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The ecology, geopolitics, and economics of managing *Lymantria dispar* in the United States

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Increases in global trade and travel have resulted in a number of species being inadvertently (or, in a few cases, deliberately) introduced into new geographical locations. In most cases, there is generally a lack of information regarding a species' biology and ecology, and its potential to cause environmental and economic harm. Regardless, management decisions concerning these new species often need to be made rapidly, even in the absence of this information. The gypsy moth, *Lymantria dispar* (L.), is an exception insofar as it is a non-native species that, due to its considerable potential for damage, has been extensively studied and managed in the United States following its introduction in 1869. In this review, we attempt to highlight the ecology, geopolitics, and economics of managing *L. dispar* in the United States, integrating the lessons learned from over 100 years of research and management. In doing so, we attempt to provide a framework that could be applicable to the management of other non-native insect species, for which we often lack information upon which to develop and implement management strategies.

Keywords: barrier zone management; biological invasions; eradication; gypsy moth; invasive species management; *Lymantria dispar*; outbreak suppression; quarantine

1. Introduction

Throughout the Earth's history, major changes in the distributions of species have repeatedly occurred due to the receding of waters, shifting of land masses, and changing of climates. Consequently, species have been introduced into new habitats, and occasionally they have dramatically altered ecosystem structure and function. However, such changes in species composition historically occurred at much slower rates (Crosby 1986; di Castri 1989) than today in an increasingly connected global human community (Mack et al. 2000; Levine and D'Antonio 2003; Hulme et al. 2008). Global trade and international travel have increased dramatically over the last several decades, connecting products and goods among countries and continents. The movement of goods can occasionally lead to the introduction of new species, such as: (i) insects and pathogens that hitch-hike within solid wood packaging materials or on imported plants (Reichard and White 2001; Brockerhoff et al. 2006; McCullough et al. 2006), and (ii) aquatic species that can be transported via ship hulls and ballast water (Carlton 1987; Drake and Lodge 2004).

Many non-native species have been introduced into new regions intentionally and with positive benefits to societies, such as many food crops worldwide (Kiple and Ornelas 2000). However, other species arrive unintentionally as a consequence of global trade, such as the wood-borers *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) and *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), both of which are presumed to have been introduced into North America through the use of infested wood packaging material (Haack et al. 1997; Poland and McCullough 2006).

The biological invasion process consists of four primary stages (Lockwood et al. 2007). The first is the arrival of a species to a new area, which can be facilitated through anthropogenic, atmospheric, or hydrologic transport mechanisms. After its arrival, a new species either establishes itself or (more often the case) does not (Simberloff and Gibbons 2004). If establishment is successful, then the invading species begins to spread and expand its distribution. The last stage is the impact stage, during which the new species can cause ecological and economic harm, which can range from zero to great (Lockwood et al. 2007).

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), was introduced from Europe into North America, outside of Boston, Massachusetts, in 1869 due to the foolhardy efforts by an amateur entomologist, Etienne Léopold Trouvelot (Liebhold et al. 1989). His exact motivations for introducing "some" (Forbush and Fernald 1896) to a "few" (Burgess 1917) *L. dispar* egg masses were unclear. Regardless, the result of Trouvelot's actions over

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100 years ago has re-shaped forests and forest pest management in the United States. In this paper, we present a review of the ecology, geopolitics, and economics of managing *L. dispar* in the United States. In doing so, we attempt to synthesize the lessons learned from over 100 years of research and management to provide a useful framework applicable to the management of other non-native insect species, particularly to those that do not have the benefit of a rich literature base such as the one that exists for *L. dispar*.

2.   Biology and ecology of *Lymantria dispar*

Lymantria dispar is a univoltine folivore, whose larvae have been recorded to exploit over 300 species of deciduous and coniferous host trees (Elkinton and Liebhold 1990; Liebhold et al. 1995), including species within the highly preferred genera of *Betula* (birch), *Crataegus* (hawthorn), *Larix* (larch), *Populus* (aspen), *Quercus* (oak), *Salix* (willow), and *Tilia* (basswood). In addition, during periods of population outbreaks, many secondary host trees, such as species within the genera of *Acer* (maple), *Carya* (hickory), *Picea* (spruce), *Pinus* (pine), and *Ulmus* (elm), are fed upon by late instars. In spring, larvae hatch from overwintering egg masses, which generally contain 300–500 eggs, and proceed through five (male) or six (female) instars (Doane and McManus 1981). After emerging from pupae in midsummer, adults are short-lived (<7 days, Doane and McManus 1981; Elkinton and Liebhold 1990; Robinet et al. 2008). Females of the *L. dispar* strain established in North America are incapable of flying (Keena et al. 2008), and generally oviposit within 1–2 m from the site of adult emergence (Odell and Mastro 1980). Females emit a sex pheromone that is attractive to males, which can fly.

Despite the fact that females do not fly, *L. dispar* can spread to new areas through both larval ballooning (using a strand of silk), which generally occurs over short distances, and through the anthropogenic movement of life-stages, which can occur both over short and very long distances (Elkinton and Liebhold 1990; Hajek and Tobin 2009). Since its introduction into Massachusetts, *L. dispar* has spread so extensively that it now occupies a range from Nova Scotia to Wisconsin, and Ontario to Virginia (Figure 1), which still represents only around one-quarter of the area in North America considered to be susceptible to *L. dispar* invasion (Morin et al. 2005). Because of the coupling of local population growth and short-range diffusive spread with long-distance spread in a process known as stratified dispersal (Okubo 1980; Hengeveld 1989; Andow et al. 1990; Shigesada and Kawasaki 1997), spread rates by *L. dispar* can be as high as 20–50 km yr^{-1} (Liebhold et al. 1992, Tobin et al. 2007a, Tobin et al. 2007b). Through stratified dispersal, new colonies form ahead of the population front that is generally expanding through local growth and diffusive

spread. These colonies can grow and eventually coalesce with the expanding front, thereby accelerating the speed of invasion over what would be expected under purely diffusive spread (Hengeveld 1989; Shigesada and Kawasaki 1997). Moreover, some colonies can form considerably ahead of the expanding front, analogous to the arrival stage of the biological invasion process, and thus constitute an invasion into a new area. This type of spread phenomenon is not unique to *L. dispar* and, in fact, tends to be a dominant form of spread in many invading species, in part due to the role that humans play in transporting life-stages to new areas (Sakai et al. 2001; Suarez et al. 2001; Gilbert et al. 2004; Liebhold and Tobin 2008). The ramifications of stratified dispersal on *L. dispar* dynamics are profound as they play both a direct or indirect role in current management strategies against this non-native forest insect pest.

