

## Chapter 4

# Recent Developments in *Lymantria dispar* Spread

Jonathan A. Walter and Andrew M. Liebhold

### Abstract

The spread of spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the “gypsy moth”), in North America arguably represents the best-studied biological invasion in the world, due in part to extensive monitoring data from the USDA National Slow the Spread (STS) Program. In this paper, we focus on recent research on spread, with particular emphasis on findings since the publication of Tobin and Blackburn (2007). Recent advances in understanding *L. dispar* spread generally fall into three categories: (1) the role of mating success and Allee effects, (2) the effects of geographical variation in climate, and (3) the genetic adaptation of local populations. Some studies have quantified how the strength of the demographic Allee effect varies regionally and interannually, due in part to differences in climate, topography, and landscape structure. Recent observations suggest that climatic suitability of the cold and warm extremes of *L. dispar*'s North American range are higher and lower, respectively, than earlier predictions, and for reasons that are not yet fully clear. Furthermore, data indicate that *L. dispar* has adapted to local climatic conditions, with convincing evidence of adaptation in traits allowing life stages to tolerate hot spring and summer temperatures in warmer parts of their range. Despite these advances, several opportunities for future research and operationalization of current knowledge remain. One area of future work of potentially high importance is the development of a realistic model of *L. dispar* spread that could be used for optimizing the STS Program decision algorithm.

**Keywords:** Allee effect, climate suitability, gypsy moth, local adaptation, spongy moth

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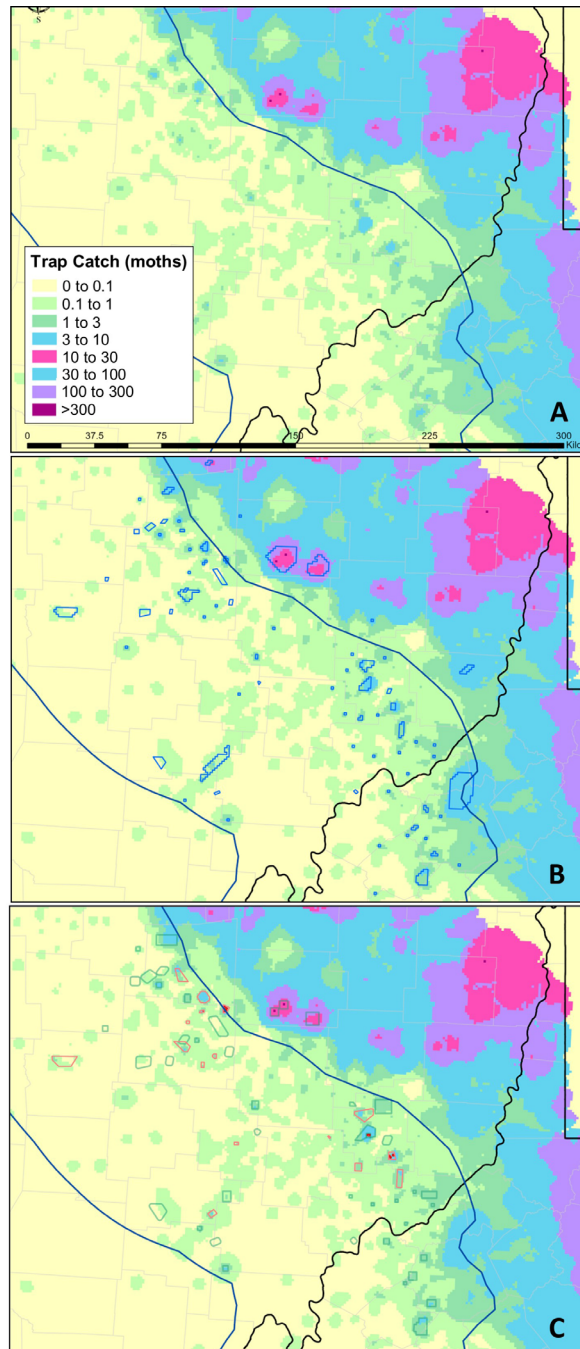
## INTRODUCTION

Once invading species found initial populations, they tend to expand their range until they have saturated the novel habitat. This phase of biological invasions, called “spread,” is one of the most studied but incompletely understood ecological processes (Hastings et al. 2005, Parry et al. 2013). A manifestation of two population processes—population growth and population dispersal—invasion spread has attracted the attention of mathematical investigators as well as applied ecologists. Their work has yielded a variety of mathematical models of invasion spread that vary from simple to complex. But like much theoretical ecology research, most of these models remain untested, largely due to a lack of rich datasets and detailed understanding of population processes necessary to evaluate nuanced population behaviors.

