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Novel insights on population and range edge dynamics using an unparalleled spatiotemporal record of species invasion

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Running headline: Range edge dynamics in gypsy moth

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Summary

1. Quantifying the complex spatial dynamics taking place at range edges is critical for understanding future distributions of species, yet very few systems have sufficient data or the spatial resolution to empirically test these dynamics. This paper reviews how data from a large-scale pest management program have provided important contributions to the fields of population dynamics and invasion biology.
2. The invasion of gypsy moth (*Lymantria dispar*) is well-documented from its introduction near Boston, Massachusetts USA in 1869 to its current extent of over 900,000 km^2 in Eastern North America. Over the past two decades, the USDA Forest Service Slow the Spread (STS) program for managing the future spread of gypsy moth has produced unrivaled spatiotemporal data across the invasion front.
3. The STS program annually deploys a grid of 60,000 – 100,000 pheromone-baited traps, currently extending from Minnesota to North Carolina. The data from this program has provided the foundation for investigations of complex population dynamics and the ability to examine ecological hypotheses previously untestable outside of theoretical venues, particularly regarding invasive spread and Allee effects.
4. This system provides empirical data on the importance of long-distance dispersal and time lags on population establishment and spatial spread. Studies showing high rates of spatiotemporal variation of the range edge, from rapid spread to border stasis and even retraction, highlight future opportunities to test mechanisms that influence both invasive and native species ranges.
5. The STS trap data have also created a unique opportunity to study low-density population dynamics and quantify Allee effects with empirical data. Notable contributions include evidence for spatiotemporal variation in Allee effects, demonstrating empirical links between Allee effects and spatial spread, and testing

mechanisms of population persistence and growth rates at range edges.

6. There remain several outstanding questions in spatial ecology and population biology that can be tested within this system, such as the scaling of local ecological processes to large-scale dynamics across landscapes. The gypsy moth is an ideal model of how important ecological questions can be answered by thinking more broadly about monitoring data.

Key-words: Allee effects, biological invasions, gypsy moth, *Lymantria dispar*, invasion front, invasive species management, low-density population dynamics, range border, spread rate

Introduction

A fundamental goal in the field of ecology is to understand how intrinsic and extrinsic factors interact to shape the size and limits of the geographic range of a species (MacArthur 1972; Brown 1995; Gaston 2003). Studies on the dynamics of borders are currently at the forefront of ecology due to increased concern about the impacts of global change on the distributions of native and non-native species (Holt & Keitt 2005; Sexton *et al*. 2009). Changes in climate and human land use patterns can alter species' distributions by opening new habitats to expansion or imposing environmental barriers that result in range retraction (Mooney & Hobbs 2000). Shifts in a species range can promote hybridization, influence community interactions, and alter ecosystem structure (Garroway *et al*. 2010; Van der Putten 2012). A multitude of factors can shape the edge of a species range, including species interactions (Holt *et al*. 2011), resource limitation (Case & Taper 2000), the physical environment (Crozier & Dwyer 2006), and dispersal limitation (Goldberg & Lande 2007).

Population dynamics at range edges ultimately determine whether a distribution is expanding, stable, or contracting. Mechanisms operating in range edge populations differ from those within the interior for several reasons. Populations at range edges often face environmental extremes that can impose physiological limits and impact population growth (Sexton *et al*. 2009). Edge populations are often at lower densities than those in the established range (Brown 1984); thus, their dynamics can be particularly susceptible to demographic stochasticity (Snyder 2003). Moreover, factors that influence population growth can operate differently across the range of a species, which may be reflected in important differences between a range edge and the established range (Sagarin, Gaines & Gaylord 2006). For example, if cues for dispersal behavior are altered at range margins, the fitness consequences of dispersal may be enhanced from a lack of competition or reduced from a lack of conspecifics beyond the range edge (Elliott & Evenden 2012). Finally, genetic structure and diversity can differ at range edges compared to the established range, often with populations experiencing reduced diversity when population sizes are small (Lee 2002; Klopfstein, Currat & Excoffier 2006). For all of these reasons, the edges of species distributions can have unique dynamics that ultimately determine the process of range shifts in current and future environments.

Many formative hypotheses concerning geographic range limits have been proposed (e.g., Caughley *et al.* 1988; Hochberg & Ives 1999; Gaston 2003). Key processes that have proposed to constrain the distribution of species include resource availability, physiological tolerances, interspecific interactions, dispersal ability, genetic isolation, and depressed growth rates in low abundance populations at range edges. Despite notable empirical studies that have provided insight into mechanisms that influence species borders (e.g., Meier *et al*. 2012; Pichancourt & van Klinken 2012; Pigot, Owens & Orme 2010), we still lack systems that provide comprehensive data on population dynamics at a range edge (Gaston 2009). The paucity of empirical data results from the very nature of range edges being highly dynamic, difficult to quantify over large scales, and often comprised of low-density populations that are hard to detect. A rapidly developing field that can provide data to address these deficiencies is the study of invasive species, which have much to offer as empirical systems for testing predictions from theoretical work on the spatial dynamics of populations and changes in species distributions (Sakai *et al.* 2001; Elith, Kearney & Phillips 2010).

This paper synthesizes research on the gypsy moth (*Lymantria dispar*) invasion front in North America and its contribution to a conceptual understanding of the processes that govern range edge dynamics. In particular, we highlight the prominent role that an unparalleled dataset generated by the gypsy moth Slow the Spread (STS) program has played in testing and advancing ecological theory. The STS data set is characterized by two decades of population abundance measures along the gypsy moth invasion front from Minnesota to North Carolina. We detail how the geographic and temporal extent of the data set combined with the local scale quantification of population dynamics has provided a useful framework for identifying cross-scale links between local population processes, dispersal, and range edge dynamics. We describe the detailed spatiotemporal patterns of invasion revealed by this system and its contributions to testing theoretical models of spatial spread. Specifically, data from the gypsy moth range edge have provided empirical evidence for models of multi-scale dispersal processes and demonstrated the role of population establishment and time lags in spatial spread. The quantification of fine-scale spatiotemporal variation in spread rates has illustrated the dynamic nature of range edges, revealing patterns of expansion and contraction, and provides promising directions for future studies. Finally, we describe the contributions of the STS data to understanding the demographic processes that govern low-density populations. In particular, we highlight the role of gypsy moth data in providing empirical tests of Allee effect theory. This body of work has provided critical insights into the dynamics of a widespread and highly destructive invasive species, while also serving as an important case study for the field of invasion ecology. These contributions have tested fundamental ecological concepts at scales where we often lack detailed empirical data.