3.   A brief history of *L. dispar* management and research in the United States

Management efforts against *L. dispar* have a long history stemming from the initial and failed eradication attempts. The earliest management tools were crude. Early trapping devices included baited live females, and control tools included oil-fuelled flame throwers to destroy life-stages and microhabitats, and arsenic-based insecticides (copper acetoarsenite and lead arsenate; Forbush and Fernald 1896). The first eradication effort, from 1890 to 1900, initially targeted a population that covered >2500 km^2 encompassing 30 cities and towns at a cost of US $1.2 million (equivalent to approximately $28 million in 2010; Forbush and Fernald 1896; Popham and Hall 1958; Dahlsten and Garcia 1989). Beginning in 1906, the United States (US) Government began efforts to import natural enemies to control *L. dispar*, including egg, larval, and pupae parasitoids (Howard and Fiske 1911; Burgess and Crossman 1929). Many of these natural enemy species became successfully established and they continue to exert some control in *L. dispar* populations (Elkinton and Liebhold 1990; Skinner et al. 1993; Gray et al. 2008), although some, such as the generalist parasitoid *Compsilura concinnata* (Meigen) (Diptera: Tachinidae), are associated with pronounced negative effects on non-target Lepidoptera (Boettner et al. 2000; Strong and Pemberton 2000). Other management programs have been attempted, such as a barrier zone in New York, Connecticut, Massachusetts, and Vermont during the 1920s, a barrier zone in New York during the 1950s, and a large-scale management effort through the use of aerial applications of DDT across several states from 1945 to 1958 (Burgess 1930; Perry 1955; Doane and McManus 1981; Dahlsten and Garcia 1989; McManus 2007). There were also earlier eradication programs, such as those in New Jersey and Michigan, which attempted to
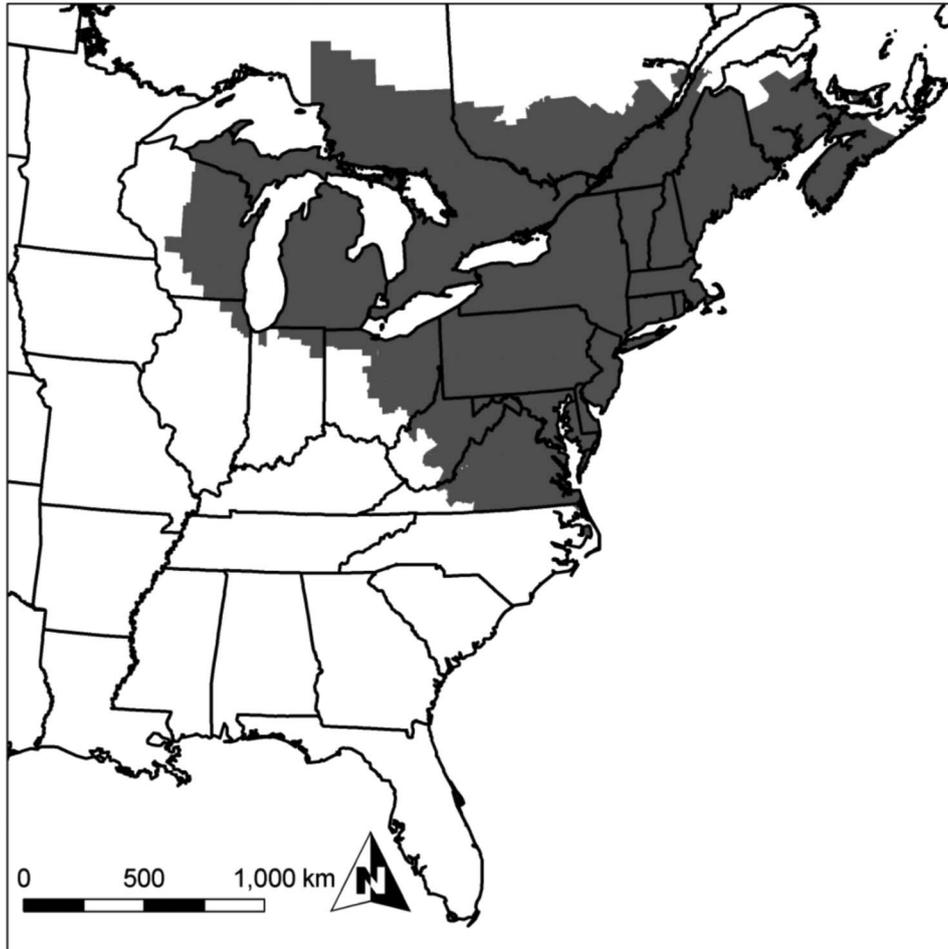
Figure 1.   The area in North America generally infested with *L. dispar* in 2010 (dark gray), which is regulated under quarantine (US Code of Federal Regulations, Title 7, Chapter III, Section 301.45-3 and Canadian Food Inspection Agency, Plant Health Division, Policy Directive D-98-09).

eliminate new populations that were spatially disjunct from the established area (Burgess 1930; Dreistadt 1983; Kean et al. 2011). Many of these earlier efforts, particularly those that attempted eradication, were unsuccessful, and *L. dispar* continued to invade new areas. However, some efforts, such as the barrier zone in New York and New England during the 1920s (Burgess 1930), were credited with slowing the rate of *L. dispar* spread (Liebhold et al. 1992) even though only crude and labor-intensive control tactics were available at the time.

Due to increases in the area infested by *L. dispar*, coupled with increases in the amount of defoliation, the US Department of Agriculture accelerated research and development on *L. dispa*, beginning with a funding allocation of $1 million in 1971 followed by annual allocations of $2.4 million from 1975 to 1978 (McManus 1978, 2007). These research efforts proved invaluable as they provided the foundation for many of the tools and much of the technology being implemented and improved upon in current *L. dispar* management efforts. Two critical gains in knowledge included: (i) the identification of the *L. dispar* sex pheromone, and

(ii) a comprehensive understanding of *L. dispar* population dynamics.

3.1.   The sex pheromone

The identification, synthesis, and development of practical applications for the *L. dispar* sex pheromone, Disparlure (cis-7,8-epoxy-2-methyloctadecane; Bierl et al. 1970), as a result of decades of research could arguably be the most significant discovery in the management of *L. dispar* as a non-native insect. Disparlure provides a highly sensitive and host-specific survey tool that is effective even when the moth occurs at very low population densities (Mastro et al. 1977; Doane and McManus 1981; Elkinton and Childs 1983; Thorpe et al. 1993). Without such a sensitive trapping tool, it would be extraordinarily challenging to engage in management efforts that depend upon early detection. For example, in eradication programs, it tends to be more feasible to eradicate low-density populations distributed over a smaller spatial scale (such as those more likely to be detected soon after arrival through a sensitive trapping tool) than higher density populations

spatially distributed over a larger area (Rejmánek and Pitcairn 2002; Liebhold and Tobin 2006; Kean et al. 2011). When considering the history of *L. dispar* eradication programs in the United States, it is perhaps not surprising that the number of attempted eradication programs increased dramatically after the discovery of Disparlure as a practical and reliable bait for use in detection (Figure 2). Indeed, the availability of a sensitive monitoring tool is virtually an absolute requirement in insect eradication efforts for the very intuitive reason that if a species cannot be detected, then it cannot be targeted for eradication. The discovery of Disparlure has also provided for the development and optimization of host-specific mating disruption tactics (Beroza and Knipling 1972; Sharov et al. 2002b; Thorpe et al. 2006) that are also useful management tools.

3.2. Population dynamics

The fundamental understanding of the population dynamics of *L. dispar* (Doane and McManus 1981; Elkinton and Liebhold 1990) and research into the mechanisms of its spread and the demographics of population growth (Johnson et al. 2006b; Liebhold and Tobin 2006; Tobin et al. 2007b) have greatly facilitated the development and improvement of the management strategies that are currently in use (Sharov and Liebhold 1998a; Sharov and Liebhold 1998b; Tobin and Blackburn 2007). Knowledge of the general population dynamics of *L. dispar* (Campbell and Sloan 1977; Elkinton and Liebhold 1990), including its interactions with natural enemies (Dwyer and Elkinton 1995; Elkinton et al. 1996), has allowed strategies to be tailored to the dynamics of the target organism. For example, regulation of outbreaks in established areas is generally due to two host-specific pathogens, the fungus *Entomophaga maimaiga* Humber, Shimazu

and Soper (Zygomycetes: Entomophthorales) and a nucleopolyhedrosis virus, *Ld*NPV (Doane and McManus 1981; Hajek 1999; Dwyer et al. 2004). Thus, *L. dispar* outbreak dynamics can differ depending on the contribution of pathogen epizootics in the density-dependent regulation of populations (Dwyer and Elkinton 1993; Dwyer et al. 2004; Siegert et al. 2009).