The invasion of North America by spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae, formerly known as the “gypsy moth”), and management efforts have created unparalleled amounts of data on spread as well as detailed knowledge of factors affecting invading populations. Between the USDA National Slow the Spread (STS) Program and surveillance programs carried out in the uninvaded states, more than 200,000 pheromone traps are deployed annually, and data from these traps represent a unique resource from which the spatial dynamics of invading populations can be deduced. Analyses of trap capture data have yielded significant insights into the mechanisms behind the spread of this species, and these findings have important implications for understanding the spread of other organisms (Grayson and Johnson 2018). For example, analyses of historical *L. dispar* trap data have identified important influences of both stratified dispersal (i.e., the combination of local diffusion and long-distance transport) (Fig. 1) and Allee effects on *L. dispar* spread, and these analyses have served as a model system for a general understanding of invasion spread (Liebhold et al. 2007, Sharov and Liebhold 1998, Tobin et al. 2009).

The uniquely detailed knowledge of *L. dispar* spread has played a crucial role in the development of the STS Program, a science-based approach to managing *L. dispar* spread in the United States. Quantification of the stratified dispersal phenomenon has allowed for the identification and optimization of an overall strategy of the STS Program, one that focuses on surveillance for the presence of isolated populations which are then suppressed (Sharov and Liebhold 1998, Sharov et al. 1998). Additional analyses of historical spread have also yielded information that has been crucial to developing the STS decision algorithm (STS DA) and solving operational problems encountered during the course of the program (Tobin et al. 2004).

Liebhold et al. (2007) summarized the state of knowledge on *L. dispar* spread using information and data analyses of *L. dispar* spread both prior to the STS Pilot Project (1900–1995) and during the STS Pilot Project (1996–1999). Since the implementation of the National STS Program and the publication of Tobin and Blackburn (2007), considerably more research has been conducted on *L. dispar* spread. Our objective here is to summarize this more recent research and discuss its relevance toward improving the efficiency of the STS Program.



**Figure 1.**— Results of stratified diffusion of *L. dispar* in West Virginia and Ohio and STS response. (A) Interpolated trap catch densities show isolated low-density populations ahead of the invasion front resulting from long-distance transport; if allowed to persist, these will coalesce through local diffusive spread. (B) Blue polygons correspond to potential problem areas (PPAs) identified under the STS decision algorithm. Note that many “hotspots” ahead of the invasion front are identified as PPAs for possible population delimitation or treatment. (C) Areas treated: mating disruption (pink), larvicides (red), and delimited (blue). Dark blue lines indicate the projected bounds of the STS action area.

## IMPORTANCE OF MATE-FINDING FAILURE AND ALLEE EFFECTS

A key topic since the publication of Tobin and Blackburn (2007) is the importance of mate-finding failure in low-density populations to *L. dispar* population establishment and spread. In eastern North America, where *L. dispar* is descended from the European strain of *L. dispar* (Wu et al. 2015), females are flightless and attract flying males using a sex pheromone. Successful reproduction, therefore, depends on a free-flying adult male locating a receptive female. The various behavioral components of *L. dispar* mate-location and their dependencies are reviewed in Cardé (1981). Sharov et al. (1995) provided the first report that *L. dispar* mating success is low in low-density, newly invaded populations. Recent developments have shed light on how the failure to find mates translates to critical population dynamic patterns that can be exploited to help manage *L. dispar* spread (Tobin et al. 2011) and how interactions between *L. dispar* biology and environmental conditions shape rates of mate-finding, and thus invasion dynamics.

Population density is the most important factor affecting mate-finding rates. Where there are many moths in an area, the likelihood that any female is successfully mated is higher than where the number of moths is fewer. In empirical field studies, Sharov et al. (1995) and Contarini et al. (2009) demonstrated that the probability of experimentally deployed *L. dispar* females being mated increased with the background population density, as measured from pheromone-baited trap catch. These studies also revealed mate-finding failure in *L. dispar* to be an important cause of Allee effects, a population dynamic phenomenon causing slow growth and extinction in small or low-density populations (Allee 1931, Courchamp et al. 1999). *Lymantria dispar* experiences strong Allee effects, which are characterized by a threshold below which populations are likely to become extinct in the absence of immigration (Tobin et al. 2009). Allee effects can be caused by a variety of mechanisms, and those effects in *L. dispar* may result from a combination of multiple factors, including mate-finding failure (Contarini et al. 2009; Robinet et al. 2007, 2008; Sharov et al. 1995; Walter et al. 2015, 2016) and predation (Bjørnstad et al. 2010, Haynes et al. 2009, Tobin et al. 2009). The empirical evidence in the cited studies on the role of mate-finding failure in driving Allee effects in *L. dispar* was foundational to research and management alike.

