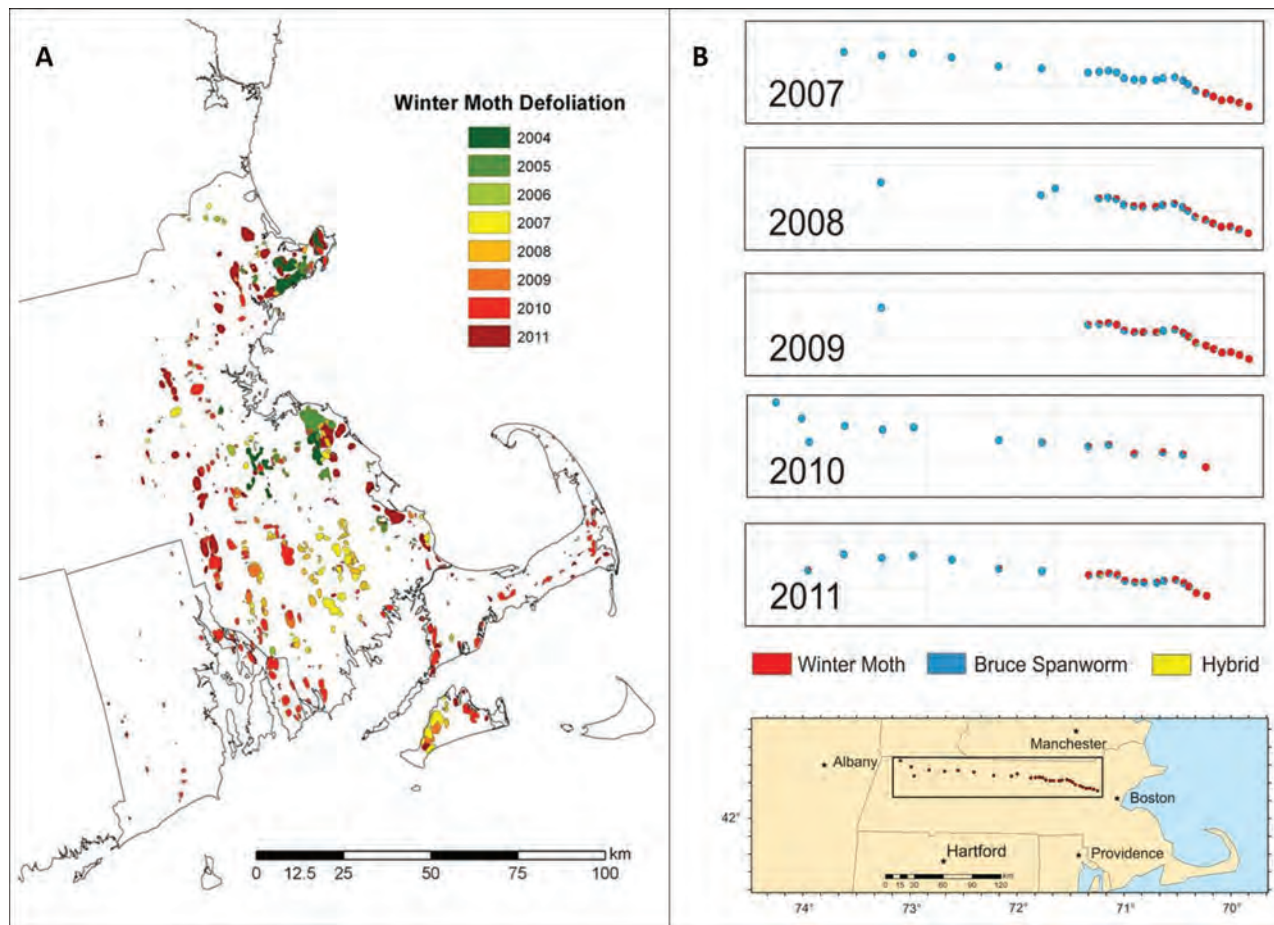


Figure 5 **A)** Winter moth (*Operophtera brumata*) defoliation in Massachusetts and Rhode Island, 2004–2011, compiled from annual aerial surveys. **B)** Winter moth and Bruce spanworm (*Operophtera bruceata*) captured in pheromone-baited traps along an east-west highway in Massachusetts, 2007–2011 (from Elkinton et al. 2014).

in both North America and in Europe, as part of a phylogeographic survey of winter moth diversity based on sequence variation of the CO1 mitochondrial gene (which included the DNA barcoding region). These sequences show high haplotype variation among winter moths from Europe, but nearly all North American winter moths are of one invariant haplotype (Fig. 6). This pattern might indicate a founder effect of a single introduction of winter moths to North America, presumably to Nova Scotia. However, the most common haplotype in North America is also the most common one in Europe, and occurs across the continent. Thus, mitochondrial diversity did not reveal the origin of North American winter moth among sampled European populations, but did provide an overview of intra-specific diversity. Similarly, there was wide variation of haplotypes among Bruce spanworm populations across North America (Gwiazdowski et al. 2013). In particular, the western Bruce spanworm

subspecies *O. bruceata occidentalis* formed a distinct clade in the mitochondrial phylogram published by Gwiazdowski et al. (2013) (Fig. 7), which included North American, European and a Japanese species of *Operophtera*. This result suggests *O. bruceata occidentalis* might be a distinct species from *O. bruceata bruceata*.

Bruce spanworm displays occasional outbreaks, especially in hardwood forests in the northern United States (Maine, Minnesota, Wisconsin, Vermont and New Hampshire), but these are very short-lived. Like winter moth, it is extremely polyphagous and is an occasional pest in apple orchards (Ives 1984). As shown by the survey conducted by Elkinton et al. (2010), (Fig. 2, page 7) and Gwiazdowski et al. (2013), Bruce spanworm is ubiquitous, except perhaps in areas where winter moth is now predominant. Elkinton et al. (2010, 2014) confirm that winter moth and Bruce spanworm hybridize to some extent, so gene flow is occurring between the two species. The extent and implications