Another important consideration of *L. dispar* invasion ecology is the understanding of initial colony establishment and growth (Liebhold and Tobin 2006). In particular, low-density colonies are often subject to a strong Allee effect (Allee 1938; Stephens et al. 1999; Taylor and Hastings 2005) from mate-finding failure (e.g. individuals in sparse populations are less likely to locate mates). Thus, the probability of females being successfully mated declines with decreasing male moth density, a finding that has been confirmed numerous times in field studies (Sharov et al. 1995; Tcheslavskaia et al. 2002; Contarini et al. 2009; Tobin et al. 2009; Figure 3). Thus, many low-density *L. dispar* populations go extinct without any management intervention, whether they arrive in uninfested areas (Liebhold and Bascompte 2003) or along the leading edge (Whitmire and Tobin 2006). When new populations are initially detected, the deployment of an intensive trapping grid can be used to better spatially define the population as well as determine if there is a persistent, reproducing population, which ultimately makes treatment decisions more economic. The presence of an Allee effect due to mate-finding failures (Tobin et al. 2009) also allows for use of mating disruption tactics against low-density populations (Thorpe et al. 2006, Tobin et al. 2011).

4. Current *L. dispar* Management Strategies in the United States

Current management programs for *L. dispar* in the United States fall into one of four categories: (i) a quarantine tactic applied in areas with established
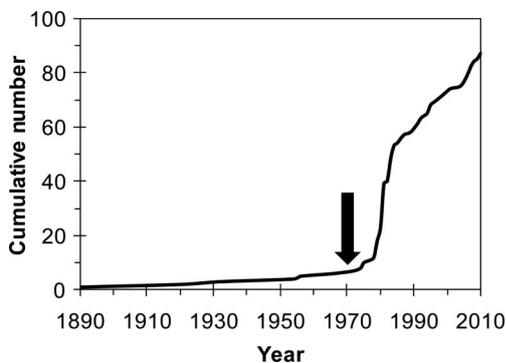

Figure 2. Cumulative number of eradication programs against the European and Asian strains of the gypsy moth in the United States and Canada, 1890–2010 (Hajek and Tobin 2009; USDA Forest Service 2011b; Kean et al. 2011). The arrow indicates the publication year of the identification of the *L. dispar* sex pheromone (Bierl et al. 1970), which is used extensively to detect new populations.
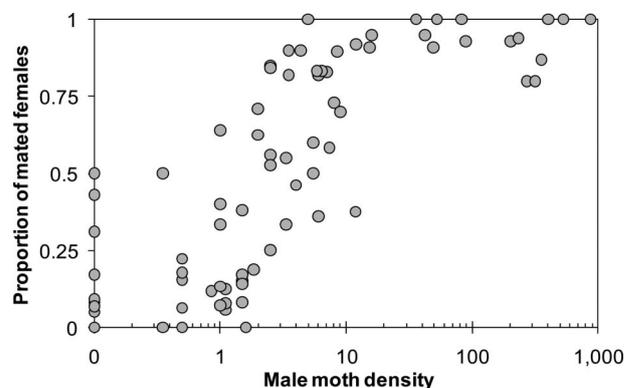

Figure 3. Results of field studies showing that the mating success of *L. dispar* females is influenced by the background male moth density (Sharov et al. 1995; Tcheslavskaia et al. 2002; Contarini et al. 2009).

populations to minimize the accidental movement of life-stages into new areas through, for example, intra-state commerce, household moves, and recreational activities; (ii) outbreak suppression in areas where gypsy moth is established and undergoes periodical outbreaks; (iii) eradication in areas where gypsy moth is not established; and (iv) barrier zone management along the leading and expanding population edge between the areas managed through the quarantine and outbreak suppression, and eradication (Figure 4). Although all of these management programs have somewhat individual objectives and challenges, an underlying factor that connects their strategies is the concept of stratified dispersal. In barrier zone management and eradication programs, the importance of stratified dispersal is intuitively clear; that is, that new colonies that form ahead of or along population front, or arrive in areas distinctly far from the population front, form a basis for both of these management programs. However, the concept of stratified dispersal is also important in areas managed under quarantine and suppression in that during years of high population densities or outbreaks, the likelihood for egg masses or other life-stages to be transported long distances, usually anthropogenically, increases. This has been observed to be the case in several eradication programs where egg masses deposited on household goods or vehicles that originated near an outbreak initiated new infestations when they were subsequently transported to areas where *L. dispar* was not already established (McFadden and McManus 1991; Liebhold and Tobin 2006; Lippitt et al. 2008; Hajek and Tobin 2009).

A time-series of the area in the United States defoliated by *L. dispar* (1924–2010) and the area treated in *L. dispar* eradication programs (1967–2010) is shown in Figure 5 and is used to underscore the connection between *L. dispar* outbreaks and new infestations. In this analysis, the autocorrelation function of the time-series of the area treated for eradication ($\log_{10}$) exhibited a strong polynomial trend, in part due to the rapid increase in eradication attempts following the identification of the *L. dispar* sex pheromone (Figure 5). This trend was removed through quadratic polynomial regression, from which the residuals were obtained. A time-series analysis to estimate the cross-correlation function between these residuals and the defoliated area ($\log_{10}$) revealed positive, significant time lags at years 3 and 4, which suggests that the area treated in eradication programs is significantly related to the area of *L. dispar* outbreaks from 3–4 years ago. A hypothesis for the 3–4 year lag period is that during outbreaks there is an increased probability that life-stages are transported by individuals from infested to uninfested areas (McFadden and McManus 1991). This action results in the establishment of new colonies that are subsequently detected and eradicated. Regardless of the mechanism of the lag period, management programs implemented in the area in which *L. dispar* is established and undergoes cyclical outbreaks (Johnson et al. 2006a; Haynes et al. 2009) can have major ramifications in areas where *L. dispar* is not yet established.

4.1. *Quarantine*

The federal quarantine for *L. dispar* is codified under the United States Code of Federal Regulations (Title 7, Chapter III, Section 301.45–3) and includes the
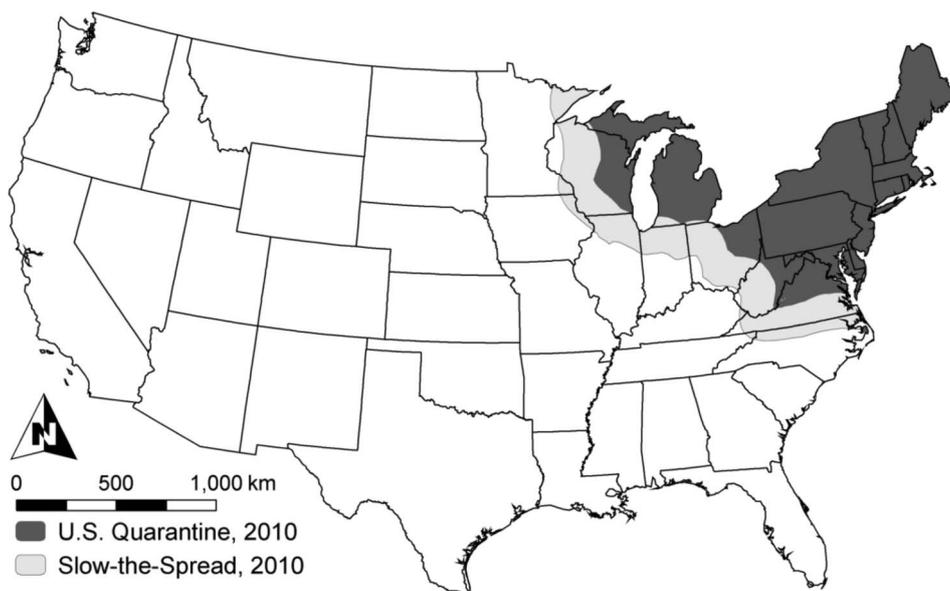

