Effects of temperature and host distribution on gypsy moth growth rates along its expanding population front

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Abstract

Gypsy moth growth rate dynamics in response to temperature and host distribution

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The gypsy moth, *Lymantria dispar* (L.), has been a major pest species in North American forests for >100 years and has caused defoliation on >369,000 km^2 since 1924. Due to the economic and ecological consequences of gypsy moth, many aspects of its population biology and ecology have been studied. However, much prior work has focused at local spatial scales and in established outbreaking populations. In contrast, gypsy moth invasion dynamics are understudied in newly established populations and across landscape scales. I first analyzed the effect of sub- and supraoptimal temperatures on nascent gypsy moth population growth rates, and the spatial patterns of growth rates, along the expanding invasion front in the eastern United States. Second, I quantified the relationship between primary and secondary host plant fragmentation and gypsy moth population growth rates along the expanding invasion front.

The data from this study indicate that there are geographical differences in how temperature and host fragmentation is affecting gypsy moth growth rates, and the spatial structure of those growth rates within expanding populations along the leading edge of the invasion front. Furthermore, the results from this study emphasize the important role that secondary hosts play in establishing populations. The results from this study could help in the development of more accurate risk assessment models pertaining to gypsy moth invasion potential.

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Chapter 1. AN INTRODUCTION TO GYPSY MOTH POPULATION DYNAMICS

The gypsy moth, *Lymantria dispar* (L.), has been a major pest species in North America for >100 years and has caused defoliation on >369,000 km^{2-} since 1924 (Elkinton & Liebhold 1990; Tobin *et al.* 2012). In addition to defoliating forests, gypsy moth populations alter carbon sequestration and nutrient cycling, biogeochemical conditions, and change the acid base status of containing catchments (Webb *et al*. 1995). Because of the severe economic and ecological consequences of gypsy moth invasion, with management costs being > $378 million since 1924 (USFS 2017), many aspects of gypsy moth population biology and ecology have been studied. This includes the relationship between gypsy moth invasion potential and climate suitability (Gray, 2004; Logan et al., 2007; Pitt *et al*., 2007; Allen *et al.*, 1993) and the relationship between gypsy moth invasion potential and density of host trees (Liebhold *et al.* 1994; Herrick & Gansner 1986). Although these dynamics are well understood in outbreak populations, they are still poorly understood in nascent gypsy moth populations.

Because of an obligatory diapause stage, gypsy moth egg masses are sensitive to suboptimal temperatures (temperatures < 28°C; Gray *et al.* 2001; Gray *et al.* 2009). Furthermore, larvae and pupae are sensitive to supraoptimal temperatures (temperatures > 28°C), resulting in reduced developmental rates (Tobin *et al.* 2014; Thompson *et al.* 2017). Extended exposure to sub- and supraoptimal temperatures causes decreased fitness with instantaneous mortality occurring at -28 °C and 32°C, respectively (Tobin *et al.* 2014; Thompson *et al.* 2017). Temperature consistency is integral in gypsy moth development, and temperature fluctuations as little as 1°C are known to change gypsy moth developmental rates and survivorship, especially when those fluctuations are on the margins of the lethal sub- and supraoptimal temperature boundary (Thompson *et al.*, 2017, Bell 1995, Summers, 1922; Sullivan & Wallace, 1972). With temperatures in the 21st century on the rise (IPCC, 2001) and range shifts in response to climate change occurring more frequently in insect species (Parmesan & Yohe, 2003; Parmesan *et al*., 1999; Warren *et al*., 2001), it has become integral to understand the effect that changing climates will have on forest insects that cause ecological and economic damage.

Despite the wide breadth of gypsy moth host species, there is much variation in defoliation rates throughout the eastern United States; this variation is believed to be a result of gypsy moth preferential feeding (Liebhold *et al.* 1994). Primary or preferred host species usually display synchronous phenology and the lack of alkaloids which often optimize larval growth and development rates as well as fecundity, survivability and size (Stoyenoff 1993; Stoyenoff *et al.* 1994b; Liebhold *et al.* 1995). Secondary or intermediate host species can be defined as those that yield slower developmental rates, lower larval weights, lower fecundity and higher mortality rates for early instars (Stoyenoff 1993; Stoyenoff *et al.* 1994a; Stoyenoff *et al.* 1994b). Secondary hosts tend to be consumed in high-density populations or during later instars when primary hosts are no longer available or are scarce. Stoyenoff (1993) found that not only did secondary host species affect larval development, relative growth rate and pupal weight, but also that consuming different host species combinations can optimize gypsy moth performance in terms of fitness.

Since 2000, the Slow-the-Spread program, implemented by the United States Forest Service, has reduced the overall rate of gypsy moth spread along its leading edge in the United States, while also providing one of the most comprehensive range-wide species distribution datasets in existence (Sharov & Liebhold, 1998; Tobin & Blackburn, 2007). In the present study, I used a 16-year spatially-referenced dataset along the gypsy moth expanding population front in the United States to quantify the effects of temperature, and primary and secondary host distribution, on nascent gypsy moth population growth rates.

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Chapter 2. EFFECTS OF TEMPERATURE ON THE SPATIAL DYNAMICS OF GYPSY MOTH POPULATION GROWTH RATES ALONG AN EXPANDING POPULATION FRONT

2.1 ABSTRACT

The gypsy moth, *Lymantria dispar* (L.), is an invasive polyphagous folivore introduced from Europe to North America. Because of economic and ecological consequences of gypsy moth invasion in North America, it is one of the more well-documented biological invasions, with much effort placed on understanding its outbreak dynamics in well-established populations. Less attention has focused on invading, newly-establishing populations across its expanding invasion front. This limits our ability to predict dynamics in invading gypsy moth populations, including its response to climate change. I used regional temperature data in combination with gypsy moth trap catch data from 1999 to 2015 to characterize the relationship between sub- and supraoptimal temperatures and local spatial dynamics of gypsy moth population growth rates across the invasion front, from Minnesota to North Carolina. Across a landscape scale, I observed different spatial structure in growth rates, and the extent to which temperatures affected the spatial pattern of growth rates. Spatial structure in the northern region of its invasion front was strongest despite the region having the most variable annual temperatures. Spatial structure in the Midwestern region was not significantly affected by either sub- or supraoptimal temperatures, while spatial structure in the southern region was more affected by supraoptimal

temperatures relative to the other regions. The data suggest that there are geographical differences in the effect of temperature on gypsy moth population growth rates, and the spatial structure of those growth rates. This finding has important consequences to the range dynamics of invading gypsy moth populations, especially in light of global climate change and predictions of range shifts in many species owing to increased temperartures.

2.2 INTRODUCTION

Physiological restraints to temperature play an important role in determining the geographic ranges of species (Lee *et al*., 2009; Butterfield, 1996; Hill *et al*., 2011). With temperatures in the 21st century on the rise and further predictions estimating increases as high as 5.6 °C (IPCC, 2001), many species are expected to experience a range shift in response as opposed to adapting to warmer temperatures *in situ* (Huntley, 1991). These changes in temperature, as well as precipitation, could have major implications for populations of poikilotherms, which respond directly to ambient temperatures (Butterfield, 1996; Addo-Bediako *et al*., 2000; Vanhanen *et al*., 2007; Hill *et al*., 2011; Bennie *et al*., 2013). For example, range shifts in response to the 20th century warming of ~ 0.6 °C occurred more frequently in those species that were most limited by temperature (*e.g.*, arctic or alpine plants) or species that are highly mobile for some of their life (*e.g.*, flying invertebrates) (Hughes, 2000). Past research has shown that in some European butterfly species, such as *Polygonia c-album*, increased temperatures resulted in a significant poleward range shift, with the expectation that many other insect species will follow suit (Parmesan & Yohe, 2003; Parmesan *et al*., 1999; Warren *et al*., 2001). Research on individual forest insect pest species' response to climate change indicate varied responses that range from intensification in all aspects of outbreak behavior and probable range expansion to unprecedented outbreak failures (Logan *et al.*, 2003; Esper *et al.* 2007). Despite this uncertainty, it remains particularly integral to understand the effect that changing climates will have on forest insects that cause ecological and economic damage.

The gypsy moth, *Lymantria dispar* (L.), is an invasive polyphagous folivore that can feed on more than 300 host tree species and has caused defoliation on >369,000 km^{2-} since 1924 (Elkinton & Liebhold 1990; Tobin *et al.* 2012). In addition to defoliating forests, gypsy moth populations alter carbon sequestration and nutrient cycling, biogeochemical conditions, and change the acid base status of containing catchments (Webb *et al*. 1995). Since its introduction from France to Medford, Massachusetts in 1869, the gypsy moth has established populations in all parts of the 19 Eastern States and the District of Columbia, or roughly one third of its potential habitat in the United States (Morin *et al*. 2005). Gypsy moth spread rates have varied through time and are believed to fluctuate as a function of variation in host availability, frequency of human transport, federal management and temporal patterns (Liebhold *et al*. 1992, Liebhold & Tobin 2006; Tobin *et al*. 2007). Once populations are established, many affected areas are susceptible to reoccurring outbreaks that follow an 8-11 year cycle (Johnson *et al.* 2005; Haynes *et al.* 2009). These outbreak dynamics ultimately reduce tree growth and increase tree dieback (Maloney *et al.* 2010). Because of the ecological and economic costs of gypsy moth outbreaks, there have been a number of gypsy moth management programs since the first eradication attempt in the 1890s (Tobin & Blackburn 2007). Since 2000, the Slow-the-Spread program, implemented by the United States Forest Service, has reduced the overall rate of gypsy moth spread along its leading edge in the United States, while also providing one of the most comprehensive range-wide species distribution datasets in existence (Sharov & Liebhold, 1998; Tobin & Blackburn, 2007).

Gypsy moth egg development is comprised of three distinct stages, each having a different developmental response to temperature. Early developing embryos are initially relatively more responsive to higher temperatures; this is known as the prediapause stage and is characterized by high respiration rates and morphological development (Gray *et al.*, 1991; Leonard, 1968). After 14-25 days in the prediapause stage (assuming a constant temperature of 20 to 30 °C), individuals enter an obligatory diapause as a pharate larva (Bell, 1996). Diapause phase is characterized by relatively low respiration rates, a virtual lack of morphological development with developmental rates being favored by low temperatures (Gray *et al.*, 2001). While exposure the cold temperatures is a requirement to terminate diapause (Grey *et al*. 2009), exposure to temperatures <–22 °C for extended periods of time has been shown to increase mortality. Supercooling points, or the temperature at which mortality is instantaneous, has been estimated at –28 °C (Summers, 1922; Sullivan & Wallace, 1972). After adequate exposure to lower temperatures, pharate larvae become responsive to higher temperatures again and enter postdiapause (Gray *et al.*, 1995). Eggs hatch into 1st instars upon completion of the postdiapause phase. Gypsy moth larvae are known to experience optimal developmental rates at ~28 °C (Logan *et al.*, 1991). Thompson *et al.* (2017) found that extended exposure to supraoptimal temperatures affected both the larval mass and developmental time to 4th instar, and reported a lethal supraoptimal temperature of ~32 °C. Because of the physiological restraints owing to suboptimal and supraoptimal temperatures, climate conditions can affect gypsy moth population dynamics and rates of spread along its population front, which extends from Minnesota to North Carolina in the United States.

Because of the economic implications of gypsy moth, with management costs in the United States ranging from $4.9-$22.5 million per year (USDA, 2017), many aspects of gypsy moth population biology and ecology have been studied. This includes the relationship between gypsy moth invasion potential and climate suitability (Gray, 2004; Logan et al., 2007; Pitt *et al.*, 2007; Allen *et al.*, 1993). Gypsy moth range expansion at the northern extent of its invasion front (e.g., Wisconsin and Minnesota) is believed to be restricted by extreme winter temperatures, which leads to increased overwintering mortality. Suboptimal temperatures also delay oviposition in northern areas; this results in a much smaller window of time in which temperatures are high enough to satisfy complete prediapause development (Sullivan & Wallace, 1972; Régnière & Nealis, 2002; Gray, 2004). Restriction in the southern extent of the invasion front (e.g., Virginia and North Carolina) has been recently attributed to supraoptimal temperatures during the larval and pupal stage (Tobin *et al.* 2014), which was subsequently linked to reduced developmental rate and fitness (Thompson *et al.*, 2017). Concurrent with climate change, the geographic margins of climatic suitability for gypsy moth will likely shift poleward with increasing temperatures (Vanhanen *et al.,* 2007).

Climate change is expected to shift the future area of suitable climate for gypsy moth in northern areas that are now marginal due to warmer winters, which reduce overwintering mortality, and warmer summers, which allow gypsy moth to complete its univoltine life cycle (Logan *et al.,* 2007). With current climate change projections, gypsy moth may pose a threat to more northern ecosystems. This is of particular concern to areas such as Quebec and Ontario, which were previously thought to be uninhabitable to gypsy moth but have since suffered multiple outbreaks as a result of steadily increasing climatic suitability since 1980 (Régnière *et al.,* 2009). Prior studies analyzing the relationship between temperature and gypsy moth distributional range have focused on regional scales, often at the state level (*e.g.* Smitley *et al., 1998*; Pitt *et al*., 2007; Allen *et al*., 1993; Régnière *et al.,* 2007). Furthermore, most studies have considered well established populations that are prone to periodical outbreaks given the interest in risk assessment. In this study, Iused a 16-year spatially-referenced dataset along the gypsy moth expanding population front to quantify the relationship between local spatial dynamics of gypsy moth growth rates and temperature.

2.3 MATERIALS AND METHODS

Spatial Scale

The spatial scale of this study encompassed the gypsy moth invasion front within the United States from 1999 to 2015, which included an area from Minnesota to North Carolina (Fig. 1). I subset the invasion front into three regions due to differences in regional range dynamics (Tobin *et al*. 2007) and temperature regimes (Gray 2004). The northern region (*i.e.*, Michigan, Wisconsin, and Minnesota) of the invasion front has displayed range expansion through time and contains the lowest average January minimums (~ –6.2 °C) and July maximums (~27.2 °C; Table 2.1; Fig. 2.1; PRISM Climate Group 2015). The Midwestern region (*i.e.*, Illinois, Indiana, Iowa, Kentucky, Ohio, and Missouri) of the invasion front has been characterized by a static range dynamic and an average January minimum and July maximum of ~ –1°C and 29°C, respectively (Table 2.1; Fig. 2.1; PRISM Climate Group 2015). The southern region (*i.e.*, North Carolina, Virginia, West Virginia, and Tennessee) has been characterized with both range expansion and retraction, but has displayed a net retraction through time (Tobin *et al* 2014*).* The southern range generally has the highest average January minimums and July maximums (~ 2.7 °C and 30°C, respectively; Table 2.1; Fig. 2.1; PRISM Climate Group 2015).

Growth Rate and Temperature

Gypsy moth growth rates were derived from monitoring data collected by the gypsy moth Slow-the-Spread program in which ~100,000 georeferenced pheromone-baited traps are deployed annually along and ahead of the gypsy moth population front (Tobin *et al*. 2012). I used data from 1999-2015 as these years generally contained a continuous trap grid across the entire invasion front. Because trap locations can shift from year-to-year, trap data from each year were interpolated using indicator kriging in GSLIB (Deutsch & Journel 1998) over a network of 5 × 5 km cells to generate a smooth surface. Growth rates were calculated for each 5 × 5 km cell. I focused on newly establishing populations; these were defined as populations with an initial interpolated value between > 0 and < 1males/trap/cell. To ensure growth rates within cells were comparable among cells through time, the data were truncated to only include those cells contained at least one value of 0 within the time sequence (1999-2015). The growth rates from year t to t+1 were calculated for each individual 5 × 5 km cell and for each pair of years (*e.g.* 1999 to 2000, 2000 to 2001, …, 2014 to 2015) according to:

$$Growth\ Rate = log_e\left(\frac{N_{t+1}}{N_t}\right), \qquad (2.1)$$

where N_{t+1} and N_t are the interpolated values (males/trap/year) in the current and prior year, respectively.

I obtained temperature data through the PRISM Climate Group (2015), This dataset contains climate data through the use of a broad range of monitoring networks and interpolates the data using a variety of modeling techniques; these data are available to the public at different spatial resolutions. Datasets are available from 1895 to the present and aim to elucidate both long term and short term spatio-temporal climate patterns. To represent the effect of sub- and supraoptimal temperatures for gypsy moth development (Logan *et al*. 1991, Tobin *et al.* 2014), Iused annual mean January minimum and July maximum temperatures at a resolution of 5 × 5 km for the years of 1999-2015 (PRISM Climate Group 2015).

Spatial dynamics of growth rate data through time

Spatial autocorrelation measures the correlation of a variable to itself through space. Spatial autocorrelation can be positive or negative. Positive spatial autocorrelation values occur when similar values are near one another in space. Negative spatial autocorrelation occurs when values are dissimilar (Moran, 1950). Iquantified spatial autocorrelation in gypsy moth growth rates across the network of 5 × 5 km cells in each region for each pair of years from 1999 to 2015. Iused the ‘ncf’ package (Bjørnstad, 2012) in R (R Development Core Team 2015) to estimate spatial autocorrelation based upon a nonparametric spatial covariance function (Bjørnstad & Falck, 2001), according to:

$$\bar{\rho}(\delta) = \frac{\sum_{i=1}^{N} \sum_{j=i+1}^{N} G\left(\frac{\delta_{ij}}{h}\right) \rho_{ij}}{\sum_{i=1}^{N} \sum_{j=i+1}^{N} G\left(\frac{\delta_{ij}}{h}\right)}, \tag{2.2}$$

where G is a kernel function with kernel bandwidth h, and ρ_{ij} refers to the correlation between a value of spatial location i and a value at spatial location j. Confidence intervals surrounding the nonparametric spatial covariance function were estimated using the 2.5 and 97.5 percentiles of a bootstrapped distribution based on 300 replications (Efron & Tibshirani, 1993). Ialso estimated spatial synchrony in gypsy moth growth rates using a nonparametric cross-correlation function (Bjørnstad 2012). Due to computation challenges, a random subset of 500 locations through time was selected for each region, from which Iestimated spatial synchrony. This was repeated 5000 times to estimate a mean and confidence interval based on the 2.5 and 97.5 percentiles of the bootstrapped distribution. Significance was noted in spatial autocorrelation and spatial synchrony when the bootstrapped confidence intervals did not include 0. Iestimated the local spatial autocorrelation and the local cross-correlation based upon the estimated y-intercept, and the spatial range as the x-intercept.

Statistical analyses

To achieve comparable sample sizes between temperature and growth rate variables, temperature variables were averaged across years and split up into categorical bins, each containing 10 bins defined by 5°C intervals. To statistically determine the relationship between sub- and supraoptimal temperatures and growth rates within specific regions, Imeasured the correlation between average growth rates and the binned January and July temperature variables within each region. To quantify the relationship between growth rates and sub- and supraoptimal temperatures across regions, Imeasured the strength of a nonlinear relationship between average growth rate and the binned January and July temperature variables across regions in R (R Development Core Team 2015).

To achieve comparable sample sizes between temperature variables and spatial autocorrelation metrics (*i.e.* local spatial autocorrelation in gypsy moth growth rates and spatial autocorrelation range), temperature variables were averaged across years. To statistically determine the relationships between estimates of local spatial autocorrelation in gypsy moth growth rates and average January minimum and July maximum temperatures within each region, Imeasured the correlation between estimates of local spatial autocorrelation growth rates and the average January and July temperature. The relationships between estimates of local spatial autocorrelation in gypsy moth growth rates and average January minimum and July maximum temperatures across regions was measured using both the strength of correlations and nonlinear models. To statistically determine the relationships between estimates of local spatial autocorrelation range in gypsy moth growth rates and average January minimum and July maximum temperatures within and across regions, Imeasured the correlation between estimates of local spatial autocorrelation range in growth rates and the average January and July temperature in R (R Development Core Team 2015).

2.4 RESULTS

Local Spatial Autocorrelation and Spatial Synchrony

When averaged across years within each region, significant local spatial was detected within the Northern region exhibiting the highest local spatial autocorrelation and the southern region exhibiting the lowest (Table 2.2; Fig. 2.2). I also found evidence of spatial autocorrelation in gypsy moth growth rates in all year pairs in all regions (Tables 2.3,2.4 & 2.5; Fig. 2.3,2.4 & 2.5). The range of spatial autocorrelation generally varied from 100 to 160 km (Fig. 2.3, 2.4 & 2.5). The northern region exhibited the largest average range of spatial autocorrelation across years (~164 km; Fig. 2.3), while the Midwestern and southern regions had comparable average ranges of spatial autocorrelation (~ 101 and 104 km, respectively; Fig. 2.4 & 2.5). I also detected significant spatial synchrony in growth rates in all regions (Table 2.6; Fig. 2.6). In all regions, spatial synchrony extended to at least 250 km while in the northern region, synchrony was measure to ~500 km (Fig. 2.6).