The key implication of strong mate-finding failure Allee effects for *L. dispar* management is that the moth's spread can be mitigated, not necessarily by driving population density to zero, but by driving population density below the Allee threshold (Liebhold and Bascompte 2003, Liebhold and Tobin 2008, Tobin et al. 2012). Once below the Allee threshold, the population is likely to decline to zero without further intervention, particularly when the population is isolated and receives few or no immigrants to supplement it (Taylor and Hastings 2005). That mate-finding failure is a key mechanism of Allee effects also affirms the value of mating disruption treatments for slowing *L. dispar* spread. Reducing rates of mate-finding effectively shifts the Allee threshold to higher densities (Liebhold and Tobin 2008; Walter et al. 2015, 2017), causing populations remaining below the elevated Allee threshold to decline toward extinction.

The strength of Allee effects in *L. dispar* populations has been found to vary across the invasion front (Tobin et al. 2007b, Walter et al. 2020), meaning that the threshold population density that determines whether a population will persist and increase in abundance or become extinct without supplementation from immigrants differs from

place to place. These differences are due to variation in environmental conditions that influence key population processes; chief among these are reproductive phenology, male flight, and mortality (Robinet et al. 2007).

The timing, or phenology, of reproductive development differs between male and female *L. dispar* and within and among *L. dispar* populations (Gray 2004). These differences are partly responsible for differences in mating success and Allee effects across the invasion front. This species exhibits protandry, in which males in a population tend to emerge as reproductive adults earlier than females, typically by a few days (Robinet et al. 2007). Additionally, within a population, individuals of each sex reach maturity over a period of days to weeks, rather than in perfect seasonal synchrony. Both the amount of protandry and the length of the period over which adults emerge are partly controlled by temperature and therefore vary across the invasion front (Gray 2004, Robinet et al. 2007, Walter et al. 2015). The degree of reproductive asynchrony (i.e., the mismatch in timing of reproductive maturation between an individual and potential mates in a population), translates to differences in mating success and Allee effects. All else being equal, increasing the mismatch between males and females in a population and spreading out the distributions of reproductive maturation dates over a longer timespan reduces mating success and strengthens Allee effects (Robinet et al. 2007, 2008; Walter et al. 2015).

