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All quiet on the western front? Using phenological inference to detect the presence of a latent gypsy moth invasion in Northern Minnesota

Patrick C. Tobin · Kimberly Thielen Cremers · Lucia Hunt · Dylan Parry

Abstract Following establishment in a new environment, invasive species expand their range through stratified diffusion, the coupling of local growth and spatial spread with long-distance movement of propagules that found new colonies. Consequently, the stages of arrival and establishment serially repeat until the entire habitat susceptible to invasion is occupied. An empirical example of such a phenomenon is the gypsy moth, *Lymantria dispar* (L.), invasion of northeastern Minnesota. Under a regional management program, a trapping grid is deployed along the *L. dispar* leading edge to detect male moth presence and inform management decisions. However, the presence of moths does not always indicate reproducing populations, and moths dispersing from populations behind the front can obscure the presence of latent invasions. We analyzed trapping data during the arrival and establishment of *L. dispar* in this region (2000–2012), supplemented with sentinel trap data to ascertain the timing of male moth flight (2005–2009), and derived yearly phenological predictions for male moth flight. We also used a male wing morphology metric (2007–2009) to further quantify spatial and temporal patterns associated with the *L. dispar* invasion. We provide evidence of an established *L. dispar* population when analyses suggest spatial randomness in trap catch data, and how the presence of phenologically distinct, immigrating adult moths from source populations outside of Minnesota recorded from sentinel traps could lead to the overestimation of the abundance of an established population. This work highlights the complexity of the initial invasion process even in a well-studied system for which a sensitive monitoring program exists.

Keywords Establishment · *Lymantria dispar* · Spread · Stratified dispersal

P. C. Tobin (✉)
School of Environmental and Forest Sciences, University of Washington, 123 Anderson Hall, 4000 15th Avenue NE, Seattle, WA 98195-2100, USA
e-mail: pctobin@uw.edu

K. T. Cremers · L. Hunt
Plant Protection Division, Minnesota Department of Agriculture, 625 Robert Street North, St. Paul, MN 55155, USA

D. Parry
College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA

Introduction

The arrival and subsequent establishment of non-native species in new environments represents a threat to native ecosystem diversity and function. Global trade and travel pathways facilitate the accidental movement of species, particularly so for insects that can clandestinely hitchhike on imported plants (Liebhold et al. 2012) or within solid wood packaging

material (Brockerhoff et al. 2006). Fortunately, though not surprisingly, successful establishment of most arriving species appears to be rare (Ludsin and Wolfe 2001; Williamson and Fitter 1996). Climatic mismatches between the native and introduced area, disparity in the seasonality of the species upon arrival, lack of host species, the length of the voyage during which populations must remain viable, and the initial population size all create formidable barriers for adventive species (Lockwood et al. 2007). The size of the founder population can be especially important, and past research has consistently highlighted the relationship between initial population size and successful establishment across a diversity of taxa (Beirne 1975; Brockerhoff et al. 2014; Colautti et al. 2006; Lockwood et al. 2009; Simberloff 2009).

Despite long odds, some species nevertheless establish, and of these, an even smaller fraction proliferates and become economically or ecologically harmful. For example, in the United States, Aukema et al. (2010) examined non-native insect establishment between 1860 and 2006, and estimated that ≈ 2.5 forest insects successfully established each year over this time period, while only ≈ 0.5 species per year caused negative impacts. Once species establish, they begin to spread and expand their geographic range, often through a process known as stratified diffusion in which local growth and dispersal is coupled with long-distance movement (Shigesada et al. 1995). Thus, after successful establishment, the arrival and establishment stages serially repeat in new locations until the entire habitat susceptible to invasion is occupied (Liebhold and Tobin 2008).

The repetitive nature of many biological invasions (i.e., arrival, establishment, and spread) is perhaps best documented by the invasion of the gypsy moth, *Lymantria dispar* (L.), in North America (Liebhold et al. 1992; Sharov and Liebhold 1998). Introduced outside of Boston in 1869 (Liebhold et al. 1989; Riley and Vasey 1870), *L. dispar* has since spread at variable rates (Sharov et al. 1995; Tobin et al. 2007) and is currently established over a range from Nova Scotia to northern Minnesota, and Ontario to Virginia (Tobin et al. 2012). The species has one generation a year with adult moths emerging in mid-to-late summer, with flightless females emitting a sex pheromone to attract males. Upon mating, females oviposit a single egg mass containing 250–500 eggs. Eggs overwinter, and neonates hatch in the following spring. Larvae are generalist folivores, capable of feeding on over 300 host trees including at least 79 species within highly preferred genera such as *Betula* (birch), *Crataegus* (hawthorn), *Populus* (aspen), *Quercus* (oak), *Salix* (willow), and *Tilia* (basswood) (Liebhold et al. 1995).