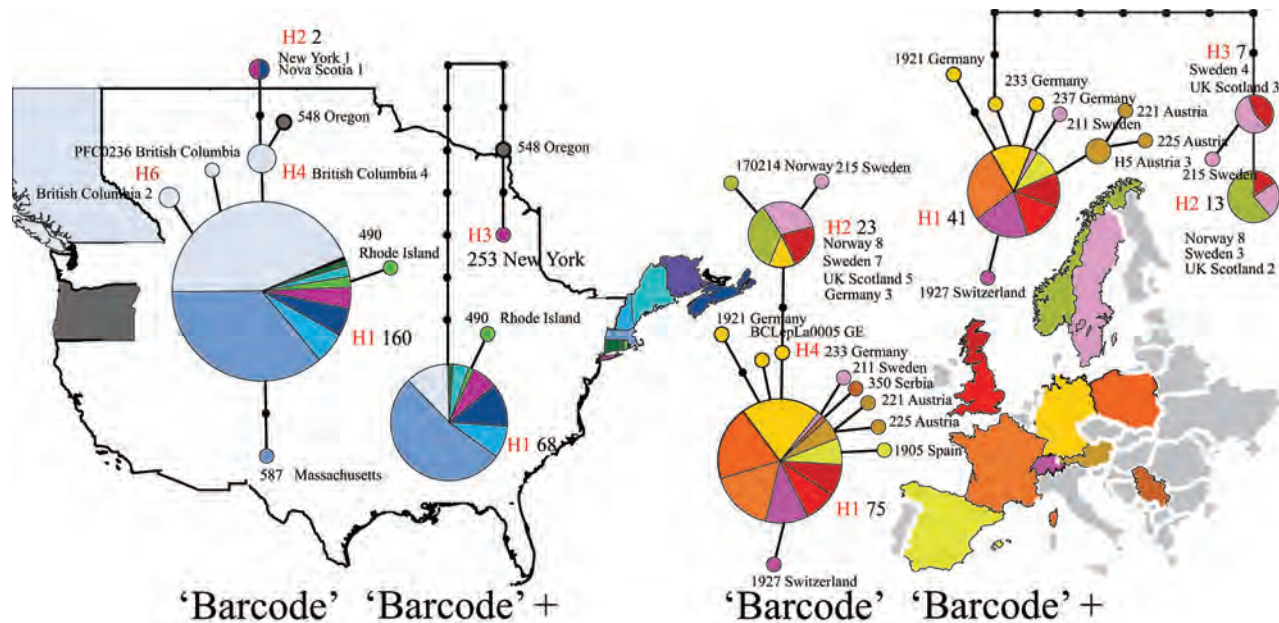


Figure 6 Haplotype networks for winter moth (*Operophtera brumata*), collected across North America and Europe. The two sets of networks display the proportion of the same genotypes collected on the respective continents. Each circle is a unique haplotype, and the area of each circle is directly proportional to the number of specimens sharing that haplotype. Colors in each circle correspond to the proportion and geographic location of specimens sharing that haplotype. Each line segment connecting haplotypes is proportional to single character-state changes (mutations) between haplotypes. Haplotype designations (e.g., H1) and the number of specimens in that haplotype are placed adjacent to the haplotype. Haplotype designations occurring in both the United States and Europe are indicated in red. Networks for each continent are divided into networks for the barcode region, as well as the combined barcode and barcode+ regions, to visualize any additional information added by the barcode+ region (Reprinted from Gwiazdowski et al. 2013).

of this gene flow remain to be determined, but could include transfer of susceptibility to the parasitoid *Cyzenis albicans* (Fallén), or the ability to tolerate cold winter temperatures.

In Europe there are two species of *Operophtera*: *O. brumata*, and the northern winter moth *O. fagata* (Scharfenberg). Large outbreaks of winter moth occur periodically in mountain birch (*Betula pubescens czereapanovii* [Ehrh.] subsp. *czereapanovii* [Orlova.]) forests in northern Fenno-Scandinavia (Tenow 1972, Jepsen et al. 2008). In this region, in response to global warming, winter moth has been moving from lower elevation coastal forests to higher elevation, where it has occupied habitat dominated by another geometrid, the autumnal moth, *Epirrita autumnata* Bkh., a species also known for periodic outbreaks (Tenow et al 2007, Jepsen et al. 2008).

Host range and damage

Winter moth is extremely polyphagous and feeds on a wide range of host trees, including oaks (*Quercus*), maples (*Acer*), birches (*Betula*) and many others (Wint 1983). It is an occasional orchard pest, and performs extremely well on apple (*Malus*). Also, it is 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. Many blueberry growers in Massachusetts have lost their entire crops amounting to thousands of dollars of losses. Winter moth is also a pest of cranberries (A. Averill, personal communication). Outbreaks of winter moth have occurred on Sitka spruce (*Picea sitchensis* [Bongard] Carr.) in Europe (Stoakley 1985, Watt and McFarlane 1991), on heather (*Calluna vulgaris* L.) in Scotland (Kerslake et al. 1996), and on mountain birch (*B. p.* subsp. *czereapanovii*) in Fenno-Scandinavia (Jepsen et al. 2008). Winter moth larvae typically hatch at or before bud-break of their

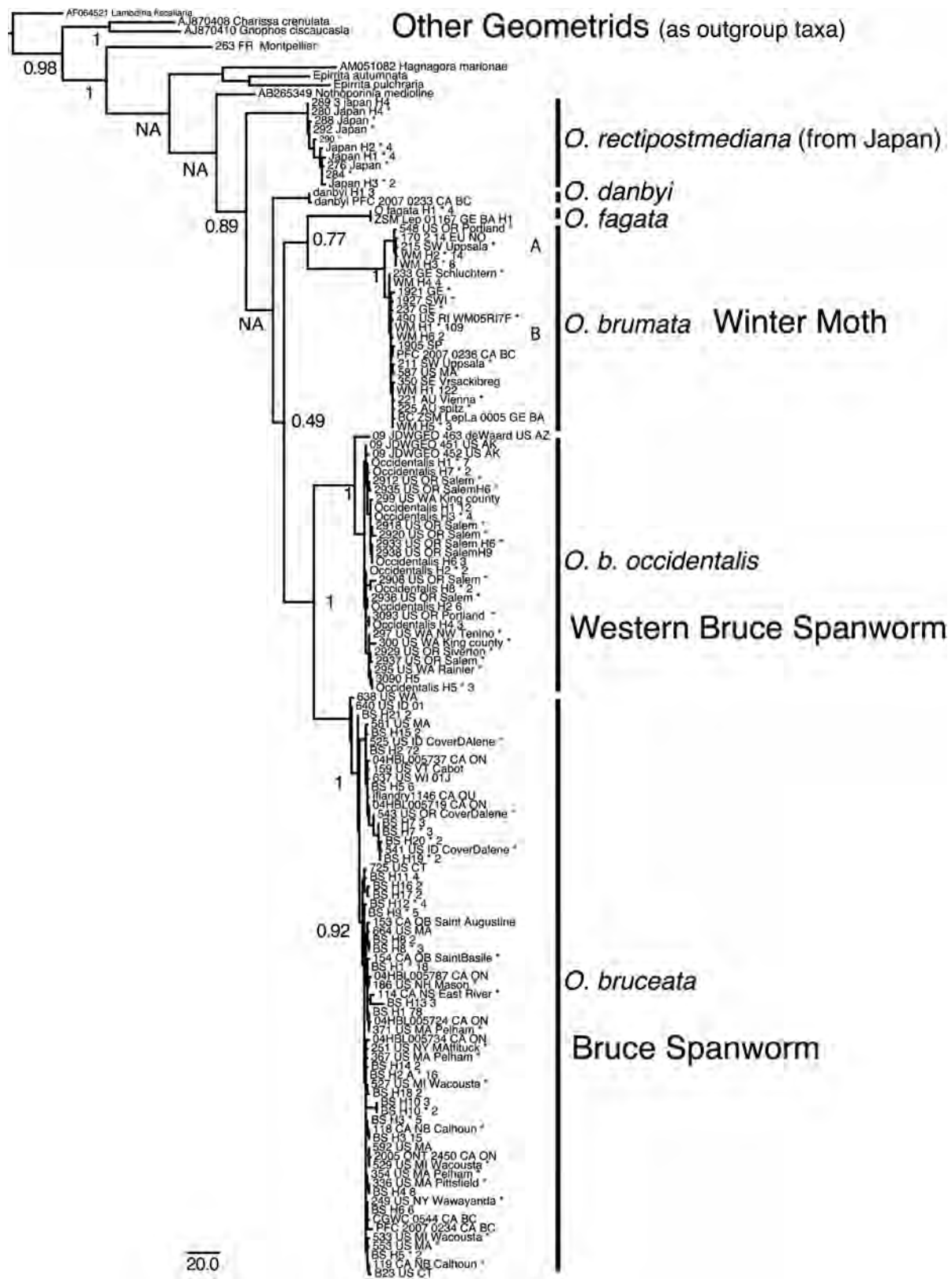


Figure 7 Mitochondrial phylogeny of *Operophtera* and outgroup taxa. Shown is a maximum parsimony topology with node labels indicating presence and support of those nodes in a Bayesian analysis. NA indicates a node not present in the Bayesian analysis. Haplotypes are designated by haplotype number, and followed by the number of specimens in that haplotype (e.g. WM H1 109). Branch lengths are directly proportional to the number of changes along that branch, and a scale bar is provided below (reprinted from Gwiazdowski et al. 2013).

host trees and the larvae bore into the expanding buds, so that much of the damage occurs before leaf expansion. Although 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. The typical damage results in partially defoliated leaves, but can cause lasting damage to the tree. 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. Annually in New England, homeowners and town tree-care professionals spend many thousands of dollars spraying for winter moth control on shade trees.