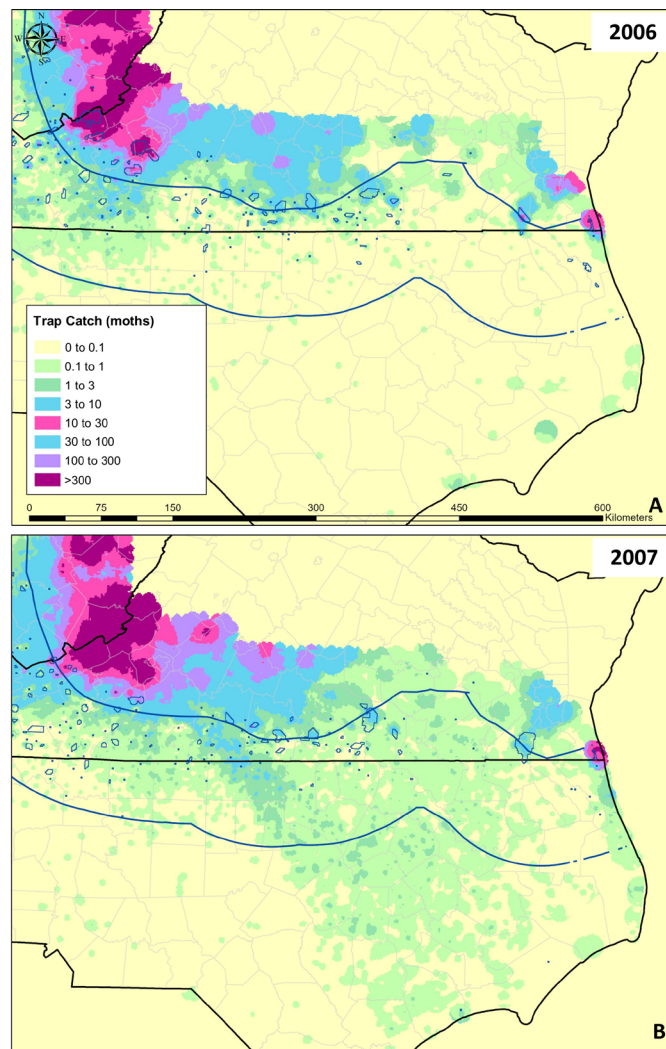
Because female *L. dispar* in eastern North America are flightless, successful mating depends on male flight. Adding to studies that have shown the general positive effect of male moth density on mating success (Contarini et al. 2009, Sharov et al. 1995), recent research has investigated how characteristics of the landscape shape male flight and mating success. Since the landscape encountered by spreading populations is a mosaic of different habitat types, some suited to *L. dispar* and others inhospitable due to lack of host resources, one focal area has been how landscape structure, such as the composition and arrangement of habitat types on the landscape, influences male flight, mating success, and spread. In a series of field experiments involving the release of laboratory-reared adult male *L. dispar*, Walter et al. (2016) found that male moths dispersed similar distances in search of mates in forested versus open field habitats but were unlikely to cross forest edges into open fields, at least in the absence of a pheromone cue from the open field. Relatedly, in an experiment where “calling” females were present in both the field and the forest, Thompson et al. (2016) observed higher mating success just inside forest edges, which could be explained by directionally unbiased mate-searching movements combined with resistance to leaving forest patches. Anecdotal evidence suggests that adult male *L. dispar* moths are visually attracted to dark colors,<sup>1</sup> which could be the mechanism behind the observed behavioral preference for forest habitats. A biologically detailed model simulating *L. dispar* spread used by Walter et al. (2016) showed that the proportion of forest in the landscape and the degree to which the forest was connected across the landscape strongly influenced the strength of Allee effects and the rate of spread through that landscape. Less connected forest meant stronger Allee effects and slower spread. Simulation results were consistent with historical patterns of spread in Virginia and West Virginia, but the model also indicated that the most important cause of this effect was that larvae dispersing into unforested areas perished.

While strong Allee effects due to mating failure fundamentally shape *L. dispar* spread and management, the tendency for populations subject to strong Allee effects to decline

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<sup>1</sup> Unpublished observation, Kyle Haynes, University of Virginia, 2019.

to extinction, provided they are below the Allee threshold, assumes that immigration is absent or minimal. While this assumption seems to hold more often than not, especially for isolated nascent populations targeted by STS, there are exceptions. Although larvae typically disperse between 10 and a few hundred of meters from the hatch site (Mason and McManus 1981), and adult males disperse similar distances (Robinet et al. 2008, Walter et al. 2016), specific meteorological conditions can result in a “blow-in” of male moths from established, higher-density areas to newly colonized areas, providing an influx of immigrants that facilitates population establishment and growth (Fig. 2) (Tobin and Blackburn 2008). Although the direction of spread is largely opposite that of prevailing winds, there is evidence that the rapid invasion by *L. dispar* of eastern Wisconsin was facilitated by storm events blowing east to west, across Lake Michigan (Frank et al. 2013). Similar long-distance, blow-in events are generally thought to be less common in other regions, but their true prevalence is unknown.



**Figure 2.**—Patterns of male *L. dispar* moth trap catch (interpolated trap catch density) suggestive of a blow-in event in the North Carolina piedmont. Note the rapid expansion of populations with very low average trap catch densities that are distributed relatively evenly and randomly over a large area in 2007 (B) compared to 2006 (A). Dark blue lines indicate the projected bounds of the STS action area in 2006.

It has also been shown that a pattern of pulsed (intermittent) advance and retreat of the *L. dispar* range boundary is related to population outbreaks (Fig. 3) (Johnson et al. 2006, Walter et al. 2015). A study focusing on spread in Virginia and West Virginia found pulsed advances of the *L. dispar* range boundary in years following outbreaks taking place up to 100 km (approximately 60 miles) behind the range boundary (Walter et al. 2015). That invasion pulses tended to lag outbreaks by a year suggests that egg masses were transported inadvertently by humans from outbreaking populations to the invasion front, where adult males arising from them were detected the following year. If invasion-front populations experienced an influx of larval or adult life stages during outbreaks, then the invasion pulse should be detected in the same year as the outbreak. Regardless of the manner in which immigrants arrive—whether blown in on storms or by accidental human transport—these inputs of immigrant moths to local, nascent populations raise local population densities, increase mating success, and enable populations to exceed the Allee threshold, become established, and facilitate further spread.