Figure 4.   Area of the contiguous United States managed under quarantine and outbreak suppression (dark gray), and the Slow-the-Spread program (light gray), 2010. Populations of *L. dispar* that arrive outside of these areas are managed under eradication programs.
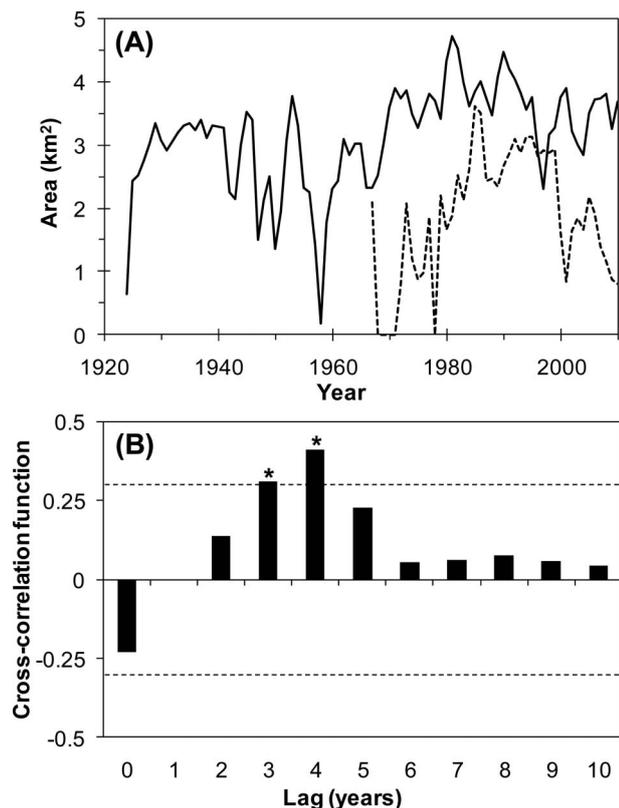
Figure 5. (A) Time-series of the area defoliated by *L. dispar* (solid lines, 1924–2010) and area treated under eradication programs (dashed line, 1967–2010, USDA Forest Service 2011a). (B) Cross-correlation function of the area treated under eradication relative to the area defoliated, showing significant lags (denoted by asterisks; the dashed horizontal lines represent significance levels at $\alpha = 0.05$). Therefore, the area treated to eradicate new infestations of *L. dispar* is positively related to the area of the outbreak from 3–4 years ago.

counties where *L. dispar* is established (Figure 1). Although this area is also managed under suppression programs during periods of population outbreaks, it often plays a role in new infestations outside of the established area when life stages are anthropogenically transported. Under the quarantine, all regulated articles are prohibited from being transported into uninfested states without proper inspection and, if necessary, treatment procedures. Regulated articles include plants with and without roots (e.g. Christmas trees), logs, pulpwood, bark and bark products, mobile homes and associated equipment, and any other product or article on which *L. dispar* life-stages can be deposited and consequential serve as a vector for introduction outside of the quarantined area. The quarantine also specifies procedures for inspection and compliance agreements that must be obtained prior to movement of regulated articles.

A recent study has highlighted the effectiveness of these quarantine measures on the movement of wood products by industry (Bigsby et al. 2011). These products are actively regulated under the quarantine,

and in an analysis of new infestations just outside of the leading edge, the movement of wood products was rarely correlated with the presence of *L. dispar*. In contrast, the movement of wood for personal household fuel use, which in theory is regulated under the quarantine but probably more difficult to enforce than industrial products, was highly correlated with new *L. dispar* infestations (Bigsby et al. 2011). Although the quarantine tactic appears to be effective in regulating industry-based commerce, in part due to established agreements between inspectors and industry, regulating the movement of personal articles by individuals remains a challenge. A recent introduction of life-stages in Oregon (where *L. dispar* is not established) through the purchase of automobile parts from a seller in Connecticut (where *L. dispar* is established) through eBay[®] (Hajek and Tobin 2009) further highlights the challenges in regulating non-traditional industries, such as e-commerce, under the *L. dispar* quarantine.

4.2. Outbreak suppression

The area of the United States where *L. dispar* has become permanently established is called the generally infested area, and covers the states of New England, mid-Atlantic, and parts of the Great Lakes (Figure 1). Periodic outbreaks in the United States occur, generally in oak forests, every 5–10 years (Haynes et al. 2009). Notable *L. dispar* outbreaks in the United States have occurred in 1980–1983 ($\approx$1,159,000 km^2) and 1989–1993 ($\approx$75,000 km^2) (Figure 5; USDA Forest Service 2011a). The first detection of the fungal pathogen *Entomophaga maimaiga* in the United States in 1989 (Hajek et al. 1995) has appeared to change the intensity of outbreaks. For example, in Pennsylvania, prior to the appearance of *E. maimaiga*, some measurable level of defoliation occurred every year and even between major outbreak peaks. Over 19,700 and 17,600 km^2 of forested areas were defoliated in Pennsylvania in 1981–1982 and 1990, respectively (Figure 6). However, following the detection of *E. maimaiga* in Pennsylvania in roughly 1992, subsequent outbreaks have been less intense; only $\approx$5490 and 8685 km^2 of forested areas in Pennsylvania were defoliated during the outbreaks in 1999–2001 and 2006–2008, respectively (Figure 6). Recent outbreaks have also been followed by 2–3 years of very low population densities with little or no defoliation, and consequently no suppression activities (Figure 6). In 2010, no defoliation was recorded in Pennsylvania for the first time since the 1960s. However, even when outbreaks are less intense, *L. dispar* can still cause widespread tree mortality (Gansner and Herrick 1984; Herrick and Gansner 1987). For example, the most recent outbreak in Pennsylvania, from 2005 to 2009, resulted in over 728 km^2 of oak mortality, leaving many high-value oak forests decimated and resulting in extensive timber salvage harvests; in some forest
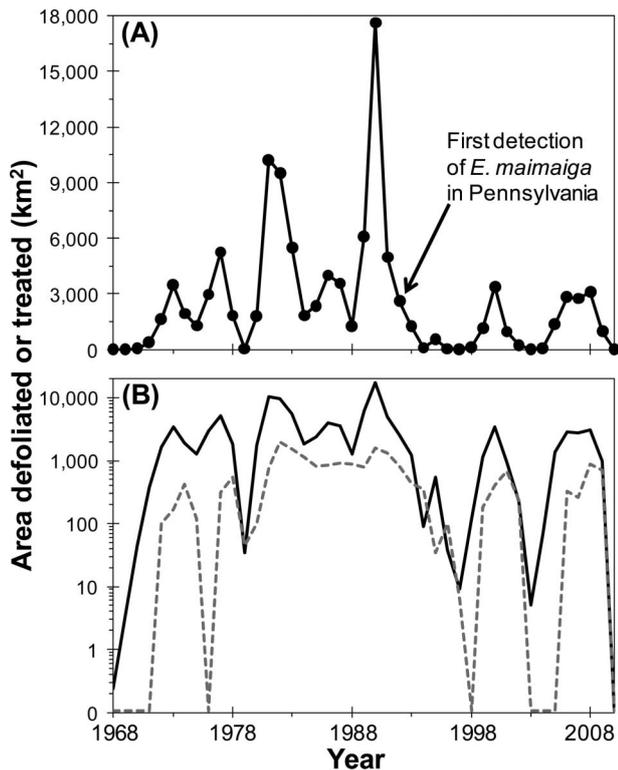
Figure 6. (A) Area defoliated by *L. dispar* in Pennsylvania, 1968–2010, showing the periodicity of outbreaks, which tend to exhibit a dominant period of 8–10 years and a subdominant period of 4–5 years (Haynes et al. 2009). The fungal pathogen *Eucalyptus maimaiga* was first detected in Pennsylvania in 1992; subsequent outbreaks have been less severe. (B) Area defoliated (solid black line) and area treated under suppression (dashed gray line) in Pennsylvania, 1968–2010.

districts, 10 yearly harvest allocations were obtained in only one year.