Traps baited with synthetic female pheromone have been deployed annually since 1996 along the *L. dispar* leading population front, which exists ahead of the established area and includes a zone from Minnesota to North Carolina (Slow-the-Spread Foundation 2013; Tobin and Blackburn 2007). These traps provide a unique and fairly high resolution perspective on the invasion dynamics of *L. dispar*, revealing both the radial diffusive spread along a leading population front, as well as the initiation of new colonies ahead of the front that arise through long-distance dispersal (Bigsby et al. 2011; Frank et al. 2013; Johnson et al. 2006; Liebhold and Tobin 2006; Tobin and Blackburn 2008). Detecting spatially disjunct incipient populations using only trapped male moths can be challenging as both locally derived moths (e.g., established, reproducing resident populations) and immigrants that arrive through long distance dispersal (e.g., life stages transported by anthropogenic or atmospheric transport mechanisms) could be simultaneously present.

One such spatially disjunct *L. dispar* population well in advance of the leading population front was observed in the northern Minnesota counties of St. Louis, Lake, and Cook (Fig. 1). A previous analysis of the spatial and temporal properties from the initial trap catch data collected from 2000 to 2005 from this region of Minnesota suggested that although there was some evidence of spatial and temporal congruence in the trap catch data, indicating the potential of established *L. dispar* populations in certain locations, considerable numbers of adult males were detected in discrete spatially random locations during different years (Tobin 2007). The fact that the northern Minnesota invasion was spatially disjunct from the established range at the time was not unique, as past records indicated that the initial colonization of Wisconsin (Frank et al. 2013; Krause et al. 1994; Tobin and Blackburn 2008) and Michigan (Hanna 1982; Tobin et al. 2015) were also spatially disjunct from the expanding population front at the time.

However, precise details of the *L. dispar* invasion of northern Minnesota are unique in that extensive monitoring records exist from 2000, when 49 moths were detected from 5085 traps that were widely
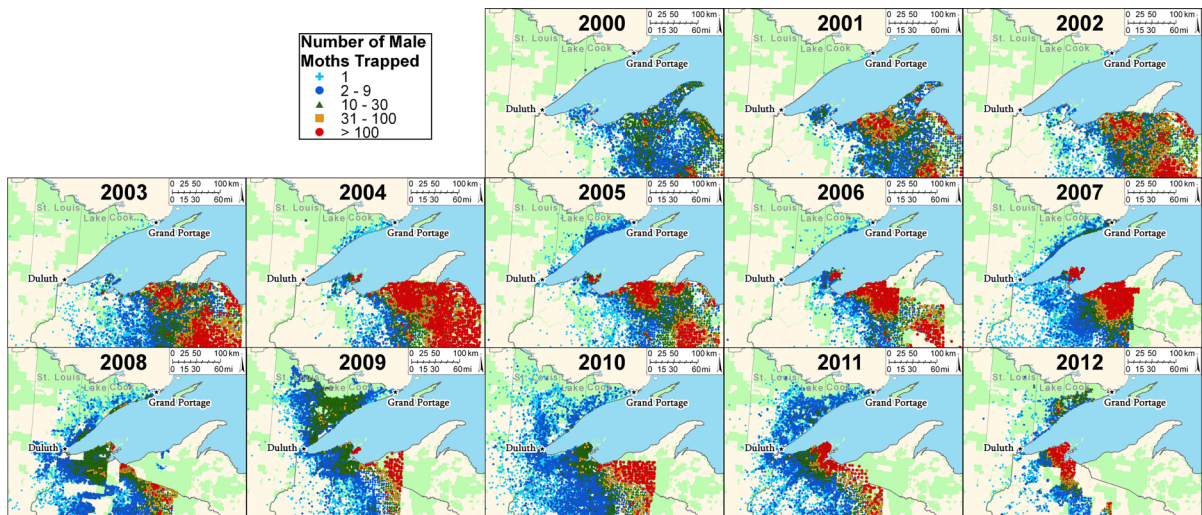
Fig. 1 Gypsy moth abundance along western Lake Superior, 2000–2012, as ascertained through the deployment of pheromone-baited traps under the gypsy moth Slow-the-Spread (STS) program (Tobin and Blackburn 2007). Note that the Keweenaw Peninsula in Michigan was only trapped in 2000 and 2001. Under the STS program, as the gypsy moth expands its range to the west, trap locations are likewise shifted to the west so that trapping is always conducted along the leading population front

deployed in St. Louis, Lake, and Cook counties. This detection event was likely soon after the initial introduction event given the lack of male moth capture in this area in all trapped years prior to 2000, albeit through a spatially much coarser-grained trapping network. This was not the case during the initial period of *L. dispar* invasion in Wisconsin or Michigan. We built upon a past assessment of the initial colonization dynamics of northern Minnesota from 2000 to 2005 (Tobin 2007) by supplementing the deployment of pheromone-baited traps under the *L. dispar* Slow-the-Spread program through the use of sentinel traps to ascertain the timing of male moth flight, phenological predictions of male moth flight in this region, and morphological measurements of male moth wings to quantify the spatial and temporal patterns encompassing its arrival and establishment in this region.