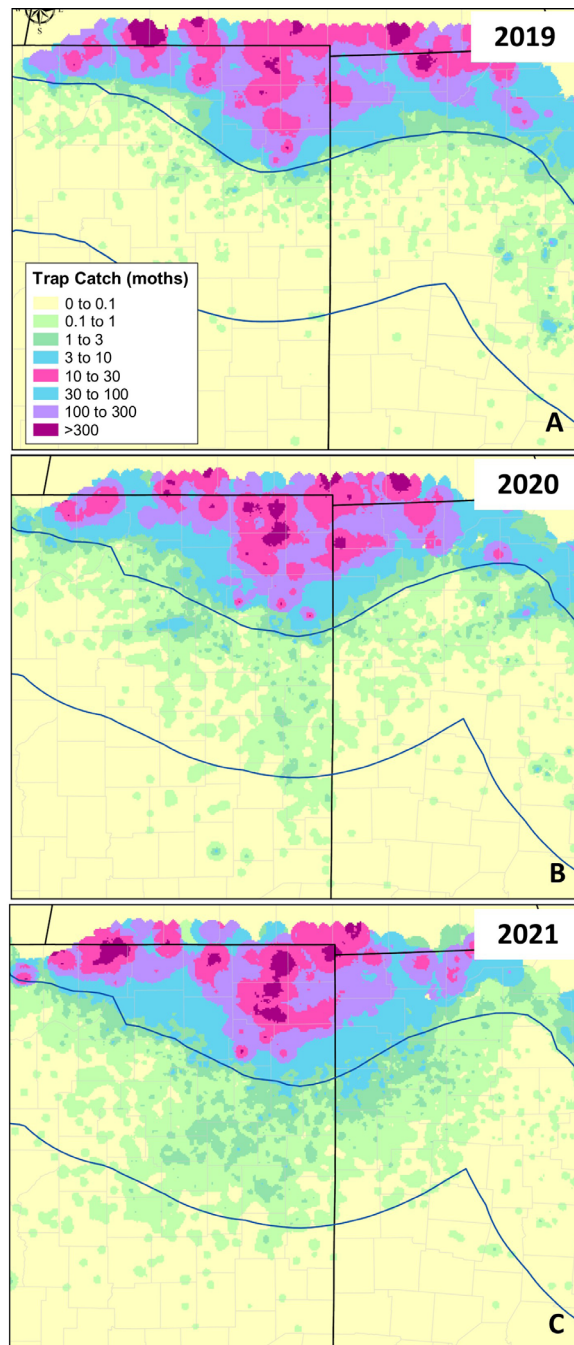
## **GEOGRAPHICAL VARIATION IN CLIMATE AFFECTS *LYMANTRIA DISPAR* SPREAD**

Across the range boundary, from North Carolina to Minnesota, rates of *L. dispar* spread vary widely on regional scales (Grayson and Johnson 2018; Tobin et al. 2007a, 2007b) and finer scales (Grayson and Johnson 2018; Walter et al. 2015, 2016). Climatic differences are one of the major drivers of spread rate variation, even at relatively fine spatial scales. It has long been known that temperature is an important factor shaping whether *L. dispar* can persist in an area (Gray 2004, Nunez-Mir et al. 2022, Sharov et al. 1999); however, some recent spread patterns have accorded poorly with earlier predictions and led to new insights into how climate shapes *L. dispar* spread.

At the southwestern edge of the expanding range front, spread appears to have slowed or stopped as a result of high summer temperatures. Tobin et al. (2014) documented range retractions in the coastal plain ecoregion of eastern Virginia and North Carolina and associated these retractions with “supraoptimal” hot temperatures, that is, those that exceed optima for growth and development. A dedicated program of research subsequently determined the likely physiological basis for this pattern, finding that extreme warm temperatures reduce egg viability, impair larval development, and lead to mortality. It has been shown for traits associated with tolerance to hot temperatures that *L. dispar* has adapted to local climate conditions, such that life stages originating from places that commonly experience hot temperatures are more tolerant of them (Banahene et al. 2018; Faske et al. 2019; Thompson et al. 2017, 2021).