Although the periodicity of *L. dispar* outbreaks, generally 8–12 years between outbreak peaks, has been observed to be consistent in many populations worldwide (Johnson et al. 2005), outbreaks conforming to a secondary period of 4–5 years have been observed (Johnson et al. 2006a; Haynes et al. 2009). Anecdotal evidence suggests that *L. dispar* populations begin to increase following warm dry springs, presumably because of reduced regulation by *E. maimaiga*, which is sensitive to temperature and moisture (Hajek et al. 1990). Regardless, populations do not necessarily increase uniformly across the landscape. For example, the most recent outbreak in Pennsylvania began in the Poconos region in 2005, which was not affected by the previous outbreak in 1999–2002, even though this region has experienced numerous outbreaks since the introduction of *L. dispar* into Pennsylvania in 1932. In this most recent outbreak, defoliation increased from about 5 km^2 in 2003 to more than 1347 km^2 in 2005, with almost all of this occurring in the Poconos region. In 2006 and 2007, an outbreak occurred in south-central and central Pennsylvania, but populations

collapsed in western Pennsylvania before they could obtain outbreak levels. Beginning in the fall of 2009 and 2010, egg mass surveys were conducted extensively throughout the state of Pennsylvania. (Fall egg mass surveys are probably the most reliable predictor of subsequent outbreak levels; Liebhold et al. 1994). In the 2009–2010 and 2010–2011 surveys, 1485 and 1048 egg mass surveys were conducted, respectively, with only 141 and 29 sites recording at least one new egg mass, respectively. New egg masses were typically found in western Pennsylvania, a region of the state that has not typically experienced many *L. dispar* outbreaks. Furthermore, when populations do begin to increase, they tend to do so in very discreet locations, such as in xeric oak sites located on ridge tops, before expanding to other areas. Anecdotal evidence suggests that atmospheric transport of the ballooning larvae can be an important mechanism of dispersal from these ridge tops to the surrounding areas, where populations are lower in density; however, it has also been observed that this type of transport did not explain outbreak patterns (Liebhold and McManus 1991). The variability in outbreak patterns highlights the challenge in coordinating and prioritizing outbreak suppression programs.

Although the primary objectives of suppression programs are to minimize defoliation and prevent tree mortality in treated areas, *L. dispar* is often referred to as a "people problem" in the states engaged in suppression activities. This is due to the considerable nuisance that *L. dispar* larvae cause, from their sheer number inducing entomophobic reactions, to allergic responses to the urticating hairs of larvae (Tuthill et al. 1984; Allen et al. 1991). Consequently, landowners, and particularly those who are well aware of the nuisance due to larvae, make their voices heard by calling state and local officials "to do something." In Pennsylvania, the Division of Forest Pest Management was created in 1972 by the state legislature to deal with the *L. dispar* problem, and has allocated funding nearly every year to its management.

Outbreak suppression programs are a cooperative effort among the United States Department of Agriculture (USDA) Forest Service, state agencies, and county or municipal governments. Each state involved in conducting suppression programs has developed Operations and Procedures guidelines detailing the roles and responsibilities of cooperating agencies (e.g. Pennsylvania Department of Conservation and Natural Resources 2009). State agencies conduct aerial spraying on non-federal lands through cooperative agreements with county or municipal governments. Requests from private landowners are coordinated by county or municipal agencies, and land managers of state managed lands make requests directly to the lead state agency. Each state conducts site-specific environmental assessments based on biological evaluations and reviews by state Natural

Heritage Programs for non-target species of concern (United States Department of Agriculture 1995). Management on federal lands is conducted by the appropriate Federal Agency with jurisdiction over the land, such as the USDA Forest Service, when suppression occurs on United States National Forests. Outbreak suppression can also be implemented outside of these efforts by individual homeowners and private communities (e.g. private golf courses).

Three insecticides are currently used in suppression programs: *Bacillus thuringiensis* var. *kurstaki* Berliner (*Btk*, Reardon et al. 1994), *Ld*NPV commercially produced and registered as Gypchek® (Reardon et al. 1996), and the insect growth regulator, diflubenzuron (United States Department of Agriculture 1995). A fourth insecticide, tebufenozide, which has been used extensively in recent years by applicators treating privately owned forests, is included in a new federal Environmental Impact Statement (EIS). Once this EIS is approved, tebufenozide will become available for use in all *L. dispar* management programs. The treatment tactic most often used is *Btk* (USDA Forest Service 2011a) due to its efficacy and reduced non-target impacts as it only affects Lepidoptera (Wagner et al. 1996; Solter and Hajek 2009). Diflubenzuron is also an effective treatment but has more pronounced non-target effects because it interferes with the moulting process of potentially all arthropods. Gypchek® is used when a non-target Lepidopteran species of concern has been identified through the environmental review process. Although Gypchek® is less effective than *Btk* or diflubenzuron, it only affects *L. dispar* and thus has no non-target effects. However, Gypchek® must be produced *in vivo* and consequently, can only be mass-produced in limited quantities, generally only enough to treat < 50 km^2 per year.

Federal funding for state cooperative suppression programs is provided from the USDA Forest Service with the requirement that there must be at least 50% in matching state funds. Federal funding for cooperative suppression programs varies each year depending upon outbreak intensity, and has ranged from $139,000 USD (in 2010) to $> $10.9 million USD (in 1990) (USDA Forest Service 2011a). The state funds required for the 50% match can be derived from in-kind services such as personnel support, appropriated funding through state governments, and local cost-share contributions. For private lands in many state suppression programs, the state agencies require a local cost-share contribution from the county or municipality (e.g. $\approx$$52/ha), or in some cases from the private landowner. Cooperative agreements are generally prepared between the state agency and the county government, detailing the cost-share amounts and the roles and responsibilities of each party.

Current costs of cooperative suppression programs are about $8600 per km^2; thus, large scale suppression projects can be very costly, and finite resources must be allocated appropriately. The capacity to conduct aerial treatments is also a constraint. In 2008, the state of Pennsylvania had the largest suppression program in the United States. Over 1680 km^2 were initially proposed for treatment in Pennsylvania, but only 894 km^2 were treated in the program at a total cost of about $7.7 million. Moreover, because federal and state budgets are rarely synchronized with the *L. dispar* population outbreak cycle, prioritization of treatment blocks must be based on available funds and the capacity to conduct large aerial spraying operations. Egg mass densities, the prior year defoliation, and land-use type are all used to establish priority of treatments. In Pennsylvania, a review of these priorities was conducted with the suggestion that high-value oak forests be given top priority when allocating scarce dollars for treatments.