Growth Rate and Temperature

Across all regions combined, growth rates were significantly affected by mean January minimum temperatures (Table 2.7, Fig. 2.7). When considering each specific region, growth rates were significantly affected by mean January minimum temperatures in the northern and southern regions, while there was a positive but non-significant trend in the Midwestern region

(Table 2.7, Fig. 2.7). This relationship in the northern region tended to reach a plateau at ~ −15°C (Fig. 2.7). This region also exhibited the greatest range in January minimum temperatures, spanning from −30 to 10 °C, and the greatest range in growth rates, from −3.3 to 0.47. In the southern region, there was a linear and positive relationship between mean January minimum temperatures and gypsy moth growth rates (Fig. 2.7).

Across all regions combined, mean July maximum temperatures significantly affected gypsy moth growth in a nonlinear manner (Table 2.8, Fig. 2.8). The highest growth rates were measured when mean July temperatures were ~28 °C (Fig. 2.8). Within the northern region, growth rates increased slightly until ~23.5 °C at which growth rates appear to plateau (Fig. 2.8). Average growth rates in the southern region remain relatively consistent until ~30 °C at which growth rates increased (Fig. 2.8). In the Midwestern region, there was no significant relationship between gypsy moth growth rates and mean July maximum temperatures (Table 2.8, Fig. 2.8).

Local Spatial Dynamics and Temperature

I detected a significant relationship between mean January minimum temperatures and the estimates of local spatial autocorrelation in gypsy moth growth rates across all regions combined (Table 2.9, Fig. 2.9). The relationship was nonlinear, and at low mean January minimum temperatures (*i.e.*, <−10°C), local estimates of spatial autocorrelation approached 0 (i.e., no spatial autocorrelation). In contrast, local estimates of spatial autocorrelation were the highest when mean January minimum temperatures were >0°C (Fig. 2.9). When examined for each region, there was only a significant association in the northern region (Table 2.9).

In contrast, I did not detect a significant relationship between mean July maximum temperature and the estimates of local spatial autocorrelation in gypsy moth growth rates across all regions combined (Table 2.9, Fig. 2.10). When examining each region separately, the southern region was the only region in which July maximum temperatures were significantly associated with local spatial autocorrelation (Table 2.9), with lower estimates of local spatial autocorrelation occurring at higher mean July temperatures (Fig. 2.10).

I detected a significant relationship between mean January minimum temperature and estimates of the range of spatial autocorrelation across all regions combined (Table 2.10). The relationship was linear and negative, with lower estimates of the range occurring at higher mean January temperatures (Table 2.10, Figure 2.11). The Midwestern region was the only region in which mean January minimum temperature were significantly associated with the range of spatial autocorrelation, with lower estimates of spatial autocorrelation range occurring at higher mean January temperatures (Table 2.10, Figure 2.11).

In contrast, I did not detect a significant relationship between mean July maximum temperatures and the estimate of the range of spatial autocorrelation in gypsy moth growth rates across all regions combined (Table 2.10, Fig. 2.12). The southern region was the only region in which July maximum temperatures were significantly associated with the range, with higher estimates of local spatial autocorrelation range occurring at higher mean July temperatures (Table 2.10, Fig. 2.12).

2.5 DISCUSSION

Across regions, mean January temperatures >–10°C were associated with increased growth rates. These findings agree with previous research that highlight mortality rates of gypsy moth egg masses at cold temperatures (Summers, 1922; Sullivan & Wallace, 1972), although this is the first attempt to quantify the effect of cold temperatures on gypsy moth population growth rates across a large and diverse landscape scale. Although colder temperatures are required to terminate the obligatory diapause stage (Gray, 2004), post-embryonic development and entry into hibernal diapause is favored by higher temperatures often within a range of 20-30°C (Lees, 1955; Tauber *et al*., 1986; Bell,1996). Exposure to temperatures <–22 °C for extended periods of time has been shown to increase mortality with instantaneous mortality occurring at ~ –28 °C (Summers, 1922; Sullivan & Wallace, 1972). In this study, I found that higher January minimum temperatures were also associated with an increase in the local estimate of spatial autocorrelation (Fig. 2.9) but with a decrease in the range of spatial autocorrelation (Fig. 2.11). Although growth rates plateau at ~ –10°C (Fig. 2.7), local spatial autocorrelation continues to increase and range continues to decrease with increasing January temperatures. These results indicate that across regions, increased January minimum temperatures could lead to greater local spatial continuity in population densities but less continuity in population densities across larger spatial scales.

Across regions, growth rates were maximized when mean July temperatures were ~28°C. These findings reinforce previous research that demonstrates gypsy moth sensitivity to warmer temperatures. Exposure to supraoptimal temperatures has been found to affect larval developmental and spread rates (Thompson *et al.,* 2017; Tobin *et al.*, 2014), with a lethal supraoptimal temperature of ~32 °C (Thompson *et al.,* 2017). Logan *et al.* (1991) found that gypsy moth larvae experience optimal developmental rates when exposed to a consistent temperature of ~28 °C when using laboratory reared populations. Thompson *et al.* (2017) reported that populations along a latitudinal gradient respond differently to supraoptimal temperatures.

I observed the largest range in gypsy moth growth rates (–3.3 to 0.47), mean July temperature (19 to 34°C), and mean January temperatures (–30 to 10°C) in the northern region. Temperature consistency is integral in gypsy moth development, and temperature fluctuations as little as 1°C are known to change gypsy moth developmental rates and survivorship, especially when those fluctuations are on the margins of lethal sub- and supraoptimal temperatures (Thompson *et al.*, 2017, Bell 1995, Summers, 1922; Sullivan & Wallace, 1972). The northern region was also the only region that contained mean January minimum temperatures close to, and in some cases less than, the suboptimal lethal limits of gypsy moth (~ –28; Summers, 1922; Sullivan & Wallace, 1972). Perhaps not surprisingly, mean January temperatures <–20°C resulted in negative growth rates (Fig. 2.7, 2.8). I also found that increased January temperatures are associated with increased values of local spatial autocorrelation in gypsy moth growth rates. Given the wide range of temperatures in the northern region relative to the Midwestern and southern regions, the northern region has the potential to likewise display the most variable gypsy moth growth rates, and the degree to which local populations are clustered in space.

Growth rates within the southern portion of the invasion front were favored by warmer January temperatures. This is not surprising given that mild winters have been shown to be beneficial for egg survival (Madrid & Stewart, 1981), and because the southern region of the gypsy moth invasion front has minimum January temperatures above gypsy moth supercooling points (Table 2.1). However, it is interesting that the southern region displayed relatively consistent growth rates, in relation to mean July temperature, until ~30°C at which point they begin to climb despite being above supraoptimal temperatures (Fig. 2.8). The southern region displayed the smallest range in July maximum temperatures (28 to 32°C) and the largest and warmest range in January temperatures (-7 to 9 °C). It has been proposed that insect populations have the potential to display local adaptations across a range, and that this is most likely to occur in populations near range edges (Sexton *et al.,* 2009; Hill *et al.*, 2011). For example, Thompson *et al.* (2017) found that southern sourced populations of gypsy moth exhibited higher performance, in terms of 4th instar and pupal mass, at higher supraoptimal temperatures than did northern sourced populations. Tobin *et al.* (2014) also found that despite more frequent exposure to supraoptimal temperatures, gypsy moth larval and pupal development rates increased with higher summer temperatures. I found that local spatial autocorrelation in gypsy moth growth rates in the southern region increased with increasing January minimum temperature (Fig. 2.9), but decreased with increasing July maximum temperatures (Fig. 2.10). However, increased July maximum temperatures in the southern region were associated with increases in the range of spatial autocorrelation (Fig. 2.10). These findings suggest that nascent gypsy moth populations in the southern region are sensitive to supraoptimal temperatures, and that supra-optimal temperatures result in reduced local spatial autocorrelation in growth rates that are also spatially autocorrelated over a larger range.

Growth rates in the Midwestern region were not affected by January minimum or July maximum temperatures. The Midwestern region also displayed intermediate January (-16 to 9°C) and July (23 to 36°C) temperatures relative to the other regions in this study. In this study I found that increased January temperatures were associated with lower estimates of spatial autocorrelation range. Given that the winters in this area do not approach suboptimal lethal limits and July temperatures have a broad enough range to support populations below supraoptimal lethal limits, temperature regimes in this region might be mild enough such that they have little effect on gypsy moth survival and population growth rates. Sharov *et al.* (1998) found that in Michigan, which is an area that also contains winter and summer temperatures within suboptimal and supraoptimal limits, respectively, there are positive gypsy moth population growth rates and considerable rates of spread. Instead of temperature, growth rates within this region might be dependent upon other factors. The Midwestern region in which the gypsy moth in invading is not well forested related to the other regions, and furthermore this region contains the least amount of basal area of host plant species preferred by gypsy moth larvae (Morin *et al.*, 2005).

The broad range of host plant species associated with gypsy moth (Liebhold *et al.* 1995) is thought to buffer nascent gypsy moth populations in new environments, and may equip populations with a higher plasticity that might also provide a safeguard to environmental change. However, past research has shown that even in widely distributed generalist species, climate change can significantly impact insect population dynamics and distributional ranges (Uelmen *et al*., 2016; Parmesan & Yohe, 2003; Parmesan *et al*., 1999; Warren *et al*., 2001). Portions of North America that were previously thought to be too cold to sustain the gypsy moth populations, such as Minnesota (Gray 2004), now seem to be within the margin of climatic suitability (Tobin *et al*. 2016). The data from this study indicate that there are geographical differences in how temperature is affecting gypsy moth growth rates, and the spatial structure of those growth rates within expanding populations along the leading edge of the invasion front. Differential selection to temperature regimes across geographical ranges has been shown to occur because of variation in thermal performance within a species (Ayres & Scriber, 1994). Given the economic and ecological importance of gypsy moth, it is important to understand these relationships under condition of changing climates.

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Chapter 3. EFFECTS OF PRIMARY AND SECONDARY HOST FRAGMENTATION ON GYPSY MOTH GROWTH RATES ALONG AN EXPANDING POPULATION FRONT

3.1 ABSTRACT

The gypsy moth, *Lymantria dispar* (L.), is an invasive polyphagous folivore that can feed on > 300 host tree species. Despite this broad spectrum of potential hosts, there is much variation in defoliation rates across the eastern United States; this variation is believed to be a result of preferential feeding. Because of dispersal limitations, host suitability is not dependent on oviposition by females, but rather the probability of larvae to disperse and find suitable hosts. Research on various insect populations, which are reliant on host species, has found that the density of insect populations often depends on the spatial arrangement of hosts. Currently, most risk assessment models associated with gypsy moth account for basal area of preferred host species, but not secondary host species. Furthermore, the role of host fragmentation has not been addressed. I used gypsy moth trap catch data from 1999 to 2015 in combination with host plant inventory data to quantify the relationship between primary and secondary host fragmentation, and gypsy moth population growth rates in nascent populations across the expanding invasion front in the eastern United States. The findings highlight the important role that secondary host species can play in establishing gypsy moth populations, as most growth rates in all regions increased with reduced fragmentation in secondary hosts. I also observed that secondary hosts are unequally represented across the gypsy moth invasion front and in those areas where

secondary hosts are sparse, growth rates decrease. The inclusion of both primary and secondary host abundance, and the degree of host fragmentation, would improve the capability of risk assessment models in predicting gypsy moth invasion dynamics.

3.2 INTRODUCTION

The gypsy moth, *Lymantria dispar* (L.), is an invasive polyphagous folivore that can feed on more than 300 host tree species and has caused defoliation on ~376,420 km^2 since 1924 (USFS 2017). In addition to defoliating forests, gypsy moth populations alter carbon sequestration and nutrient cycling, biogeochemical conditions, and change the acid base status of containing catchments (Webb *et al.* 1995). Since its introduction from France to Medford, Massachusetts in 1869, the gypsy moth has established populations in all parts of the 19 Eastern States and the District of Columbia, or roughly one third of its potential habitat in the United States (Morin *et al.* 2005). Gypsy moth spread rates have varied through time and are bateelieved to fluctuate as a function of variation in host availability, frequency of human transport, federal management and temporal patterns (Liebhold *et al.* 1992, Liebhold & Tobin 2006; Tobin *et al.* 2007). Once populations are established, many affected areas are susceptible to reoccurring outbreaks that follow an 8 to 11 year cycle (Johnson *et al.* 2005; Haynes *et al.* 2009). These outbreak dynamics ultimately reduce tree growth and increase tree dieback. (Maloney *et al.* 2010). Because of the potential harm to forests, there have been a number of gypsy moth management programs since the first eradication attempt in the 1890s (Tobin & Blackburn 2007). Since 2000, the Slow-the-Spread program implemented by the United States Forest Service has reduced the overall rate of gypsy moth spread along its leading edge in the United States, while also providing one of the most comprehensive range-wide species distribution datasets in existence (Sharov & Liebhold 1998; Tobin & Blackburn 2007).

Gypsy moth range expansion along a population front does not strictly follow a reaction diffusion model, but rather, like many invasive species, follows a stratified diffusion model (Shigesada *et al.* 1995). This model of invasion is characterized by both long-range and short-range dispersal events (Hengeveld 1989). Female gypsy moths are winged but lack the ability of flight; therefore, gypsy moth range expansion is heavily reliant upon mechanisms such as larval crawling, windborne dispersal of first instars, and human transport (Elkinton & Liebhold 1990; Liebhold & Tobin 2006, Hajek & Tobin 2009). Long-range dispersal is often a result of accidental human transport of egg masses into uninfested yet susceptible areas (Liebhold & Tobin 2006; Hajek & Tobin 2009). Long-range dispersal plays an integral role in gypsy moth range expansion as it provides an opportunity for populations to expand well beyond the invasion front (Sharov & Liebhold 1998). However, the expansion of these less dense isolated populations are reliant upon short-range dispersal mechanisms such as first instar wind-borne movement and larval crawling, to ultimately coalesce with the main invasion front (Sharov & Liebhold 1998; Liebhold & Tobin 2008).

Research on various insect populations, which are reliant on host species, has found that occurrence and density of insect populations may depend on the area, isolation and quality of habitat patches (Biederman 2002; Hunter *et al.* 2002; Collinge 2000). In many cases, the immigration and emigration from habitat patches is affected by patch size and spatial distribution across the landscape (Connor *et al.* 2000; Cronin 2003). Grilli and Bruno (2007) observed that populations of *Delphacodes kuscheli*, a highly dispersive specialist agricultural pest, was affected by the distribution and condition of host patches. Host area, cohesion, connectivity and dominance of host patches have direct effects on the consuming insect populations (Grilli & Bruno 2007). In many cases, patches with greater host area yield higher population densities

(Denno *et al.* 1981). In species with high dispersal capabilities, there is a higher probability of patches being reached (Biederman 2002), but patch connectivity is a critical factor that affects patch occupancy and regional dynamics within isolated or patchy insect populations (Hanski, 1999). Those host patches which are isolated have been found to have low population densities, regardless of the dispersal quality of insects, because greater interpatch separation yields increased mortality rates associated with dispersal (Matter *et al.*, 2004). Grilli and Bruno (2007) also found that high population abundances were positively correlated with primary host plant dominance; this was a result of *D. kuscheli* increased fitness while feeding on primary host species (Biederman, 2002). The dominance of these host species within a stand also provides shelter for egg masses (Claridge *et al.* 1977), ample nutrition for larval development (Backus 1985), and consequently higher reproductive rates.

The probability of establishment of non-native species within a system is often directly dependent upon the size of the initial population and the ability of that species to disperse (MacArthur & Wilson 1967; Mollison *et al.* 1986). Less dense, nascent populations are often subject to strong Allee effects, which in turn affect the rate of spread (Lewis & Kareiva 1993; Tobin *et al.* 2007). An Allee effect refers to a decrease in the per capita growth rate of a population as a result of a reduction in cooperative interactions among individuals in small population sizes (Allee *et al.* 1949; Dennis 1989). Such interactions include anything that hinders adequate frequency of encounters between individuals that would otherwise facilitate population growth (Allee *et al.* 1949; Dennis 1989). Allee effects often impose population density thresholds, below which lower density populations often go extinct (Tobin *et al.* 2007). These Allee effects can be integral in populations that display a consumer-host dynamic. Although the Allee effect of mate-finding failure has been shown to play an essential role in the rate of spread and population growth of the gypsy moth (Contarini *et al.* 2009; Tobin *et al.* 2013), the demographic consequences of Allee effects may be influenced by other forms of density dependence within populations, such as interactions between different trophic levels (Courchamp *et al.* 1999).

Because female gypsy moths are unable to fly, host plant suitability is not directly influenced by ovipositing females (Lance & Barbosa 1982), who generally oviposit within 1–2 m from the site of adult emergence (Odell & Mastro 1980). This necessitates the location and selection of suitable host species by larvae through crawling or ballooning (Lance & Barbosa 1982). First instars are well adapted for dispersal having dorsal aerostatic and lateral aculminate hairs, which increase the surface area and aids in buoyancy and wind dispersal (Burgess 1913). Larval dispersal has been found to be directly related to host nutritional qualities, crowding dynamics, starvation and temperature (Leonard 1971). Lance and Barbosa (1982) found that larval dispersal events increase as the suitability of available foliage decreases. This is believed to be partially a product of nutritional experience of the maternal parent on egg quality and size (Rossiter *et al.* 1987). Females which consume more suitable host species produce egg masses with a higher mean egg size than those females that were raised on less suitable host species regardless of whether or not those females emerged from small or larger eggs themselves (Capinera & Barbosa 1976). Larvae that hatch from larger eggs with greater yolk content often display a greater tendency to disperse away from the population foci; furthermore, these larvae were also found to disperse greater distances despite being larger (Capinera & Barbosa 1976). Thus, gypsy moth larvae exhibit a behavioral or functional polymorphism reflected in egg size which varies, in part, as a function of host suitability (Capinera & Barbosa 1976; Barbosa & Capinera 1978). The rate of larval dispersal is also a function of crowding dynamics. Those females that feed on less suitable hosts produce greater amounts of eggs with a smaller mean egg size causing populations with high proportions of residents and non dispersants, usually yielding high core population density (Barbosa & Capinera 1978). When exposed to unfavorable hosts or lack of hosts, which often happens in high density populations due to intraspecific competition and therefore primary host depletion, dispersal by both large and small larvae increases significantly (Capinera & Barbosa 1976). Linde (1971) has suggested the occurrence of mass dispersal of gypsy moth larvae based on the lack of food or when the available food is unsuitable.