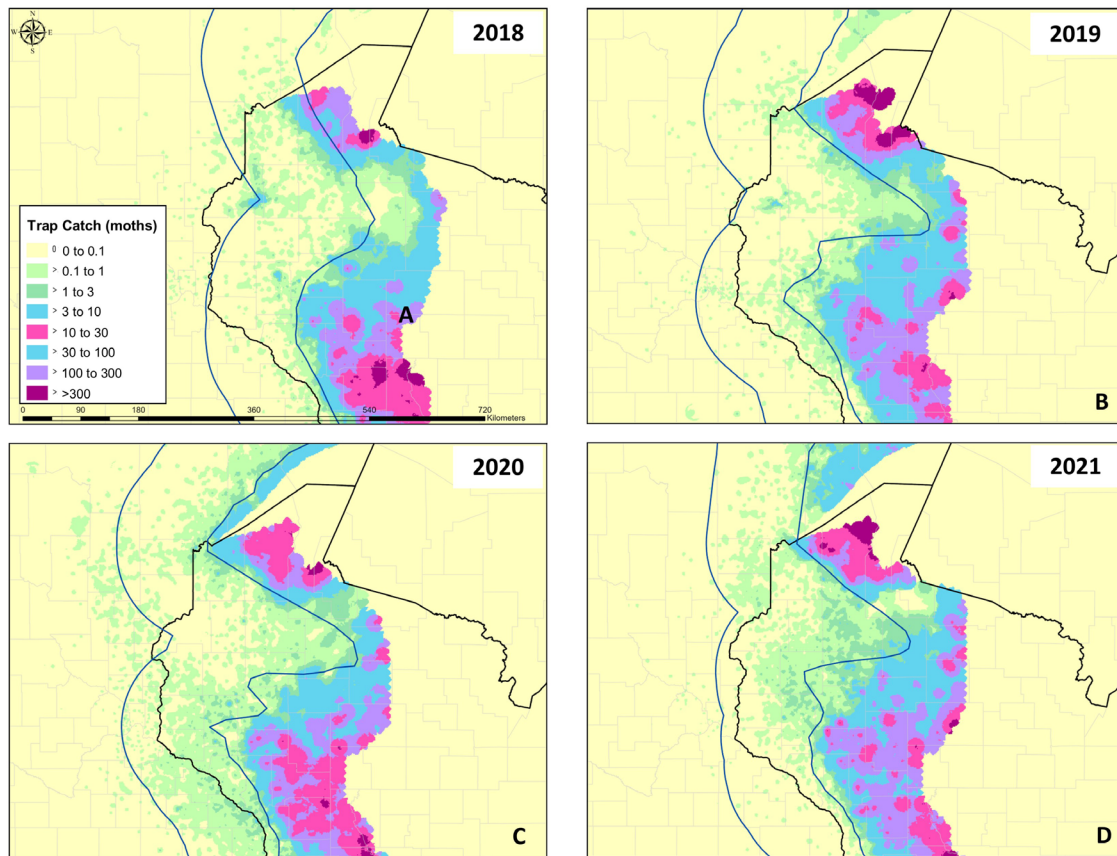
At the other end of the range, *L. dispar* has expanded its northwestern range into areas predicted to have low climatic suitability due to cold temperatures (Fig. 4). One contributing factor may be the role of snowpack in insulating egg masses from extreme cold air temperatures (Streifel et al. 2019), but further research is needed to examine this and other mechanisms that potentially allow *L. dispar* to persist in areas previously thought to be too cold, whether due to lethal extreme cold temperatures or insufficient warmth to complete development. Tests of geographic variability in tolerance to cold temperatures are forthcoming (Hafker et al. 2021). Adaptation of *L. dispar* to local climates will be discussed further in the next section.





**Figure 3.**— The *L. dispar* invasion front can surge forward, creating a pulsed invasion dynamic, particularly when populations in established areas behind the invasion front are high and there is substantial defoliation. Low-density populations surged forward between 2019 (A) and 2020 (B), and in 2021 (C) were largely persistent and had expanded somewhat from their 2020 distribution in Indiana and Ohio. Dark blue lines indicate the projected bounds of the STS action area.





**Figure 4.**— Models of *L. dispar* development (Gray et al. 2004) predict low climatic suitability for *L. dispar* in northernmost Wisconsin and the arrowhead region of Minnesota, but from 2019 to 2021 (A, B, C, and D), populations became established and reached high densities in these areas. Dark blue lines indicate the projected bounds of the STS action area.