Gypsy moth biology and the North American invasion

The gypsy moth in North America is arguably one of the best-documented biological invasions in the world. Since its introduction in 1869, the range of gypsy moth has expanded to encompass over 900,000 km^2 in Eastern North America across divergent climates and forest types (Tobin *et al*. 2012). Gypsy moth is a generalist feeder of broad-leafed trees, with aspen, birch, oak, and willow topping a list of over 300 potential host species (Liebhold *et al.* 1995). The life cycle is univoltine; larvae hatch in spring, and adults emerge in summer to mate and lay eggs, which overwinter in an obligate diapause (Gray, Ravlin & Braine 2001). In North America, gypsy moth females are flightless, consistent with Western European populations (Wu *et al*. 2015), and release a pheromone to attract flying males (Doane & McManus 1981). Natural dispersal occurs over relatively short distances driven by larval ballooning and male flight. Both processes are influenced largely by prevailing wind patterns and topographic features (Mason & McManus 1981). Inadvertent transportation of egg masses by humans is thought to be the dominant mode of long-distance dispersal and can result in satellite populations establishing beyond the invasion front (Liebhold & Tobin 2006). Established gypsy moth populations are characterized by dramatic changes in population density, where populations can synchronously increase to outbreak levels. This results in large-scale defoliation, which can cause extensive ecological and economic damage (Elkinton & Liebhold 1990; Williams & Liebhold 1995). Defoliation records have provided nearly a century of data on the outbreak dynamics of gypsy moth, where the degree of damage to the forest canopy each year provides a spatiotemporal series of the extent and magnitude of gypsy moth populations. These data have enabled a substantial body of work on the dynamics of periodic cycles (e.g., Johnson, Liebhold & Bjørnstad 2006) and population synchrony in insect outbreaks (e.g., Peltonen *et al*. 2002; Johnson *et al.* 2005; Haynes *et al*. 2013).

Unlike many invasions, the native source, as well as the year and location of primary introduction, are known for the gypsy moth in North America. The invasion can be traced back to the residence of Étienne Léopold Trouvelot, an artist and amateur entomologist interested in silk production. It is believed that he brought gypsy moth egg masses from his native France to his home in Medford, MA where individuals escaped around 1869 (Riley & Vasey 1870). Despite considerable effort, eradication during the early stage of the invasion failed as did subsequent barrier zones to prevent further spread (McManus 2007). While subsequent introductions may have occurred after the initial colonization, genetic analyses point to the Medford population as the origin of the main North American invasion (Bogdanowicz *et al*. 1997; Wu *et al*. 2015).

Since its initial establishment, the gypsy moth has spread slowly across the landscape. Its range currently comprises the entirety of the Northeastern United States into Canada (Régnière, Nealis & Porter 2009) and extends into the Mid-Atlantic and Midwestern United States (Fig. 1). Detections over the last decade have resulted in new populations as far west as the arrowhead region of Minnesota (Tobin *et al*. 2016). Research on gypsy moth outbreaks and how to contain future spread has resulted in a vast body of work on gypsy moth life history, natural enemies, interspecific interactions, and methods of detection and control (Doane & McManus 1981). Despite the vast area of Eastern North America currently infested with gypsy moth, this range represents less than one-third of the susceptible habitat in the United States (McFadden & McManus 1991; Morin *et al*. 2004). Large areas of economically and environmentally important forests in the Southern Appalachian Mountains, Ozark Mountains, Northern Minnesota, and Northwestern US are at risk from further spread of the gypsy moth (Liebhold *et al*. 1997). In addition, increases in temperature under future changes in climate are predicted to increase the total North American range size (Gray 2004). Unabated spread of gypsy moth and the economic costs associated with increasing forest damage and management in the 1980s led to the implementation of the STS program as the lead initiative for invasion front management (Sharov *et al*. 2002; Roberts & Ziegler 2007). This program provided a coordinated effort between the USDA Forest Service and state governments along the gypsy moth invasion front to reduce the spread of gypsy moth from the established range into uninfested areas. At the same time as these management goals have been achieved, the STS program has resulted in one of the most extensive and detailed spatiotemporal records of a species border ever attempted.

Slow the Spread: Unparalleled detail at the invasion front

It has long been understood that complete eradication of gypsy moth from North America is infeasible. Similarly, as failure of early barrier zones illustrated, complete containment of gypsy moth spread is also highly unlikely (Sharov *et al*. 2002). However, given the susceptibility of the next tier of states in advance of the invasion front in the 1990s, where 50 - 80% of forested land was classified as highly at risk (Morin *et al*. 2004), it was recognized that slowing the spread was not only economically viable, but highly beneficial (McManus 2007). Several assessments have shown a positive benefit to cost ratio of delaying the spread of gypsy moth and reducing costs related to pest management that will substantially increase as the amount of infested forest acreage increases (e.g., Leuschner *et al*. 1996; Tobin 2008). Based on strategies and detection techniques in earlier programs, such as the Appalachian Integrated Pest Management Program from 1988 - 1992, the STS program was piloted from 1993 - 1998 and integrated with the national strategy for managing gypsy moth in 1999 (McManus 2007).

The management objective of the STS program is to reduce spread rates of gypsy moth through monitoring and local suppression of isolated populations beyond the advancing front. Monitoring is achieved by annually trapping males using delta or milk carton style traps that are baited with disparlure, the synthetic version of the gypsy moth pheromone, and deploying the traps in an extensive spatially referenced grid both along and ahead of the invasion front (Sharov *et al*. 2002). The trapping program focuses on the ‘transition zone’ between the generally infested area, where populations are established, and the uninfested area (Liebhold, Sharov & Tobin 2007; Fig. 2). Between 60,000 - 100,000 georeferenced traps are annually deployed in a 100 - 170 km band proximal to the generally infested area across the entire gypsy moth invasion front in the United States (Fig. 2A). Trap catches provide quantitative counts of adult males and are highly effective at detecting low-density populations (Tobin *et al*. 2007). The trapping area currently spans from Minnesota to North Carolina, where traps are deployed at 2 - 8 km intervals to provide robust annual measurements of abundance across the range margin (Roberts & Ziegler 2007). Trap density is lower adjacent to the established range (the northern and eastern portion of the trapping band) and increases to the south and west of the trapping band to improve detection of low-density populations and monitor uninfested areas. The nature of trapping a moving band, where specific trap locations vary year to year and variation in trap density (both by design and through fluctuations in state and federal budgets), requires interpolating gypsy moth abundance to compare trap catch data across years and measure spread rates. Median indicator kriging, an estimation method for interpolation based on the geospatial relationships among measured points, is used to generate a continuous surface of male gypsy moth abundance from the trapping data each year (Isaaks & Srivastava 1988; Fig. 2B,C).