Population ecology

Winter moth is one of the world's most widely studied insects in terms of population ecology. Classic ecological studies (Varley and Gradwell 1960, 1968, Varley et al. 1973) helped introduce the analysis of life tables to insect ecology and promoted the use of key-factor analysis to identify the main determinants of population density change. These authors studied winter moths in an oak forest near Oxford, England, and concluded that winter moth populations were regulated at low density by predation on pupae in the soil or leaf litter beneath the study trees. Mortality during the egg and larval stages, which they called "overwintering mortality," accounted for most of the year-to-year variation in winter moth density. Although this mortality was the key factor responsible for population density change, it was not density dependent, and thus did not serve to regulate winter moth densities. They believed that overwintering mortality was dominated by starvation/dispersal due to asynchrony of winter moth hatch with bud-break. Subsequent research suggested that pupal predation was mainly caused by staphylinid and carabid beetles (Frank 1967). Mortality caused by the tachinid *C. albicans* was not a major factor in these low-density populations.

European studies in recent years have focused on the outbreaks of winter moth in northern Fenno-Scandinavia (Tenow et al 2007, Jepsen et al. 2008). Winter moth outbreaks occur approximately every 10 years in the mountain birch (*B. p.* subsp. *czerepanovii*) forests of that region in synchrony with, but lagging 2–3 years behind, those of the well-studied geometrid autumnal moth, *Epirrita autumnata* (Tenow 1972, Tenow et al. 2007). Jepsen et al. (2009) used satellite data of leaf out and defoliation to show that favorable synchrony of winter moth hatch with bud-break fueled the synchronous outbreak of winter moths during the increase phase of the population cycle. The synchrony was reduced during the peak and declining phases of the outbreak. Analyses by Tenow et al. (2013) showed that waves of defoliation by winter moth spread from east to west across Europe approximately every 10 years. The underlying causes of this phenomenon are not understood.

Vinstad et al. (2013) reported the complex of larval parasitoids attacking winter moth and autumnal moth in northern Norway and compared that to reports from other sites in Western Europe. A total of 18 species (five ichneumonids, three braconids, nine tachinids and one eulophid) comprise most of this fauna. The majority of these species occur on winter moth in northern Fenno-Scandinavia, except the tachinids, including *C. albicans*, which does not occur there, but is very common elsewhere (Vinstad et al. 2013). Recent studies by Schott et al. (2010) of mortality caused to winter moth by these other larval parasitoid species showed they often cause levels of mortality exceeding 50% in northern Norway, but do not appear 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 by invertebrate predation at low density. It is evident that, despite all this research, the role of natural enemies in the dynamics of winter moth in northern Fenno-Scandinavia remains unresolved.

Epizootics of nuclear polyhedrosis virus (NPV) in winter moth populations occasionally have been reported in the European literature (Wigley 1976,

Graham et al. 2004). In North America, Burand et al. (2011) reported an NPV recovered from cadavers of winter moth reared from larvae collected in Massachusetts. However, between 2004 and 2014, we have reared tens of thousands of winter moths collected as late instar larvae from high-density populations throughout the northeastern United States, British Columbia and northern Norway. Nearly all of these larvae survived to the pupal stage. Mortality from pathogens is a major feature that reliably terminates the outbreak populations of many forest Lepidoptera, such as gypsy moth (*Lymantria dispar* [L]) (Elkinton and Liebhold 1990) and forest tent caterpillar (*Malacosoma disstria* Hübner). In contrast, outbreak populations of winter moth seem remarkably free of such epizootics.

Embree (1965) analyzed life table data he collected from winter moth populations beginning in 1954 in a red oak (*Q. rubra*) stand in Nova Scotia before and after the onset of high parasitism by *C. albicans* beginning in 1960. *Cyzenis albicans* and *Agrypon flaveolatum* Gravenhorst (Hymenoptera: Ichneumonidae) were released in Nova Scotia as biological control agent beginning in 1954. Before these parasitoids were established, variation in larval survival accounted for most of the changes in winter moth population density. Embree believed (as did Varley and Gradwell, above) that asynchrony of hatch with bud-break, especially when the spring was late, was the main cause of larval mortality. Embree's life table shows high levels of mortality occurring in the late larval instars, possibly due to avian predation. After 1960, when *C. albicans* and *A. flaveolatum*, achieved high levels of parasitism, variation in pupal mortality, including parasitism by these two species, became the main cause of population density change.

Biological control

The biological control of winter moth in Canada represents one of the most famous of all biological control successes in forest entomology (Caltagironi 1981, Roland and Embree 1995). Biological control efforts began in Nova Scotia in the 1950s, where winter moth had invaded in the 1930s (Hawboldt and Cuming 1950). Natural enemies were collected in France and Germany (Roland and Embree 1995) with the help of the Commonwealth Institute of Biological Control. A total of 63 parasitoid species known to attack winter moth in Europe were considered for release in Nova Scotia (Wylie 1960). The most abundant species

collected were the tachinids *Lypha dubia* (Fallén) and *C. albicans* (Fig. 8A, B) and the ichneumonid *A. flaveolatum* (Fig. 8C, D).

Between 1954 and 1957, annual releases of *C. albicans* (Fig. 9A) were made at one location (Oak Hill) in Nova Scotia (Graham, 1958). In addition, 250 *A. flaveolatum* (Fig. 9A) were released in 1956. Releases of both parasitoids continued elsewhere in Nova Scotia until 1965. Before 1963, the parasitoids were collected in Europe; thereafter they were collected at sites in Nova Scotia where the parasitoids had become abundant. Other species released were the tachinids *L. dubia* and *Phorocera obscura* Fallén, and the ichneumonids, *Phobocampe crassiuscula* Gravenhorst and *Pimpla turiaonellae* L. (Graham 1958, Roland and Embree 1995), but these species were not recovered.

Cyzenis albicans lays microtype eggs along the edges of partially defoliated leaves, and each fly can lay more than 1000 eggs (Embree and Sisojevic 1965). Winter moth larvae ingest the eggs as they feed. As this occurs, the eggs hatch and the neonate fly maggots migrate to the caterpillar's salivary glands, where they remain until the winter moth larva drops out of the canopy and completes development to the pupal stage. The immature *C. albicans* then complete development and form puparia inside the pupa of the winter moth host in early summer. The fly puparia remain in the soil until the following spring, when the adult flies emerge at approximately the same time that winter moth larvae hatch. There is one generation per year. The flies mate and then require about two weeks before they are ready to lay eggs (Embree and Sisojevic 1965). Oviposition begins about the same time winter moth larvae are in the third instar and are large enough to consume the *C. albicans* eggs. Roland (1986) showed that *C. albicans* flies aggregate to oak and apple foliage that has been fed upon by winter moth, and he identified a volatile compound (borneol) from oak leaves that attracts the fly (Roland 1990a, Roland et al. 1995).

