Chapter 20

Biological Control Success Against Winter Moth in the Northeastern United States

Joseph S. Elkinton[1]*, George H. Boettner[1], Hannah J. Broadley[2]

[1] Department of Environmental Conservation, University of Massachusetts, Amherst, MA
*elkinton@umass.edu, boettner@umass.edu
[2] USDA-APHIS-PPQ, Science and Technology, Buzzards Bay, MA hannah.j.broadley@usda.gov

NON-TECHNICAL SUMMARY

Winter moth, *Operophtera brumata* (Lepidoptera: Geometridae), is native to Europe. It invaded the northeastern United States in the late 1990s, where it caused widespread defoliation of forests and shade trees. In Massachusetts, the defoliated area ranged from 2,266 to 36,360 ha (5,600–89,848 acres) per year between 2003 and 2015. In 2005, we initiated a biological control program against winter moth in Massachusetts, using the specialist tachinid parasitoid *Cyzenis albicans*. We chose this species because it had been introduced (along with the generalist ichneumonid parasitoid *Agrypon flaveolatum*) and successfully controlled winter moth in Nova Scotia in the 1950s and on Vancouver Island, Canada in the 1970s. Because *A. flaveolatum* potentially posed some risk to non-target insects, we introduced only the specialist *C. albicans*. Each year for 14 years, we collected several thousand *C. albicans* in British Columbia and released the adults the following year at widely-spaced sites in the northeastern United States. As of 2020, we had established *C. albicans* at 41 of 44 sites from southeastern Connecticut to coastal Maine. Beginning in 2005, we made yearly estimates of winter moth density. By 2016, winter moth density had declined from 100–500 pupae/m^2 to 0–10 pupae/m^2 (9–46 pupae/ft^2 to 0–1 pupae/ft^2) at these sites, an average reduction of 98%. This drop in winter moth density was coincident with the onset of 10–40% parasitism by *C. albicans*. At a site in Wellesley, Massachusetts, this decline occurred in 2012, and winter moth densities have remained low there through the present (2022). Defoliation by winter moth in Massachusetts has been undetectable by aerial survey since 2016. Studies of predation on winter moth pupae at these and other sites revealed that predation rates became density-dependent only after *C. albicans* had reduced pupal densities to a level that is now comparable to the density reported at a site in England where winter moth is not an outbreak species.

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HISTORY OF INVASION AND NATURE OF PROBLEM

The Species Invasion

In the late 1990s, defoliation by a green inchworm was first detected near Boston, in the northeastern United States. At first it was assumed to be a native inchworm, such as fall cankerworm, *Alsophila pometaria*. However, a flight of male moths in late December of 2002 suggested it might be the European species known as winter moth, *Operophtera brumata* (Lepidoptera: Geometridae). It is called winter moth because it flies in early winter. Our taxonomic collaborators confirmed this identification in 2003 (Elkinton et al., 2010, 2015). There had been three previous invasions of winter moth in North America, one to Nova Scotia in the 1930s, a second to Oregon in the 1950s, and a third to Vancouver Island in British Columbia in the 1970s; none of these invasive populations spread much beyond the region of their initial invasion. Andersen et al. (2021) showed that all four introductions to North America originated independently from Europe.

In 2005, we initiated a regional survey of winter moth in the northeastern United States and adjacent parts of Canada using pheromone-baited traps (Elkinton et al., 2010) (**Fig. 1**). With the help of various collaborators, we deployed traps from Long Island (near New York City), New York and southeastern Connecticut, northward to Maine, New Brunswick, and Nova Scotia, Canada. Unfortunately, winter moth shares the same pheromone with a native North American species known as Bruce spanworm, *Operophtera bruceata*. This species is ubiquitous across northern North America, even though it almost always remains