4.3.   Eradication

The area of the United States where *L. dispar* is not established is called the uninfested area, and is located west and south of the leading population edge that is managed under the Slow-the-Spread program, a barrier zone management that aims to limit *L. dispar* range expansion (discussed in section 4.4). The uninfested area covers more than three-quarters of the land mass of the contiguous United States (Figure 4). The introduction of *L. dispar* within the uninfested area typically occurs when life-stages, often egg masses, are anthropogenically transported from infested areas (Doane and McManus 1981; McFadden and McManus 1991; Hajek and Tobin 2009). Additionally, egg masses or other life-stages of the Asian strain, *L. dispar asiatica* Vnukovskij, can arrive at coastal states from ships originating in Asia (Hajek and Tobin 2009). Because human-assisted introduction is generally the only manner by which *L. dispar* can arrive to many uninfested areas, these infestations tend to be spatially isolated and occur sporadically. The management strategy for the uninfested area relies first upon quarantine and prevention strategies to minimize the introduction of life stages from the established area. However, new infestations still occur. Eradication programs then depend upon surveillance detection, and eradication if a reproducing *L. dispar* population is confirmed or suspected to be present.

4.3.1.   Surveillance detection

Delta traps baited with Disparlure are deployed in systematic grids to detect adult males, and are effective at attracting both the European and Asian strains of *L. dispar* (United States Department of Agriculture 2009). Trapping grids are usually placed in areas where the introduction of *L. dispar* is more likely to occur, such as in populated areas, along transportation hubs and routes, and in campgrounds and nurseries.

In detection efforts, a standard trap density is 1 trap/ 10.4 km^2 (e.g. 1 trap/4 mi^2) in rural areas and 1 trap/ 2.6 km^2 (e.g. 1 trap/mi^2) in towns and cities (United States Department of Agriculture 2009). Upon detection of *L. dispar*, additional traps are set around positive traps if the male flight period is ongoing. Beginning in the next season, delimitation trapping is conducted generally for the next two years. The standard delimitation trap density in the first year following the positive catch is 16–36 traps/2.6 km^2 centered on the location of the positive trap, and trapping grids extend outward to areas where *L. dispar* was not detected (United States Department of Agriculture 2009). Under certain circumstances, such as in the case of sensitive habitats, trap grid intensity can be increased and/or extended over a larger area. If no additional moths are detected, a delimitation trap density of 16 traps/2.6 km^2 is used during the second year. If no moths are trapped during the second year as well, the site is considered to be devoid of a reproducing *L. dispar* population and the site returns to a standard detection trap density. The cost of surveillance detection is about $30–40/trap. Each year, states not infested with *L. dispar* place over 150,000 traps for use in detection according to estimated risk levels for each state. In the coastal states of Oregon and Washington, over 12,000 and 21,000 traps, at the cost of about $498,000 and about $1,800,000, respectively, were placed in 2010. Data are maintained by the cooperating states and the USDA through the Co-operative Agricultural Pest Survey, and are accessible online through the National Agricultural Pest Information System (2011).

4.3.2. Eradication

When surveillance detection efforts reveal: (i) the presence of multiple life-stages in the same year at the same site, or (ii) positive traps at the same site for two or more years in a row and an increasing number of trapped males, an eradication program is initiated. Both conditions suggest that an established, reproducing *L. dispar* population could be present. Not all detections of *L. dispar* result in an eradication program (Figure 7); however, in the case of *L. dispar asiatica*, a single moth catch will trigger eradication, and this policy exists because females of this subspecies are able to fly and also have a broader host range than *L. dispar dispar* (Keena et al. 2008). In eradication, the most commonly used pesticide is *Btk* (Reardon et al. 1994), which can be applied from the ground or air depending on, for example, the size of the eradication area, location, terrain, and accessibility. Smaller eradication blocks with high accessibility are often treated using ground applications, while larger eradication blocks with low accessibility, such as in areas of uneven terrain or forested areas, are often treated using aerial applications that are more economically feasible.
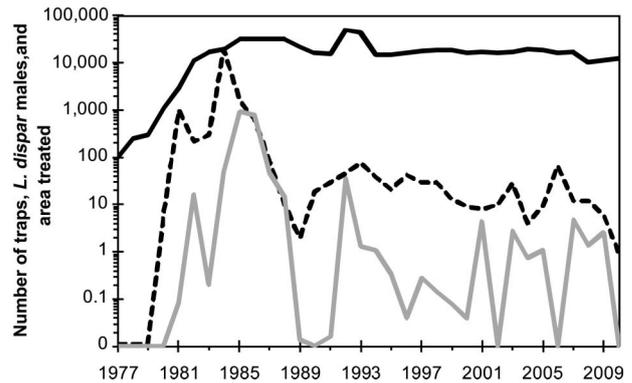

Figure 7. Number of deployed traps (solid black line), male *L. dispar* detected (dashed black line) and area treated in eradication (km^2, gray line), in Oregon, United States, 1977–2010.

To evaluate the success of eradication, delimitation trapping grids are deployed for 2–3 years and eradication success can only be declared when traps fail to record any *L. dispar* for at least two consecutive years.

Since the isolation of the *L. dispar* sex pheromone in 1970, a number of eradication projects, including those that have targeted *L. dispar asiatica*, have been conducted in the United States (Figure 2), with many of these implemented in the west-coastal states of Washington, Oregon, and California (Hajek and Tobin 2009, USDA Forest Service 2011b). For example, the Oregon Department of Agriculture has conducted 26 *L. dispar dispar* and three *L. dispar asiatica* eradication projects on over 1,800 km^2 since 1981. During this time, eradication blocks have ranged in size from 0.02 km^2 (Clackamas County, 1991) to 910 km^2 (Lane County, 1985), with a corresponding cost of $267,000 to $9.5 million, respectively. Due to the optimization of surveillance and detection efforts over the last decade by, for example, prioritizing trapping in high-risk areas, eradication projects have tended to be smaller in scale, because new populations are detected earlier; consequently, in recent years, treatment areas have rarely exceeded 4 km^2 (Figure 7). Detecting populations early greatly reduces the costs of eradication and increases the likelihood of eradication success.

One major challenge encountered in *L. dispar* eradication efforts is the public opposition to any kind of pesticide application, including *Btk*, and especially in aerial applications (Hajek and Tobin 2010). A recent advance in more benign treatment tools is the development of organic formulations of *Btk*, which would allow treatments to be applied in areas of organic farming without jeopardizing the ability to obtain a certified organic label. However, some sections of the general public still oppose any kind of aerial application based upon health and other non-target concerns. This challenge underscores the importance of public education and outreach during an eradication campaign.

Eradication programs against *L. dispar* are a federal and state cooperative program. Whenever eradication is proposed, state departments of agriculture, forestry, natural resources, or similar agencies in charge of pest prevention, work with federal agencies such as the USDA Animal and Plant Health Inspection Service and the USDA Forest Service to write site-specific Environmental Assessments and to conduct the eradication treatments. Using a management strategy that incorporates quarantine and prevention with surveillance detection and eradication of any reproducing populations, uninfested states, especially those along the west coast, have been successful in eliminating *L. dispar* populations for more than three decades (Kean et al. 2011). This has consequently prevented the ecological and economic damage associated with *L. dispar*. A key attribute to this success is early detection followed by a rapid response of eradication.