Analyses using gypsy moth data demonstrate successful approaches to the methodological challenges of demarcating a range boundary and its dynamics. The transition zone at a range edge is rarely an abrupt transition, but instead is often characterized by a noisy gradient from a contiguous population to increasingly fragmented populations at lower densities. Thus, a clear definition of the population boundary is critical. Multiple methods were considered in the establishment of a standard metric for estimating gypsy moth population boundaries (Sharov et al. 1995; Sharov, Liebhold & Roberts 1996b; Sharov, Liebhold & Roberts 1997). From the abundance surface, the locations of population boundaries are delineated where spatially interpolated captures average 1, 3, 10, 30, 100, and 300 male moths per trap. Annual rates of gypsy moth spread are estimated by measuring the spatial displacement of these population boundaries in successive years (Sharov, Liebhold & Roberts 1997). Prior to the STS program, historic rates of gypsy moth spread were reconstructed from county-level presence/absence data from quarantine records (Liebhold, Halverson & Elmes 1992), which provide relative congruence with trapping data for broad estimates of spread (i.e., regional estimates of mean annual spread rate; Tobin, Liebhold & Roberts 2007). This similarity is encouraging for systems with coarser scale occurrence or survey data, where more detailed information is unfeasible. The level of detailed information from the STS program on the spatial and temporal variability in spread, as well as population abundance, generates unrivaled and unique opportunities for scientific inquiry along a dynamic range edge.

The abundance data are used to optimize the application of management interventions through a decision algorithm that objectively identifies areas ahead of the invasion front with elevated moth counts (Sharov & Liebhold 1998; Tobin *et al*. 2004; Tobin & Sharov 2007). Potential problem areas are identified based on trap catches that greatly exceed the average abundance in a 40 km × 40 km area, both for the current and previous year. These areas are then prioritized based on distance from the established range edge and moth abundance in the surrounding area. The usual course of action for priority areas includes finer-scale trapping to more precisely delimit the spatial extent of an isolated colony, followed by treatment with disparlure to cause mating disruption or application of a biological insecticide (*Bacillus thuringiensis kurstaki* or *Btk*; Tobin *et al*. 2013). The goal of management actions in areas prioritized by the decision algorithm is preventing colonies ahead of the invasion front from growing and reducing their contribution to range expansion. Across the transition zone area of over 340,000 km^2, these intensive trapping areas and interventions represent less than 2% of the monitoring area (Tobin *et al*. 2007). Despite treating a relatively small area, the STS program has reduced gypsy moth spread by at least 60% (Slow the Spread Foundation, 2016) relative to a historical average estimated at 21 km/yr from 1966 – 1989 (Liebhold, Halverson & Elmes 1992). Over the 17-year period from 2000 – 2016 spread rate averaged 4.0 km/yr, a rate that prevents infestation of more than 150 million acres over the next 20 years (Slow the Spread Foundation 2016).

The success of the STS program, with the invasion experiencing an overall reduction in spread rate and populations in treated areas experiencing reduced growth or local extirpation, raises a valid concern about using this data to generate and test ecological theory. However, as these areas are georeferenced and occur over a relatively minimal area, data from treated populations can be excluded or specifically included based on the research question. For example, studies that use data on changes in abundance over time can easily institute a buffer around treated areas and exclude these when testing processes that impact local population dynamics. Alternatively, the analysis of areas trapped at a finer resolution in subsequent years (delimiting surveys) has proved a useful tool for testing ecological theories related to time lags, the population dynamics of early invasion stages, and space–time properties of emerging invasions (Tobin 2007; Tobin *et al*. 2013). Using an objective decision algorithm means that STS treatments are generally consistently applied across the invasion front and natural spatiotemporal variation in spread rates is still apparent across the range (see Fig. 3). Furthermore, populations in the transition zone proximal to the established range are not treated, as limited resources are prioritized for isolated colonies identified at the distal edge the invasion front, and mechanisms that influence natural spread operate undisturbed from the contiguous range in this area. While the invasion is substantially slower due to the reduction in satellite populations established through long-distance dispersal, this has not obscured dynamic patterns in the range edge nor the relative relationships between landscape variables and spatial spread. In comparison to spread information for other invasive species, where smaller-scale monitoring or county-level occurrence data are typically available, the application of a detailed trapping grid over the extensive landscape of the gypsy moth invasion front has provided much greater resolution for characterizing extent, shape, and abundance along a dynamic range border (Tobin, Liebhold & Roberts 2007).

Contributions to understanding spatial spread

Understanding changes in species distributions requires accurate models that describe the dynamics of dispersal and spread (Shigesada & Kawasaki 1997). Measuring changes in range extent are complicated by the need to confirm both the presence and absence of a species, as well as detecting rare long-distance dispersal events. The STS gypsy moth data provides one of the most compelling systems to study spatial spread and dispersal due to the trapping band extending so far ahead of the edge of the established range (Fig. 2; Sharov & Liebhold 1998). Early reaction-diffusion models assume random walk movement with a diffusion parameter (*d*) for dispersal and the intrinsic rate of increase (*r*) for population growth to describe spatial spread in non-native species (Skellam 1951). When these two parameters are constant, predictions of border expansion occur at a constant speed (C) where $C = 2\sqrt{rd}$ in a homogenous environment. However, the assumption of random walk movement is unrealistic for many systems, as spread is often complicated by long-distance dispersal events and cryptic life stages. It has been demonstrated using theoretical models that temporal variation in these parameters can accelerate spread rates (Ellner & Schreiber 2012). One of the greatest theoretical advances in modeling spatial spread is the incorporation of long-distance dispersal (Kot, Lewis & van den Driessche 1996), while one of the most significant barriers in the field is the empirical estimation of these low frequency events (Hastings *et al.* 2005). Even though long-distance dispersal events are usually quite rare compared to local-scale movements, they can be the most important determinants of invasion rates (Shigesada, Kawasaki & Takeda 1995). In the case of gypsy moth, simple reaction-diffusion models parameterized with field data on natural dispersal generally predict spread rates of approximately 2.5 km/yr, which is far less than observed rates (Liebhold, Halverson & Elmes 1992; Tobin, Liebhold & Roberts 2007). This difference has been linked to stratified dispersal, which is the coupling of local population expansion with long-distance dispersal events. Long-distance dispersal events in gypsy moth typically occur through human transportation, resulting in populations popping up well in advance of the range edge, persisting, coalescing, and contributing to increased spread (Sharov & Liebhold 1998). Inadvertent anthropogenic transportation is well-known to play a large role in the introduction of invasive species (e.g., Floerl & Inglis 2005) and the gypsy moth system provides a clear example where this process continues to contribute to spatial spread.