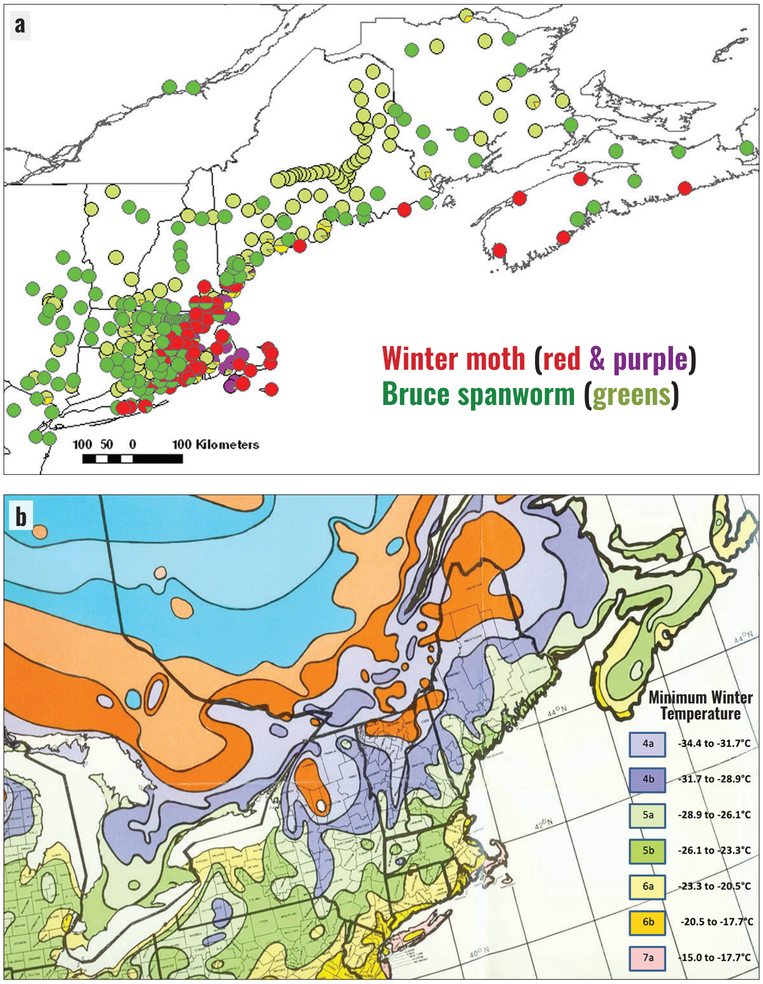

Figure 1. (a) Distribution of winter moth (*Operophtera brumata*) and Bruce spanworm (*Operophtera bruceata*) catches in pheromone-baited traps in northeastern North America, 2005–2007. Most moths were Identified via DNA , red for winter moth, dark green for Bruce spanworm. Others were identified by dissection of genitalia, purple for winter moths, light green for Bruce spanworm. A few moths had intermediate genitalia (yellow). Each circle represents a pie diagram indicating the proportion of 10 moths in each category, in each trap. (b) Plant cold hardiness zone map for northeastern North America. (a: modified from Elkinton et al., 2010; b: modified from Cathey, 1990 and Elkinton et al., 2010)

at low density. Thus, all the traps we deployed filled up with little brown moths, some of which were winter moths and some Bruce spanworm. The two species are not easy to tell apart as wing patterns are not reliable. Instead, we examined the male genitalia, which have a slightly different shape between the two species (Eidt et al., 1966). Unfortunately, we encountered many with genitalia whose shapes were intermediate in form, suggesting that hybridization was occurring between the two species. This conjecture was later confirmed by DNA analysis. For a more reliable distinction between the two species, we turned to extraction and sequencing of the CO1 "barcoding gene", a mitochondrial gene that has become a central tool for insect identification (Hebert et al., 2003).

Identification of moths from survey traps (**Fig. 1a**) revealed a maritime distribution for winter moth that closely matched the USDA Plant Hardiness Zone Map (Cathey, 1990), which is based on minimum winter temperatures (**Fig. 1b**). This pattern of distribution possibly explains why winter moth remained confined to Nova Scotia for many decades after its invasion there in the 1950s. Presumably, winter moth was unable to penetrate the much colder regions immediately to the west in New Brunswick (**Fig. 1b**). This plant hardiness zone map also suggested that the warmer temperatures that may have allowed the winter moth outbreak to occur in Massachusetts also occur elsewhere in the eastern United States. Thus, we suspected that we were on the verge of a major defoliator invasion analogous to that of *Lymantria dispar* (formerly known as gypsy moth). Over the decade following 2003, winter moth became a major defoliator all over eastern Massachusetts, including Cape Cod and Martha's Vineyard, as well as in Rhode Island (Elkinton et al., 2014) (**Fig. 2**). At the same time, winter moth was spreading west across Massachusetts, as documented by pheromone-baited traps deployed along an east-west highway. Between 2005 and 2011, winter moth spread 50 km (31 mi) into the central part of the state (Elkinton et al., 2014). During this same period, however, virtually no defoliation occurred in central Massachusetts, at least as recorded by aerial surveys (**Fig. 2**). In 2012, defoliation by winter moth occurred for the first time along the coast of Maine, a phenomenon that was likely linked to the warming temperatures in the Gulf of Maine (Elkinton et al., 2015).