Despite the wide breadth of gypsy moth host species, there is much variation in defoliation rates throughout the eastern United States; this variation is believed to be a result of gypsy moth preferential feeding (Liebhold *et al.* 1994). Gypsy moth feeding may be divided into two phases: early larval feeding (instars 1 to 3), and late larval feeding (instars 4 to 5/6). Early larval feeding is initiated in the spring as gypsy moth eggs hatch, a process that typically extends over a three-week period (Stoyenoff 1993). Early-instars have more dietary limitations relative to late instars because the former are not metabolically adapted to process defensive chemical compounds such as alkaloids (Barbosa & Capinera 1978, Barbosa & Krisdchik 1987). Barbosa and Krisdchik (1987) found that host species in the field that were rejected by early instar dispersants were associated with alkaloids. Alkaloids are heterogeneous compounds characterized by the presence of nitrogen, usually in a ring structure (Pelletier 1983). Such defensive chemicals, when incorporated into the diets of gypsy moth larvae, produced reduced survival, increased developmental time, and reduced late-instar weight (Miller & Feeny 1983). Host suitability is also dependent upon host plant phenology. For example, the phenology of bud and leaf development of a potential host determines subsequent larval performance and whether or not feeding is pursued (Chilcote 1990). Therefore, a primary or preferred host species is defined as those species that displays a phenology that maximizes host biomass and digestibility at the time of gypsy moth egg hatching. Primary host species also usually lack alkaloid chemicals that gypsy moth larvae are not adapted to process metabolically. Synchronous phenology and the lack of alkaloids, often optimize larval growth and development rates as well as fecundity, survivability and size (Stoyenoff 1993; Stoyenoff *et al.* 1994b; Liebhold *et al.* 1995). Once an initial host plant has been accepted, larvae typically remain on it and feed for the first three instars (Doane & McManus 1981). At the end of the early feeding period, larvae show a change in feeding behaviors and begin to undergo a process known as host switching (Lance & Barbosa 1982). Most of the defoliation can be attributed to late instars that have the ability to consume additional host species due to their ability to detoxify certain compounds. Therefore, late instars often exhibit a broader diet (Barbosa & Capinera 1978). Using a mark and recapture study, Lance and Barbosa (1982) observed a good deal of intertree movement of late larvae within stands, even in endemic populations. They also found that larvae must undergo considerable amounts of larval crawling to sample acceptable foliage as they are incapable of wind dispersal. Larvae in mixed stands will often be exposed to foliage which varies suitability (Lance & Barbosa 1982). When a host of marginal suitability is encountered the larvae must decide to stay and feed upon the host, or risk further starvation and predation by crawling onto a different host (Lance & Barbosa 1982). Feeding on less suitable hosts often produces longer development time and lower fecundity (Barbosa & Greenblatt 1979). Stoyenoff (1993) found that not only did secondary host species affect larval development, relative growth rate and pupal weight, but also that different host species combinations optimize gypsy moth performance during different stages of the host switching process. For example, northern red oak, *Quercus* *rubra*, optimized gypsy moth larval fitness when serving as the first host, while quaking aspen, *Populus tremuloides*, optimized larval fitness when consumed as a second host; furthermore, feeding on *P. tremuloides* was found to produce females that were 1.5 times larger than those that did not switch to *P. tremuloides* (Stoyenoff 1993; Stoyenoff *et al.* 1994a; Stoyenoff *et al.* 1994b). Host combinations that optimize larval fitness throughout period of larval development, which typically lasts ~8 weeks, are integral in maintaining population size and growth because longer development times potentially expose larvae to mortality factors such as predators, parasites and pathogens for greater lengths of time (Beckwith 1976). Secondary or intermediate host species can therefore be defined as those that yield slower developmental rates, lower larval weights, lower fecundity and higher mortality rates for early instars (Stoyenoff 1993; Stoyenoff *et al.* 1994a; Stoyenoff *et al.* 1994b). Secondary hosts tend to be consumed in high-density populations or during later instars when primary hosts are no longer available or are scarce.

A considerable amount of research, yielding models of various levels of complexity, has been devoted to identifying attributes that quantify forest susceptibility to gypsy moth outbreaks. One of the more prominent attributes is the proportion of basal area within the stand classified as gypsy moth preferred host species (Herrick & Gansner 1986). A quantitative study conducted by Liebhold *et al.* (1994), which used historical defoliation rates, showed that forest susceptibility to outbreak defoliation rates were the greatest when the forest stands were composed of >20% of gypsy moth preferred host species. Although this relationship has been well studied in outbreak populations, the effect of host plant composition, including the proportion of primary and secondary host availability, on nascent populations is still poorly understood. Furthermore, most of the research on gypsy moth outbreak dynamics has been conducted at the spatial scale of the forest stand (Liebhold *et al.* 1994). In this study, I quantified the effects of primary and secondary host species density and fragmentation on nascent gypsy moth populations at a landscape scale. I hypothesized that the spatial distribution of primary and secondary hosts affects the rate of gypsy moth population growth rate along its leading invasion front.

3.3 MATERIALS AND METHODS

Spatial Scale

The spatial scale of this study encompassed the gypsy moth invasion front within the United States from 1999 to 2015, which included an area from Minnesota to North Carolina (Fig. 1). I subset the invasion front into three regions due to differences in regional range dynamics (Tobin *et al.* 2007), host coverage (Morin *et al.*, 2005), and temperature regimes (Gray 2004). The northern region (i.e., Michigan, Minnesota, and Wisconsin) of the invasion front has displayed range expansion through time and is relatively well forested with gypsy moth preferred host species (Figs. 3.1, 3.2 & 3.3). The Midwestern region (i.e., Illinois, Indiana, Iowa, and Ohio) of the invasion front has been characterized by a static range and poorly forested areas with lower estimated basal area of preferred gypsy moth host species (Figs. 3.1, 3.2 & 3.3). The southern region (i.e., Kentucky, North Carolina, Tennessee, Virginia and West Virginia) has been characterized with both range expansion, stasis, and retraction (Tobin *et al.* 2014). The southern range generally has the greatest area containing high estimates of forest cover and estimated basal area of preferred gypsy moth host species (Figs. 3.2 & 3.3).

Temperature Data

I obtained temperature data through the PRISM Climate Group (2016). This dataset contains climate data through the use of a broad range of monitoring networks and interpolates the data using a variety of modeling techniques; these data are available to the public at different spatial resolutions. Datasets are available from 1895 to the present and can be used to elucidate both long term and short term spatio-temporal climate patterns. To represent the effect of suboptimal temperatures to which diapausing eggs are exposed, and supraoptimal temperatures to which developing gypsy moth larvae are exposed (Logan *et al.* 1991, Tobin *et al.* 2014), I used annual mean January minimum and July maximum temperatures, respectively, at a resolution of 5 × 5 km over the gypsy moth invasion front (Fig. 3.1) for each year from 1999-2015 (PRISM Climate Group 2016).

Gypsy Moth Growth Rates

Gypsy moth growth rates were derived from monitoring data collected by the gypsy moth Slow-the-Spread program in which ~100,000 georeferenced pheromone-baited traps are deployed annually along and ahead of the gypsy moth population front (Tobin *et al.* 2012). I used data from 1999-2015 as these years generally contained a continuous trap grid across the entire invasion front. Because trap locations can shift from year-to-year, trap data from each year was interpolated using indicator kriging in GSLIB (Deutsch & Journel 1998) over a network of 5 × 5 km cells to generate a smooth surface. Growth rates were calculated for each 5 × 5 km cell. I focused on newly establishing populations; these were defined as populations with an initial interpolated value between >0 and <1 males/trap/cell. To ensure growth rates within cells were comparable among cells through time, the data was truncated to only include those cells that contained at least one value of 0 within the time sequence (1999-2015).

In my analysis of the effect of host distribution on gypsy moth growth rates, I also considered different stages of gypsy establishment. To do this, I subset the data using 4 population thresholds over the time sequence: (1) cells that achieved < 10 males/trap; (2) cells that achieved between 10 and 19 males/trap; (3) cells that achieved between 20 and 29 males/trap; and (4) cells that achieved ≥30 males/trap. Due to a small sample size in the Midwestern region at higher population thresholds, I merged subsets 2-4, yielding two subsets for the Midwestern region (< 10 males/trap and ≥ 10 males/trap). Growth rates from year t to t+1 were calculated for each individual 5 × 5 km cell and for each pair of years (*e.g.*, 1999 to 2000, 2000 to 2001, …, 2014 to 2015) according to:

$$Growth\ Rate = log_e\left(\frac{N_{t+1}}{N_t}\right), \tag{1}$$

where N_{t+1} and N_t are the interpolated values (males/trap) in the current and prior year, respectively.

Primary and Secondary Host Fragmentation

Forest inventory data were obtained from the U.S. Forest Service Forest Inventory Analysis (FIA) as an ArcGIS layer at a scale of 240 × 240 m (www.fia.fs.fed.us). In the eastern United States, these data are available for both private and federal lands. These inventories are typically conducted every 5-15 years and include more than 1,000 plots within each state (www.fia.fs.fed.us). All inventory data contains information about both the individual tree and whole plots. From this inventory, proportion basal area attributed by each tree species is available for each state within the gypsy moth invasion front. Using the above data set, tree species were classified into two categories based on Liebhold *et al.* (1995). The first category includes tree species classified as primary host species and the second category includes tree species classified as secondary host species. Common primary host tree genera in the current gypsy moth invasion front include aspen (*Populus* spp.), birch (*Betula* spp.), hawthorn (*Crataegus* spp.), larch (*Larix* spp.), oak (*Quercus* spp), and willow (*Salix* spp). Common secondary host tree genera include beech (*Fagus* spp.), elm (*Ulmus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), pine (*Pinus* spp.), and walnut (*Juglans* spp.). A previous study by Morin *et al.* (2005) provided an interpolated map of the basal area of gypsy moth preferred host species (Fig. 3.3). To complement this map, I interpolated a map of the basal area of gypsy moth secondary host species (Fig. 3.4).

I used FRAGSTATS 3.3 (McGarial *et al.* 2012) to estimate mean patch cohesion for the primary and secondary host species layers based upon FIA data compiled at a scale of 240 × 240 m. Mean patch cohesion across the network of 240 × 240 m cells was estimated at a 5 × 5 km resolution that could then be linked to both weather data and gypsy moth growth rates. The patch cohesion index quantifies the connectivity of a specific host type patch within the entirety of the landscape. Patch cohesion increases as the host type patch becomes more clumped or aggregated within the landscape. This index will approach 0 as a particular host type becomes more subdivided and less physically connected within the landscape. Patch cohesion index, PCI, is estimated according to:

$$\mathrm{PCI} = \left[1 - \frac{\sum_{j=1}^{n} p_{ij}}{\sum_{j=1}^{n} p_{ij}\sqrt{a_{ij}}}\right]\left[1 - \frac{1}{\sqrt{A}}\right]^{-1} \cdot (100), \qquad (2)$$

where p_{ij} is the perimeter of patch *ij* in terms of the number of cell surfaces, a_{ij} is the area of patch in terms of the number of cells, and A is the total number of cells within the landscape.

Spatial Autocorrelation Correction

I quantified spatial autocorrelation in gypsy moth growth rates across the network of 5 × 5 km cells in each region and population threshold for each pair of years from 1999 to 2015. Within each region, estimates of spatial autocorrelation were averaged across population thresholds. I used the ncf package (Bjørnstad 2012) in R version 3.4.2 (R Development Core Team 2015) to estimate spatial autocorrelation, $\bar{\rho}(\delta)$, based upon a nonparametric spatial covariance function according to:

$$\bar{\rho}(\delta) = \frac{\sum_{i=1}^{N}\sum_{j=i+1}^{N} G\left(\frac{\delta_{ij}}{h}\right)\rho_{ij}}{\sum_{i=1}^{N}\sum_{j=i+1}^{N} G\left(\frac{\delta_{ij}}{h}\right)}, \qquad (3)$$

where G is a kernel function with kernel bandwidth h, and ρ_{ij} refers to the correlation between a value of spatial location i and a value at spatial location j. Confidence intervals surrounding the nonparametric spatial covariance function were estimated using the 2.5 and 97.5 percentiles of a bootstrapped distribution based on 1000 replications (Efron & Tibshirani, 1993).

Correlograms indicated that gypsy moth growth rates were spatially autocorrelated up to a distance of ~100 km in the Midwestern and southern regions, and up to ~160 km in the northern region (Table 3.1, Fig. 3.5). Spatial autocorrelation in population growth rate was accounted for in subsequent generalized additive models by including the distance-weighted mean of the growth rate as a term in the model (Walter *et al.* 2014). Within the Midwestern and southern regions, points > 100 km were assigned a weight of zero. Within the northern region, points > 160 km were assigned a weight of 0. Otherwise, the weight (w_{ij}) was calculated based on the fitted relationship between autocorrelation and distance in each region according to:

Northern: $w_{ij} = 6.7 - 0.54 \cdot \log_{10}(5.445e^{4} + d_{ij})$; (4)

Midwestern: $w_{ij} = -0.16 - 0.94 \cdot \exp(-1.9e^{-5} + d_{ij})$; (5)

Southern: $w_{ij} = -4.4\, e^{-2} - 0.51 \cdot \exp(-1.6e^{-5} + d_{ij})$; (6)

where *dij* is the straight-line distance between the focal points *i* and *j* (Anselin & Bera 1998). The distance-weighted mean growth rate, $\bar{\lambda}_m$, was then calculated as:

$$\bar{\lambda}_m = \frac{\sum_{j=1}^{n} w_{ij}\lambda_j}{\sum_{j=1}^{n} w_{ij}}\,, \tag{7}$$

where λ_j are the mean growth rates within the previously defined spatial autocorrelaation neighborhood.

Statistical Methods

I used generalized additive models (GAMs) to assess the influence of primary and secondary host species basal area and cohesion on gypsy moth population growth rates of each population threshold in each region. GAMs combine properties of generalized linear models and additive models, allowing the replacement of linear regression coefficients with nonparametric smooth functions such as splines (Hastie & Tibshirani 1987). Using smoothed estimates for covariates is advantageous as it allows for the detection of nonlinear relationships, such as those between environmental covariates and aspects of gypsy moth population dynamics (Sharov *et al.* 1997; Haynes *et al.* 2012). In GAMs, smooth functions are penalized for increased nonlinearity to balance model fit and complexity. Temperature was included in the model by incorporating January minimum and July maximum temperatures averaged across the 15 years. Because past work has shown that gypsy moth spread can be related to the proportion of preferred host basal area (Sharov *et al.* 1999), I included interaction terms between primary and secondary host basal area, and primary host cohesion and secondary host cohesion as well as host basal area and corresponding cohesion. I used a backward selection protocol, based on Wood & Augustin (2002), to arrive at a parsimonious model for each population threshold for each region starting with the full model:

$$\lambda_m = s\left(\bar{\boldsymbol{\lambda}}_{\boldsymbol{m}}\right) + s(\mathbf{Jan\ min\ avg}) + s(\mathbf{July\ max\ avg}) + s(\mathbf{prim\ coh}) + s(\mathbf{sec\ coh}) + s(\mathbf{prim\ BA}) + s(\mathbf{sec\ BA}) \qquad (8)$$

$$+\boldsymbol{te}(\mathbf{prim\ coh}, \mathbf{sec\ coh}) + \boldsymbol{te}(\mathbf{sec\ BA}, \mathbf{prim\ BA}) + \boldsymbol{te}\ (\mathbf{sec\ coh}, \mathbf{sec\ BA}) + +\boldsymbol{te}\ (\mathbf{prim\ coh}, \mathbf{prim\ BA})\ \ ,$$

in which the growth rate was predicted by mean January minimum temperature $(\mathbf{Jan\ min\ avg})$, mean July maximum temperature $(\mathbf{July\ max\ avg})$, primary and secondary host cohesion $(\mathbf{prim\ coh}\ , \mathbf{sec\ coh})$, primary and secondary host basal area $(\mathbf{prim\ BA}, \mathbf{sec\ BA})$, the distance-weighted mean growth rate $\left(\bar{\boldsymbol{\lambda}}_{\boldsymbol{m}}\right)$ and interaction terms between basal area and cohesion. Within the full model, *s* indicates smooth spline functions of the covariates and *te* indicates a tensor product smooth. Following Wood & Augustin (2002), variables were removed from the model if: (1) the estimated degrees of freedom for that term were close to 1; (2) the confidence region for the smooth function included zero for all values of the independent variable; and (3) the generalized cross-validation (GCV) score for the full model decreases if the term is removed. GAMs were implemented using the mgcv package (Wood 2006) in R version 3.4.2 (R Development Core Team 2015).

3.4 Results

Model Parameterization

Distance weighted mean growth rate was the only variable that consistently met all criteria and was retained in all GAM models; details of all GAM models are presented in Table 3.2. January and July temperature were retained in most models, the exceptions being a few models in the southern region that corresponded to the intermediate ($10 \leq N < 20$ and $20 \leq N < 30$ males/trap) population thresholds. Each GAM retained at least one of two interaction terms. The model corresponding to the $10 \leq N$ population threshold in the Midwestern region was the only model to retain two interaction terms. The model corresponding to the lowest population threshold ($N < 10$ males/trap) within the Midwestern region was the only model display no significant interaction terms. The models corresponding to the $N < 10$ males/trap population threshold displayed some of the highest GCV values as well as some of the lowest adjusted R^2 values. In contrast, the models corresponding to the intermediate population thresholds ($10 \leq N < 20$ and $20 \leq N < 30$ males/trap) displayed some of the lowest GCV values and the highest R^2 values.

Gypsy Moth Growth Rates and Temperature

Mean estimates of gypsy moth growth rates by region and population threshold are presented in Table 3.3. Mean gypsy moth growth rate predictions based on the GAM models as well as observed growth rates in this study can be found in Figure 3.6. All growth rate estimates in all population thresholds corresponding to the northern (Tables 3.4-3.7) and Midwestern regions (Tables 3.8-3.9) were significantly affected by both January minimum temperatures and July maximum temperature. Growth rate estimates in all population thresholds within the southern region, except the lowest intermediate threshold ($10 \leq N < 20$ males/trap), were significantly affected by July maximum temperature (Tables 3.10-3.13).

Growth Rates at the Lowest Population Threshold ($N <10$ males/trap)

At the lowest population threshold, mean growth rates varied from 0.19 to 0.27, and this threshold also tended to have the most variable estimates of growth rates (Table 3.3). Growth rate estimates in the lowest population threshold were significantly affected by a primary and secondary host cohesion interaction in the northern (Table 3.4) and southern regions (Table 3.10). Within the northern region, estimates of growth rates were highest when primary host cohesion was < 50 and secondary host cohesion > 80 (Fig. 3.7). In contrast, estimates of growth rates within the southern region were highest when primary host cohesion > 50 and secondary host cohesion was > 80 (Fig. 3.7). Growth rate estimates of the lowest population threshold in the Midwestern region were only significantly affected by temperature (Table 3.8).

Growth Rates at the Lower-Intermediate Population Threshold (10 ≤ N < 20 males/trap)

Mean estimates of gypsy moth growth rates in the lower-intermediate population threshold varied from 0.23 to 0.66 (Table 3.3). This population threshold was the only population threshold to be significantly affected by a secondary host basal area and secondary host cohesion interaction in the northern (Table 3.5) and southern (Table 3.11) regions. Within the northern region, growth rate estimates were highest when secondary host cohesion was > 50 regardless of secondary host basal area (Fig. 3.8). For example, when secondary host basal area was < 10 m^2/ha, growth rates were high even at low values of secondary host cohesion (Fig. 3.8). Estimates of growth rates within the southern region were highest when secondary host basal area ranged from 15 to 25 m^2/ha and secondary host cohesion ranged from 70 to 80 (Fig. 3.8).

Growth Rates at the Higher-Intermediate Population Threshold (20 ≤ N < 30 males/trap)

Mean estimates of gypsy moth growth rates in the higher-intermediate population threshold varied from 0.25 to 0.56 (Table 3.3). Growth rate estimates corresponding to this population threshold in the northern (Table 3.6) and southern (Table 3.12) regions were significantly affected by a primary and secondary host cohesion interaction. The highest growth rate estimates within the northern region corresponded to primary host cohesion values > 60 regardless of secondary host cohesion (Fig. 3.9). If primary host cohesion was < 60, higher estimates of growth rates corresponded to secondary host cohesion values < 40 (Fig. 3.9). In contrast, the highest growth rate estimates within the southern region corresponded to secondary host cohesion values > 95 and primary host cohesion values < 90 (Fig. 3.9).

Growth Rates at the Higher Population Threshold (10 ≤ N) in the Midwest

Estimates of growth rates in the intermediate-higher subset within the Midwestern region were the lowest, having an average of 0.1, when compared to all other subsets in all other regions (Table 3.3). Growth rate estimates corresponding to this population threshold within this region were significantly affected by both a secondary host cohesion and secondary host basal area interaction and a primary host and secondary host cohesion interaction (Table 3.9, Fig. 3.10). Growth rates estimates were highest when secondary host cohesion values < 40 and secondary host basal area values > 10 m^2/ha (Fig. 3.10). When considering the primary and secondary host cohesion interaction, growth rate estimates were highest when primary host cohesion values were < 60 and secondary host cohesion values were > 50 (Fig 3.10).

Growth Rates at the Highest Population Threshold (30 ≤ N males/trap)

Mean estimates of gypsy moth growth rates in the highest population threshold varied from 0.21 to 0.77 (Table 3.3). Growth rate estimates corresponding to this population threshold in the northern (Table 3.7) and southern (Table 3.13) regions were significantly affected by a primary and secondary host cohesion interaction. Growth rate estimates within the northern region were highest when primary host cohesion was > 80 and secondary host cohesion < 40 or when secondary host cohesion was > 80 and primary host cohesion < 20 (Fig. 3.11). Growth rate estimates within the southern region were high when primary host cohesion ranged from 40 to 80 and secondary host cohesion < 90 (Fig. 3.11).