Research to understand the dynamics of spatial spread and the role of multiple dispersal processes in gypsy moth also made important contributions to statistical methods for measuring spread rates and invasion (Sharov & Liebhold 1998; Sharov, Liebhold &

Roberts 1998; Lewis, Petrovskii & Potts 2016; Tisseuil *et al*. 2016). Initial evidence to identify the important role of isolated colonies in gypsy moth range expansion was provided by the spatial aggregation and autocorrelation of elevated trap capture in transition zone traps (Sharov, Liebhold & Roberts 1996a). Further investigation into the dynamics of these locations resulted in the estimation of colony formation rate and the ability to quantify the contribution of isolated colonies to spatial spread beyond simple dispersal in Skellam's model. Sharov & Liebhold (1998) applied a coalescing colony model to the gypsy moth invasion front, with the novel addition of simulated variation in colony formation distance. While this model was motivated by testing the effectiveness of various barrier zone management strategies, it provided a formal framework for including stratified diffusion into spatial spread models (Liebhold, Sharov & Tobin 2007; Gilbert and Liebhold 2010). These foundational methods have been applied in a wide range of studies on dispersal and invasive species spread (e.g., Gilbert *et al*. 2004; Taylor & Hastings 2004; Gosper, Stansbury & Vivian-Smith 2005; Robinet, Suppo & Darrouzet 2017). For example, Gilbert *et al*. (2004) demonstrate the utility of applying stochastic stratified dispersal models to account for two-scale dispersal processes in spatial spread data.

Another benefit of the STS data is the ability to monitor the fate of newly established populations. During the early stages of the invasion process, time lags in population growth are often observed and these effects are important components of models predicting spatial spread (Sakai *et al*. 2001). While several theories have been proposed to explain the role of time lags in the growth and expansion of founding populations, the STS data are unique in their ability to test these hypotheses by providing a large-scale matrix for detecting newly established populations and following their fate over time. Liebhold & Tobin (2006) used historical data to estimate the time lag associated between initial introduction and detectable spread. They then used STS trap catch data to measure annual radial expansion of isolated colonies well ahead of the invasion front where eradication treatments were not applied. Their analyses showed that time lags can be substantially longer than predicted by simple reaction-diffusion models and the inclusion of stochasticity in population growth rates is important for explaining the expansion or decline of an isolated, newly established population. While variation in invasion rates is often perceived to be a function of varying diffusion rates, an analysis of the STS trap catch data revealed that gypsy moth spread rates are at least partially affected by the variation in local extinction probability of isolated nascent populations beyond the invasion front (Whitmire & Tobin 2006). For species detected by trap catch, particularly those with a highly sensitive bait such as pheromones, the dispersal of flying males by wind can be a contributing factor to detection of isolated colonies and time lags in establishment (Frank *et al.* 2013). These results have important implications for accurately modeling the early stages of invasion and developing risk assessments and optimal management plans.

Theoretical work has been recently developed to explore trophic interactions and the role of predators at range margins (Holt & Barfield 2009). On this topic, the STS gypsy moth spread rate data provide an important empirical component to studies that examine the prevalence of two natural enemies, a nucleopolyhedrovirus (*Ld*NPV) and an introduced fungus (*Entomophaga maimaiga*) at the range edge. Research has found low infection levels in low-density populations at the advancing front, but demonstrated that pathogens can rapidly spread in populations behind the invasion front and influence growth in newly established areas (Hajek, Elkinton & Witcosky 1996; Hajek & Tobin 2011). The fungus *E. maimaiga* can be more commonly found in lower-density host populations than *Ld*NPV, but further connecting the effects of this pathogen with range edge dynamics requires additional investigation. While a large body of work has examined gypsy moth pathogens and natural enemies in the established range (e.g., Gould, Elkinton & Wallner 1990; Skinner *et al.* 1993), this system has important potential for testing further theory about the effects of host-pathogen interactions at range edges. In particular, the STS data set can aid in investigations that explore the potential role of *E. maimaiga* in altering the spread of gypsy moth, and whether the effect is governed by landscape, geographic, or temporal variation in the environment.

Annual estimates of the continuous gypsy moth range boundary across the entire invasion front in the United States has resulted in highly detailed measures of spatial displacement over a lengthy time series. These data have revealed extremely dynamic spatial variation in spread rates across the full range border, with regions experiencing expansion, stasis, and contraction (Fig. 3). Gypsy moth spread rates also show varying degrees of temporal variation, where some areas experience dramatic fluctuations in the amount and direction of change at the range edge, while other areas advance more steadily (Tobin *et al.* 2007). At the southern range edge, border expansion, stasis, and retraction were all found to occur across a relatively narrow region (Tobin, Gray & Liebhold 2014). The potential for the STS data to elucidate the underlying mechanisms of range expansion is just beginning to be tapped. Forest susceptibility metrics, such as the density of preferred hosts have not provided a singular explanation for variation in spread rates (Sharov *et al.* 1999; Whitmire & Tobin 2006), although the absence of forest is likely a strong barrier in the highly fragmented forests from Illinois to eastern Ohio (Morin *et al.* 2004). Despite predictions from a detailed climatic suitability map for gypsy moth in North America (Gray 2004), climate has been shown to pose unexpected limits to the gypsy moth range edge. For example, the patterns of range edge dynamics in eastern Virginia, characterized by overall stasis and range retraction with high temporal variability (Fig. 3), were unexpected given the suitability of winter climate in the southeastern United States for gypsy moth. Spread rates in this region were found to be negatively correlated to hours of spring/summer temperature above optimal for gypsy moth growth (Tobin, Gray & Liebhold 2014). Elevational gradients may also play a role by creating phenological differences between adjacent populations, which can affect spread rates (Walter *et al*. 2015a). Research that partitioned potential anthropogenic factors found that personal firewood use had the strongest relationship to gypsy moth spread rates (Bigsby, Tobin & Sills 2011). With the complexity of factors impacting spread rates, understanding the multi-scale contributions that drive spatial dynamics is the next frontier. While initial attempts have been made to partition the relative contributions of multiple drivers of spread (e.g., Sharov *et al*. 1999), the accumulation of spatiotemporal data from the STS program over the last two decades provides the opportunity to apply new statistical approaches and combine multiple sources of information to identify how multiple factors interact in populations at the range edge. Additionally, given the divergent climate gradients being experienced by populations across the gypsy moth invasion front, this system has untapped potential for examining the significance of evolutionary changes at range margins.

Contributions to understanding range edge population dynamics

Gypsy moth studies have made significant contributions to our understanding of population cycles in outbreak species and the phenomenon of spatiotemporal population synchrony. High amplitude population cycles are uncommon among most taxonomic groups, although are fairly prevalent among forest Lepidoptera (Berryman 1996), rodent (Krebs *et al.* 1973), and grouse species (Moss & Watson 2001). Here, we focus on contributions from the STS data for understanding population dynamics at range edges and in nascent populations beyond range edges. Although range edge gypsy moth populations may be influenced by cycles and dynamics in the established range, their dynamics are predominately defined by their being at low densities and founding nascent populations. Therefore, insights from this system are relevant to a conceptual understanding of range edge dynamics across taxonomic groups.