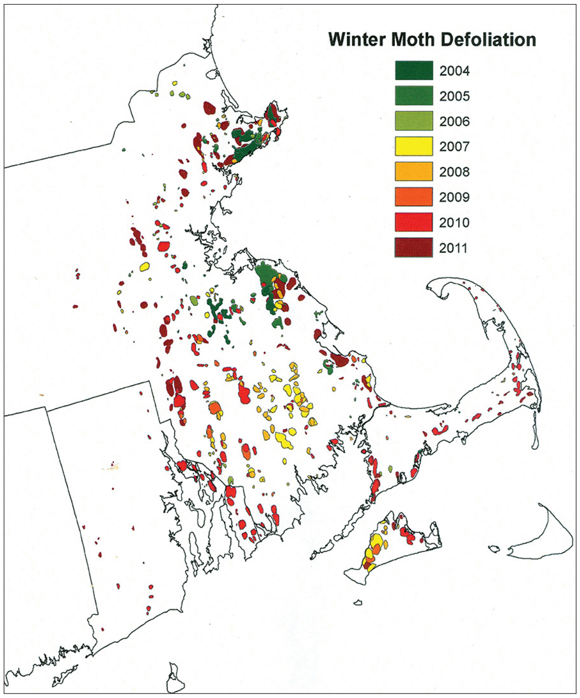

Figure 2. Spread of defoliation by winter moth (*Operophtera brumata*) across eastern Massachusetts from 2004–2011, compiled from annual aerial surveys. (modified from Elkinton et al., 2014)

NATURE OF THE PROBLEM

Winter moth is extremely polyphagous, feeding on a wide range of host plants, including oaks (*Quercus*), maples (*Acer*), birches (*Betula*), and many others (Wint, 1983). It is a potential orchard pest, and larvae develop well on apple (*Malus*). In Massachusetts and Rhode Island, winter moth was especially damaging to blueberry (*Vaccinium*) crops. Larvae feed inside the buds, where they are inaccessible to most pesticides, destroying the developing berries before the buds open. Many blueberry growers in Massachusetts lost whole crops during the winter moth outbreak, amounting to thousands of dollars of losses each. Winter moth is also a pest of cranberries (*Vaccinium*; A. Averill, pers. comm.). Winter moth eggs typically hatch at or before bud-break of the host plant, and the larvae (**Fig. 3a**) 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 rarely reached 100% (in Massachusetts and Rhode Island at least), presumably because the larvae finish feeding and pupate in late May before defoliation is complete. Larvae then drop to the ground where they pupate (**Fig. 3b**) inside earthen cocoons near the soil surface beneath the tree. Pupae remain in the soil until November and December, when the adults (**Fig. 3c,d**) emerge. The female, as in many inchworm (geometrid) species, has no wings (**Fig. 3d**). Instead of flying, she spends all of her energy on egg production. Females emit pheromone to attract the flying males. After mating, females climb the trunk of the host tree, laying about 250 eggs singly on the tree bark.

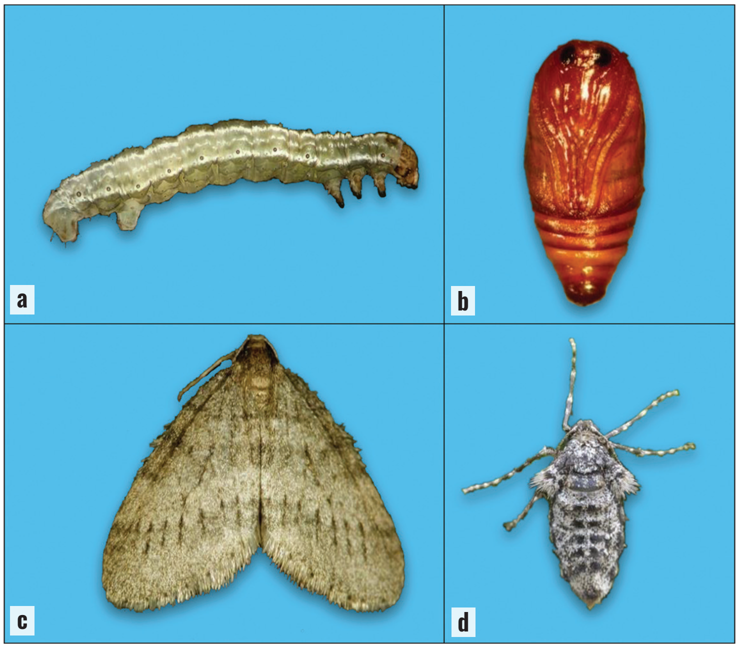

Figure 3. Winter moth (*Operophtera brumata*) life stages: (a) larva; (b) pupa; (c) adult male; (d) adult female. (a–d: D. Wagner; reprinted from Elkinton et al., 2018)

The typical damage caused by winter moth is partial defoliation of the leaves, which can cause lasting damage to the tree. Simmons et al. (2014) showed that defoliation by winter moth caused significant decline in growth in red oak (*Quercus rubra*) in Massachusetts, as measured by growth increments seen in 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.

Unlike other defoliators, such as *L. dispar* (formerly gypsy moth) or forest tent caterpillar (*Malacosoma disstria*), whose outbreaks are terminated by disease epizootics, winter moth outbreaks suffer no such epizootics, even though the moth does have a viral disease (Graham et al., 2004; Burand et al., 2011). Consequently, winter moth defoliation persisted year after year in Nova Scotia in the 1950s (Embree, 1965; Elkinton et al., 2015) and, later, in Massachusetts (Elkinton et al., 2021). As a result, many forest and shade trees started to die after several consecutive years of defoliation.