Materials and methods

Study region

We considered the invasion dynamics of *L. dispar* within the northern Minnesota counties of St. Louis, Lake, and Cook, which collectively comprise the Arrowhead Region of Minnesota. At the time of initial trapping in this region (2000), this area represented the most western extent of the expanding *L. dispar* population front (Fig. 1). The region is classified as a Laurentian mixed forest characterized by a transitional area between the deciduous forests to the south and the boreal forests to the north (Minnesota Department of Natural Resources 2015). In this region, the dominant host species preferred by *L. dispar* are quaking aspen (*Populus tremuloides*), yellow birch (*Betula alleghaniensis*), and white birch (*B. papyrifera*) (U.S. Forest Service 2016). The mean annual temperature ranges from 2 to 4 °C, while mean January temperatures are generally −10 °C with daily temperatures that are often <−30 °C during some portion of the winter (National Oceanic and Atmospheric Administration 2015).

Regional trapping data

Under the *L. dispar* Slow-the-Spread program, ≈ 100,000 georeferenced pheromone-baited traps are deployed annually along and ahead of the *L. dispar* population front, which currently extends from Northern Minnesota to southeastern North Carolina, to ascertain the spatial location of new colonies and prioritize management interventions (Tobin and Blackburn 2007). Under this program, traps are

generally deployed from 2 to 8 km apart, with delimiting trapping grids with a smaller intertrap distance (250–500 m) deployed after new colonies are first detected. In northern Minnesota, traps were deployed in July, removed in early October, and the number of males trapped in each trap was recorded. As part of the Slow-the-Spread program, 1453–7972 traps were deployed each year (median of 4479 traps per year) in Northern Minnesota (St. Louis, Lake, and Cook counties) from 2000 to 2012, which corresponds to the time period when *L. dispar* was first invading and subsequently establishing. Indeed, Lake and Cook counties were first proposed to be included in the *L. dispar* Federal quarantine for generally infested areas in Spring 2013 based upon 2012 trap catch data and the presence of alternative life stages (e.g., egg masses) detected in autumn 2012; these counties were officially quarantined, as codified by the U.S. Code of Federal Regulations (Title 7, Chapter III, Sect. 301.45-3), in early 2014.

Spatial dynamics of trap catch data through time

We used the regional trapping data to measure the spatial autocorrelation in the number of male moths per trap in each year from 2000 to 2012. Spatial autocorrelation was estimated using a nonparametric spatial covariance function (Bjørnstad and Falck 2001) and the ncf package (Bjørnstad 2012) in R (R Development Core Team 2015). This approach incorporates a bootstrap method to generate confidence intervals around the estimated nonparametric covariance function; we estimated the 95 % confidence intervals of the nonparametric spatial covariance function using the 2.5 and 97.5 percentiles of the bootstrapped distribution based upon 250 replications (Bjørnstad and Falck 2001; Efron and Tibshirani 1993). We noted significant spatial autocorrelation in the number of males per trap when the bootstrapped confidence intervals for the local estimate of spatial autocorrelation (i.e., the estimate when the distance between two trapping locations approaches 0) did not include 0.

Sentinel trapping data

In each year from 2005 to 2009, 60–80 additional pheromone-baited traps (188 and 126 traps in 2005 and 2007, respectively) were deployed beginning in mid-to-late June and sampled 1–3 times per week until mid-October to better quantify male moth flight seasonality. Traps were placed along Minnesota State Highway 61 from Two Harbors to Grand Marais, MN. In addition, approximately 4–6 transects emanating northwest from Highway 61 (and Lake Superior) were used; most were approximately 3–5 km in length while one extended 25 km north of Silver Bay and to Murphy City.

L. dispar phenology data

Estimates of the seasonal distribution of male moth flight was based upon the Gray phenology model (Gray 2009; Gray et al. 2001) interpolated over a digital elevation model using the BioSIM software (Régnière and Sharov 1998). Daily surface maximum and minimum temperatures from the National Climatic Data Center (2015) were used to estimate the 5th and 95th percentiles of expected male moth flight for each year corresponding to the years of sentinel trap data from northern Minnesota (2005–2009). Estimates were obtained for Duluth and Grand Portage, Minnesota, which represent the southern and northern extent, respectively, of sentinel trap locations. The estimates of the 5th and 95th percentiles of expected male moth flight for Duluth and Grand Portage were then averaged by year to ascertain the predicted male moth flight period in northeastern Minnesota.