O'Hara and Cooper (1992) reviewed six species of Nearctic *Cyzenis* flies. *Cyzenis albicans* and *C. pullula* (Townsend), which attacks Bruce spanworm, are closely related sister species. There is one report of *C. pullula* from winter moth on Vancouver Island, but that may represent a misidentification of the host. Four other species of *Cyzenis* are widespread in North America and attack various species in the family Tortricidae,

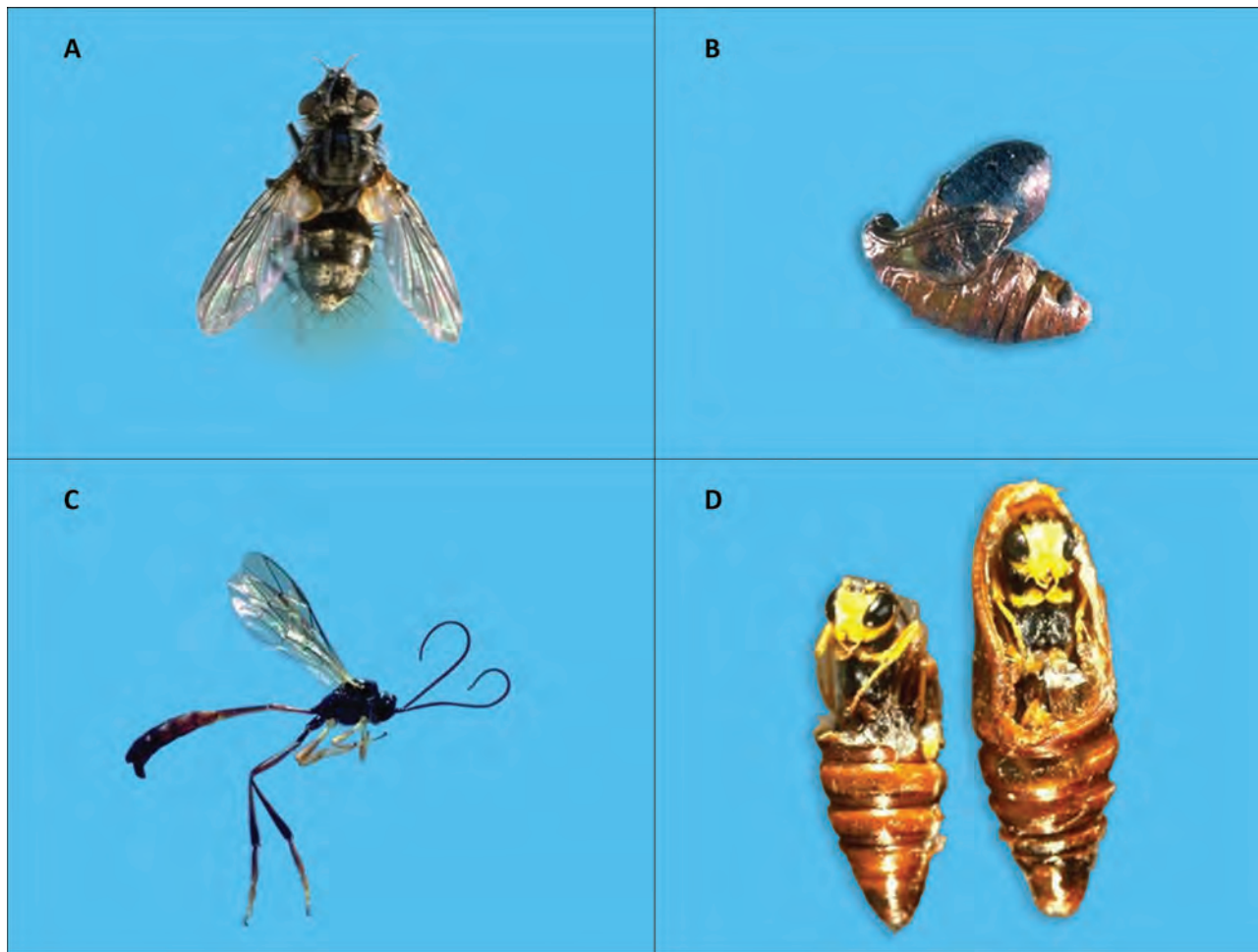


Figure 8 A) Adult *Cyzenis albicans*, B) *C. albicans* puparium inside winter moth pupa, C) adult *Agrypon flaveolatum*, D) pharate adult *A. flaveolatum* inside winter moth pupae (photos by Nicholas Condor).

including the spruce budworm, *Choristoneura fumiferana* (Clemens). No *Cyzenis* of any species were recovered from thousands of winter moth larvae reared from many sites in the northeastern United States before the deliberate release of *C. albicans* in the region.

Embree and Sisojevic (1965) were unsuccessful in laboratory attempts to rear *C. albicans* on the geometrid *A. pomataria*, the lasiocampid *Malacosoma americanum* (Fabricius), or the olethreutid *Pseudexentera improba* (Walker), but they did rear it successfully on Bruce spanworm, *O. bruceata*. Roland and Embree (1995) state that *C. albicans* rarely attacks Bruce spanworm in the field, and is unlikely to have a major impact on this species.

The ichneumonid *Agrypon flaveolatum* (Figs. 8C, D) attacks the larval stage of winter moth and has one generation per year. Adults overwinter inside the winter moth pupae (Fig. 8D) and emerge in the spring.

Roland and Embree (1995) report the highest levels of parasitism from this species occur in low-density populations of winter moth. Because of uncertainties in its taxonomy and host range, *A. flaveolatum* has not been considered for release in the current biological control effort in the northeastern United States. Dasch (1984) reported that *A. flaveolatum* might be synonymous with *A. alaskensis* Ashmead in the Pacific Northwest and northern Canada. Schmid (1970) and Marsh and Carlson (1979) believed it to be synonymous with *A. provancheri* Dalla Torre. *Agrypon provancheri* is widespread across North America (Marsh and Carlson 1979) and has a wide host range among the Geometridae, including *O. bruceata* and *Melanolophia imitata* Walker (Barron 1989). However, no *Agrypon* spp. have been recovered in ten years of rearing many thousands of winter moth larvae in Massachusetts (Elkinton and Boettner, unpublished data). Barron (1989) found morphological differences between *A. flaveolatum*, *A. provancheri*, and *A. alaskensis*.