WHY CONTROL THIS INVASIVE SPECIES?

By 2010, winter moth was causing widespread defoliation of the dominant deciduous forest and shade trees across eastern Massachusetts and Rhode Island (**Fig. 2**). It was causing complete losses of blueberry crops and was a serious pest of apples and cranberries—all important, traditional crops in southern New England. The defoliation continued year after year, and many valuable shade trees were dying across the region. Town managers and homeowners in eastern Massachusetts were spending millions of dollars each year on pesticides to protect shade trees or to remove and replace dying or dead trees. A successful biological control effort, such as that previously achieved in Nova Scotia and in the Vancouver region of British Columbia, would permanently solve these problems and save these annual costs.

PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

Biological control efforts against winter moth in North America began in Nova Scotia in the 1950s, where winter moth had invaded in the 1930s (Hawboldt and Cuming, 1950). Natural enemies for release in Nova Scotia 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* and *Cyzenis albicans* and the ichneumonid *Agrypon flaveolatum*.

Between 1954 and 1957, releases of more than 1,000 *C. albicans* were made at one location (Oak Hill) in Nova Scotia (Graham, 1958). In addition, 250 *A. flaveolatum* 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 they had become abundant. Two other species of tachinids, including *L. dubia*, and two other ichneumonid species were released (Graham, 1958; Roland and Embree, 1995), but these species were not recovered.

Parasitism by both *C. albicans* and *A. flaveolatum* increased at the Oak Hill site in Nova Scotia beginning in 1959 and reached a peak of about 40%, by both species together, in 1962, whereupon winter moth densities declined to undetectable levels (Embree, 1965) and have remained at low density ever since. Subsequent work showed that low densities of winter moth persisted in Nova Scotia apple orchards over the following decades (McPhee et al., 1988), but that parasitism by *C. albicans* and *A. flaveolatum* declined to around 10%. Predators of winter moth pupae in the soil are now thought to prevent low-density populations from increasing (Pearsall and Walde, 1994).

A repetition of this winter moth biological control program (based on the same two parasitoids) was later carried out on Vancouver Island in western Canada after winter moth invaded the area in the 1970s (Gillespie et al., 1978). Winter moth populations declined, mainly due to *C. albicans*, within several years of the first parasitoid releases (Embree and Otvos, 1984). The rapid success of this project, compared to the one in Nova Scotia or the subsequent one in the northeastern United States, was likely due to the larger number of *C. albicans* flies that were released into a winter moth population that covered a much smaller geographical area than was the case in the other two invaded areas (Elkinton et al., 2021).

In Massachusetts, we decided to release only *C. albicans* (**Fig. 4**) and not *A. flaveolatum*, because the latter species is thought to attack the larvae of several non-target moth species. Furthermore, preliminary DNA evidence suggests that *A. flaveolatum* may be a group of unseparated cryptic species needing further taxonomic work. In contrast, Embree and Sisojevic (1965) showed that *C. albicans* was a specialist attacking only winter moth.

To collect *C. albicans*, we traveled to locations where the fly was established and collected late-instar winter moth larvae, some of which had larval *C. albicans* immature stages inside them. In 2004, we attempted to collect *C. albicans* in Nova Scotia, but the densities of winter moth were too low to do so. In subsequent years, we traveled to Vancouver Island, where winter moth densities had remained sufficiently high to enable us to collect many thousands of winter moth larvae over several weeks before larvae in the field pupated. We reared the collected larvae to their pupal stage and then dissected the winter moth pupae in mid-summer to determine the proportion that were parasitized by *C. albicans*. From parasitized winter moth pupae, we

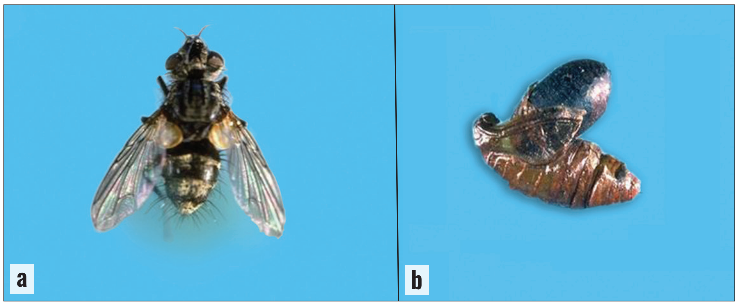

Figure 4. *Cyzenis albicans* (a) adult and (b) puparium inside winter moth pupa. (a,b: Nicholas Condor; reprinted from Elkinton et al., 2018)

obtained *C. albicans* puparia by rearing. These puparia were then held over the summer months in Petri dishes in growth chambers at 12°C (54°F) in summer and fall, and then dropped to 4°C (39°F) in winter. In April, fly puparia were moved to room temperature to induce adult fly emergence. Once flies had emerged, they were allowed to mate, and we then took the flies and released them at new release sites each year (Elkinton et al., 2021). At each site, our goal was to release 1,500–2,000 flies. In 2014, we started to recover large numbers of *C. albicans* near an early release site in Wellesley, Massachusetts, and so we switched our *C. albicans* collection efforts to that location to support more releases elsewhere.