3.5 DISCUSSION

Across regions and regardless of population thresholds, except for a few (*i.e.* the highest and high-intermediate population thresholds in the northern region and the low-intermediate population threshold in the Midwestern region), growth rate estimates were the highest when secondary host cohesion was high (Figs. 3.5-3.8). These findings emphasize the important role that secondary host species have in supporting nascent gypsy populations. Secondary host species are known to be more likely to be fed upon in high-density populations, and especially outbreak populations (Liebhold *et al.* 1986). However, in this study, I observed that these secondary hosts can play an important role in facilitating gypsy moth population growth rates along its expanding population front. Previously, Stoyenoff (1993) reported that gypsy moth larvae consuming combinations of primary and secondary host species can optimize developmental rate. Furthermore, the findings from this study highlight the importance of the placement of those host species in space. Because of the dispersal limitations of adult females, host plant suitability is not directly influenced by ovipositing females (Lance & Barbosa 1982; Odell & Mastro 1980). This necessitates the location and selection of suitable host species by larvae through crawling or ballooning (Lance & Barbosa 1982). Indeed, Lance and Barbosa (1982) observed a good deal of intertree movement of late instars within stands, even in endemic populations.

The effect of secondary host species is further exemplified in the low-intermediate population threshold, in which growth rate estimates were significantly affected by both secondary host basal area and secondary host cohesion (Fig. 3.7). In the northern region, growth rate estimates were highest when secondary host cohesion was higher, while in the southern region there was a more balanced effect in which growth rate estimates were highest when secondary host basal area was 15 to 25 m^2/ha and secondary host cohesion was between 75 and 85. This might be a result of the southern region having a well-represented range of secondary host basal area (Fig. 3.5). The representation of secondary host basal area and cohesion within the southern range could allow for more variation across the landscape in terms of secondary host cohesion and basal area interactions, which could help maximize growth rate estimates within a range of secondary host basal area and cohesion.

Growth rate estimates pertaining to the Midwestern region were unique in that they could not be attributed to any one population threshold above the lowest population threshold because higher population thresholds were often not obtained. For example, the lowest population threshold accounted for ~88% of the data from the Midwestern region. Furthermore, growth rate estimates of the lowest population threshold were only significantly affected by temperature (Table 3.8). This is not surprising given that gypsy moth egg masses undergo an obligatory diapause during which they are sensitive to suboptimal temperatures (Gray *et al.* 2001; Gray *et al.* 2009). Furthermore, larvae and pupae are sensitive to supraoptimal temperatures, resulting in reduced developmental rates (Tobin *et al.* 2014; Thompson *et al.* 2017). In regions like the Midwest, which do not display high growth rates, these temperature fluctuations could have profound effects on gypsy moth populations across this region. Temperature is integral in gypsy moth development, and temperature fluctuations as little as 1°C can alter gypsy moth developmental rates and survivorship (Sullivan & Wallace, 1972; Bell 1996; Thompson *et al.* 2017). Higher growth rate estimates within the higher population thresholds in the Midwestern region corresponded to higher basal area and lower cohesion. Secondary host basal area, was relatively sparse in the Midwestern region (Fig. 3.5), except for some areas in Indiana and Illinois which displayed relatively high secondary host basal area and higher growth rate estimates (Fig. 3.6). Although spatial distribution of hosts is important, it is not a measurement of abundance. Because these species were sparse in the Midwestern region, it is possible that the abundance of secondary hosts was the limiting factor in this region as opposed to the spatial arrangement of those hosts.

The highest population threshold (i.e., areas that achieved at least 30 males/trap), within the northern and southern regions were significantly affected by primary and secondary host cohesion (Tables 3.7 and 3.13, respectively). High-density gypsy moth populations are more likely to display intraspecific competition, which results in primary host depletion and exposure to unfavorable hosts (Capinera & Barbosa 1976). Capinera & Barbosa (1976) reported that larval dispersal increased significantly with increased exposure to unfavorable hosts. Because ovipositing females do not fly, neonates within high-density populations are often forced to disperse to find suitable hosts (Barbosa & Capinera, 1978; Capinera & Barbosa 1976; Linde, 1971). Furthermore, early instars are particularly reliant upon primary host species due to diet limitations, mostly pertaining to their lack of ability to metabolically process alkaloids (Barbosa & Capinera 1978, Barbosa & Krisdchik 1987).

Risk assessment models associated with invading insect species, including gypsy moth, tend to focus on the basal area of preferred host species (Morin *et al.* 2005), as well as climatic constraints (Gray 2004). The data from this study indicate the importance of secondary hosts to establishing gypsy moth populations, as well as the spatial arrangement of secondary host species. This is especially the case in populations at intermediate densities. This study also provides evidence that secondary hosts are unequally represented across the gypsy moth invasion front (Fig. 3.4). Prior research on other insect species, which are reliant on host plant species, has observed that occurrence and density of insect populations may be a function of the distribution of those hosts across the landscape (Biederman, 2002; Hunter *et al.* 2002; Collinge, 2000). Host distribution is also important in nascent gypsy moth populations given their limited dispersal ability (Barbosa & Capinera, 1978; Capinera & Barbosa 1976; Linde, 1971). The inclusion of both primary and secondary host composition, and host fragmentation metrics, may improve the predictive capability of risk assessment models.

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Tables

Table 2.1: Mean January minimum and July maximum temperatures (± standard deviation) from 1999 to 2015 each region in the study (PRISM Climate Group 2015)

Region	Mean January Minimum (°C)	Standard Deviation of Average January Minimum (°C)	Mean July Maximum (°C)	Standard Deviation of Average July Maximum (°C)
Northern	-6.2	±2.2	27.2	±1.2
Midwestern	-1.0	±1.0	29.0	±0.6
Southern	2.7	±1.9	30.0	±1.8

Table 2.2: Estimates (±bootstrapped 95 % confidence intervals) of the local spatial autocorrelation in gypsy moth growth rates averaged across years within each portion of the invasion front.

Region	**Local Spatial Autocorrelation**	**95% confidence interval**	
		Lower (2.5%)	Upper (97.5%)
Northern	0.82	0.66	0.95
Midwest	0.77	0.37	1.31
Southern	0.49	0.25	0.81

Table 2.3: Estimates (±bootstrapped 95 % confidence intervals) of the local spatial autocorrelation in gypsy moth growth rates across the northern portion of the invasion front.

Year	**Local Spatial Autocorrelation**	**95% confidence interval**	
		Lower (2.5%)	Upper (97.5%)
1999-2000	0.991	0.93	1.05
2000-2001	0.997	0.83	1.11
2001-2002	0.968	0.80	1.10
2002-2003	0.951	0.82	1.06
2003-2004	0.967	0.86	1.07
2004-2005	0.527	0.45	0.64
2005-2006	0.988	0.93	1.09
2006-2007	0.932	0.78	1.05
2007-2008	0.799	0.71	0.90
2008-2009	0.986	0.88	1.06
2009-2010	0.920	0.83	1.02
2010-2011	0.772	0.67	0.91
2011-2012	0.879	0.75	1.03
2012-2013	0.759	0.69	0.86
2013-2014	0.876	0.78	0.95
2014-2015	0.850	0.75	0.97

Table 2.4: Estimates (±bootstrapped 95 % confidence intervals) of the local spatial autocorrelation in gypsy moth growth rates across the Midwestern portion of the invasion front.

Year	**Local Spatial Autocorrelation**	**95% confidence interval**	
		Lower (2.5%)	Upper (97.5%)
1999-2000	0.988	0.85	1.18
2000-2001	0.978	0.83	1.19
2001-2002	0.962	0.78	1.23
2002-2003	0.672	0.50	0.84
2003-2004	0.727	0.54	0.93
2004-2005	0.579	0.41	0.74
2005-2006	0.645	0.51	0.78
2006-2007	0.996	0.75	1.24
2007-2008	0.744	0.62	0.85
2008-2009	0.771	0.61	0.93
2009-2010	0.904	0.70	1.13
2010-2011	0.802	0.72	0.86
2011-2012	0.652	0.51	0.79
2012-2013	0.808	0.69	0.94
2013-2014	0.788	0.65	0.92
2014-2015	0.755	0.64	0.86

Table 2.5: Estimates (±bootstrapped 95 % confidence intervals) of the local spatial autocorrelation in gypsy moth growth rates across the southern portion of the invasion front.

Year	**Local Spatial Autocorrelation**	**95% confidence interval**	
		Lower (2.5%)	Upper (97.5%)
1999-2000	0.829	0.73	0.92
2000-2001	0.848	0.77	0.93
2001-2002	0.647	0.56	0.72
2002-2003	0.854	0.76	0.94
2003-2004	0.792	0.71	0.87
2004-2005	0.677	0.59	0.76
2005-2006	0.722	0.64	0.81
2006-2007	0.744	0.69	0.79
2007-2008	0.702	0.65	0.75
2008-2009	0.663	0.57	0.74
2009-2010	0.567	0.49	0.64
2010-2011	0.544	0.40	0.67
2011-2012	0.693	0.60	0.77
2012-2013	0.928	0.82	1.05
2013-2014	0.898	0.74	1.03
2014-2015	0.849	0.73	0.96

Table 2.6: Estimates (±bootstrapped 95 % confidence intervals) of the spatial synchrony in gypsy moth growth rates across all portions of the invasion front.

Region	**Synchrony**	**95% confidence interval**	
		Lower (2.5%)	Upper (97.5%)
Northern	0.79	0.78	0.81
Midwest	0.77	0.75	0.88
Southern	0.7	0.68	0.72

Table 2.7: Formula and estimates of the relationship between average annual January minimums °C and gypsy moth growth rates

Region	**Formula**	**p-value**	**Adjusted R^2**
Northern	$y=-0.35 + 2.00x - 2.29x^2 + 1.28x^3$	**0.001**	0.95
Midwest	$y=-0.079 + 0.27x$	0.206	0.21
Southern	$y=-0.01 + 0.48x$	**0.026**	0.68
Overall	$y=-0.16 + 1.95x - 2.01x^2 + 1.53x^3 - 0.86x^4$	**2.12×10^{-7}**	0.87

Table 2.8: Formula and estimates of the relationship between average annual July maximums °C and gypsy moth growth rates

Region	**Formula**	**p-value**	**Adjusted R^2**
Northern	$y=-0.11+ 0.86x -1.19x^2+ 0.76x^3$	**0.007**	0.82
Midwest	$y=-0.08 - 0.003x$	0.999	0.21
Southern	$y=0.11+ 0.13x +0.25x^2+ 0.18x^3$	**0.046**	0.72
Overall	$y=-0.02 + 0.59x+-0.88 x^2$	**0.025**	0.22

Table 2.9: Formula and estimates of the relationship between average annual July maximums and January minimums and local spatial autocorrelation in gypsy moth growth rates

Region	**Temperature Regime**	**Formula**	**p-value**	**Adjusted R^2**
Northern	Mean January Minimum	$y=-0.05 + 0.29x$	**0.02**	0.26
Northern	Mean July Maximum	$y=-0.05 - 0.03x$	0.82	0.07
Midwest	Mean January Minimum	$y=-0.09 + 0.22x$	0.11	0.68
Midwest	Mean July Maximum	$y=-0.09 - 0.07x$	0.65	0.05
Southern	Mean January Minimum	$y=-0.15 - 0.45x$	**0.056**	0.23
Southern	Mean July Maximum	$y=-0.15 - 0.35x$	0.10	0.1
Overall	Mean January Minimum	$y= -0.07 \cdot (exp(0.16 \cdot x))$	-	-
Overall	Mean July Maximum	$y=-0.1 - 0.02x$	0.9	0.02

Table 2.10: Formula and estimates of the relationship between average annual July maximums and January minimums and spatial autocorrelation range in gypsy moth growth rates

Region	Temperature Regime	Formula	p-value	Adjusted R^2
Northern	Mean January Minimum	$y=-160 - 108x$	0.09	0.14
Northern	Mean July Maximum	$y=-160 - 91x$	0.15	0.07
Midwest	Mean January Minimum	$y= -118 - 91x$	**0.005**	0.39
Midwest	Mean July Maximum	$y=-118 + 27.4x$	0.45	0.02
Southern	Mean January Minimum	$y=-150 + 50x$	0.41	0.02
Southern	Mean July Maximum	$y=-150 + 131.89x$	**0.014**	0.38
Overall	Mean January Minimum	$y= -138 - 2x$	**0.04**	0.11
Overall	Mean July Maximum	$y=-175 - 1.14x$	0.78	0.02

Table 3.1: Estimates (±bootstrapped 95 % confidence intervals) of the local spatial autocorrelation in gypsy moth growth rates within each portion of the invasion front.

Region	**Local Spatial Autocorrelation**	**95% confidence interval**	
		Lower (2.5%)	Upper (97.5%)
Northern	0.82	0.66	0.95
Midwest	0.77	0.37	1.31
Southern	0.49	0.25	0.81

Table 3.2: Whole GAM model statistics for each region and population threshold; variable specific statistics can be found in Tables 3-12.

Whole GAM model statistics for each region and population threshold; variable specific statistics can be found in Tables 3-12.

Region	**Population Threshold (males/trap)**	**Most parsimonious model**	**GCV**	**Adj. R^2**	**Deviance explained (%)**
Northern	N< 10	$\lambda_m = s(\bar{\lambda}_m)$ + *s* (jan min avg) + *s* (july max avg) + *s* (sec coh) +*te* (sec coh, prim coh)	0.19	0.36	37
Northern	10 ≤ N < 20	$\lambda_m = s(\bar{\lambda}_m)$ + *s* (jan min avg) + *s* (july max avg) + *te* (sec coh, sec BA)	0.01	0.77	79
Northern	20 ≤ N < 30	$\lambda_m = s(\bar{\lambda}_m)$ + *s* (jan min avg) + *s* (july max avg) + *te* (sec coh, prim coh)	0.01	0.67	73
Northern	30 ≤ N	$\lambda_m = s(\bar{\lambda}_m)$ + *s* (jan min avg) + *s* (july max avg) + *te* (sec coh, prim coh)	0.02	0.68	68
Midwestern	N< 10	$\lambda_m = s(\bar{\lambda}_m)$ + *s* (jan min avg) + *s* (july max avg) + *te* (sec coh, prim coh)	0.3	0.46	47
Midwestern	10 ≤ N	$\lambda_m = s(\bar{\lambda}_m)$ + *s*(jan min avg) + *s* (july max avg) +*s* (sec coh)+ *te* (sec coh, prim coh) + *te* (sec coh, sec BA)	0.008	0.74	77
Southern	N< 10	$\lambda_m = s(\bar{\lambda}_m)$ + *s*(jan min avg) + *s* (july max avg) + *s* (coh.prim) + *te* (coh.prim, coh.sec)	0.32	0.21	21
Southern	10 ≤ N < 20	$\lambda_m = s(\bar{\lambda}_m)$ + *s* (sec coh) +*te* (sec coh, sec BA)	0.16	0.91	93
Southern	20 ≤ N < 30	$\lambda_m = s(\bar{\lambda}_m)$ + *s* (july max avg) + *te* (sec coh, prim coh)	0.61	0.55	63
Southern	30 ≤ N	$\lambda_m = s(\bar{\lambda}_m)$ + *s*(jan min avg) + *s* (july max avg) +*s* (sec BA)+ *te* (sec coh, prim coh)	0.26	0.78	79

Table 3.3: Mean, standard deviation, and range of the estimated gypsy moth growth rate for each region and population threshold. N refers to the number of males/trap in the population threshold

Region	**Population threshold**	**Mean (λ_m)**	**SD (λ_m)**	**Range (λ_m)**
Northern	$N < 10$	0.27	±0.33	2.47
Northern	$10 \leq N < 20$	0.23	±0.18	0.83
Northern	$20 \leq N < 30$	0.25	±0.15	0.75
Northern	$30 \leq N$	0.21	±0.2	0.73
Midwestern	$N < 10$	0.21	±0.51	3.50
Midwestern	$10 \leq N$	0.10	±0.14	0.93
Southern	$N < 10$	0.19	±0.29	1.74
Southern	$10 \leq N < 20$	0.66	±1.13	7.52
Southern	$20 \leq N < 30$	0.56	±0.77	5.10
Southern	$30 \leq N$	0.77	±0.96	9.26

Table 3.4: Variable specific statistics for GAM model corresponding to the N < 10 population threshold within the northern region

Variable	**estimated df**	**F**	**p-value**
λ_m	8.4	177	< 0.001
January Minimum	6.8	2.1	0.03
July Maximum	5.8	3.8	< 0.001
Secondary Host Cohesion	4.8	3.6	< 0.001
<u>Interactions:</u>			
Primary Cohesion x Secondary Cohesion	10.03	3.1	< 0.001

Table 3.5: Variable specific statistics for GAM model corresponding to the $10 \leq N < 20$ population threshold within the northern region

Variable	**estimated df**	**F**	**p-value**
λ_m	8.6	25.4	< 0.001
January Minimum	7.9	6.2	< 0.001
July Maximum	7.9	6.1	< 0.001
Interactions:			
Secondary Basal Area x Secondary Host Cohesion	9.5	4.2	< 0.001

Table 3.6: Variable specific statistics for GAM model corresponding to the $20 \leq N < 30$ population threshold within the northern region

Variable	estimated df	F	p-value
λ_m	8.5	9.8	< 0.001
January Minimum	8.5	5.9	< 0.001
July Maximum	8.2	4.5	< 0.001
<u>Interactions:</u>			
Primary Cohesion x Secondary Cohesion	11.3	5.3	0.005

Table 3.7: Variable specific statistics for GAM model corresponding to the $30 \leq N$ population threshold within the northern region

Variable	**estimated df**	**F**	**p-value**
λ_m	8.7	424	< 0.001
January Minimum	8.5	3.6	< 0.001
July Maximum	8.8	8.7	< 0.001
Interactions:			
Primary Cohesion x Secondary Cohesion	8.8	3.9	< 0.001

Table 3.8: Variable specific statistics for GAM model corresponding to the N < 10 population threshold within the Midwestern region

Variable	estimated df	F	p-value
λ_m	8.3	172	< 0.001
January Minimum	4.1	2.7	0.01
July Maximum	7.3	2.3	0.01
<u>Interactions:</u>			
Primary Cohesion x Secondary Cohesion	7.5	1.3	0.2

Table 3.9: Variable specific statistics for GAM model corresponding to the $10 \leq N$ population threshold within the Midwestern region

Variable	estimated df	F	p-value
λ_m	8.4	63	< 0.001
January Minimum	3.9	2.5	< 0.001
July Maximum	5.4	4	< 0.001
Secondary Host Cohesion	7.6	3.4	< 0.001
Interactions:			
Primary Cohesion x Secondary Cohesion	8.8	3.1	< 0.001
Secondary Basal Area x Secondary Host Cohesion	8.6	1.2	0.002

Table 3.10: Variable specific statistics for GAM model corresponding to the N < 10 population threshold within the southern region

Variable	estimated df	F	p-value
λ_m	8.6	168	< 0.001
January Minimum	8.7	14	< 0.001
July Maximum	8.5	8.2	< 0.001
Primary Host Cohesion	7.1	2.2	0.02
<u>Interactions:</u>			
Primary Cohesion x Secondary Cohesion	3.1	7.4	< 0.001

Table 3.11: Variable specific statistics for GAM model corresponding to the $10 \leq N < 20$ population threshold within the southern region

Variable	**estimated df**	**F**	**p-value**
λ_m	8.8	169	< 0.001
Secondary Host Cohesion	3.3	2.7	0.02
<u>Interactions:</u>			
Primary Cohesion x Secondary Cohesion	6.3	1.7	0.09
Secondary Basal Area x Secondary Host Cohesion	11.4	1.2	0.01

Table 3.12: Variable specific statistics for GAM model corresponding to the 20 ≤ N < 30 population threshold within the southern region

Variable	**estimated df**	**F**	**p-value**
λ_m	5.6	13.1	< 0.001
July Maximum	8.1	2.8	< 0.001
<u>Interactions:</u>			
Primary Cohesion x Secondary Cohesion	11.03	3.6	< 0.001

Table 3.13: Variable specific statistics for GAM model corresponding to the 30 ≤ N population threshold within the southern region

Variable	estimated df	F	p-value
λ_m	7.6	145	< 0.001
January Minimum	7.1	10.1	< 0.001
July Maximum	8.9	10.2	< 0.001
Secondary Host Basal Area	5.6	2.6	0.007
Interactions:			
Primary Cohesion x Secondary Cohesion	5.9	2.45	0.01