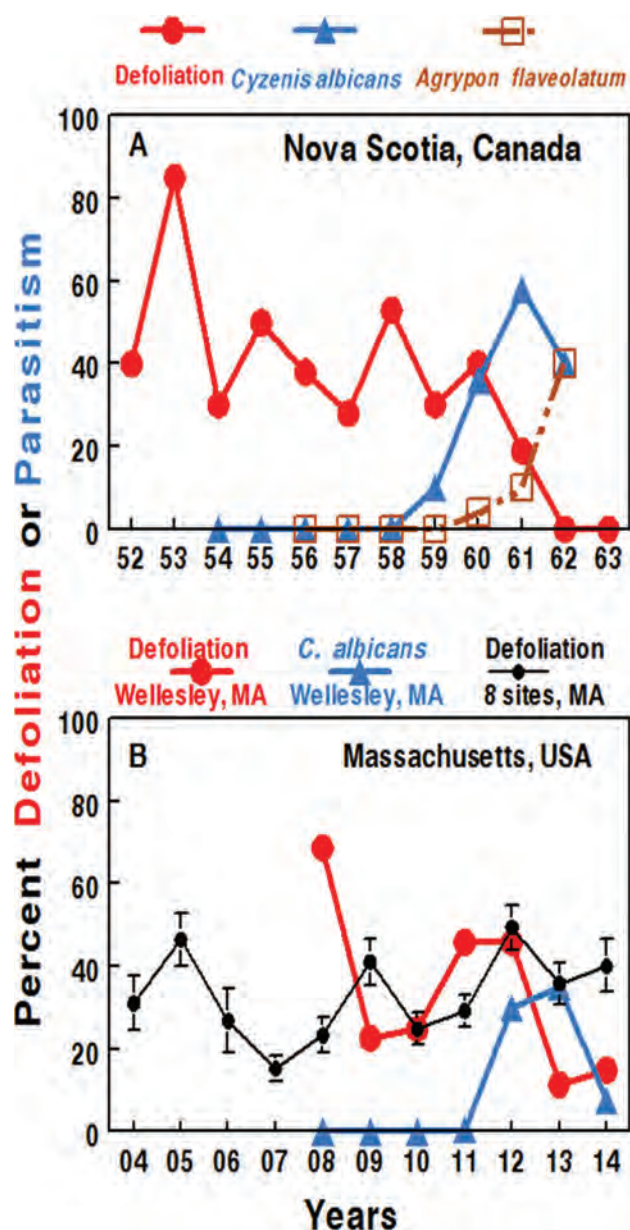


Figure 9 Defoliation by winter moth (*Operophtera brumata*) and percentage of parasitism by *Cyzenis albicans* and *Agrypon flaveolatum* in **A**) Nova Scotia in the 1950s (adapted from Embree 1965) or **B**) in eastern Massachusetts, 2004–2014. Black line is defoliation (on oak and maple) averaged from eight sites, Red line represents defoliation (on red oak and red maple) in Wellesley, Massachusetts, beginning with first parasitoid releases at this site occurring in 2008.

The first recovery of *C. albicans* at the release site in Nova Scotia was made in 1956. By 1959, the parasitism was approximately 10%; this increased to more than 70% by 1961 (Fig. 9A). The winter moth populations in Nova Scotia started to decline in

1962 as parasitism exceeded 78% (Fig. 9A). *Agrypon flaveolatum* was recovered in 1957, one year after its release. Parasitism by this species peaked in 1962 (Fig. 9A). In subsequent years, winter moth populations in Nova Scotia remained at low density, except for minor and short-lived eruptions (Embree 1991, Roland and Embree 1995).

Between 1979 and 1980, and 15,085 *C. albicans* and 3354 *A. flaveolatum* adults were released evenly across 33 locations over an area of 600 km² in Victoria, Vancouver Island, British Columbia (Embree and Otvos 1984, Roland and Embree 1995). Releases occurred primarily in stands of Garry oak (*Quercus garryana* [Douglas ex Hook]). Nearly all parasitoids came from Nova Scotia and the rest from Germany. Parasitism by *C. albicans* quickly rose to levels exceeding 50%, causing a dramatic reduction in winter moth densities two or three years after release. In 1982, 3745 *C. albicans* and 1595 *A. flaveolatum* were released in 11 commercial filbert orchards in Oregon. Recoveries were made the following year (Kimberling et al. 1986). Although follow-up studies were not conducted in Oregon, winter moth has not been a problem there in subsequent years.

Following the establishment of winter moth (*C. albicans*) in British Columbia, Roland (1994) studied its impact on winter moth population dynamics. He presented evidence that *C. albicans* reduces winter moth densities to a level at which pupal predation caused density-dependent mortality and regulated low-density populations, much as it does in England (Varley et al. 1973). Research by Pearsall and Walde (1994) in Nova Scotia also supports this view. They showed that mortality in low-density populations in apple orchards was dominated by pupal predation and that parasitism by *C. albicans* varied between 4 and 28%, far lower than the initial values in 1960–1962 reported by Embree (1966) (Fig. 9A). Studies in England by Raymond et al. (2002) indicate that in some habitats, predation by pupal predators declines with higher-density populations of winter moth, potentially allowing winter moth to escape into an outbreak phase.

Embree (1991) continued to follow densities of winter moth through the 1980s in Nova Scotia. He believed that *C. albicans* was mainly responsible for the decline of winter moth densities following the establishment of that species in Nova Scotia and British Columbia. However, subsequent analyses by

Roland (1988, 1990b) indicated that the decline in winter moth density at both of these locations was more closely associated with increased pupal predation, than it was with increased parasitism by *C. albicans*. In other words, it appeared that parasitism by *C. albicans* was somehow synergized by pupal predation. Roland postulated three possible mechanisms for this effect. As one explanation, he argued that, because the unparasitized winter moths emerge as adults in November, the presence of *C. albicans* puparia in the soil might provide a food source for predators in spring that would otherwise be absent. This food source might induce a numerical buildup of predatory beetles that then would feed on the next generation of winter moth pupae. As another explanation, Roland (1990b) provides evidence that predators prefer unparasitized winter moth pupae over those that had immature *C. albicans* inside them; he postulated that this might raise the attack rates on unparasitized pupae, causing a synergistic effect. Finally, Roland argued that *C. albicans* propelled winter moth densities to a lower value that allowed the pupal predators to cause higher mortality, as explained above. Embree (1991) expressed doubt about the idea that predators were responsible for the decline of winter moth densities in Nova Scotia. He pointed out that the decline occurred across a wide variety of habitats with vastly different predator communities. In the northeastern United States, we now have another opportunity to test these ideas as *C. albicans* becomes established.

In Massachusetts and Rhode Island, we decided to release only *C. albicans* because, unlike *A. flaveolatum*, it was very host-specific, and because it had caused higher levels of parasitism in Canada, especially in British Columbia, than did *A. flaveolatum*. Parasitized larvae were collected from Victoria, British Columbia, in 2004, and reared. Releases in New England began in 2005, with approximately 250 *C. albicans* mated females released at one site in Massachusetts. Annual releases were made through 2015 at one or two Massachusetts sites per year, each site receiving 700–2000 mated *C. albicans* adults. Beginning in 2011, we increased our collection to approximately 100,000 winter moth larvae each year in Victoria, British Columbia, of which about 50% were parasitized by *C. albicans*. This allowed an increase in the number of release sites, while maintaining the number of flies

released to between 1600 and 2000 flies (both sexes, combined) per site. In 2014 we released 28,000 flies across ten new sites from southeast Connecticut to Vinalhaven, Maine (Fig. 10). As in Nova Scotia, it took several years to recover the first flies at any release site. We made the first recoveries in 2010, and by 2014 we had established *C. albicans* at 11 sites. At one site in Wellesley, Massachusetts, parasitism by *C. albicans* had reached approximately 35% in 2012 and was accompanied by a decline in winter moth density, measured by pupae per square meter and defoliation (percent) (Figs. 9B, 11). Samples of winter moth larvae collected in the town of Wellesley at various distances from the central release site show levels of parasitism by *C. albicans* between 20% and 50% everywhere in town within 2 km from the release site (Fig. 12). This means we have a large population of *C. albicans* ready to spread into neighboring towns in 2015. We will document the rate of spread of these flies.