In 2016, we altered our release strategy. Instead of releasing adult flies in the spring, in November we placed *C. albicans* puparia in peat moss inside screen cages and partially buried the cages in the soil at the intended release site. This allowed flies to emerge in spring as dictated by local temperatures. When flies had emerged inside cages, we opened the cage to allow them to escape. This release method resulted in higher rates of *C. albicans* establishment (Elkinton et al., 2021).

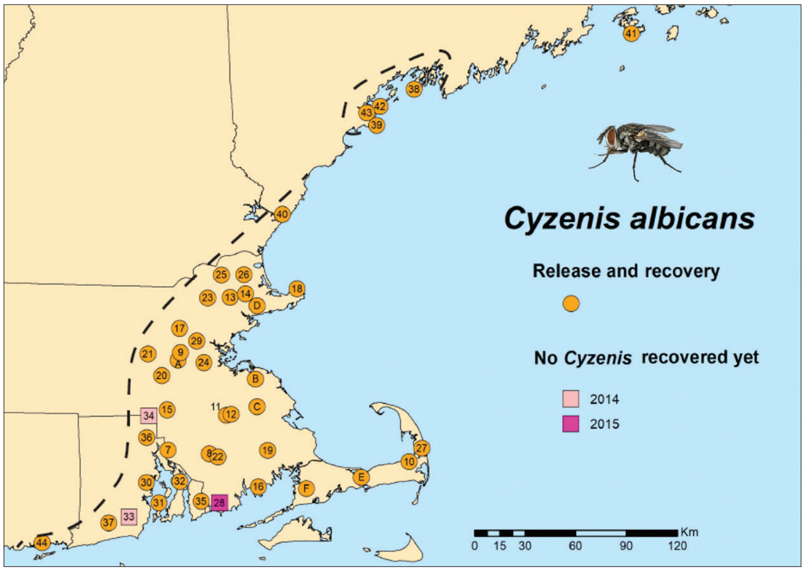

Figure 5. *Cyzenis albicans* release and recovery locations in New England, 2005–2018. Dotted line delineates the boundary of the area with defoliating populations of winter moth, numbers refer to site IDs. As of 2020, we had not yet recovered *C. albicans* from several sites where releases had been made in 2014 or 2015, as indicated by purple squares. (reprinted from Elkinton et al., 2021 with permission from Wiley)

HOW WELL DID IT WORK?

By 2021, we had introduced >80,000 *C. albicans* flies, distributed across 44 sites in eastern Massachusetts, Rhode Island, Connecticut, and Maine, and establishment of the fly had been confirmed at 41 of them (**Fig. 5**) (Elkinton et al., 2021). Similar to events in Nova Scotia in the 1950s (Embree, 1965), we found that in Massachusetts, 3–6 years were required after release before we recovered *C. albicans* at our release sites. Because there is only one generation per year of both the fly and the winter moth, several years were needed for the 1,500–2,000 flies released per site to catch up with the millions of winter moth larvae at a site and become detectable in field-collected larvae.

We made our first recovery of *C. albicans* at the Wellesley, Massachusetts site in 2010, following a 2008 first release there (**Fig. 6a**). By 2016, at each of our six long-term study sites (**Fig. 6**), winter moth densities had declined from 100–500 pupae/m^2 to 0–10 pupae/m^2 (9–46 pupae/ft^2 to 0–1 pupae/ft^2), and these low densities persisted in subsequent years. This decline coincided with the year when parasitism reached 10–40%.

From 2003 to 2018, personnel from the Massachusetts Department of Conservation and Recreation conducted annual aerial surveys in June, when winter moth defoliation had reached peak levels. Surveyors sketched the location of defoliation onto topographic maps, and this information was digitized as GIS polygons whose areas were then summed (**Fig. 7**). Ground survey crews checked each defoliated site to verify that winter