Male moth wing length

In 2007–2009, we measured the length of the right forewing in all male moths collected from sentinel traps, and a randomly selected subset from regional traps. We used wing length as a proxy for male moth size, which in turn reflects larval fitness as the adults do not feed. Past research has shown that during outbreaks where *L. dispar* larvae face intense intraspecific competition for foliage, adult males are significantly smaller than conspecifics that developed from larvae feeding under less competition (Carter et al. 1991). Moths collected from sentinel traps were of a known date given the frequency at which these traps were checked. In addition, traps from the regional trapping dataset were checked at least once at approximately the middle of the male moth flight season for quality control purposes, and many were checked more frequently. In these cases, trapping personnel noted the presence of live moths in the trap (traps contain a

Tanglefoot® interior on which the male is entrapped, but not immediately killed) and indicated the date. In all years, any live-trapped moths were automatically selected for wing measurement. A total of 2292, 3734, and 7991 moths were measured from northern Minnesota in 2007, 2008, and 2009, respectively.

In 2012, we also monitored a *L. dispar* population from Kirkville, New York, where gypsy moth have been established since the 1950s (officially placed under the *L. dispar* quarantine in 1973) yet had no history of irrupting into outbreak densities. In recent years, detectable levels of *L. dispar* egg masses were present annually, but late instars were only occasionally found. This population was sampled from a stand co-dominated by red and sugar maple (*Acer rubrum* and *A. saccharum*, respectively), American beech (*Fagus grandifolia*), and black cherry (*Prunus serotina*), all considered secondary *L. dispar* hosts; <20 % of the stand was comprised of preferred host plants, which were *P. tremuloides*, northern red oak (*Quercus rubra*), swamp white oak (*Q. bicolor*), and *B. papyrifera* (Liebhold et al. 1995). We monitored two pheromone-baited traps daily from mid-June, which was prior to the onset of male moth flight for this area, and continued until 1 week after the last male was caught. Moths were collected daily and identified with a date stamp. In 2013, we repeated this effort but also added two sites (with similar host tree composition as the Kirkville site): one in Green Lakes State Park ≈ 6 km from the first site, and another near Sennett, New York, ≈40 km from the Kirkville site. Two pheromone-baited traps were placed in each site. Traps in 2013 were monitored daily in Kirkville, every other day at the Green Lakes site, and every third day at the Sennett site from mid-June until a week after the last male moth was recorded. In addition to the seasonality dynamics from a long established *L. dispar* population, we also measured the right forewing length in all moths for each collection date if the number was ≤30 moths, or from a randomly selected sample of 30. Across all New York sites in 2012 and 2013, a total of 2142 and 3966 male moth wings were measured, respectively.

Moth wing measurements from Minnesota and New York provided an expected distribution of wing length, and its relationship to male moth flight seasonality. Moths collected from traps containing Tanglefoot were immersed in Histo-Clear (National Diagnostics, 305 Patton Drive, Atlanta, Georgia) for 24 h to remove males from the Tanglefoot. Wings were carefully removed from the body and then measured across the widest point to nearest 0.01 cm using a digital micrometer. Observations were made under a table-mounted magnifier or stereomicroscope (10 ×). We measured Pearson's correlation coefficient (ρ) between wing length and capture date to determine seasonal trends in male moth wing size for each location and year (2007–2009 for Minnesota and 2012–2013 for New York). We also measured ρ in a subset of moths from Minnesota that were trapped prior to the predicted male moth flight period for the specific year, and in the subset of moths trapped during the predicted flight period. Finally, we compared the distribution of moth wing lengths in moths collected from Minnesota that were trapped prior to or during the predicted flight period for each year (2007–2009) using a two-tailed *t* test. Analyses were conducted in R (R Development Core Team 2015).

Results

### Spatial dynamics of trap catch data through time

We did not find evidence of spatial autocorrelation in the number of male moths trapped in any year from 2000 to 2006 (Table 1, Fig. 2). During this time, the number of male moths per trap was <0.2, and was approximately 0.01 males/trap from 2000 to 2003 (Fig. 3). Male moth abundance increased tenfold beginning in 2007, and we detected significant spatial autocorrelation in the regional trapping data in each year from 2007 to 2012 (Table 1, Fig. 2). The presence of spatial autocorrelation indicates clustering at local spatial scales, which is suggestive of successful population establishment. In each year from 2007 to 2012, we detected spatial autocorrelation generally at ranges from 10 to 20 km. Particularly strong local spatial autocorrelation was detected in 2007 and 2008 when *L. dispar* populations were beginning to increase exponentially (Fig. 3). Relatively weaker local spatial autocorrelation was detected in 2009 and 2012, which were the years of highest recorded *L. dispar* abundance from regional traps.