Interestingly, parasitism at the initial release site in Wellesley was only about 7% in 2014 (Figs. 11, 12) compared to much higher levels in the previous two years and other sites across the town of Wellesley in 2014 (Fig. 12). We suspect this reflects the much lower densities of winter moth at the initial release site. That's what happened in Nova Scotia in the 1960s. Winter moth densities there declined to innocuous levels, but so did parasitism by *C. albicans*. Parasitism values on the order of 5% have been reported there in subsequent years (Pearsall and Walde 1994). So it appears that *C. albicans* serves to knock down high densities of winter moth, which are then maintained at lower densities by other factors, such as pupal predation (Roland 1994). Hannah Broadley is conducting experiments in the Elkinton laboratory to document the impact of predators on winter moth densities at these sites.

As of 2014, *C. albicans* is established at 11 sites in the northeastern United States, has achieved parasitism in excess of 20% at three sites, and appears to have lowered the density of winter moth at one site, so far. Based on the success of biological control in Nova Scotia and the Pacific Northwest, principally by *C. albicans*, it is highly likely that *C. albicans* will have a similar effect on winter moth in the northeastern United States. However, it remains to be seen what will happen to winter moth densities in New England, following the establishment of *C. albicans*. Thus, it

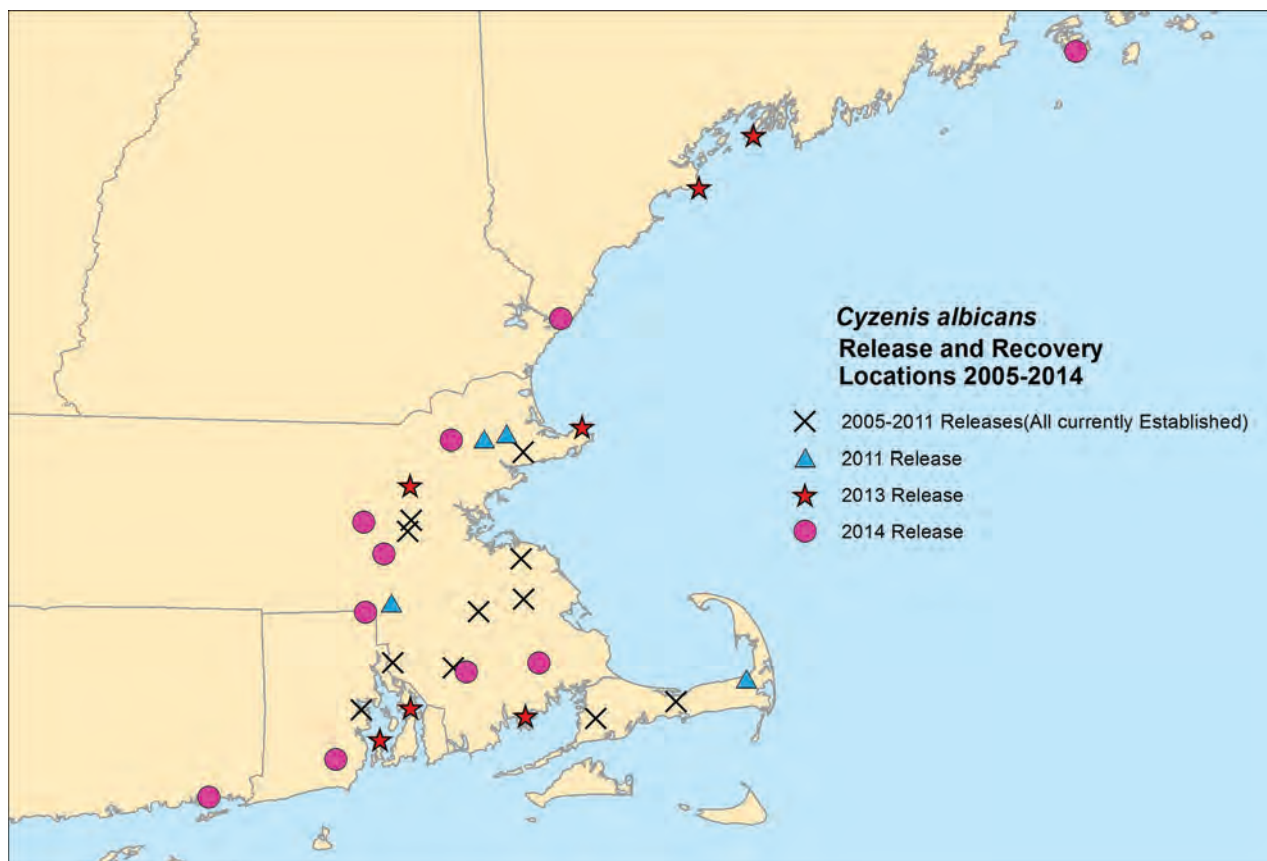


Figure 10 *Cyzenis albicans* release and recovery sites in New England, 2005–2014.

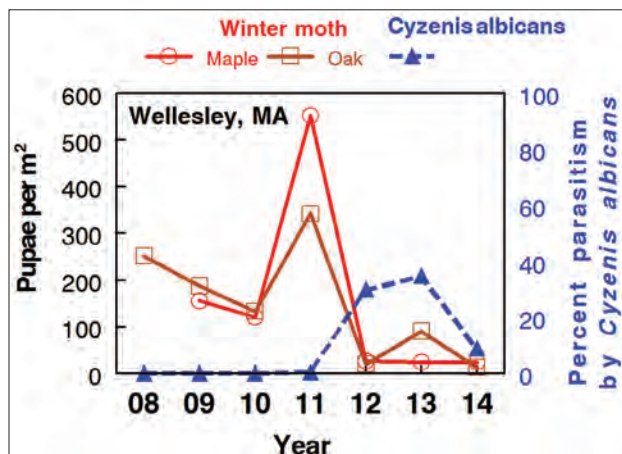


Figure 11 Density of winter moths (*Operophtera brumata*) (pupae per m²) beneath oak and maple trees and percent parasitism of winter moth pupae by *Cyzenis albicans* following release in 2008 at a site in Wellesley, Massachusetts.

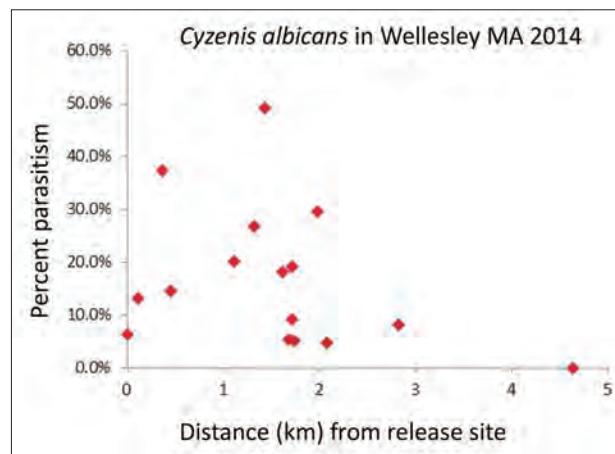


Figure 12 Percent parasitism of winter moth larvae by *Cyzenis albicans* collected in 2014 at sites in the town of Wellesley, Massachusetts, at various distances from the 2008 central release site.

is critically important to collect life-table data from the long-term plots we are monitoring, so we can document changes in winter moth density and causes of mortality due to *C. albicans* and other factors. That is our plan for the coming years.