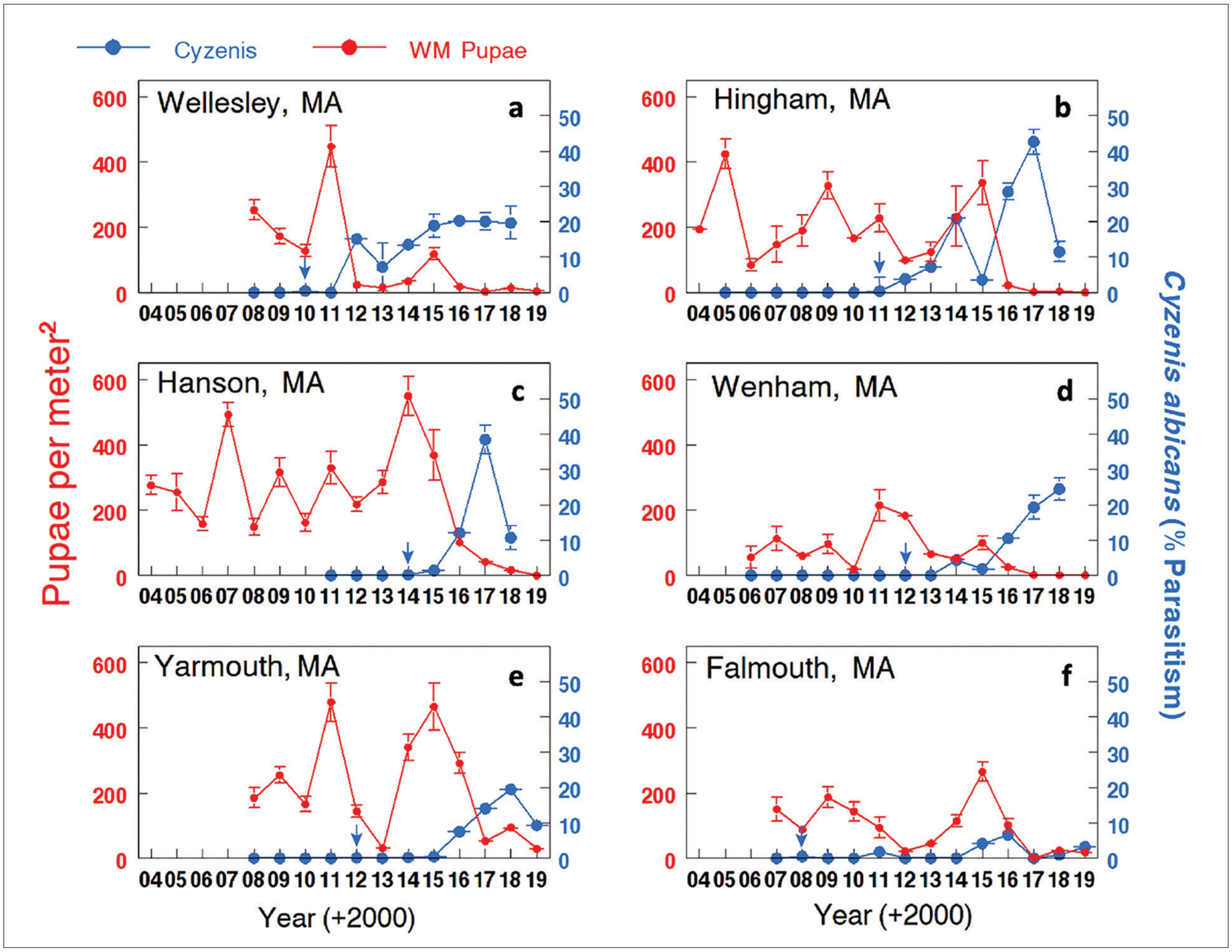

Figure 6. Yearly density of winter moth (*Operophtera brumata*) pupae (red) and percent parasitism by *Cyzenis albicans* (blue) following release at six widely spaced release sites in Massachusetts. Blue arrows indicate year of first recovery of *C. albicans*. (reprinted from Elkinton et al., 2021 with permission from Wiley)

moth was the cause of the defoliation. Annual defoliation by winter moth in Massachusetts ranged from 2,266 to 36,360 ha (5,600–89,848 acres) between 2003 and 2015, but defoliation declined to undetectable levels from 2016 to 2018 (**Fig. 7**). The decline coincided with the widespread occurrence of parasitism by *C. albicans*.

We conclude that releases of *C. albicans* converted winter moth into a non-pest in eastern Massachusetts and Rhode Island. We expect that these low densities will persist indefinitely as they have in Nova Scotia and in the Vancouver region of Canada.