Phenology of trap catch

In 2005, and 2007–2009, we recorded male moths from sentinel traps over 65–88 days (Fig. 4), longer
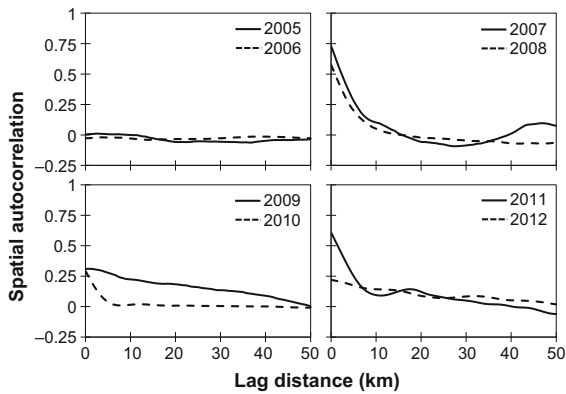
Fig. 2 Spatial autocorrelation in the number of male moths per trap from St. Louis, Cook, and Lake Counties, Minnesota, 2005–2012. Data from 2000 to 2004 are not shown but the respective autocorrelation function for these years was the same as 2005 and 2006 (i.e., no spatial autocorrelation). In each year from 2007 to 2012, significant spatial autocorrelation was detected (bootstrapped 95 % confidence intervals are not shown; estimates of the local spatial autocorrelation and confidence intervals for all years, 2000–2012, are shown in Table 1)
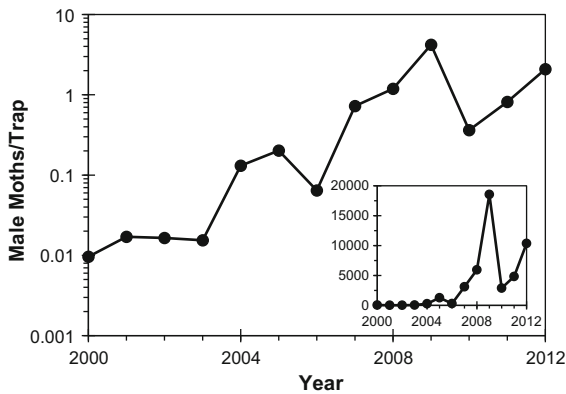
Fig. 3 Number of male moths per trap in St. Louis, Lake, and Cook counties, Minnesota, 2000–2012. The *inset graph* indicates the total number of moths trapped over the same time period. The number of traps deployed per year ranged from 1453 (in 2002) to 7972 (in 2010)

than the 6–8 week period of male moth flight typically reported (Régnière and Sharov 1998, 1999; Tobin et al. 2009). In 2006, males were recorded over 39 days. However, in all years, including 2006, male moths were trapped at least 2 and sometimes as much as 6 weeks prior to the expected period of male moth flight based upon phenological predictions for northeastern Minnesota (Fig. 4). Male moths, however, were also consistently trapped during the expected
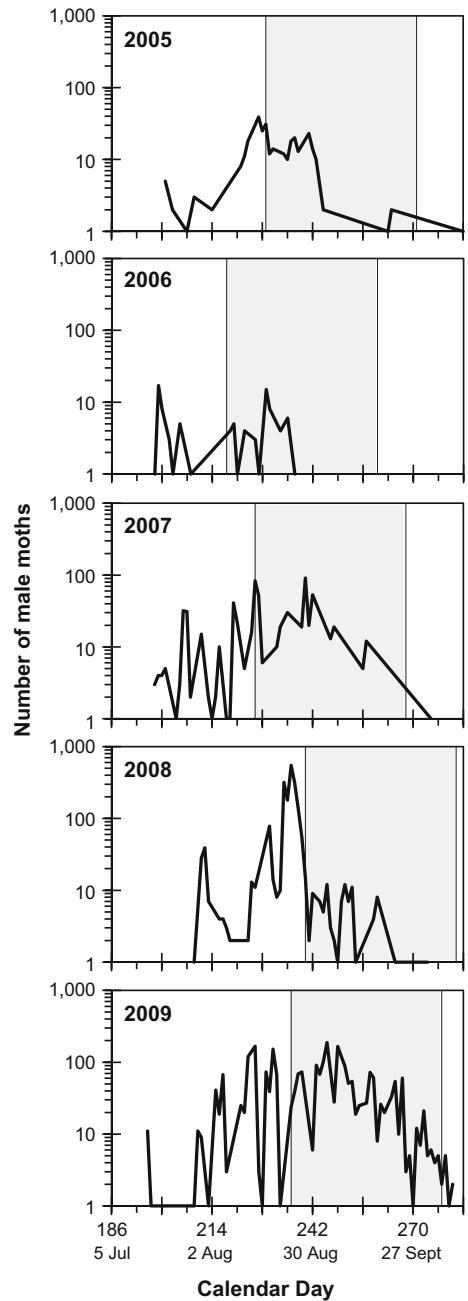
Fig. 4 The number of male moths trapped per day in northern Minnesota, 2005–2009, as ascertained from sentinel traps. The *grey shaded area* is the predicted gypsy moth flight period in this region for each year

period of male moth flight for this region. Because northeastern Minnesota represents the most northern extent of the gypsy moth distributional range in North America, and undeniably the coldest region in which

gypsy moth currently is distributed, phenological predictions of male moth flight are consequently the latest predicted dates over its range (Régnière and Sharov 1998, 1999). It also noteworthy that male moths were trapped during the expected phenological period for this region in both 2005 and 2006, even though we detected no evidence of spatial autocorrelation in these two years.