Research in Canada by both Roland and Embree illustrates that it is important to understand the impact of *C. albicans* in the context of all the other sources of mortality and causes of population density change occurring in the winter moth system. If we achieve

the same success with our biological control in the northeastern United States as that achieved in Canada, we will have permanently converted winter moth into a non-pest and saved millions of dollars in pesticide spray applications against this serious defoliator of forests and shade trees. This is especially true given that winter moth continues to spread south and west and will soon be a threat to much of the eastern United States. If we can establish *C. albicans* in sufficient numbers across the infested region in New England, the fly should spread along with winter moth across the rest of the country and prevent a national calamity.

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References

- Barron, J. R. 1989. Status of the parasite *Agrypon flaveolatum* (Gravenhorst) (Hymenoptera, Ichneumonidae), introduced to control the winter moth in Nova Scotia and British Columbia. *The Canadian Entomologist* 121: 11–26
- Burand, J. P., W. Kim, A. Welch, and J. S. Elkinton. 2011. Identification of a nucleopolyhedrovirus in winter moth populations from Massachusetts. *Journal of Invertebrate Pathology* 108: 217–219.
- Caltagirone, L. E. 1981. Landmark examples in classical biological-control. *Annual Review of Entomology* 26: 213–232
- Cathey, H. M. 1990. USDA plant hardiness zone map. USDA Misc. Publ. No. 1475.
- Dasch, C. E. 1984. Ichneumon-flies of America north of Mexico: 9. Subfamilies Theriinae and Anomaloninae. *Memoirs of the American Entomological Institute*, Ann Arbor, Michigan, USA, 36.
- Elkinton, J. S. and A. M. Liebhold. 1990. Population dynamics of gypsy moth in North America. *Annual Review of Entomology* 35: 571–596.
- Elkinton, J. S., G. H. Boettner, M. Sremac, R. Gwiazowski, R. Hunkins, J. Callahan, S. B. Schuele, C. Donahue, A. H. Porter, A. Khrimian, B. M. Whited, and N. K. Campbell. 2010. Survey for winter moth, (Lepidoptera: Geometridae) in northeastern North America with pheromone-baited traps and hybridization with the native Bruce spanworm. *Annals of the Entomological Society of America* 103: 135–145.
- Elkinton, J. S., A. M. Liebhold, G. H. Boettner, and M. Sremac. 2014. Invasion spread of *Operophtera brumata* in northeastern United States and hybridization with *O. bruceata*. *Biological Invasions* 16: 2263–2272.
- Elkinton, J. S. and G. H. Boettner. 2014. Winter moth, pp. 221–230. In: Van Driesche, R. and R. Reardon (eds.). *The Use of Classical Biological Control to Preserve Forests in North America*. FHTET–2013–2. USDA Forest Service, Morgantown, West Virginia, USA.
- Embree, D. G. 1965. The population dynamics of the winter moth in Nova Scotia, 1954–1962. *Memoirs of the Entomological Society of Canada*, Vol 97, Supplement S46: 5–57.
- Embree, D. G. 1966. Role of an introduced parasitoid in control of winter moth in Nova Scotia. *The Canadian Entomologist* 98: 1159–1168.

- Embree, D. G. 1967. Effects of winter moth on growth and mortality of red oak in Nova Scotia. *Forest Science* 13: 295–299.
- Embree, D. 1970. The diurnal and seasonal pattern of hatching of winter moth eggs, *Operophtera brumata* (Geometridae: Lepidoptera). *The Canadian Entomologist* 102: 759–768.
- Embree, D. G. 1991. The winter moth *Operophtera brumata* in eastern Canada, 1962–1988. *Forest Ecology and Management* 39: 47–54.
- Embree, D. G. and I. S. Otvos. 1984. *Operophtera brumata* (L.), winter moth (Lepidoptera: Geometridae), pp. 353–357. In: Kelleher, J. S. and M. A. Hulme (eds.). *Biological Control Programmes Against Insects and Weeds in Canada 1969–1980*. Commonwealth Agricultural Bureaux (CAB), Slough, UK.
- Embree, D. G. and P. Sisojevic. 1965. The bionomics and population density of *Cyzenis albicans* (Fall.) (Tachinidae:Diptera) in Nova Scotia. *The Canadian Entomologist* 97: 631–639.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth larvae. *Ecology* 51: 565–581
- Frank, J. H. 1967. Insect predators of pupal stage of winter moth *Operophtera brumata* (L.) (Lepidoptera: Hydrimenidae). *Journal of Animal Ecology* 36: 375–389.
- Gillespie, D. R., T. Finlayson, N.V. Tonks, and D. A. Ross. 1978. Occurrence of winter moth, *Operophtera brumata* (Lepidoptera: Geometridae), on southern Vancouver Island, British Columbia. *The Canadian Entomologist* 110: 223–224.
- Graham, A. R. 1958. Recoveries of introduced species of parasites of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae), in Nova Scotia. *The Canadian Entomologist* 90: 595–596.
- Graham, R. I., W. I. Tyne, R. D. Possee, S. M. Sait, and R. S. Hails. 2004. Genetically variable nucleopolyhedroviruses isolated from spatially separate populations of the winter moth *Operophtera brumata* (Lepidoptera: Geometridae) in Orkney. *Journal of Invertebrate Pathology* 87: 29–38.
- Gwiazdowski, R.S., J.S. Elkinton, J.R. Dewaard and M. Sremac. 2013. Phylogeographic diversity of the winter moths (Lepidoptera: Geometridae: *Operophtera*) *O. brumata*, and *O. bruceata* in Europe and North America. *Annals of the Entomological Society of America* 106: 143–151
- Hawboldt, L. S. and F. G. Cuming. 1950. Cankerworms and European winter moth in Nova Scotia. Dominion Department of Agriculture Science Service Division Entomology, Forest Insect Investigation, *Bi-Monthly Progress Report* 6: 1–2.
- Hibbard, E. M. and J. S. Elkinton. 2015. Effect of spring and winter temperatures on winter moth (Geometridae: Lepidoptera) larval eclosion in the northeastern United States. *Environmental Entomology* (in press).
- Ives, W. G. H. 1984. *Operophtera bruceata* (Hulst), Bruce Spanworm (Lepidoptera: Geometridae), pp. 349–351. In: Kelleher, J. S. and M. A. Hulme (eds.). *Biological Control Programmes Against Insects and Weeds in Canada 1969–1980*. Commonwealth Agricultural Bureaux (CAB), Slough, UK.
- Jepsen, J. U., S. B. Hagen, R. A. Ims, and N. G. Yoccoz. 2008. Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology* 77: 257–264.
- Jepsen, J. U., S. B. Hagen, S. R. Karlsen, and R. A. Ims. 2009. Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. *Proceedings of the Royal Society B: Biological Sciences* 276(1676): 4119–4128.
- Kerslake, J. E., L. E. B. Kruuk, S. E. Hartley, and S. J. Woodin. 1996. Winter moth (*Operophtera brumata*) (Lepidoptera: Geometridae) outbreaks on Scottish heather moorlands: Effects of host plant and parasitoids on larval survival and development. *Bulletin of Entomological Research* 86: 155–164.
- Kimberling, D. N., J. C. Miller, and R. L. Penrose. 1986. Distribution and parasitism of winter moth, *Operophtera brumata* (Lepidoptera, Geometridae), in western Oregon. *Environmental Entomology* 15: 1042–1046.
- Kimberling, D. N. and J. C. Miller. 1988. Effects of temperature on larval eclosion of the winter moth, *Operophtera brumata*. *Entomologia Experimentalis et Applicata* 47: 249–254.
- Klemola, N., T. Andersson, K. Ruohomäki, and T. Klemola. 2010. Experimental test of parasitism hypothesis for population cycles of a forest lepidopteran. *Ecology*, 91(9), 2506–2513.