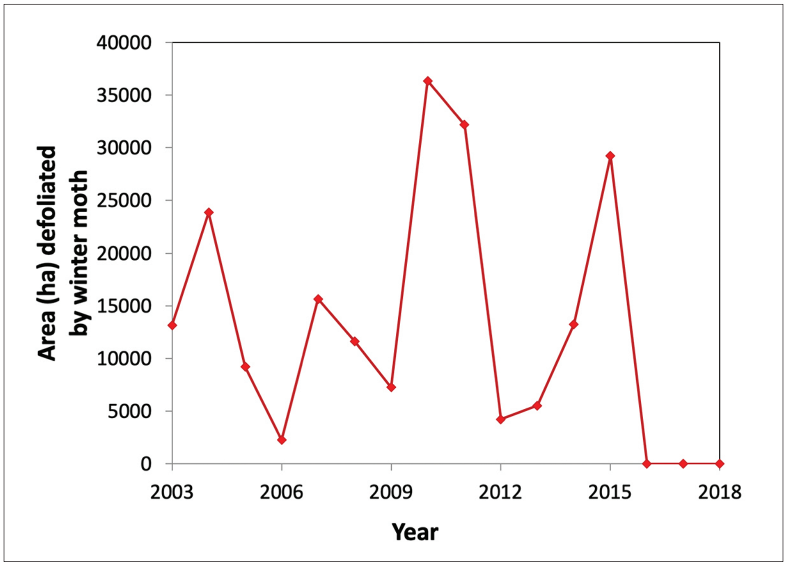

Figure 7. Area (ha) defoliated by winter moth (*Operophtera brumata*) in Massachusetts from 2003–2018 based on aerial survey followed by confirmation by ground surveyors. (reprinted from Elkinton et al., 2021 with permission from Wiley)

THE ECOLOGY OF THE BIOCONTROL PROGRAM

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 moth in an oak forest near Oxford, England, and they concluded that its population was 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 between years, it was not density dependent, and thus did not serve to regulate winter moth densities. They believed that overwintering mortality was dominated by starvation and dispersal due to asynchrony of winter moth larval hatch with budburst. 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.

On Vancouver Island, British Columbia, Roland (1994) studied factors governing the dynamics of invasive winter moth following *C. albicans* establishment. 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) (**Fig. 8a**). 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). Studies in England by Raymond et al. (2002), however, 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 (**Fig. 8b**). This result implies that above some threshold density of winter moth, predators in the soil become saturated and cannot keep up with, or regulate, winter moth densities.

In Massachusetts, we studied predation on winter moth pupae at sites across Massachusetts, including those illustrated in **Fig. 6**, to see if these earlier findings applied to winter moth populations in New England (Broadley, 2018; Broadley et al., in press). The soil-dwelling predator community at these sites consisted of many species of predatory beetles and two species of shrews. With predator exclusion experiments that involved placing pupae in wire-mesh cages of different mesh sizes, we demonstrated that many of these predators were feeding on winter moth pupae. Pupal predation was found to increase with winter moth density, but only after *C. albicans* was established at the study sites (**Fig. 8c**). The role of *C. albicans*, therefore, appears to be to stabilize winter moth pupal populations at a low enough density for pupal predators to regulate winter moth populations, as Roland (1994) had demonstrated on Vancouver Island. Indeed, the