4.4.   *Barrier zone management*

Between the areas in which *L. dispar* is targeted for eradication and outbreak suppression is an expanding leading edge that is currently managed under the Slow-the-Spread program (Sharov et al. 2002a; Tobin et al. 2004; Tobin and Blackburn 2007; Figure 4). Because of the importance of stratified dispersal in this and other biological invasions, *L. dispar* does not spread continuously along the edge of the established area; rather, colonies arrive and establish beyond the expanding front. The importance of stratified dispersal in the context of barrier zone management was illustrated by Liebhold et al. (1992), who used demographic data on *L. dispar*, parameterized from field studies, to formulate a model of diffusive spread, which was estimated to be about 3 km yr^{-1}. They then estimated a rate of spread based upon county quarantine records, which was about 21 km yr^{-1} (Liebhold et al. 1992). The difference in rates of spread highlighted the importance of "jump" dispersal of new colonies, their growth, and eventual coalescence with the established area. This study also provided a scientific basis for managing *L. dispar* spread using a barrier zone strategy.

The premise of the Slow-the-Spread program is to deploy a network of pheromone-baited traps across the leading population front that extends from the established area by approximately 170 km, encompassing more than 190,000 km^2 (Figure 4). Within this zone, newly founded colonies are most likely to be detected (Sharov and Liebhold 1998a; Sharov and Liebhold 1998b). Traps are deployed every 2–8.0 km, with a finer spatial grid used in the areas farthest from the established area where populations are expected to be absent or low. Upon initial detection of a new colony, a management priority is placed upon the area depending on its contribution to *L. dispar* spread; generally, colonies that are the largest in density and

farthest away from the established area increase spread rates the most and hence are given the highest priority (Tobin et al. 2004). Colonies that are selected for management are first delimited, in the following year, using a finer grid of traps (0.5–1 km apart). In doing so, the spatial extent of the colony and the population peak are better defined. In the year after delimitation, the colony is treated using one of several options, such as mating disruption or *Btk* (Tobin and Blackburn 2007; United States Department of Agriculture 1995). The strategy of the initial detection, delimitation, treatment, and post-treatment evaluation in the Slow-the-Spread program is illustrated in Figure 8. The Slow-the-Spread program is evaluated by estimating yearly spread rates obtained from the yearly displacement in population boundaries (Sharov et al. 1997; Tobin et al. 2007). Since 2000, this program has reduced *L. dispar* spread from historical rates of about 21 km yr^{-1} (Liebhold et al. 1992) to less than 4 km yr^{-1} (Roberts et al. 2011), which is estimated to have prevented *L. dispar* infestation on more than 400,000 km^2 between 2000 and 2010.

The reduction in *L. dispar* spread and consequent infestation to other areas has considerable economic benefits. Previous economic analyses on the benefit of barrier zone programs against *L. dispar* have consistently shown a benefit-to-cost ratio of at least 3 : 1 (Leuschner et al. 1996), with the primary benefit resulting from delaying the onset of impacts that occur as gypsy moth invades new areas. A recent economic assessment estimated a 20-year net present value of the Slow-the-Spread program, after subtracting its costs, ranging from $184 million to $348 million (Sills 2007). These prior economic assessments have highlighted that the delay in impacts resulting from *L. dispar* invasion can affect multiple sectors, including timberland and forest resources, recreational services and amenities, nuisance to humans in areas experiencing outbreaks, and intra- and interstate commerce due to quarantine restrictions that regulate the movement of articles from areas infested by *L. dispar* to areas not infested (Blacksten et al. 1978; Leuschner et al. 1996; Sills 2007). In addition, invasion by *L. dispar* can incur costs that are challenging to estimate, such as impacts upon native species, biodiversity, and ecosystem function and services (Herrick 1981; Thurber et al. 1994; Redman and Scriber 2000).

The implementation of the *L. dispar* Slow-the-Spread program involves a number of entities including the US Government (through the USDA), several state governments, and two universities. In addition, the program operates over a mosaic of private, local, state, federal, and tribal-owned or managed lands. For example, on lands managed by the US Government alone, it is not atypical for program personnel to interact with over 50 separate federal entities – such as US national forests and federally protected wilderness areas, military bases, and aquatic areas managed by the
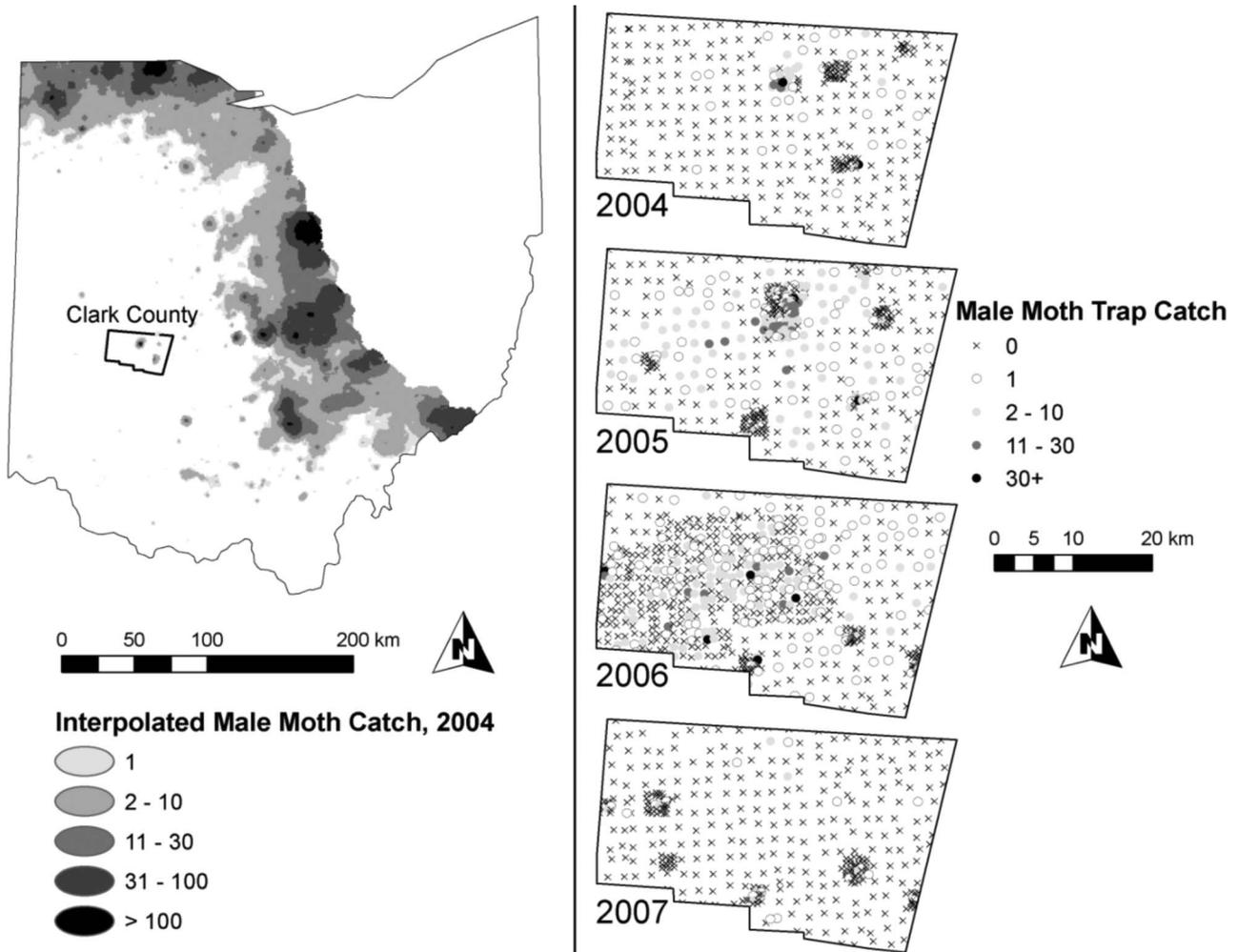
Figure 8. Conceptual outline of barrier zone management for *L. dispar* under the Slow-the-Spread program (Tobin and Blackburn 2007). Trap catch data revealed the presence of a colony ahead of the leading edge in Clark County, Ohio in 2004. Trapping delimits were conducted in 2005, treatments were deployed in 2006, and post-treatment evaluation in 2007 suggested that the colony had been largely eliminated.