One of the most noteworthy contributions of STS data has been in characterizing the role of Allee effects in range edge populations. Allee effects, the depression of population growth rates at low densities, have received a surge of interest over the last decade for their role in increasing extinction risk in low-density populations (Berec, Angulo & Courchamp 2007; Courchamp, Berec & Gascoigne 2008). Below a critical population density, an unstable equilibrium termed the Allee threshold, population growth is negative and populations deterministically approach extinction (Boukal & Berec 2002). Allee effects have been documented in a diversity of species, although we lack evidence for how widespread Allee effects are in natural populations (Kramer *et al.* 2009; Gregory *et al*. 2010). In addition to extinction, Allee effects can impact a multitude of population processes such as invasion, metapopulation dynamics, species' distributions, and disease dynamics (Regoes, Ebert & Bonhoeffer 2002; Taylor & Hastings 2005; Astudillo Fernandez, Hance & Deneubourg 2012).

Many mechanisms can result in Allee effects including mate limitation, reduced cooperative behaviors, generalist predators, and inbreeding depression (Courchamp, Berec & Gascoigne 2008). These mechanisms result in component Allee effects, where an isolated fitness parameter is reduced in small populations (Stephens, Sutherland & Freckleton 1999). Component Allee effects have been found in a wide variety of species through comparisons between low and high density populations. The most likely mechanisms driving component Allee effects in gypsy moth have been identified as mate-finding failure and inability to satiate predators (Sharov, Liebhold & Ravlin 1995; Contarini *et al*. 2009; Tobin *et al*. 2009; Tobin, Onufrieva & Thorpe 2013). Gypsy moth protandry, where adult males eclose earlier than adult females, can magnify mate-finding Allee effects (Robinet *et al.* 2008; Tobin *et al.* 2009).

Much more difficult to test empirically is the manifestation of Allee effects on growth rates at the population level, termed demographic Allee effects. Evidence for demographic Allee effects is largely lacking in empirical studies (Gregory *et al*. 2010; but see Kramer & Drake 2010). Theoretical studies have demonstrated that demographic Allee effects can reduce colonization rates and rates of spread. In some cases, demographic Allee effects prevent range expansion, termed ‘invasion pinning’, creating stable well-defined range borders (Dennis 1989; Keitt, Lewis & Holt 2001; Taylor & Hastings 2005). Threshold-like responses due to demographic Allee effects can result in abrupt shifts in range border dynamics between stable, advancing, and contracting range boundaries (Keitt, Lewis & Holt 2001).

Inherent difficulties to studying rare populations has limited tests of how Allee effects operate in natural populations. Gypsy moth is one of the few systems, along with other notable examples (Davis *et al.* 2004; Angulo *et al.* 2007), providing empirical evidence of demographic Allee effects. An important advancement was developing a metric to quantify Allee effects from empirical data and measure the Allee threshold. Tobin *et al*. (2007) used trap catch data from the STS program and applied a network grid to the interpolated gypsy moth abundance surface and extracted population estimates from areas with successive years of overlap. They defined the Allee threshold as the population density where the proportion of locations able to achieve the sample density or higher in the successive year equals 0.5. The vast amount of data from across the range over 8 successive years permitted high resolution estimates of the Allee threshold and further generated hypotheses regarding variation in Allee thresholds over time and space. This study is the first, to our knowledge, to demonstrate variation in the Allee threshold across multiple regions of an invasion front. Wisconsin achieves population replacement in greater than half of locations that capture 2.2 moths/trap or more (Fig. 4A), while the estimate of the Allee threshold for the southeastern portion of the range was 20.7 moths/trap (Fig. 4B). This threshold could not be quantified in the Midwest due to consistently low population replacement rates (Fig. 4C). Importantly, the geographic and temporal variation in the strength of the Allee effect was negatively linked to variation in the rate of spread along the gypsy moth invasion front. In years with Allee effects at higher population densities, the spread rates dropped and faster spread rates were associated with lower Allee thresholds (Tobin *et al*. 2007; Tobin *et al*. 2009; Fig. 4D). These findings using STS empirical data validated theoretical predictions regarding the negative outcomes of strong Allee effects for spatial spread (e.g., Lewis & Kareiva 1993).

The ability to quantify Allee effects at the gypsy moth range edge has facilitated additional studies that examine the resulting impacts on low-density population dynamics. Robinet *et al*. (2008) used an individual-based model to identify how Allee effects can result from the inability to locate mates in low-density populations. These mate-finding Allee effects have been shown to reduce establishment rates at the gypsy moth range edges (Robinet & Liebhold 2009). In addition to intraspecific interactions, landscape features that reduce local population sizes and limit dispersal have been found to exacerbate Allee effects (Vercken *et al*. 2011). Testing these types of models with empirical data requires large-scale abundance data from the range edge of a species over multiple years. While these data are available for gypsy moth, such expansive data collection is logistically infeasible for the majority of field research programs.

The combination of detailed data on both low-density population dynamics and spread rates have led to further studies on the mechanisms that underlie temporal variation in range expansion. Johnson *et al.* (2006) found that gypsy moth range expansion occurs in periodic pulses of approximately every 4 years. A simulation model was used to show that stratified diffusion and Allee effects in gypsy moth populations together, but neither alone, could produce the observed periodic pulses of gypsy moth invasion (Johnson *et al.* 2006). More recent research presents a non-mutually exclusive alternative hypothesis, that synchronous peaks in population cycles behind the invasion front may facilitate pulses of spread by increasing dispersal beyond the range edge and potentially overcoming Allee effects through inflated immigration (Walter *et al.* 2015b). These results provide a novel conceptual framework for testing theoretical models predicting non-constant rates of range expansion and the processes that underlie this variation.

Discussion

Ecologists are often encouraged to connect the results of basic research to applications for managing our environment and natural resources. By improving our underlying knowledge of biological processes we can then further inform decision making in ecological systems. This synthesis presents a perspective from the other direction, by highlighting the opportunities that can arise when large-scale management data is applied to fundamental research questions. While the STS program was founded with targeted goals for managing and containing the spread of gypsy moth, an invasive forest pest species, we show how this landscape-scale management program has made significant contributions to ecological theory. The grid-trapping scheme and study design for the program were designed specifically to collect data necessary to identify areas for targeted suppression and eradication treatments in keeping with the program goal of reducing gypsy moth spread. However, the magnitude of spatiotemporal abundance data collected through this program has provided research opportunities realized in a wide range of studies. The STS data has provided empirical insights on fundamental ecological processes such as spatial spread, stages of invasion, low-density population dynamics, and Allee effects.