FIGURES

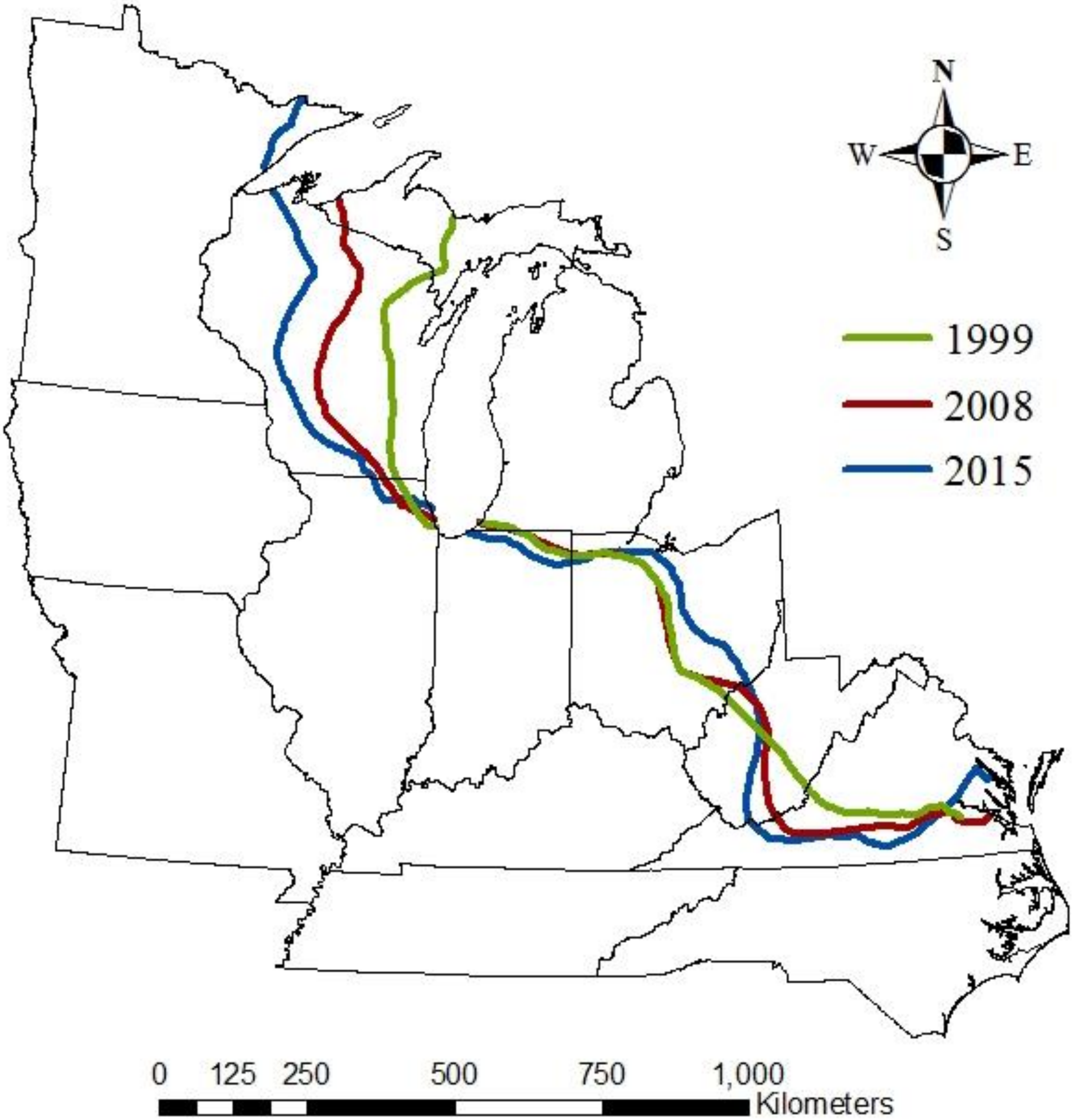


Figure 2.1: Range dynamics of the gypsy moth, based upon the 10-moth population abundance boundary in 2001, 2008 and 2015.

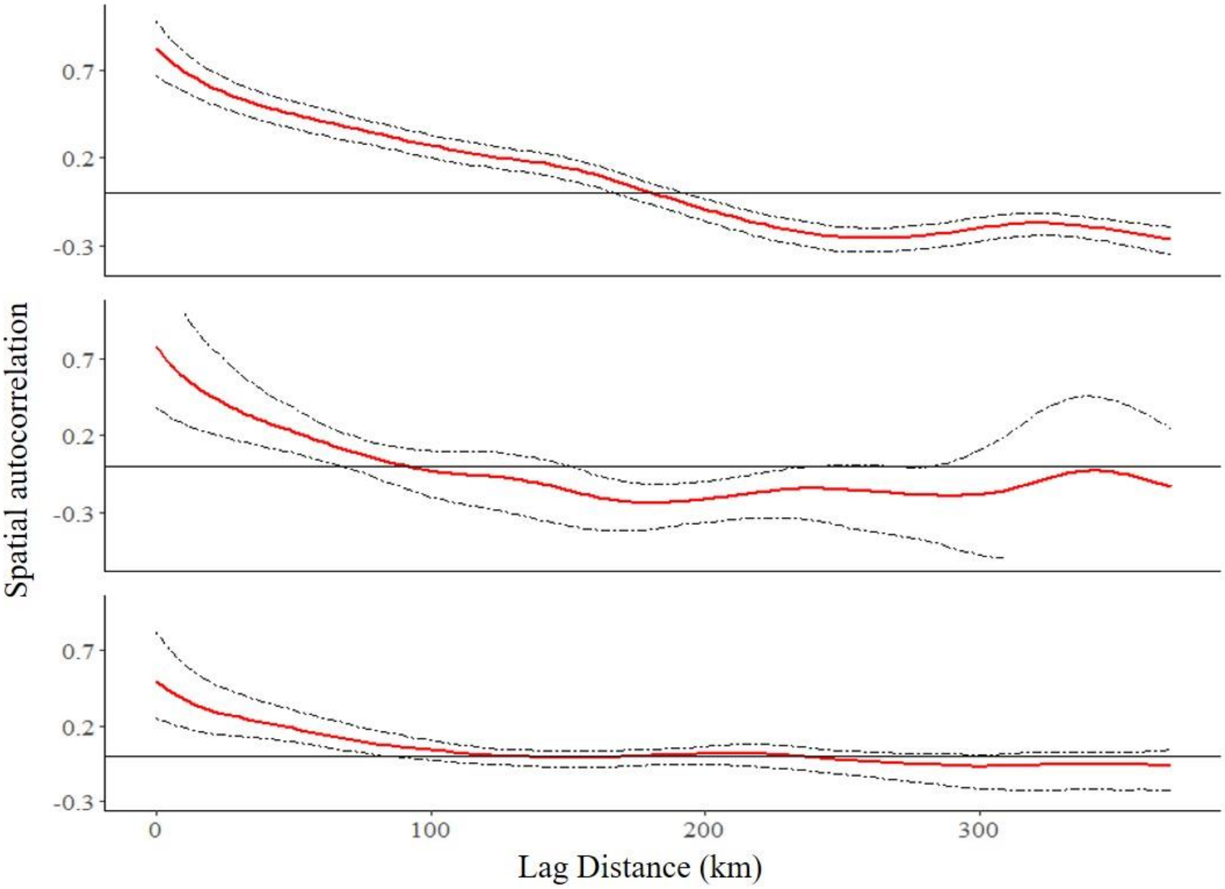


Figure 2.2: Spatial autocorrelation across years in gypsy moth growth rate within all portions of the invasion front with bootstrapped 95 % confidence intervals.

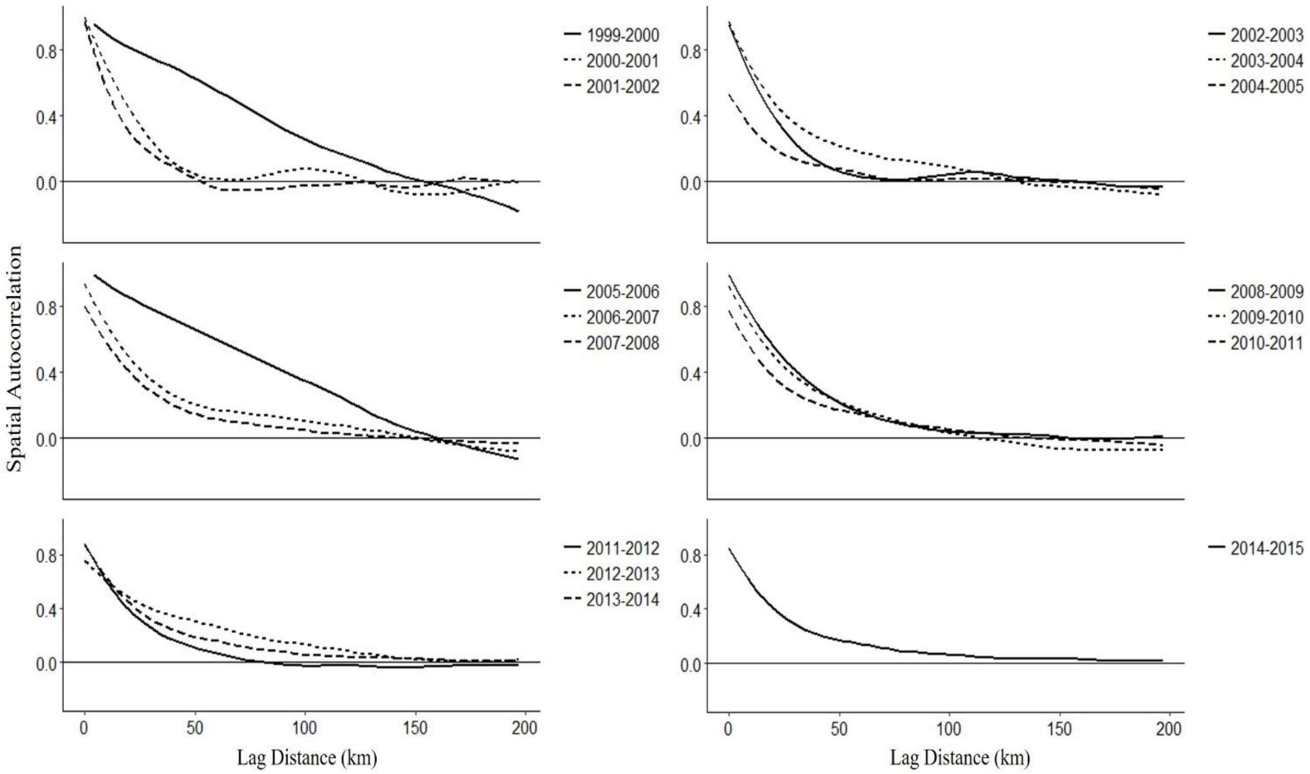


Figure 2.3: Spatial autocorrelation in gypsy moth growth rate within the northern portion of the invasion front. In each year pair, significant spatial autocorrelation was detected (bootstrapped 95 % confidence intervals are not shown; estimates of the local spatial autocorrelation and confidence intervals for all years, are shown in Table 2.3)

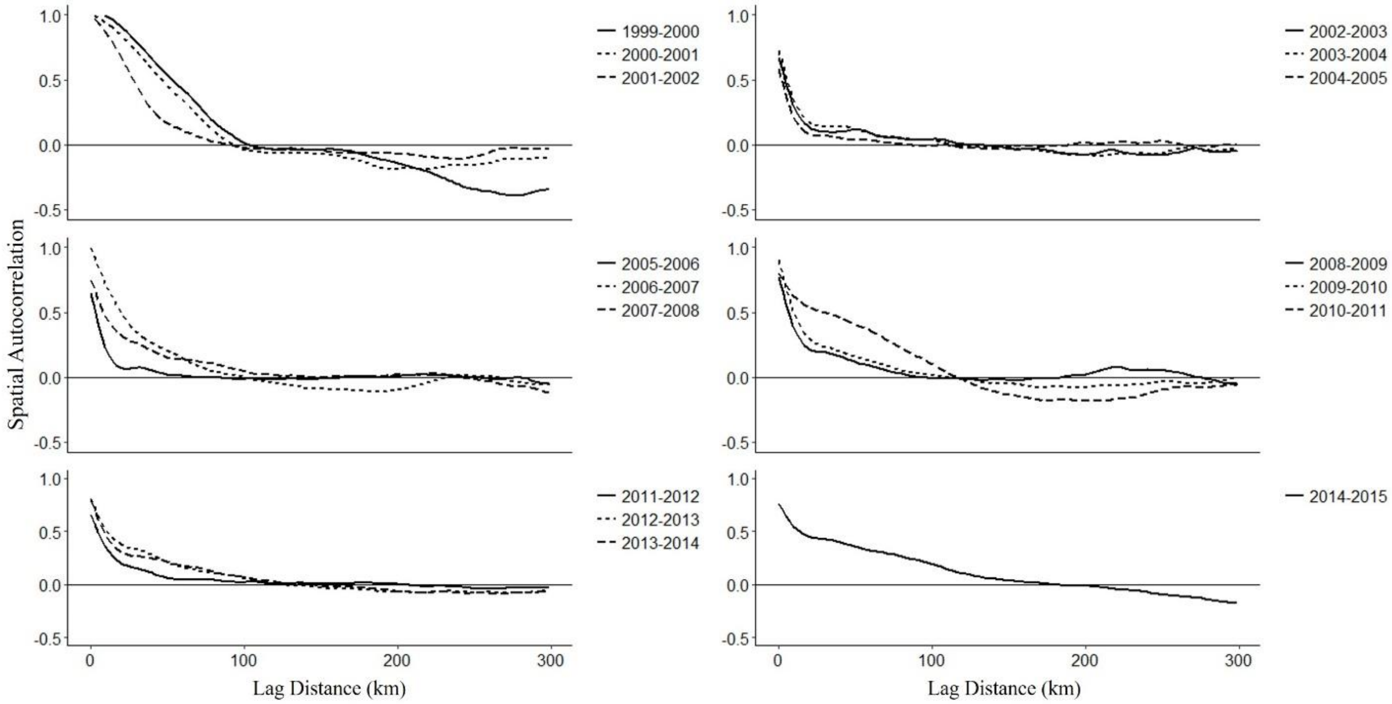


Figure 2.4: Spatial autocorrelation in gypsy moth growth rate within the midwestern portion of the invasion front. In each year pair, significant spatial autocorrelation was detected except for the year pairs of 2002-2003 and 2003-2004 (bootstrapped 95 % confidence intervals are not shown; estimates of the local spatial autocorrelation and confidence intervals for all years, are shown in Table 2.4)

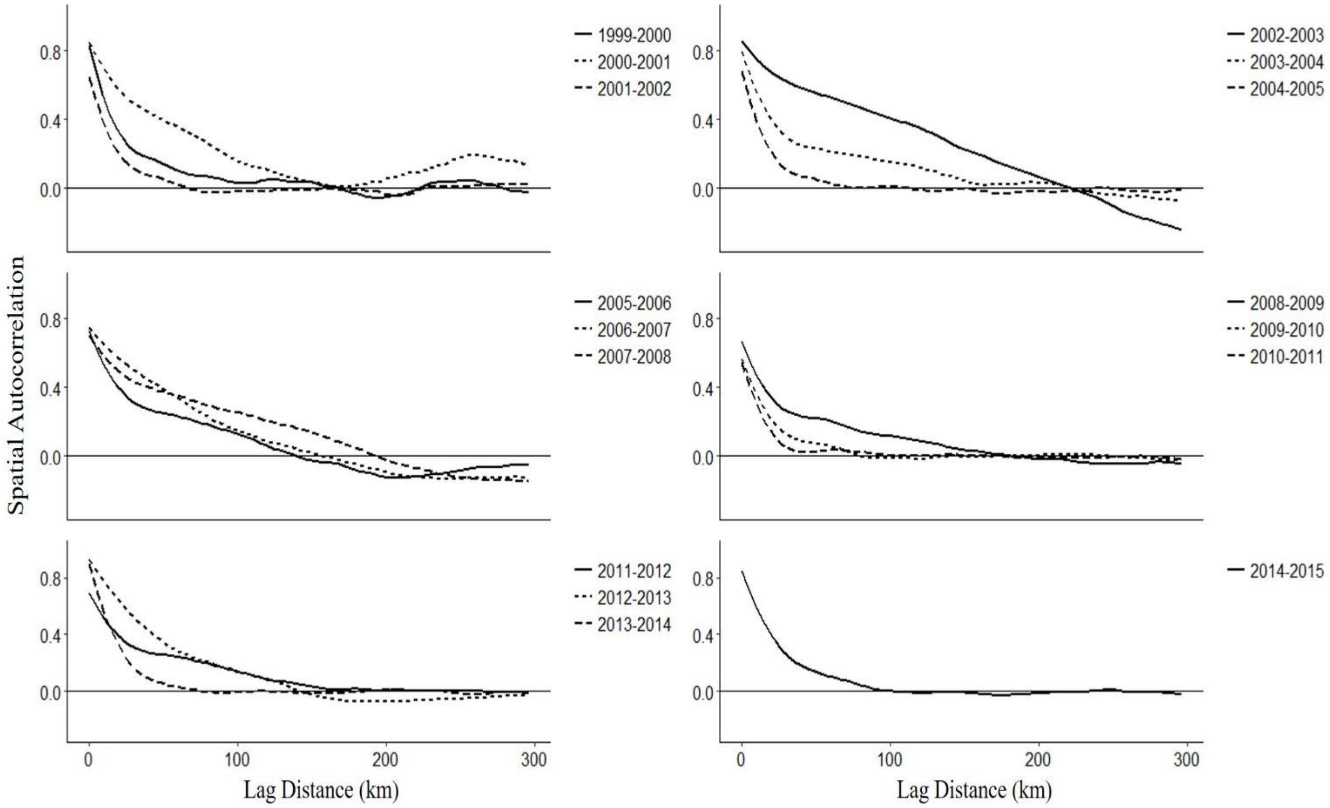


Figure 2.5: Spatial autocorrelation in gypsy moth growth rate within the southern portion of the invasion front. In each year pair, significant spatial autocorrelation was detected (bootstrapped 95 % confidence intervals are not shown; estimates of the local spatial autocorrelation and confidence intervals for all years, are shown in Table 2.5)

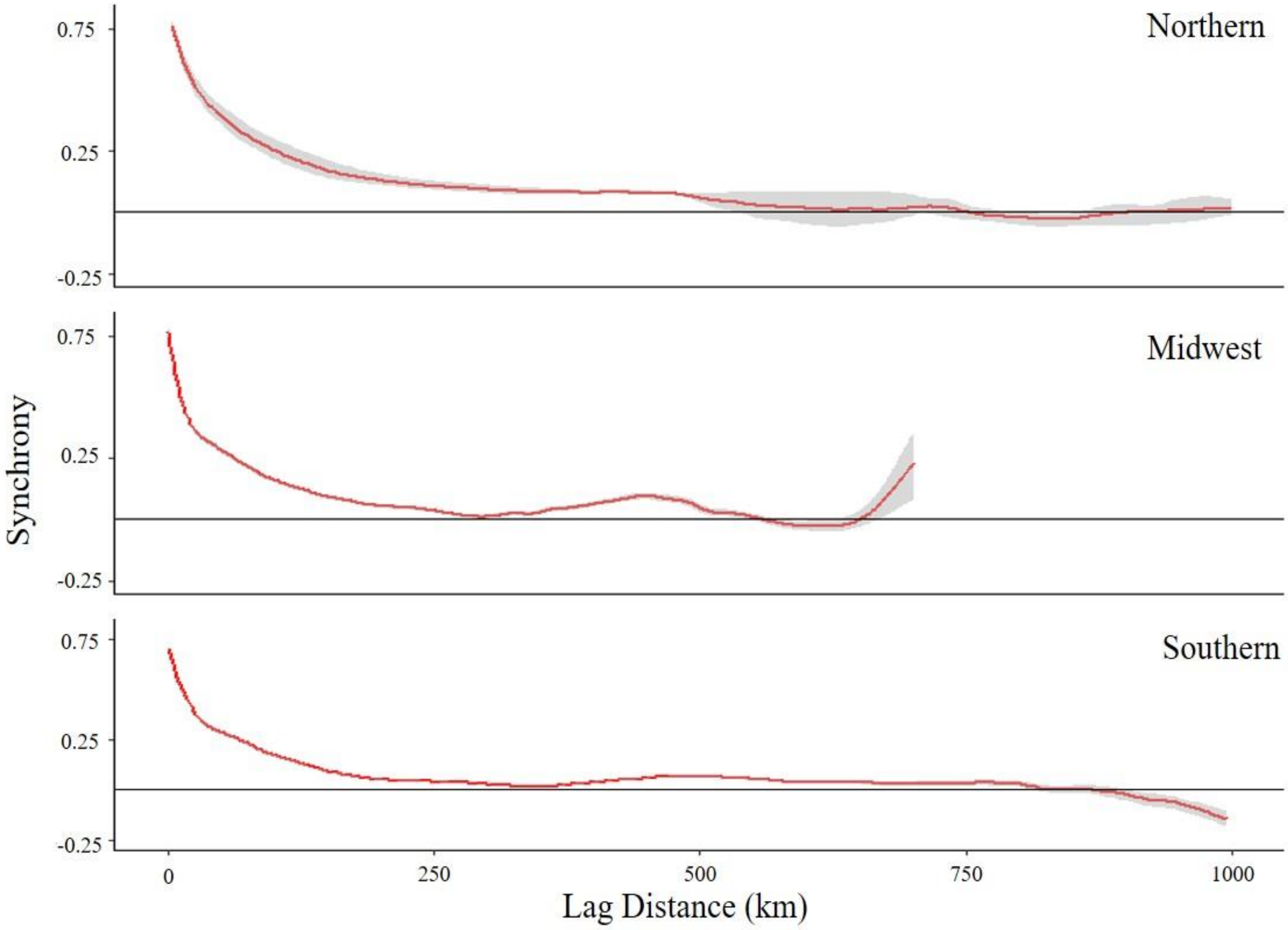


Figure 2.6: Spatial synchrony across years in gypsy moth growth rate within all portions of the invasion front in the United States with bootstrapped 95 % confidence intervals