US Army Corps of Engineers, fish and wildlife refuges, and US parks and national monuments – in a given year. For the Slow-the-Spread program to operate effectively there must be a consistent sampling protocol and a management strategy that transcends geopolitical boundaries. Thus, a critical component to this, as well as other barrier zone management programs, is the ability to formulate and implement management decisions that are biologically based.

5. Lessons learned and applicability to other non-native insects

Several key attributes have greatly facilitated a biologically-based management approach for *L. dispar* over a variable geopolitical landscape in the United States. One extremely important tool is the development of sampling techniques. Pheromone-based trapping systems, which are imperative in eradication and Slow-the-Spread programs, are highly

sensitive and effective at low pest densities, and are critical in both initial detection and evaluation of the effectiveness of treatments deployed to eradicate new populations (Elkinton and Cardé 1980; Elkinton and Childs 1983; Elkinton and Cardé 1988). At high population densities that are common prior to and during *L. dispar* outbreaks, research that has elucidated the relationship of life-stage densities, such as for egg masses, to the expected level of defoliation allows for generalized predictions of damage (Williams et al. 1991; Liebhold et al. 1993; Liebhold et al. 1994), which in turn can be used to prioritize resources for mitigating *L. dispar* outbreaks through suppression activities.

The enhanced understanding of *L. dispar* invasion ecology and population dynamics is another factor that has improved management decisions. One aspect of the invasion dynamics of *L. dispar* is the concept of latency in which there is a period time between the first arrival of new *L. dispar* reproducing populations, such as

through the importation of egg masses, and its population growth to damaging levels (Liebhold and Tobin 2006). This latency is thought to occur in many biological invasions (Shigesada and Kawasaki 1997; Sakai et al. 2001). In *L. dispar* management efforts, such latency allows for the use of delimiting trapping grids, so that the full extent of the infestation and its population peaks can be spatially identified, which then allows for the more precise treatment applications (Sharov et al. 2002a; Tobin et al. 2004). In the established area, identifying the periodicity of *L. dispar* outbreaks (Johnson et al. 2006a; Haynes et al. 2009) and the role of entomopathogens in the collapse of outbreaking populations (Dwyer et al. 2004) can facilitate decision-making in suppression. Finally, the development of molecular tools to genetically differentiate among *L. dispar* subspecies (Bogdanowicz et al. 1997), such as between the Asian subspecies, *L. d. asiatica*, and the European subspecies, *L d. dispar*, is an important advancement, as different subspecies of *Lymantria* could trigger different management decisions. For example, *L. d. asiatica* could be more damaging than *L. d. dispar* due to many factors including its broader host range (Keena et al. 2008). Coupled with the fact that *L. d. asiatica* is not established in North America, when males of this subspecies are detected in pheromone-baited traps, there is usually a more aggressive management response.

A third attribute that facilitates *L. dispar* management activities is the availability of effective treatment tactics, including host-specific tactics with little or no non-target effects for use in ecologically sensitive areas. The identification of the *L. dispar* sex pheromone is not only useful in detection, but also in the development and optimization of very host-specific mating disruption tactics (Beroza and Knipling 1972; Thorpe et al. 2006). The pheromone has no known deleterious environmental effects. Mating disruption tactics are the primary control tactic in the Slow-the-Spread program (Tobin and Blackburn 2007; Gypsy Moth Slow-the-Spread Foundation Inc. 2011), and also has been used in eradication programs (USDA Forest Service 2011b). Another important tactic is the biopesticide *Btk* (Solter and Hajek 2009), which is used in suppression, Slow-the-Spread program, and eradication, and is the dominant tactic in eradication and suppression programs. Although *Btk* can affect other Lepidoptera, it still has fewer non-target effects than the broad-spectrum chemical-based insecticides. A third treatment tactic exists in the commercial formulation of Gypchek®, which only affects *L. dispar* populations and is used in all three management programs where there are immediate non-target concerns (Reardon et al. 1996). A significant contribution related to these treatment tactics is the innovations in application technology, especially in aerial applications, that were developed and optimized under *L. dispar* management programs in the United States over the decades. Many of the generic aspects of these advances in application technology are directly applicable to other insect management programs.

A final characteristic of *L. dispar* management in the United States is arguably a paramount attribute when managing, or attempting to manage, a non-native species: an assessment of the economics of *L. dispar* and evidence to support its designation as an actionable pest. In the case of *L. dispar*, several economic assessments have consistently concluded, given then extent of the *L. dispar* range and the amount of susceptible habitat that remains uninfested, that the benefits of management efforts outweigh the costs of control (Blacksten et al. 1978; Leuschner et al. 1996; Sills 2007). The primary costs of *L. dispar* infestation in new areas include residential, recreational, and timber impacts; consequently, the primary benefits of *L. dispar* management activities include the postponement of costs associated with maintaining a quarantine, and the cost of outbreak suppression to mitigate impacts to forested areas and urban forests on public and private lands. Due in part to the economic benefits of *L. dispar* management efforts, there exists a legal authority to regulate populations through quarantine measures in the established area (United States Code of Federal Regulations, Title 7, Chapter III, Section 301.45–3) and through the eradication of populations that form outside of the established area (United States Department of Agriculture 2009).

6.   Discussion

In many new biological invasions, initiating a management policy can be challenging, given the uncertainty associated with the invasiveness and potential economic and ecological impact of the new species. Most arrivals of a non-native species are thought to fail to become establish due to, for example, small founder sizes, climate unsuitability, and a lack of suitable hosts (Williamson and Fitter 1996; Simberloff and Gibbons 2004), and only a minority of those that do become established are considered to pose significant economic and ecological harm (Mack et al. 2000). Among forest insects and pathogens, recent work has suggested that approximately 2.5 non-native species successfully establish in the United States each year, while those species posing high risks to ecosystem function and services establish approximately once every 2 years (Aukema et al. 2010). Regardless, for those species that do pose economic and ecological harm, or those that are deemed to be an "actionable pest," there is often a lack of existing management guidelines upon which to formulate an appropriate response, in part because many of these species do not pose the level of damage and concern in their native environment (Herms 2002; Yan et al. 2005).

Because of the need to respond to non-native species, even in the absence of specific knowledge of the species, examining the experience and practices from other non-native species for which there is past knowledge could be a viable approach. In *L. dispa*, over 100 years of research and management experience has been accumulated (e.g. Doane and McManus 1981; Elkinton and Liebhold 1990), and although tailored to *L. dispar*, many of the conceptual principles that form the basis of its management are applicable to other non-native species. We also contend that there are other surrogate species that could provide a basis of management for other non-native species. For example, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), which has recently invaded California, is another well-studied species that could serve as a model for in the development of management programs against related non-native species (Suckling and Brockerhoff 2010).

With the current trends in global trade and travel, new species will likely continue to arrive to new areas (Levine and D'Antonio 2003; Work et al. 2005; McCullough et al. 2006; Dehnen-Schmutz et al. 2007). Although challenges remain in the classification of actionable pests, those that are deemed environmentally and ecologically damaging require a sound and rationale basis for developing management protocols, often in the absence of species-specific knowledge. Past research and management knowledge of *L. dispar*, as well as other species both native and non-native, could thus serve as important surrogate species in the formulation of management guidelines and strategies for new invaders.

Acknowledgments

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