Male moth wing length

Male moth wing lengths from northeastern Minnesota, and from an endemic, long established population in New York, are shown in Fig. 5 and reveal several patterns. First, the distribution of wing length, regardless of the population source, was generally normally distributed (Fig. 5). Across all years and sampling locations (N = 14,572), the mean and median wing length were 20.28 and 20.35 mm, respectively, and wing lengths ranged from a minimum of 13.62 mm to a maximum of 25.44 mm. Second, male moths from New York decreased in length through the course of the season; the correlation between calendar day and wing length was significantly negative in both 2012 ($\rho = -0.73$, $P < 0.01$) and 2013 ($\rho = -0.44$, $P < 0.01$). We also note that the period of male moth flight from New York lasted ≈ 6 to 8 weeks, which is consistent with prior observations of the male moth flight period (Régnière and Sharov 1998, 1999; Tobin et al. 2009). In contrast, moths from northeastern Minnesota were collected over a longer period of time, generally up to 12 weeks, which also, in some years, extended beyond the range of the predicted flight period based upon temperature accumulation (Fig. 4).

The association between collection day and wing lengths from northeastern Minnesota was less consistent that those observed from New York. This could be due to the fact that Minnesota represents a newer, more recently established population, or the fact that moths from Minnesota were collected from multiple locations over a much larger area than the New York sites. Regardless, we observed a reduced level of association even when separately examining moths that were trapped prior to the expected phenological period of male moth flight. Only in 2009, the year of the highest male moth trap catch in northeastern Minnesota, did we measure a significantly negative correlation between collection day and wing length from moths trapped during the resident phenological

period ($\rho = -0.16$, $P < 0.01$), while in 2007 we measured a significantly positive correlation ($\rho = 0.28$, $P < 0.01$; Fig. 5). In 2008, we measured a significantly negative correlation between collection day and wing length from moths trapped prior to the resident phenological period ($\rho = -0.20$, $P < 0.01$; Fig. 5).

Despite the lack of consistency between collection day and wing length in moths from northeastern Minnesota, a final observation is the tendency for male moths, in each year, to be significantly smaller when collected prior to the resident predicted phenological period (2007: $t = 2.89$; df = 238; $P < 0.01$; 2008: $t = 11.28$; df = 874; $P < 0.01$; 2009: $t = 21.57$; df = 1411; $P < 0.01$). Male moths trapped prior to the predicted male moth flight period had a mean ($\pm$SE, N) wing length of 19.85 (0.13, 89), 19.17 (0.05, 788) and 19.58 (0.06, 466) mm in 2007, 2008, and 2009, respectively. In contrast, male moths trapped during the predicted male moth period had a mean ($\pm$SE, N) wing length of 20.32 (0.10, 151), 20.78 (0.14, 88), and 21.11 (0.04, 947) in 2007, 2008, and 2009, respectively. These differences represent a 2.3, 8.1, and 7.5 % increase in wing length in male moths collected during the predicted phenological period, as opposed to those collected prior to the predicted phenological period, for northeastern Minnesota, for 2007, 2008, and 2009, respectively.

Discussion

The arrival stage of a biological invasion includes the initial introduction of a species from its native range, a process strongly facilitated by global trade and travel (Liebhold et al. 2016; McCullough et al. 2006; Work et al. 2005). Such anthropogenic movement allows for species to be translocated across geographic barriers, such as oceans, that are not easily traversed through natural dispersal. However, the arrival stage is also a recurrent process in biological invasions given its role in post-establishment spread through stratified dispersal, a process likely common to most species invasions (Lewis and Kareiva 1993; Liebhold and Tobin 2008; Shigesada et al. 1995), even though the precise mechanisms of long-distance dispersal are not always known or easily quantifiable. The serial repetition of the arrival stage as part of spread can be synergized by an expanding population front, which provides a