More subtly, temperature also influences the degree of reproductive asynchrony in a population. Walter et al. (2015) found that temperature creates different levels of reproductive asynchrony and mating success across broad climatic zones encompassed by the invasion front as well as locally with changes in elevation. In colder climates, the interval between the emergence of adult males and adult females (i.e., protandry) is longer, and the distribution of maturation dates for each sex is broader. In other words, the effective population density is smaller because as a population's reproductive maturation extends over a longer period and *L. dispar* also perish, a smaller fraction of the total population is reproductively mature at any given time. This strengthens Allee effects and slows population growth and spread. Although subtler than regional differences in reproductive asynchrony, the authors found that effects of climate on reproductive asynchrony and mating success are substantial enough that populations at different elevations can experience differences in mating success, and populations in areas of high topographic variability may have reduced mating success due to increased reproductive asynchrony.

## GENETIC ADAPTATION OF INVADING *LYMANTRIA DISPAR* POPULATIONS

Changes in the genetic composition during the spread phase is a phenomenon observed in many different invading species (Baker and Stebbins 1965, Keller and Taylor 2008). These changes may result from stochastic effects (e.g., founder effects), selection unique to the establishment of populations at the invasion front, or long-term selection acting upon established populations. Despite the enormous economic importance of *L. dispar* and its presence in North America for more than 150 years, relatively little is known about genetic changes that have occurred during its invasion. Part of the reason for this lack of evidence of genetic changes during the *L. dispar* invasion of North America is the general lack of genetic variation within the North American population, presumably a result of a genetic bottleneck occurring during initial establishment (Wu et al. 2015).

Recently, Friedline et al. (2019) investigated genetic variation as a result of divergent selection. The authors compared phenotypic and genetic variation among six North American populations with varying dates of initial invasion. Among phenotypic traits tested, geographical variation in larval developmental time was strongest, with relatively little variation found in either pupal mass or pupal duration. The authors also made genome-wide analyses (based on single nucleotide polymorphisms, or SNPs) to investigate the genetic basis for each trait and to search for evidence of selection on those genes. Evidence indicated a polygenic architecture for each trait. Similar to other studies, the authors found low levels of genetic structure across the North American range as well as evidence of bottlenecks occurring during historical range expansion. They also found evidence of historical divergent natural selection on larval developmental time and pupal mass with strongest signals of such selection present in relatively new populations at the range margin. The authors conclude that local adaptation has contributed to the ability of *L. dispar* to spread and establish in new regions of North America that differ in climate and other environmental characteristics. However, the question of how such adaptation has affected rates of spread and how this adaptation might affect the success of the STS Program remains an open question.

As described in the preceding section, *L. dispar* has encountered highly divergent climatic conditions as it has expanded its North American range, and there is ample evidence that this climatic variation has translated into variable rates of spread across the range. A good example of this effect is seen in the markedly slower rate of spread (i.e., zero spread or retraction) in the coastal plain of Virginia (Tobin et al. 2014). Fasje et al. (2019) conducted transplant experiments using insects collected both inside and outside of this region, which were reared simultaneously inside and outside of the same regions. Similarly, Thompson et al. (2017) simulated transplant experiments by rearing populations sourced in different regions under different temperature regimes. Fasje et al. (2019) found that all populations exhibited lower fitness when reared in the coastal plain, supporting the hypothesis that climatic conditions in the coastal plain adversely affect *L. dispar* performance and spread. Thompson et al. (2017) found that northern populations exhibited greater larval mortality and that eggs collected from populations in the coastal plain region survived at higher rates than other populations when reared in the coastal plain climate. These results provide more evidence for local adaptation of *L. dispar* to climatic extremes that they encounter as they expand their range.

## AREAS OF FUTURE RESEARCH

Even though the invasion of *L. dispar* is better understood than that of most non-native species, many aspects remain unclear. Improved understanding of spread holds potential for increasing the effectiveness and cost efficiency of the STS Program.

The STS DA currently applies criteria for decision-making that are largely constant across the entire action area (i.e., the *L. dispar* transition zone). However, environmental factors such as climate, forest composition, and human activities vary across the invasion front and likely influence local *L. dispar* reproduction and spread, and how they do so is not completely understood. Deeper knowledge of these influences could potentially be used to prioritize trapping and treatments in certain areas, which could potentially lead to cost savings and increased effectiveness of the STS Program.