In turn, insights into the ecological mechanisms of the invasion process can bring new strategies into management practices as well. While the STS program has greatly enhanced our understanding of ecological theory and invasion, it has become an effective program because of its incorporation of fundamental ecological concepts and studies on invasive species spread. As an example of this bridge, Bigsby, Tobin & Sills (2011) used trap catch data to partition the anthropogenic drivers of gypsy moth spread at the invasion front. This work not only empirically demonstrated the role of human modification in species invasions, but also indicated that public firewood use is contributing more to spread than movement of wood by industry. Developing a model using empirical data that tests the contributions of anthropogenic processes to spread is an important contribution to invasion biology, but, in this case, it also informs management. Investigations of Allee effects and stratified dispersal using data from the gypsy moth invasion front have provided significant insights into theoretical expectations for low-density population dynamics and spatial spread of invasive species. These advances have not only impacted gypsy moth management, but also been incorporated into the management of spread rates in other of pest species (Liebhold & Tobin 2010). Work demonstrating the role of isolated advanced colonies in spatial spread has been influential in guiding STS program design (Sharov & Liebhold 1998; Liebhold, Sharov & Tobin 2007) and has been applied in other systems (e.g., parasitoids of fire ants, LeBrun, Plowes & Gilbert 2008). Data on lag times indicate that management action does not need to occur immediately, providing the opportunity to further delimit the population, increasing our data on the dynamics of isolated colonies, and reducing the number and extent of treatment applications (Tobin *et al*. 2013).

Allee effects in particular have gained attention as an important consideration for management against invasive species establishment and spread, where different management tactics can have interacting effects on low-density population dynamics (Blackwood *et al*. 2012; Suckling *et al*. 2012). A recent theoretical study demonstrated how geographic variation in the strength of Allee effects in gypsy moth may affect the optimal management strategy (Chan, Kent & Johnson 2017). Estimations of the Allee threshold can provide target densities below which the population is unlikely to persist. For example, eradication of isolated, low-density colonies of gypsy moth only requires a treatment mortality greater than 80% to ultimately achieve population extinction (Liebhold & Bascompte 2003). Examples from other species include models of density-based eradication strategies for *Spartina alterniflora*, an invasive grass, that incorporate Allee effects (e.g., Taylor & Hastings 2004) and understanding the role of Allee effects in population establishment of *Vincetoxicum rossicum*, an invasive vine (Cappuccino 2004). Our enhanced knowledge of Allee effects from research in the gypsy moth system has not only provided grounds for testing and developing new ecological theory, but also provided insights that can be applied to risk assessments to prioritize resources for invasive species management (Tobin, Berec & Liebhold 2011).

Despite the prolific work and novel contributions over the last two decades, the STS program presents many opportunities for continued research on range borders and spatial population dynamics. A major advancement in spread models is the use of a landscape perspective to directly test the effects of spatial population structure on invasion dynamics (With 2002). However, a better understanding is needed of how cross-scale landscape features affect range expansion and interact with the local dynamics (e.g., Walter *et al.* 2016).

A recent study suggests that forest edges may enhance mate-finding ability in gypsy moth (Thompson, Grayson & Johnson 2016), which could have large effects on spread by reducing Allee effects in fragmented landscapes. Further investigations that partition the contributions of the natural and human landscape can add new insights into gypsy moth range expansion in a rapidly changing environment.

In advancing the study of low-density population dynamics, gypsy moth data provide an important opportunity to test underlying mechanisms of Allee effects and gain insights on patterns of natural variability. Largely because of data limitations, most studies must treat Allee effects as spatiotemporal constants or, at best, varying only at large scales. In natural systems, population parameters vary across spatiotemporal scales, and the same is likely true for Allee effects. For example, populations can fluctuate over space and time between strong Allee effects, where there is a threshold density for population growth, and weak effects where the depression in population growth does not cross an Allee threshold (Tobin *et al.* 2007). Studies examining the interactions between multiple mechanisms influencing Allee effects can benefit from using the “Allee slope” to characterize variability in the system. This metric describes the magnitude of the positive relationship between population size and per-capita growth rate at low densities (Walter, Grayson & Johnson 2017). Application of models and analytical approaches that explicitly account for measurement and process error, such as Bayesian analyses, will likely result in better measurements of Allee effects, which are plagued by the high demographic stochasticity characteristic of low-density populations. Also, models and statistical approaches that account for immigration into low-density populations, which would tend to mask Allee effects, would be beneficial toward estimating these effects. Together, we contend that applying these new methods to the study of Allee effects and other low-density population dynamics using gypsy moth data will facilitate a more complete understanding of species border dynamics. Despite the impressive research and insights made possible by the STS data, this data set has much more to offer to our understanding of population theory; thus, we assert that the gypsy moth system remains one of the best venues for testing questions related to spatial spread and population dynamics at range borders.

Data Accessibility

Information on the data from the Slow the Spread program, including annual trap catch, spread rates, and treatment blocks, can be accessed from the Decision Support page of the STS Foundation: http://yt.ento.vt.edu/da/

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Author Contributions

KG conceived the synthesis, developed the framework, and led the writing of the manuscript. The ideas represent the intellectual contributions of both KG and DJ. DJ contributed to writing and editing. Both authors gave final approval for publication.

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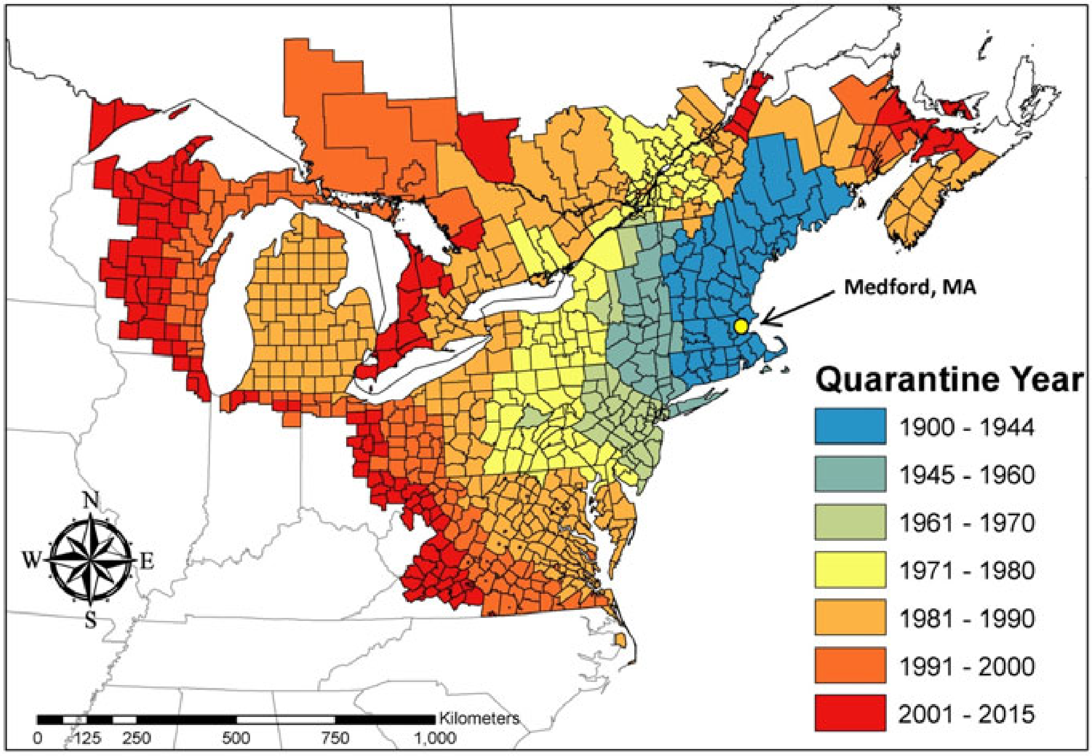
Figures