- Marsh, M. M. and R. W. Carlson 1979. Superfamily Ichneuemonidae, pp 143–741. *In*: Krombein, K. V., P. D Hurd, Jr, D. R. Smith, and B. D. Burks (eds.). *Catalog of Hymenoptera in America North of Mexico. Vol. 1. Symphyta and Apocrita (Parasitica)*. Smithsonian Institution Press, Washington, D.C, USA.
- O'Hara, J. E. and B. E. Cooper. 1992. Revision of the nearctic species of *Cyzenis* Robineau-Desvoidy (Diptera, Tachinidae). *The Canadian Entomologist* 124: 785–813.
- Pearsall, I. A. and S. J. Walde. 1994. Parasitism and predation as agents of mortality of winter moth populations in neglected apple orchards in Nova Scotia. *Ecological Entomology* 19: 190–198.
- Raymond, B., A. Vanbergen, A. Watt, S.E. Hartley, J.S. Cory and R.S. Hails. 2002. Escape from pupal predation as a potential cause of outbreaks of the winter moth, *Operophtera brumata*. *Oikos* 98: 219–228.
- Roelofs, W. L., A. S. Hill, C. E. Linn, J. Meinwald, S. C. Jain, H. J. Herbert, and R. F. Smith. 1982. Sex-pheromone of the winter moth, a geometrid with unusually low-temperature pre-copulatory responses. *Science* 217: 657–659.
- Roland, J. 1986. Parasitism of winter moth in British Columbia during buildup of its parasitoid *Cyzenis albicans*: Attack rate on oak vs. apple. *Journal of Animal Ecology* 55: 215–234.
- Roland, J. 1988. Decline in winter moth populations in North America: Direct versus indirect effect of introduced parasites. *Journal of Animal Ecology* 57: 523–531.
- Roland, J. 1990a. Parasitoid aggregation: chemical ecology and population dynamics, pp. 185–211 *In*: Mackauer, M., L.E. Ehler and J. Roland (eds.). *Critical Issues in Biological Control*. Intercept, Andover, Harts, UK.
- Roland, J. 1990b. Interactions of parasitism and predation in the decline of winter moth in Canada. Pgs. 289–302, *In*: Watt, A. D., S. R. Leather, M. D. Hunter, and N. A. C. Kidd (eds.), *Population Dynamics of Forest Insects*. Intercept, Andover, Harts, UK.
- Roland, J. 1994. After the decline: What maintains low winter moth density after successful biological control. *Journal of Animal Ecology* 63: 392–398.
- Roland, J. and D.G. Embree. 1995. Biological control of the winter moth. *Annual Review of Entomology* 40: 475–492.
- Roland, J., K. E. Denford, and L. Jimenez. 1995. Borneol as an attractant for *Cyzenis albicans*, a tachinid parasitoid of the winter moth, *Operophtera brumata* L. (Lepidoptera Geometridae). *The Canadian Entomologist* 127: 413–421.
- Schmid, J. M. 1970. Notes on the Nearctic *Agrypon* (Hymenoptera: Ichneumonidae). *The Canadian Entomologist* 102: 1539–1541.
- Schott, T., S. B. Hagen, R. A. Ims, and N. G. Yoccoz. 2010. Are population outbreaks in sub-arctic geometrids terminated by larval parasitoids? *Journal of Animal Ecology* 79: 701–708.
- Schott, T., L. Kapari, S. B. Hagen, O. P. L. Vindstad, J. U. Jepsen, and R. A. Ims. 2013. Predator release from invertebrate generalists does not explain geometrid moth (Lepidoptera: Geometridae) outbreaks at high altitudes. *The Canadian Entomologist*, 145: 184–192.
- Simmons, M. J., T. D. Lee, M. J. Ducey, J. S. Elkinton, G. H. Boettner, and K. J. Dodds. 2014. Effects of invasive winter moth defoliation on tree radial growth in eastern Massachusetts. *Insects* 5: 301–318.
- Stoakley, J. T. 1985. Outbreaks of winter moth, (*Operophtera brumata* L.) (Lep., Geometridae) in young plantations of Sitka spruce in Scotland: Insecticidal control and population assessment using the sex attractant pheromone. *Zeitschrift für Angewandte Entomologie* 99: 153–160.
- Tenow, O. 1972. Outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862–1968. *Zoologiska bidrag från Uppsala*, Suppl 2:1–107.
- Tenow, O., A. C. Nilssen, H. Bylund, and O. Hogstad. 2007. Waves and synchrony in *Epirrita autumnata* / *Operophtera brumata* outbreaks. I. Lagged synchrony: Regionally, locally and among species. *Journal of Animal Ecology* 76: 258–268.
- Tenow, O., A. C. Nilssen, H. Bylund, R. Pettersson, A. Battisti, U. Bohn, F. Carouille, C. Ciornei, G. Csóka, H. Delb, W. De Prins, M. Glavendekić, Y. I. Gninenko, B. Hrašovec, D. Matošević, V. Meshkova, L. Moraal, C. Netoiu, J. Pajares, V. Rubtsov, R. Tomescu, and I. Utkina. 2013. Geometrid outbreak waves travel across Europe. *Journal of Animal Ecology* 82: 84–95.
- Troubridge, J. T. and S. M. Fitzpatrick. 1993. A revision of the North American *Operophtera*. *The Canadian Entomologist* 125: 379–397.

- Varley, G. C., and G. R. Gradwell. 1960. Key factors in population studies. *Journal of Animal Ecology*. 29: 399–401.
- Varley, G. C., and G. R. Gradwell. 1968. Population models for the winter moth, pp. 132–142. In: Southwood, T.R.E. (ed.). *Insect Abundance*. Symposium of the Royal Entomological Society of London No. 4, Blackwell Scientific Publications, Oxford, UK.
- Varley, G. C., G. R. Gradwell, and M. P. Hassell. 1973. *Insect Population Ecology: An Analytical Approach*. University of California Press, Berkeley and Los Angeles, California, USA.
- Vindstad, O. P. L., T. Schott, S. B. Hagen, J. U. Jepsen, L. Kapari, and R. A. Ims. 2013. How rapidly do invasive birch forest geometrids recruit larval parasitoids? Insights from comparison with a sympatric native geometrid. *Biological Invasions* 15: 1573–1589.
- Visser, M. E. and L. J. M. Holleman. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B- Biological Sciences* 268: 289–294.
- Wigley, P. J. 1976. The epizootiology of a nuclear polyhedrosis virus disease of the winter moth, *Operophtera brumata* L., at Wistman's Wood, Dartmoor. Ph.D. dissertation, Oxford University, Oxford, UK.
- Watt, A. D. and A. M. McFarlane. 1991. Winter moth on Sitka spruce: Synchrony of egg hatch and budburst, and its effect on larval survival. *Ecological Entomology* 16: 387–390.
- Wint, W. 1983. The role of alternative host-plant species in the life of a polyphagous moth, *Operophtera brumata* (Lepidoptera: Geometridae). *Journal of Animal Ecology* 52: 439–450.
- Wylie, H.G. 1960. Insect parasites of the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae) in Western Europe. *Entomophaga* 5: 111–129.