Fig. 5 Male moth wing
length by capture date in
Minnesota (2007–2009) and
New York (2012–2013). In
Minnesota, data are divided
into an early period (*grey*) in
which trap catch precedes
the predicted male moth
flight period and a normal
period (*black*), in which trap
catch occurs during the
predicted period; values of
Pearson's correlation
coefficient are noted in the
respective colored font.
Note the strong significant
negative correlation
between wing length and
date in a well-established
population from New York,
while the correlations from
Minnesota indicate a mix of
significantly negative,
significantly positive, and no
correlation. The
corresponding histograms
(also by *color* in Minnesota)
illustrate the overall
distribution of male moth
wing length
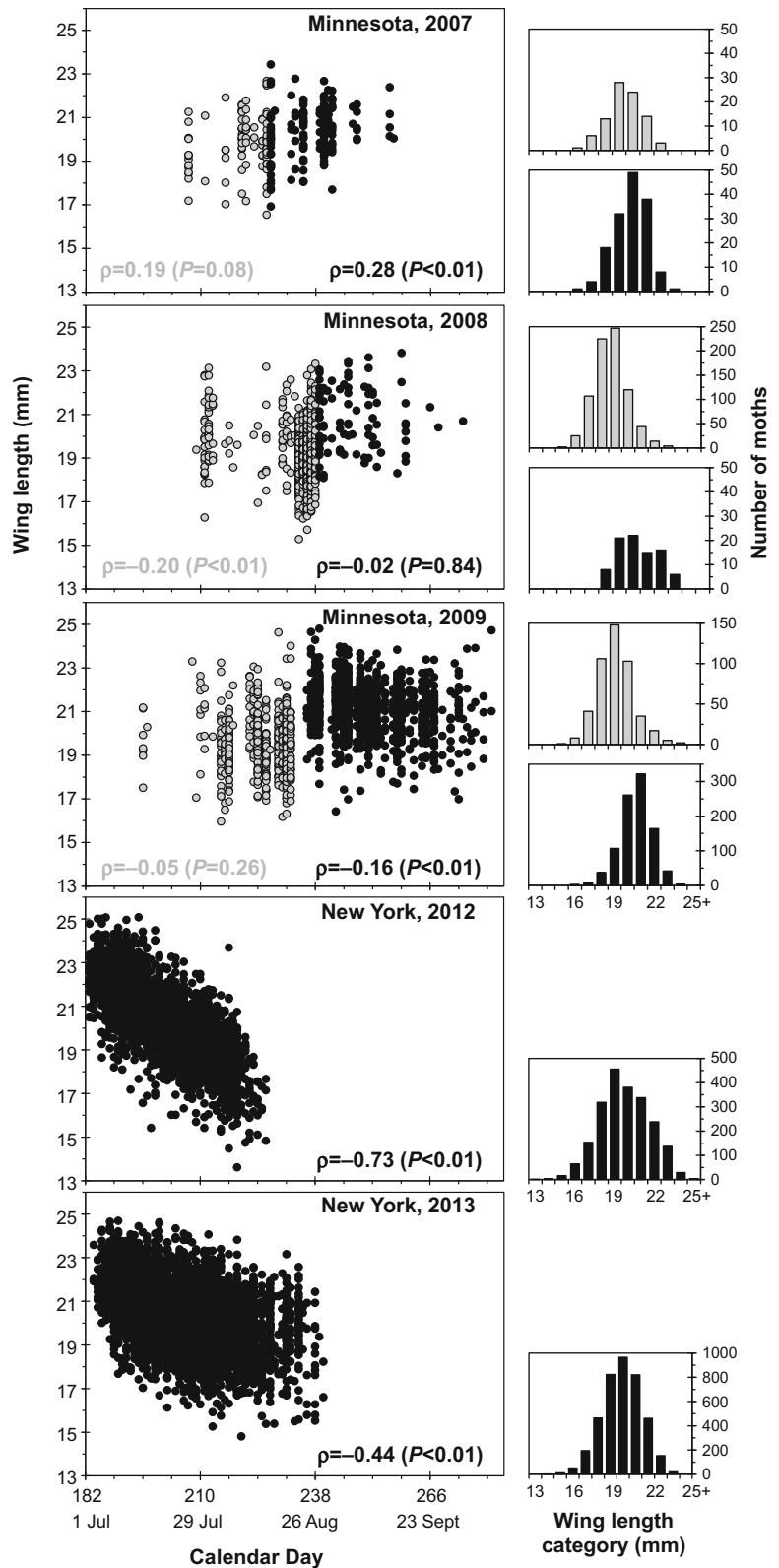
nearby source of propagules that can be moved through both anthropogenic and biological means.

In this paper, we provide evidence that individuals from at least two population sources were present during the initial stages of *L. dispar* establishment in an area that was spatially disconnected from its current geographic range in North America. One population source was non-resident and comprised of immigrants from a phenologically distinct area, while another source was a resident population that developed under local climatic conditions. We also revealed that the spatial autocorrelation function did not always reveal spatial clustering, even when the timing of adult male flight was consistently linked to local phenological conditions. Spatial clustering would be expected in an established insect population, and especially so for *L. dispar* as adult females are incapable of sustained flight, which restricts the spatial diffusion of egg masses. Climatic conditions in northeastern Minnesota are particularly unique across the current *L. dispar* range in North America because egg hatch from overwintering egg masses, and subsequent immature development and adult emergence, occur later in the year than elsewhere (Régnière and Sharov 1999). Moreover, adult *L. dispar* are short-lived and do not feed; most are thought to live 1–2 days in nature (Robinet et al. 2008). Therefore, adult males trapped during the predicted *L. dispar* flight period for northeastern Minnesota, and especially moths that comprised the tail end of the flight distribution (e.g., mid-to-late September, Fig. 4), are unlikely to have come from an established population outside of northeastern Minnesota. The same rationale can be applied to adult males trapped prior to the predicted *L. dispar* flight period for northeastern Minnesota, and especially those that comprised the front end of the flight distribution (e.g., mid-July, Fig. 4) are unlikely to have come from an established population within northeastern Minnesota. The mixing of the two (i.e., immigrating and resident individuals) presents a complex picture of the invasion dynamics of *L. dispar* in this area. Based upon robust spatial and temporal trapping records, which are generally not available in the majority of invasive species, both the observed male moth flight period and abundance of established populations are overestimated, which complicates the biological interpretation of the trap catch data and the corresponding management response.