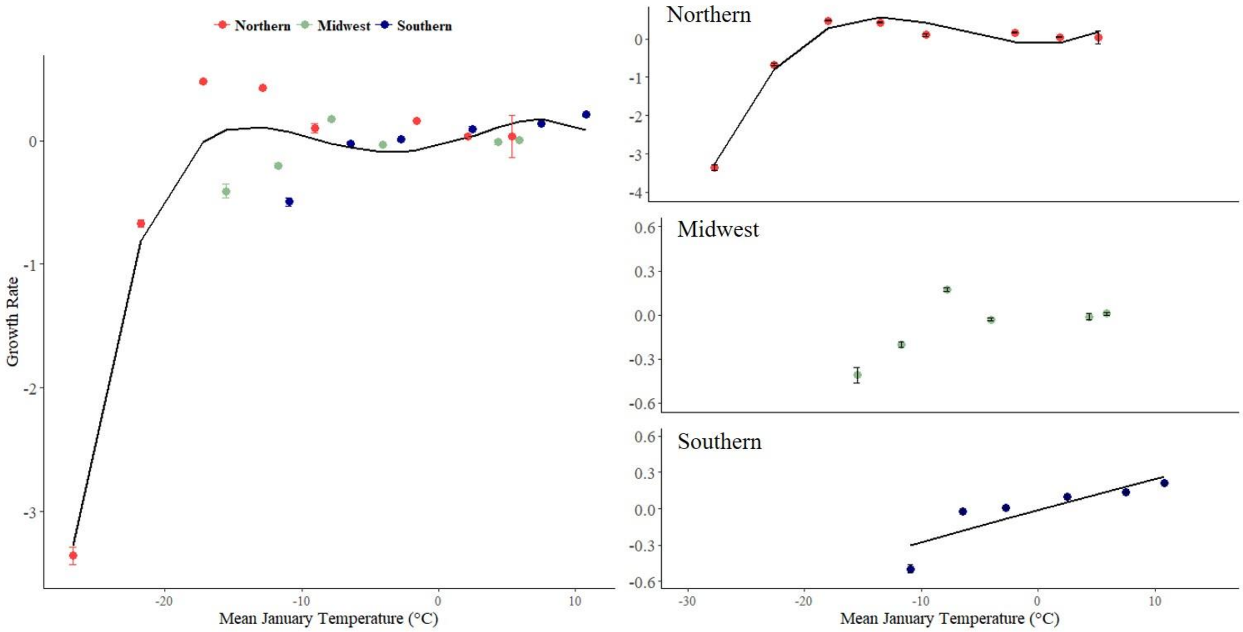


Figure 2.7: Relationships between mean annual January minimum temperatures and gypsy moth growth rates in all regions combined (left), and in each specific region (right). Model parameter estimates along with corresponding statistics are shown in Table 2.7.

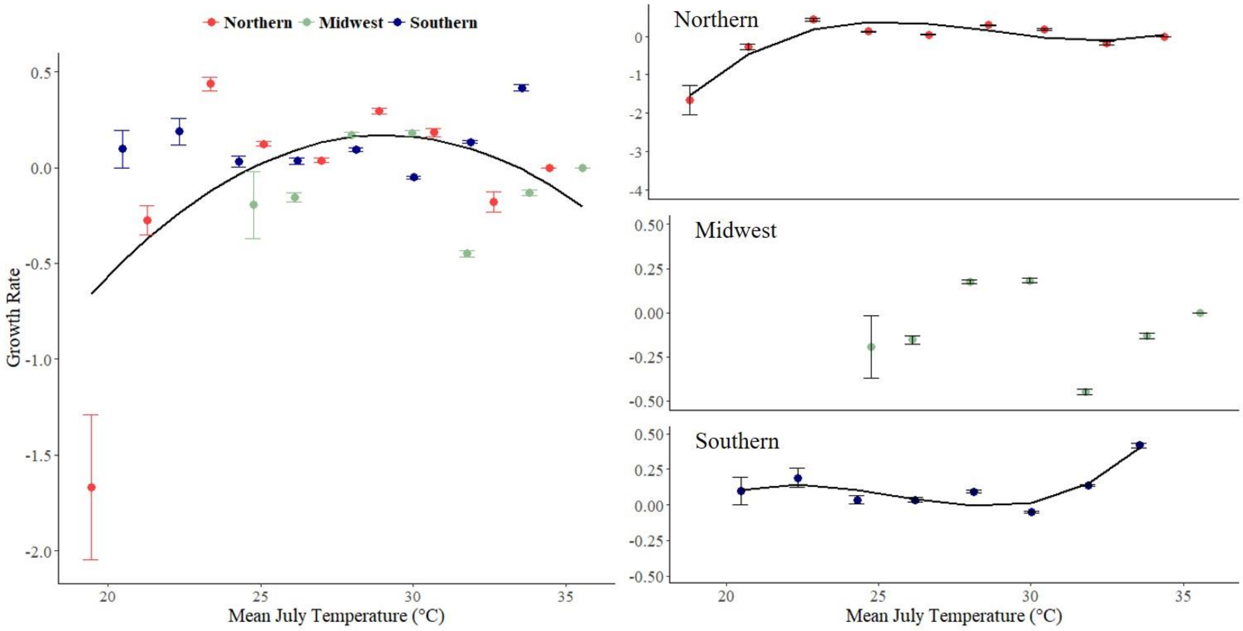


Figure 2.8: Predicted relationships between mean annual July maximum temperatures and gypsy moth growth rates, shown both regardless of region (left) and as a function of region (right). Formulas and parameter estimates along with corresponding statistics are shown in Table 2.8.

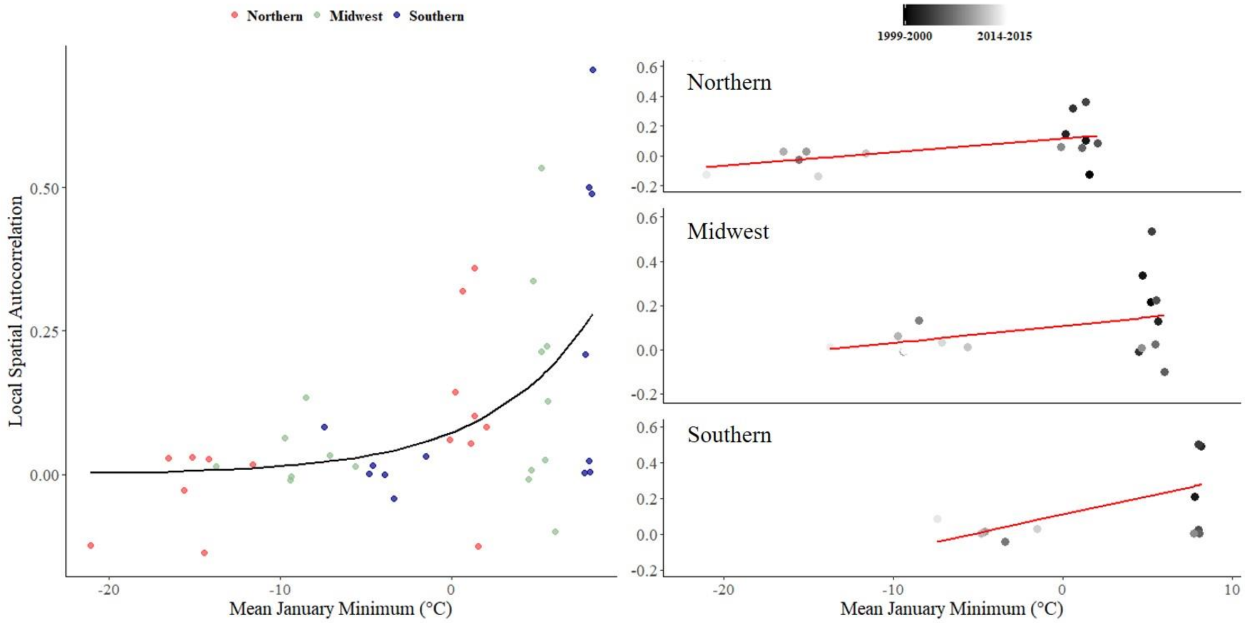


Figure 2.9: Relationships between local spatial autocorrelation in gypsy moth growth rates and mean January minimum temperatures across all regions (left), and in each specific region (right). Parameter estimates along with corresponding statistics are shown in Table 2.9.

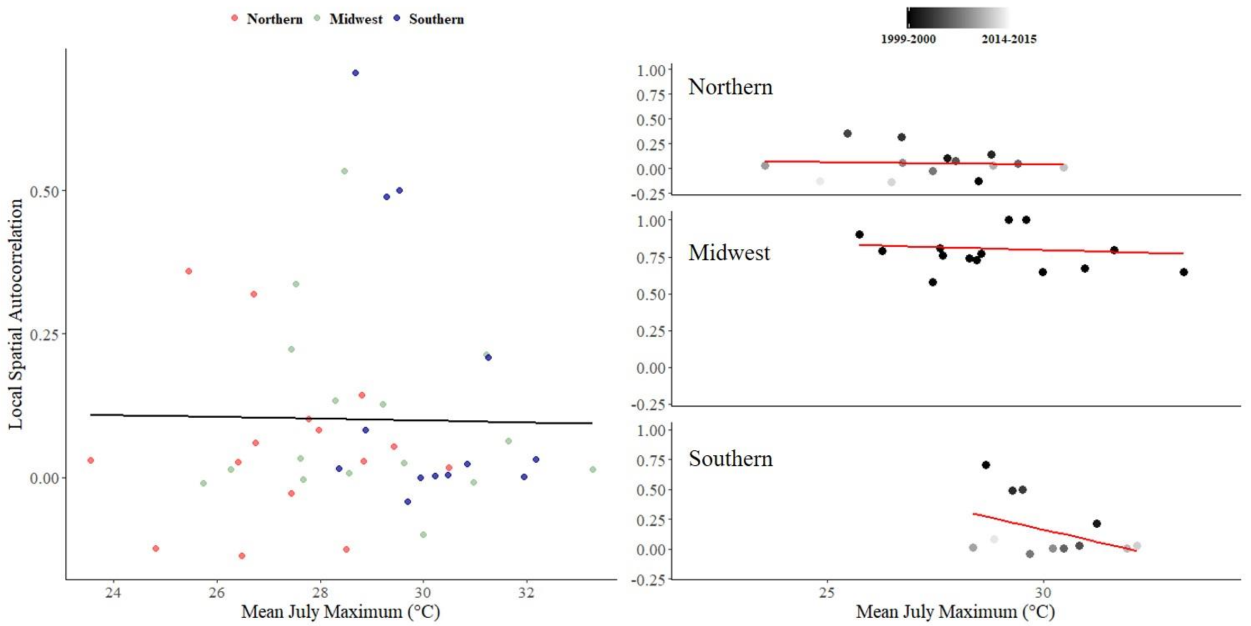


Figure 2.10: Relationships between local spatial autocorrelation in gypsy moth growth rates and mean July maximum temperatures across all regions (left), and in each specific region (right). Parameter estimates along with corresponding statistics are shown in Table 2.9.

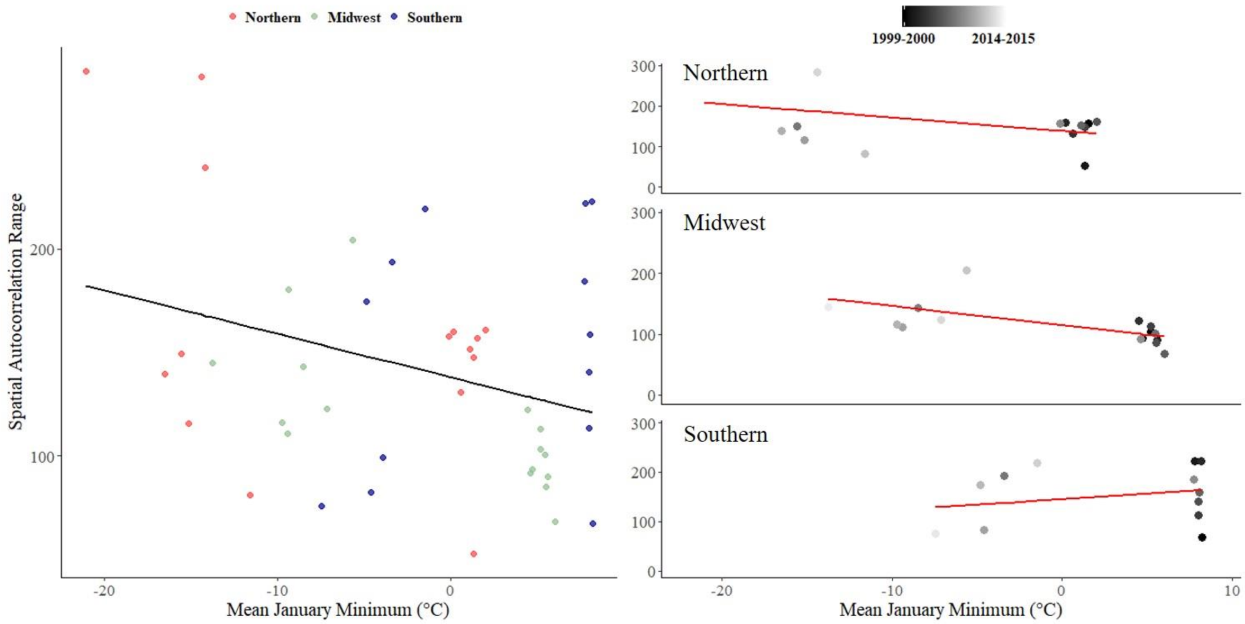


Figure 2.11: Relationships between local spatial autocorrelation range in gypsy moth growth rates and annual January minimum temperatures, shown both regardless of region (left) and as a function of region (right). Formulas and parameter estimates along with corresponding statistics are shown in Table 2.10.

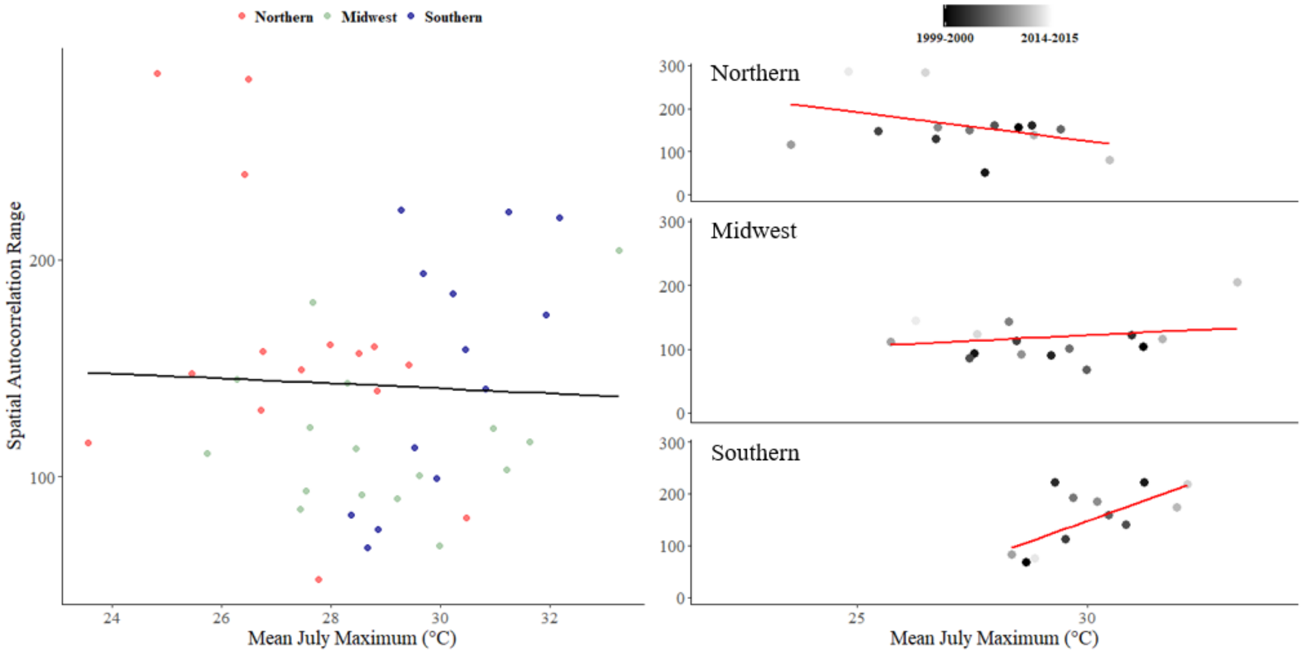


Figure 2.12: Predicted relationships between local spatial autocorrelation range in gypsy moth growth rates and annual July maximum temperatures, shown both regardless of region (left) and as a function of region (right). Formulas and parameter estimates along with corresponding statistics are shown in Table 2.10.

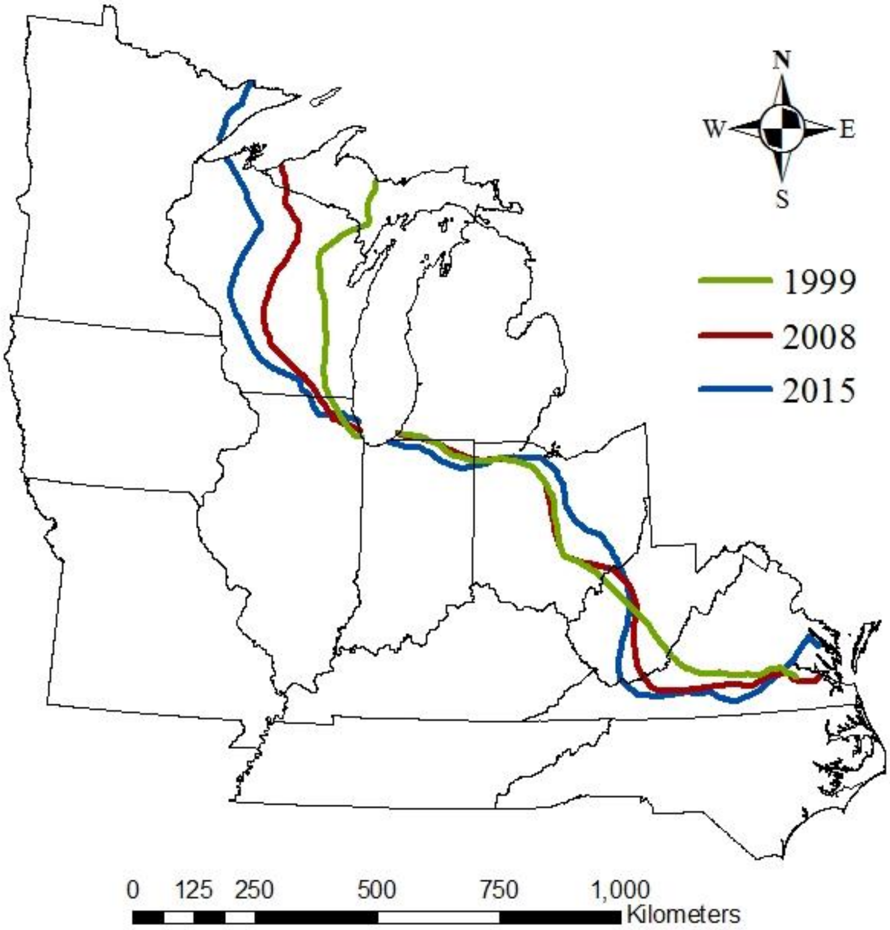


Figure 3.1: Range dynamics of the gypsy moth, based upon the 10-moth population abundance boundary in 2001, 2008 and 2015.