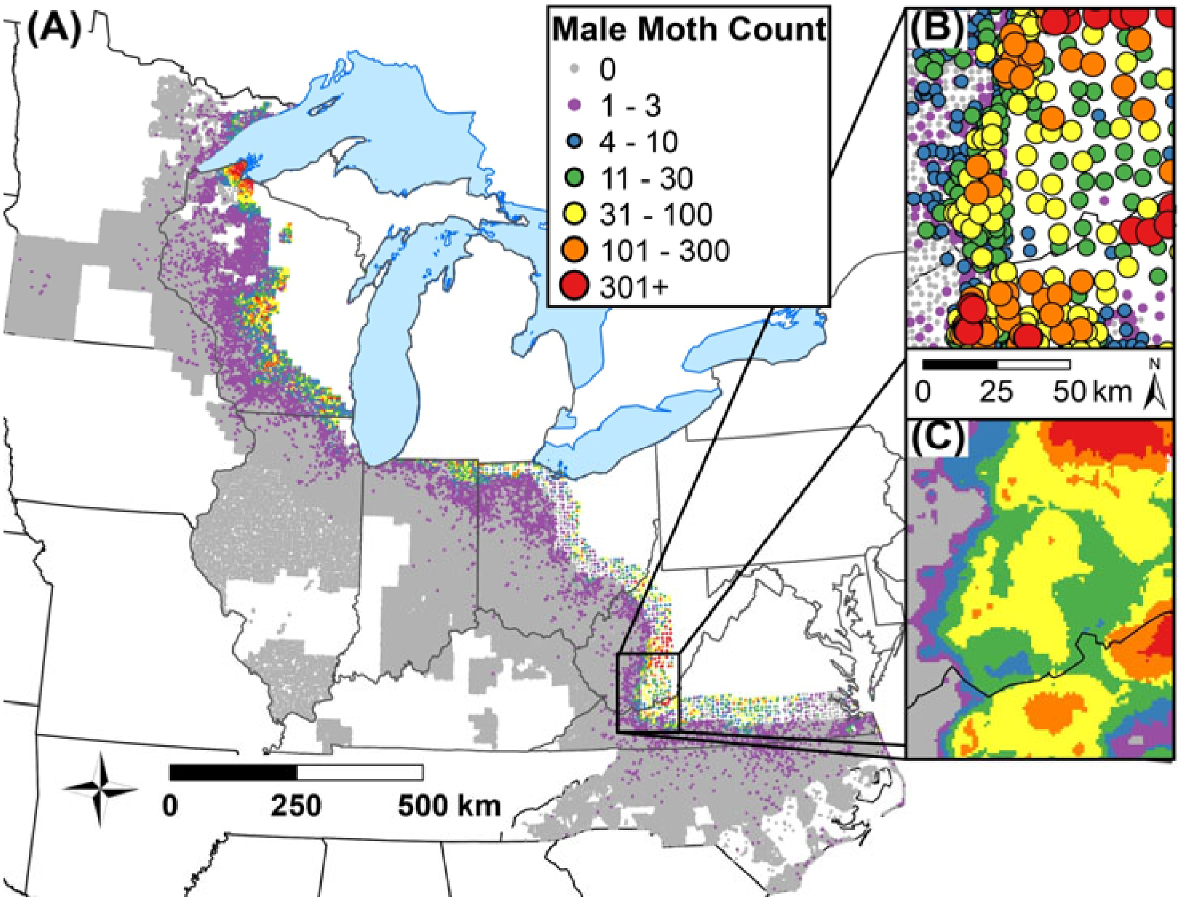
Fig. 1. Gypsy moth spread in the United States and Canada based on county quarantine records. Quarantines are a regulatory mechanism in which a geopolitical unit is considered generally infested in an effort to limit movement of non-native species to uninfested areas (data provided by the US Code of Federal Regulations, Title 7, Chapter III, Section 301.45 and the Canadian Food Inspection Agency, Plant Health Division, Policy Directive D-98-09, digitized by the US Forest Service, and mapped by B. Lind and L. Thompson).

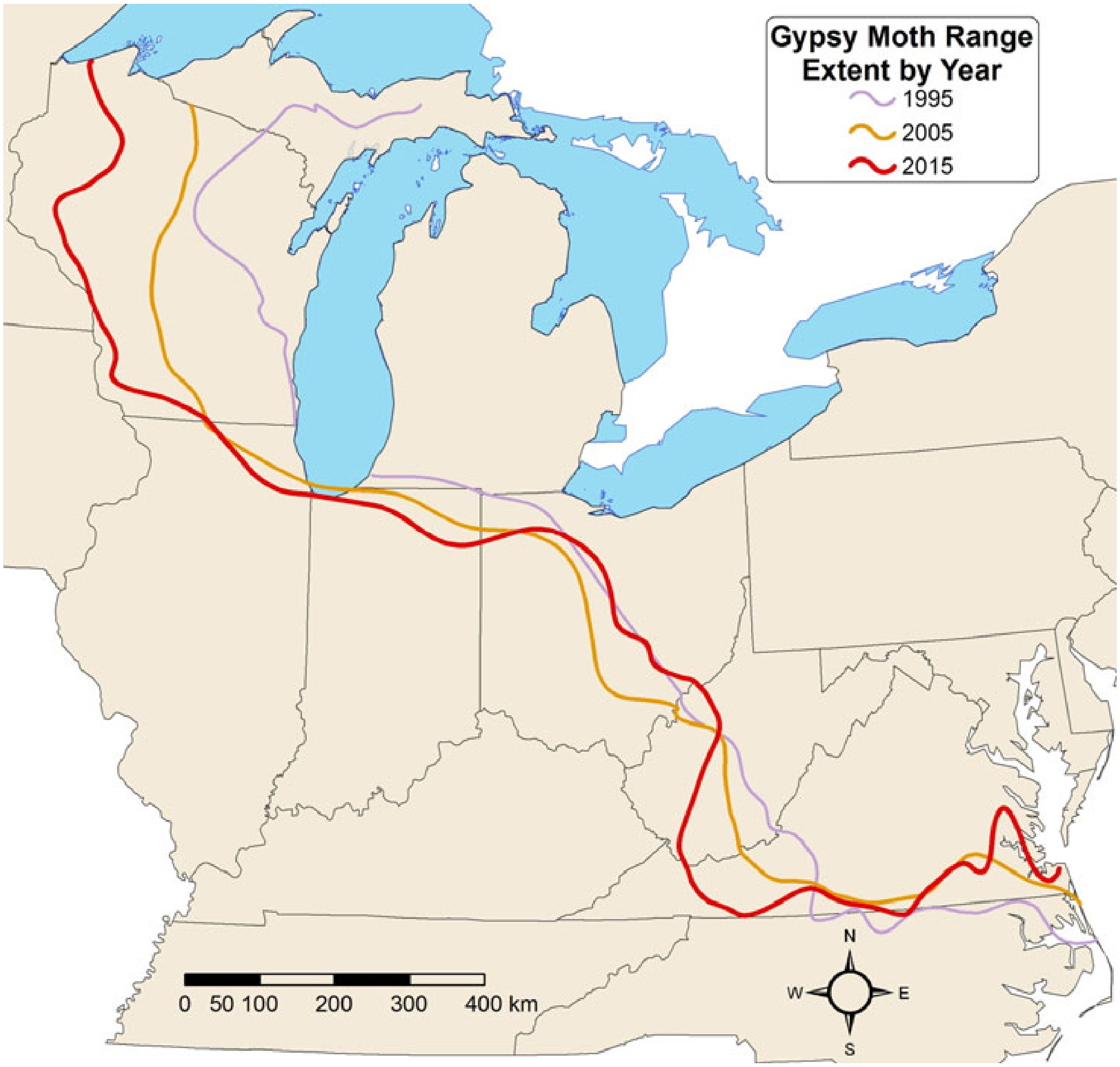
Fig. 2. (A) Area trapped under the Slow the Spread program in 2012 where each dot represents an individual gypsy moth trap and the associated captures of male moths. (B) Individual trap catch data, shown from a subset region, is used to spatially interpolate (C) a continuous surface of gypsy moth abundance. Graphic by P. Tobin and L. Blackburn.