A largely unknown aspect of *L. dispar* spread is the role of natural enemies (predators, parasitoids, and pathogens) in influencing patterns of spread. Results from one study (Hajek and Tobin 2011) indicated that the pathogens *L. dispar* nucleopolyhedrovirus (LdNPV) and *Entomophaga maimaiga* Humber, Shimazu, and R.S. Soper (Entomophthorales: Entomophthoraceae), as well as the parasitoid *Compsilura concinnata* Meigen (Diptera: Tachnidae) are present in populations near the expanding *L. dispar* population front. However, it is not clear how these agents are affecting host populations and ultimately how these effects are influencing rates of spread. Less is known about how populations are affected directly after initial colonization; unfortunately, low population densities preclude meaningful sampling of larval populations that exist at the time of initial colonization. Even less is known about the effects of predators on spread. Studies within the generally infested area indicate that predation by small mammals is the largest source of mortality in low-density populations, yet almost nothing is known about impacts of predators on spread. Predator population densities are known to vary considerably among different forest types, and this variation potentially could influence spread rates. Knowledge of geographical predator variation could potentially be incorporated into the STS DA.

Even though the STS Program is designed to find and suppress isolated populations ahead of the expanding population front, little information exists about the principal pathways responsible for the founding of these isolated populations. In one study, Bigsby et al. (2011) examined statistical correlates of the presence of isolated *L. dispar* populations for counties falling in the transition zone. They found that the use of wood for home heating was positively correlated with the occurrence of new isolated populations, suggesting that accidental movement of life stages (e.g., egg masses) with firewood is a likely invasion pathway that facilitates local spread. Other studies of *L. dispar* establishment in more distant uninfested areas (e.g., California) indicate the importance of accidental transport of life stages with household moves as a key invasion pathway (McFadden and McManus 1991). A refined understanding of important invasion pathways in the transition area as well as identification of mitigative procedures could ultimately lead to greater effectiveness of the STS Program, in particular the regulatory component.

The STS Program relies on the use of pheromone-baited traps to locate isolated colonies that are targeted for treatment. In most cases, this approach works well; however, data show that in certain areas and in certain years, large numbers of adult males disperse long distances from outbreak areas into STS trapping grids, and their presence in the

grids may obscure the presence of locally reproducing isolated populations. Evidence for this phenomenon can be found in reports of captures of males in STS trapping grids during times other than the seasonal period of locally developing adult males (Régnière and Sharov 1998, Tobin et al. 2009). Unfortunately, the phenomenon of mass migration by *L. dispar* males is poorly understood, although one study (Frank et al. 2013) found that such long-distance transport events may be associated with specific meteorological conditions. More work that clarifies the identity of these conditions and explains why the phenomenon is more common in certain regions would be useful. In addition to obscuring the detection of isolated populations in trapping grids, these mass dispersal events may strongly influence *L. dispar* spread. Considerable evidence indicates that *L. dispar* spread is limited by the failure of males to find females for mating at low densities; however, dispersal of large numbers of males into distal portions of the transition area may greatly elevate mating success in these areas and cause increases in spread rate. More work is needed to clarify this situation.

Predictions of *L. dispar* phenology (i.e., the timing of insect development) are used for various purposes in the STS Program. For example, the timing of trap placement and recovery as well as the timing of mating disruption treatments are all based on predictions of the timing of the *L. dispar* adult developmental periods. This information comes from *L. dispar* phenology models that are linked with raster climatic data in the BioSim model (Régnière et al. 2014). This approach is quite effective, although evidence suggests that phenology predictions are less accurate in more northerly portions of the STS action area. Thus, there is a continuing need to improve phenology models for use across a diversity of climatic conditions. Furthermore, incorporation of information about local adaptation of *L. dispar* populations to climate (Faske et al. 2019, Thompson et al. 2017) may also contribute to more accurate phenology predictions.

Since the beginning of the STS Pilot Project and through the operational program to the present, the STS DA has been continually modified. The initial decision algorithm was very simple, and most aspects of decisions were made based on visual assessment of trap data. Over time, refinements of the algorithm have improved its capacity to better mimic these assessments, thereby reducing subjectivity and increasing consistency. However, aside from the initial selection of the width of the action area (Sharov and Liebhold 1998), none of the refinements of the STS DA have been made based on evidence that they will increase the effectiveness of the program. This is because it has not been possible to test the efficacy of modifications relative to a counterfactual. To make such comparisons, there would be value in the development of a very realistic model of *L. dispar* spread that incorporates treatment impacts. Such a model would likely have to be spatially explicit and account for the stochastic nature of *L. dispar* spread dynamics. With such a model in hand, it would be possible to test various modifications to the STS DA and optimize its performance.

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