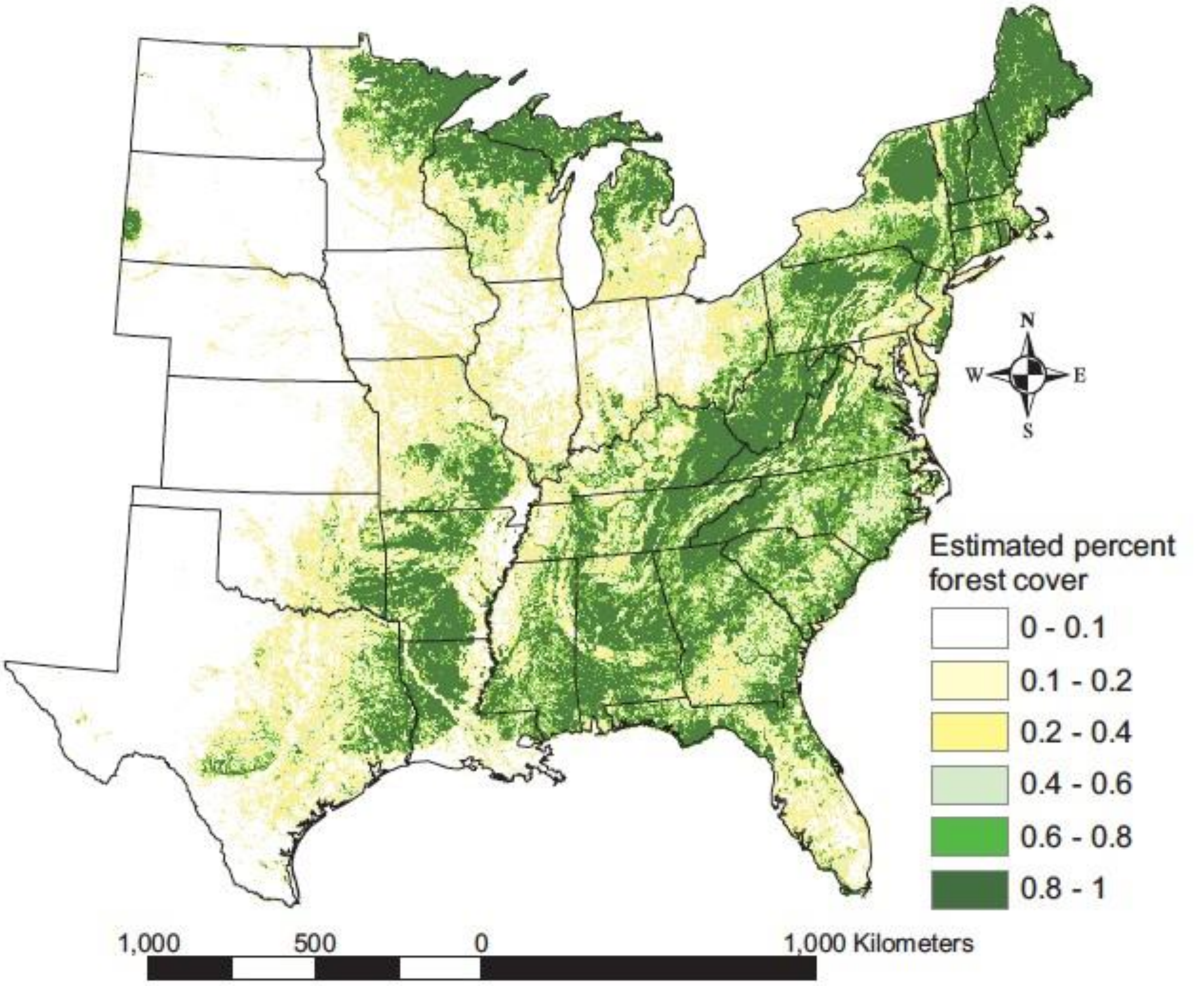


Figure 3.2: Estimated percent of forest cover across the eastern United States (from Morin et al. 2005).

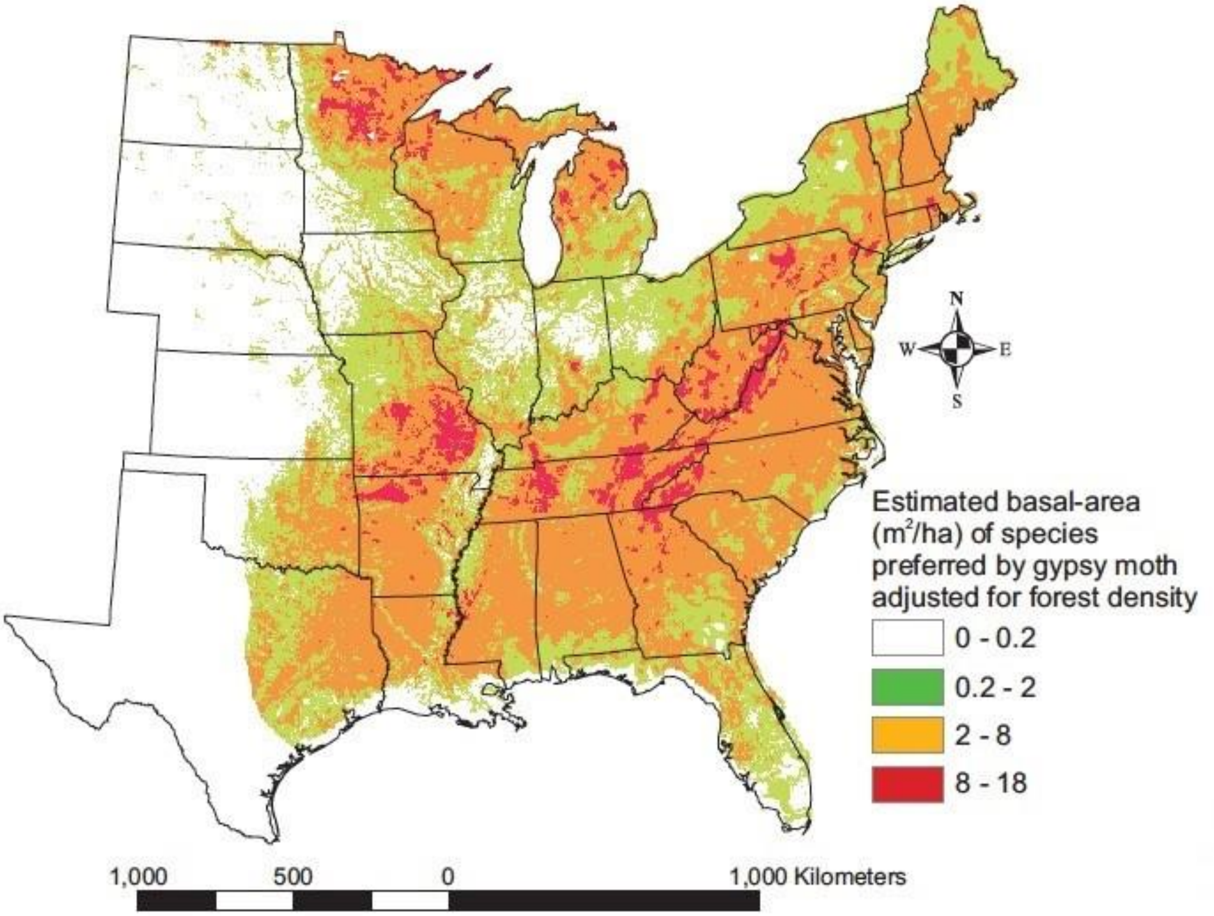


Figure 3.3: Estimated basal area of preferred gypsy moth host species cover across the eastern United States when adjusted for forest density (from Morin et al. 2005).

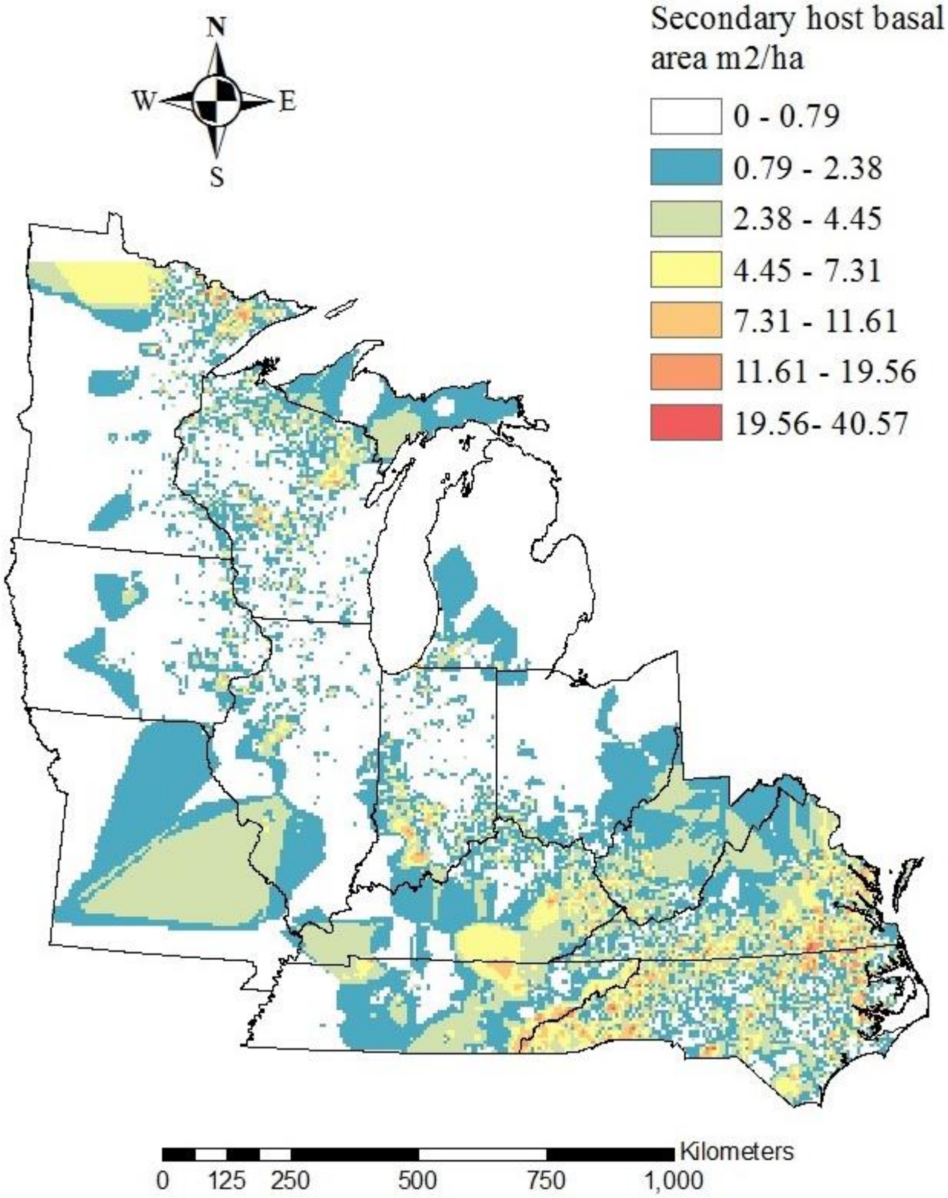


Figure 3.4: Estimated basal area (m2/ha) of secondary gypsy moth host species (based on Liebhold et al. 1995) across the eastern United States.

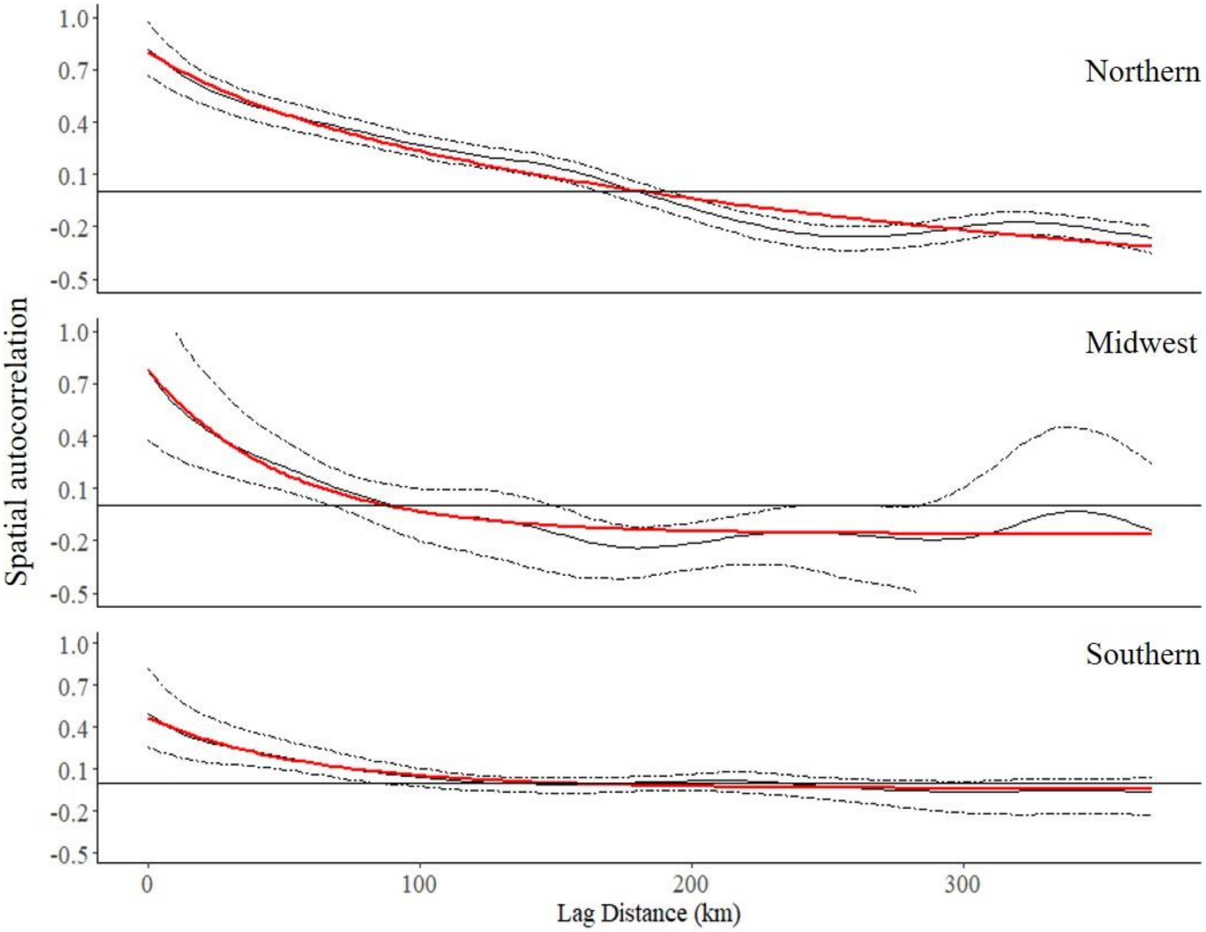


Figure 3.5: Spatial autocorrelation in gypsy moth growth rate in the northern, Midwestern, and southern regions (solid line; bootstrapped 95 % confidence intervals shown as dashed lines and corresponding spatial weight fit shown as the red line).

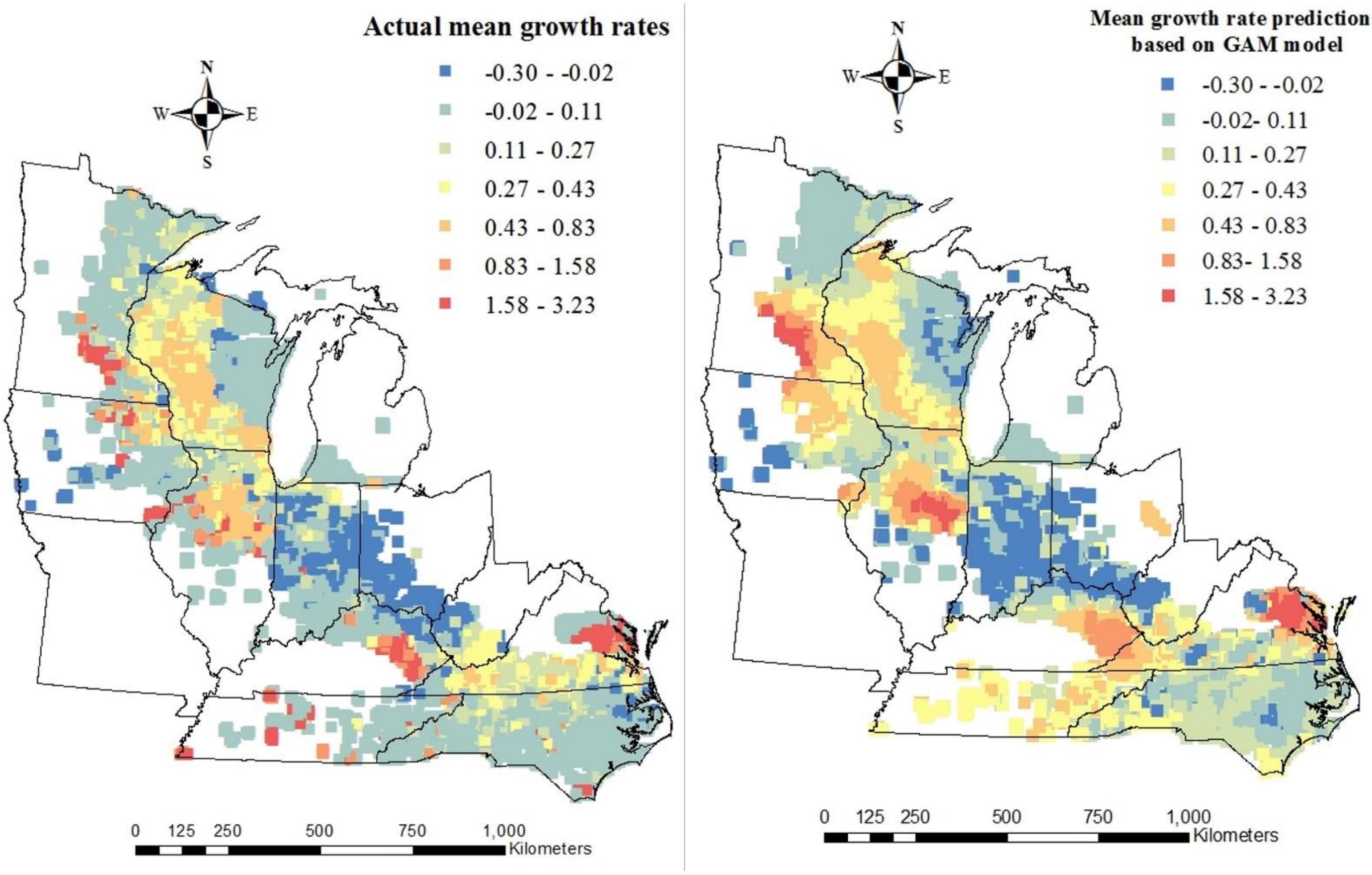
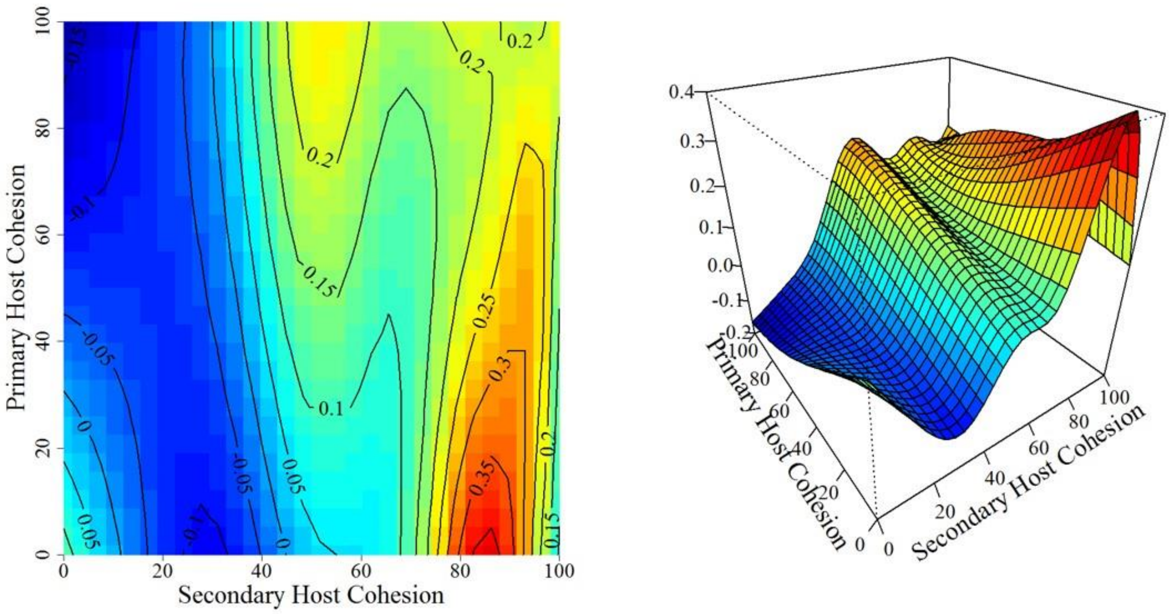
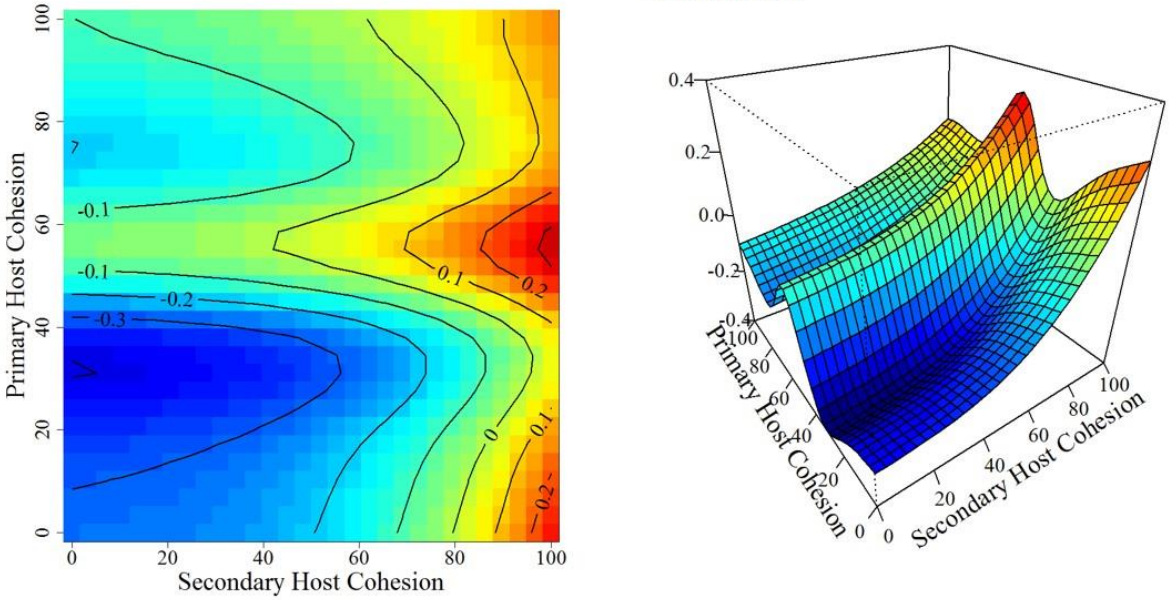