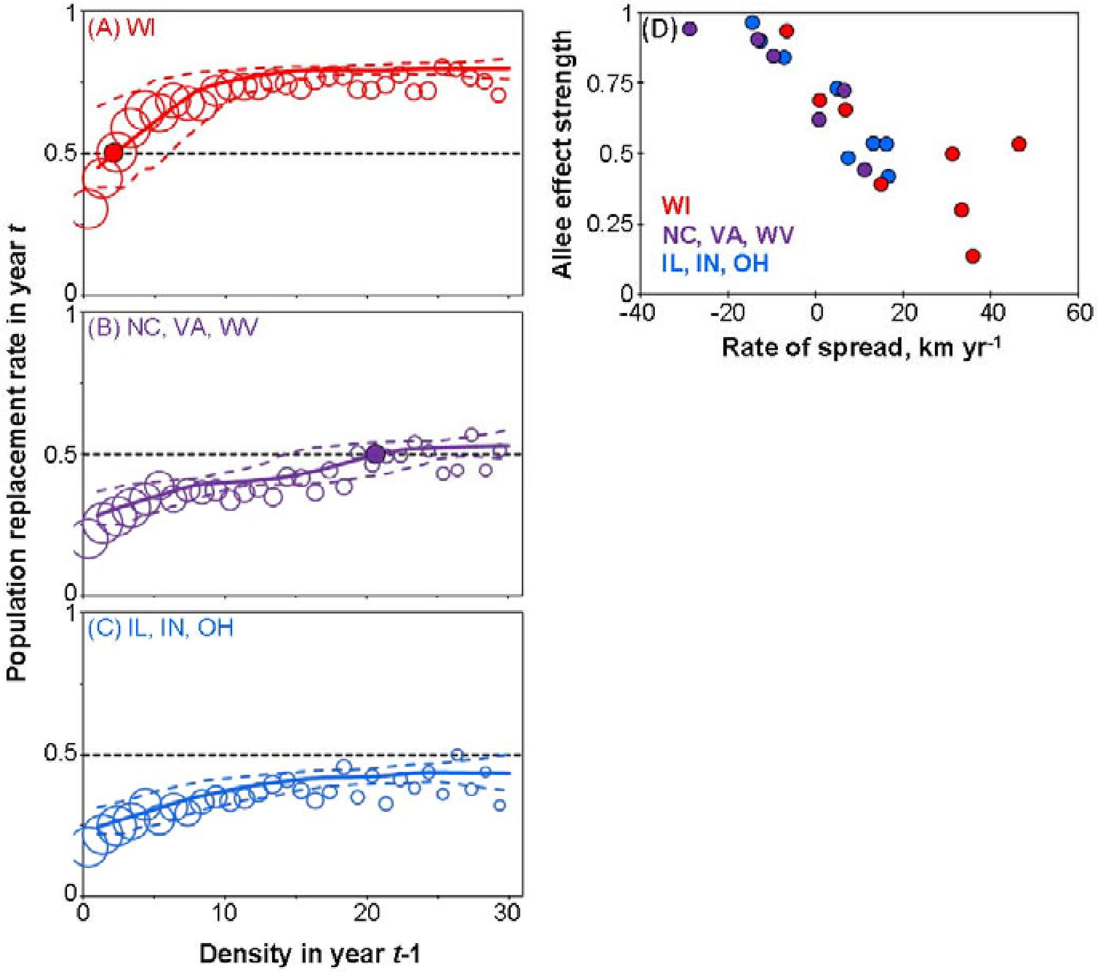
Fig. 3. Geographic variation across the gypsy moth invasion front in the United States between 1995 and 2015. The border here is the smoothed isocline where mean abundance is 0.5 – 1 moths/trap using interpolated Slow the Spread trap catch data. Graphic by L. Blackburn.

Fig. 4. Region-specific relationships between population replacement rate in year t and initial population density in year t-1 for trapping areas with ≤ 30 gypsy moths for the northern range edge in Wisconsin (A), the southern range edge in North Carolina, Virginia, and West Virginia (B), and the Midwest in Illinois, Indiana, and Ohio (C). Data is pooled across all pairs of years from 1996 – 2004. Population replacement rates below the dashed line indicate that fewer than 50% of populations at that density maintained their population size or grew. The solid circle indicates estimates of the Allee threshold; no estimate was found in (C) due to replacement rates consistently below 0.5. Open circle size reflects the sample size and the solid line indicates the mean with the 95% CI as dashed lines. For each region and pair of consecutive years, the relative strength of the Allee effect was negatively correlated with spread rate (D). Redrawn from Tobin et al. 2007.




(A)
Male Moth Count
0
1 - 3
4 - 10
11 - 30
31 - 100
101 - 300
301+
(B)
0
25
50 km
N
(C)
0
250
500 km


Gypsy Moth Range
Extent by Year
1995
2005
2015
0
50
100
200
300
400 km
N
W
E
S


(A) WI
(B) NC, VA, WV
(C) IL, IN, OH
(D)
Population replacement rate in year t
Density in year t-1
0
0.5
1
0
10
20
30
Allee effect strength
0
0.25
0.5
0.75
1
Rate of spread, km yr-1
-40
-20
0
20
40
60
WI
NC, VA, WV
IL, IN, OH