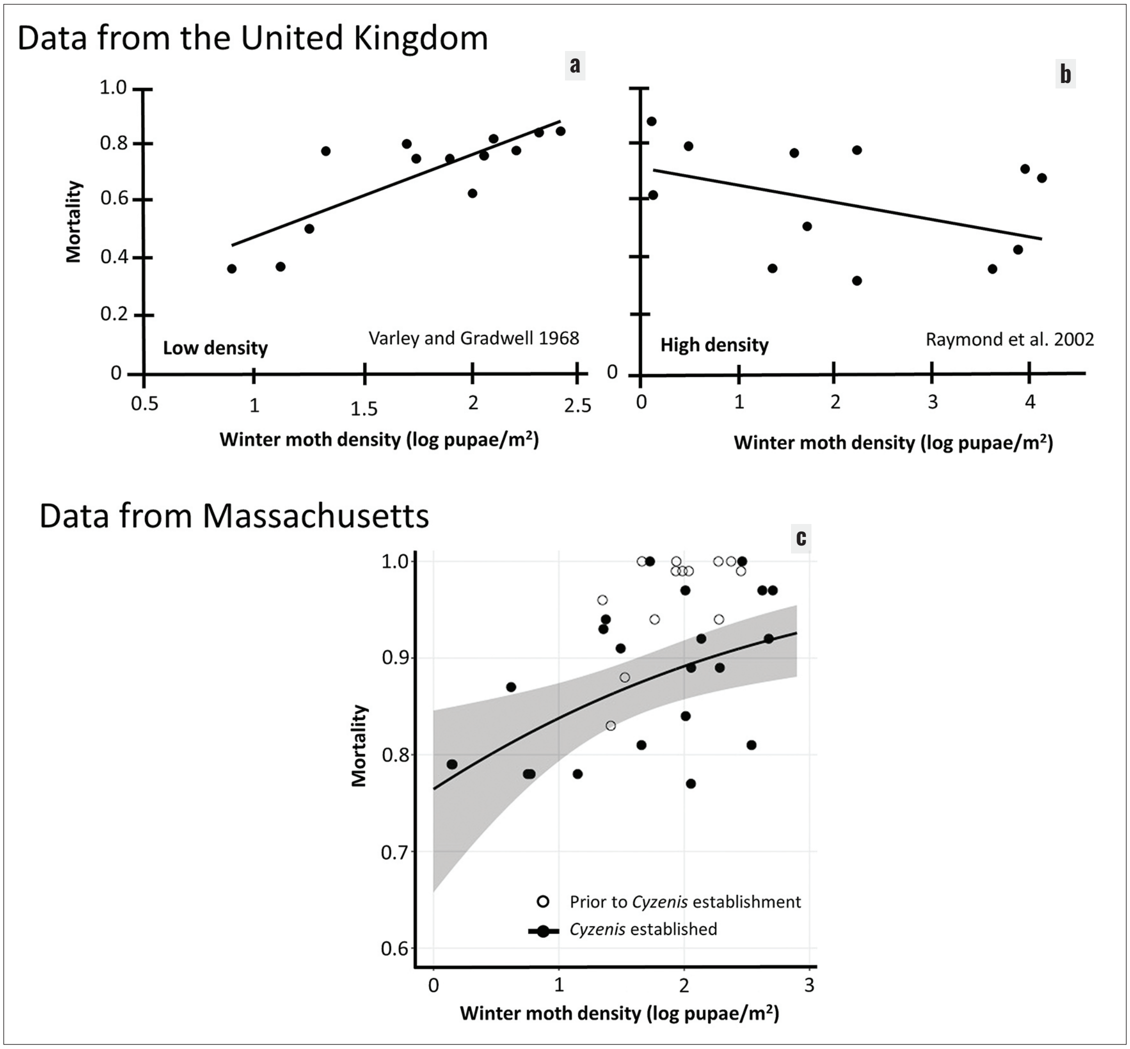

Figure 8. Yearly proportion of winter moth (*Operophtera brumata*) pupae eaten by predators at (a) a site near Oxford England; (b) on a moor in Scotland; and (c) at sites in eastern Massachusetts. (a: modified from Varley et al., 1973; b: modified from Raymond et al., 2002; c: modified from Broadley, 2018; Broadley et al., in press)

densities of winter moth pupae at our sites in Massachusetts are now comparable to those reported by Varley et al. (1973) in England (**Fig. 8a**). Before the establishment of *C. albicans*, pupal densities were higher, and there was no evidence of density-dependent pupal predation, presumably because some of the important predators were approaching saturation (Broadley et al., in press). But the very high densities (10,000 pupae/m^2) reported by Raymond et al. (2002) at outbreak sites in England were never observed in Massachusetts (**Fig. 8c**). Broadley et al. (in press) noted that mortality to winter moth from soil predators in Massachusetts decreased following the establishment of *C. albicans*, in contrast to the data from Nova Scotia and British Columbia, as presented by Roland (1994), where mortality increased following establishment of *C. albicans*. A likely explanation for this difference is that the predator community at the sites in Nova Scotia and British Columbia may be less robust than at the sites in Massachusetts, so that the predators were well above the saturation threshold at outbreak densities, as in **Fig. 8b**, whereas at our sites in Massachusetts at winter moth's highest densities, predation rates were at peak values close to, but not above the saturation threshold (**Fig. 8c**).

Cyzenis albicans achieves its highest rates of parasitism at high winter moth densities because *C. albicans* is attracted to partially defoliated leaves (Roland et al., 1995) and lays tiny eggs along the margins of damaged leaves. Parasitism of winter moth larvae occurs when they consume those eggs. When defoliation levels decline, it is more difficult for *C. albicans* to find suitable leaves on which to lay its eggs. This relationship explains why parasitism by *C. albicans* declined in Nova Scotia following the decline of winter moth populations to low density after 1962. The same is likely to happen in eastern Massachusetts and Rhode Island. Nevertheless, *C. albicans* will remain available to respond to any increases in winter moth density with increasing parasitism rates. In this way, *C. albicans* may resemble other high-density specialists in other population systems, such as the LdMNPV virus of *L. dispar* (formerly gypsy moth) that reliably causes the collapse of high-density populations but causes minimal mortality in low-density populations (Elkinton and Liebhold, 1990).

This research illustrates why it is important to understand the impact of *C. albicans* in the context of all the other causes of mortality occurring in the winter moth system. It is vital that we try to quantify and explain the other factors influencing winter moth densities, in addition to *C. albicans*. This is only sometimes accomplished in other biological control projects.

BENEFITS OF BIOLOGICAL CONTROL OF WINTER MOTH

Winter moth, once a major forest and shade-tree defoliator in southeastern New England, is now a non-pest and is likely to remain so permanently. This biological control project has saved municipalities and homeowners in this region millions of dollars through avoidance of frequent pesticide application costs and has likely had conservation benefits for non-target species likely to be affected by such pesticide applications. The blueberry growers in the region no longer face losses of their crops, and winter moth no longer has the potential to become a major new invasive defoliator across larger portions of the eastern United States.

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