Figure 3.6: Maps displaying the actual observed mean growth rates (left) and the mean growth rates as estimated by the GAM models in this study (right) across the eastern United States.



Northern



Southern

Figure 3.7: Two-dimensional contour plots (left) with corresponding 3-dimensional surface plots (right) depicting mean gypsy moth growth rate (estimated from the GAM model) as a function of primary and secondary host cohesion at the N<10 population threshold in the northern and southern regions

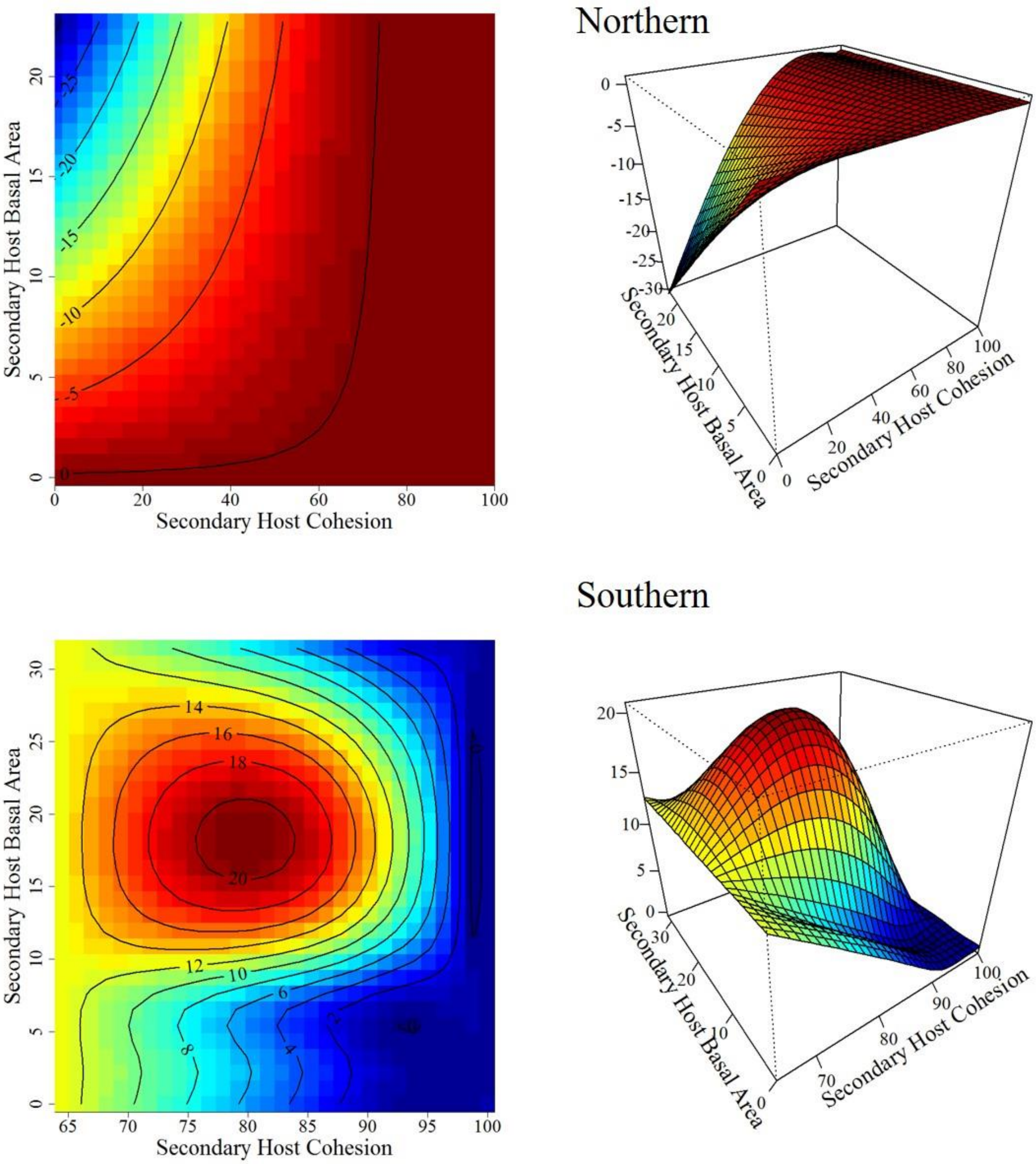
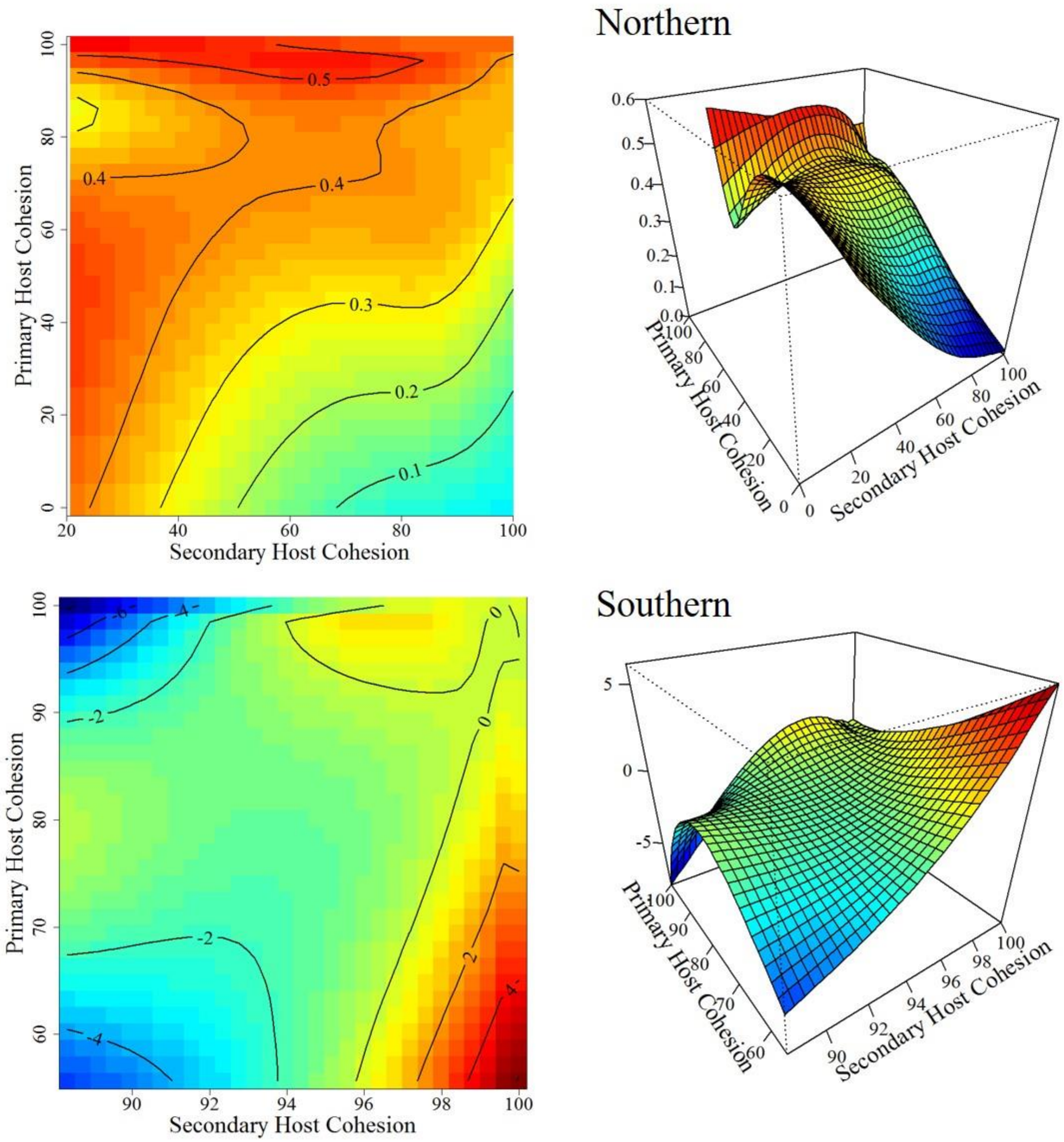


Figure 3.8: Two-dimensional contour plots (left) with corresponding 3-dimensional surface plots (right) depicting mean gypsy moth growth rate (estimated from the GAM model) as a function of primary and secondary host cohesion at the 10 ≤ N < 20 population threshold in the northern and southern region.



Northern

Southern

Figure 3.9: Two-dimensional contour plots (left) with corresponding 3-dimensional surface plots (right) depicting mean gypsy moth growth rate (estimated from the GAM model) as a function of primary and secondary host cohesion at the 20 ≤ N < 30 population threshold in the northern and southern regions.

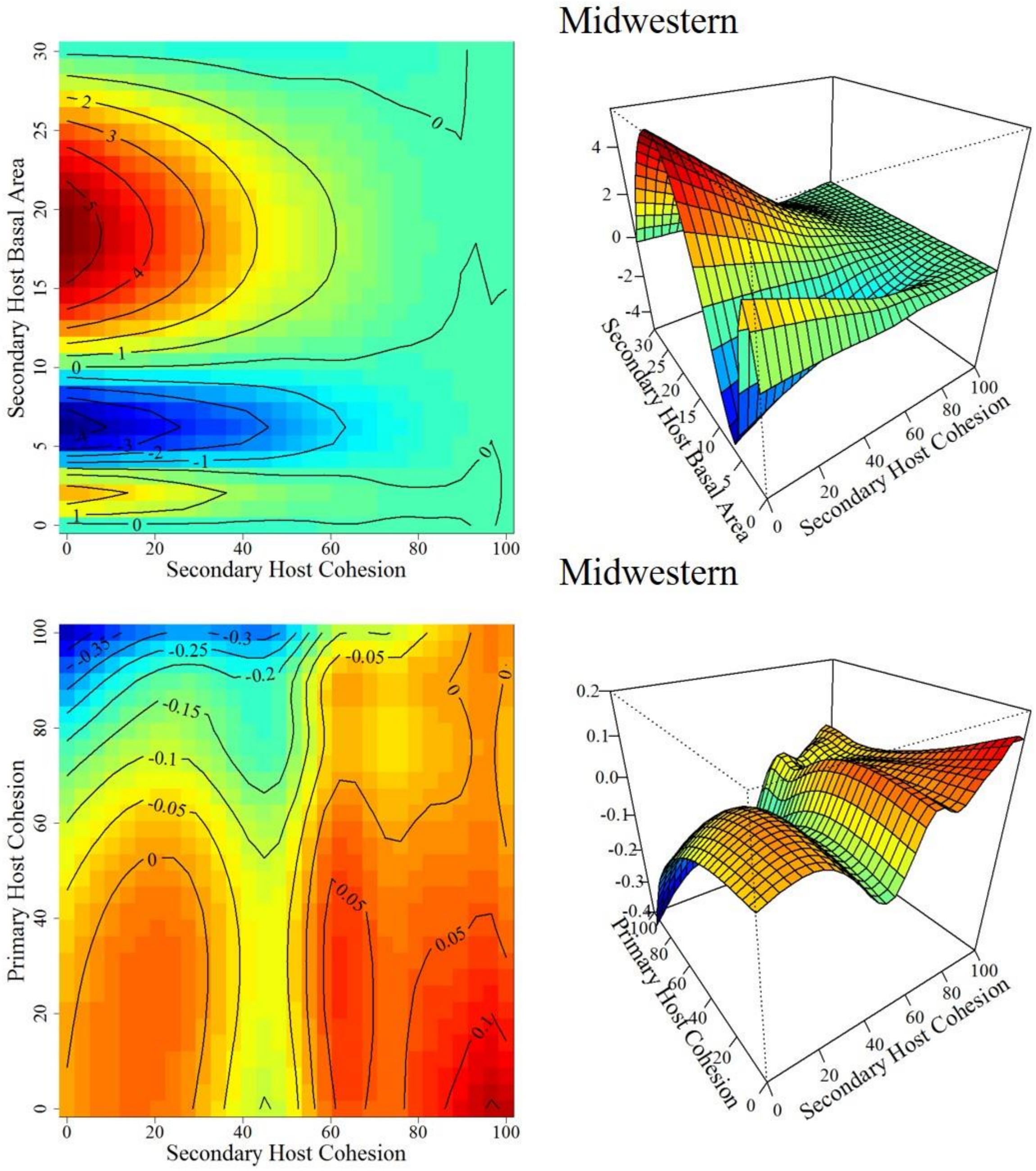


Figure 3.10: Two-dimensional contour plots (left) with corresponding 3-dimensional surface plots (right) depicting mean gypsy moth growth rate (estimated from the GAM model) as a function of primary and secondary host cohesion at the 10 ≤ N population threshold in the Midwestern region.

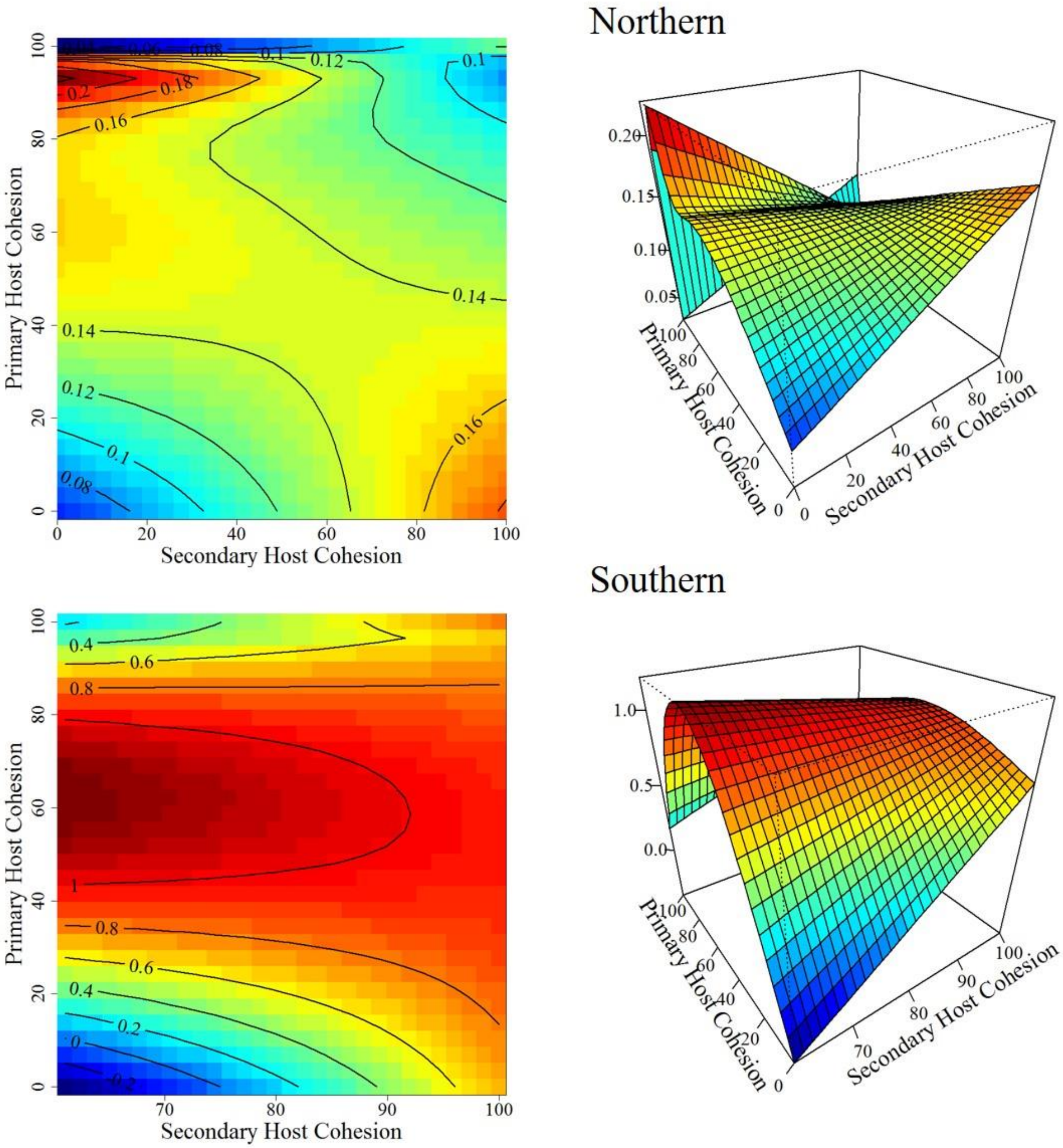


Figure 3.11: Two-dimensional contour plots (left) with corresponding 3-dimensional surface plots (right) depicting mean gypsy moth growth rate (estimated from the GAM model) as a function of primary and secondary host cohesion at the 30 ≤ N population threshold in the northern and southern regions.