The exact source of the immigrating individuals is unknown in the absence of mark-recapture studies. However, we did record male moths from an early period of trap capture and prior to the estimated period of moth flight for northeastern Minnesota beginning in mid-July to approximately mid-August (Fig. 4). A prior study by Régnière and Sharov (1999) used 30-year normals (1960–1990) to predict male moth flight across northeastern North America, including Minnesota, and showed that peak male moth flight during mid-July to mid-August occurred from southern Wisconsin and Michigan, to northern Illinois, Indiana, and Ohio. A more recent study by Tobin et al. (2009), conducted from 2004 to 2008 and hence a study conducted under more recent climate conditions, showed that the location of male moth catch in mid-July to mid-August had shifted north to include primarily only Wisconsin and Michigan, including northern Wisconsin and the Upper Peninsula of Michigan. Given the proximity of northern Wisconsin and the Upper Peninsula of Michigan to northeastern Minnesota, these areas would be a likely source of immigrants, especially since both had established *L. dispar* populations in 2000 and particularly high population densities by 2004 (Fig. 1).

Although only male moths were recorded in this study, as locating alternate life stages of *L. dispar* in low density populations is prohibitively difficult, it is possible to consider the life stage of immigrants given the wealth of information on gypsy moth biology, phenology, and invasion ecology (e.g., Doane and McManus 1981; Elkinton and Liebhold 1990; Liebhold and Tobin 2006; Régnière and Sharov 1998). Adult females are not capable of sustained flight, and are thought to oviposit within 1–2 m from where they emerged from pupae (Odell and Mastro 1980), which limits natural dispersal of this species. Neonate ballooning is one mechanism of natural dispersal, and larval dispersal from the closest area of *L. dispar* established populations (northern Wisconsin and the Upper Peninsula of Michigan) is phenologically possible. A study by Gray (2004) demonstrated that hatch from overwintering egg masses occurs from late May to early June in northern Wisconsin and the Upper Peninsula of Michigan. Bud burst of quaking aspen, *Populus tremuloides*, one of the primary host plants for *L. dispar* (Liebhold et al. 1995) and one that is present in Northern Minnesota (U.S. Forest Service 2016), begins in early May (Uelmen et al. 2016), and

thus would be available to ballooning larvae. *Lymantria dispar* neonates are thought to balloon only in the first few days after hatch (Mason and McManus 1981), and are dependent upon newly expanded foliage during a critical and short phenological window for survival. Although past studies have shown that certain host plants, including oak and aspen, can be suitable for neonates several weeks after budburst (Hunter 1993; Raupp et al. 1988), neonates under laboratory conditions survive <6 days in the absence of food (Capinera and Barbosa 1976; Stockhoff 1991). Thus, neonate dispersal from the closest area of *L. dispar* established populations is phenologically possible, but would require larvae to traverse >50 km. This distance is considerably farther than what past studies have shown, which is that passive larval dispersal is generally limited to <200 m (Mason and McManus 1981; Weseloh 1985).

The anthropogenic movement of egg masses is another potential source of introduction, and has been linked to the initialization of other *L. dispar* populations outside of the established range (Hajek and Tobin 2009; Liebhold and Tobin 2006). Northeastern Minnesota is a heavily used recreational area and includes state and Federal forest lands, and the Boundary Waters Canoe Area Wilderness, which is considered to be the most visited wilderness area in the United States, attracting ≈250,000 visitors per year (Dvorak et al. 2012). Eggs are also the longest lived stage of *L. dispar*, spending roughly 8 months per year as an egg, and as a sessile stage can be transported

anthropogenically. However, the introduction of egg masses does not provide a suitable explanation for early season male moth flight because such eggs would be subject to local weather conditions in northeastern Minnesota as developing larvae and pupae and hence would emerge as adults in synchrony with resident adult moths.

A final consideration to explain the early season occurrence of male moths is perhaps the most parsimonious explanation: immigration of adult males. Adult male "blow-in" from a phenologically distinct area was thought to underlie early male moth trap catch in Wisconsin (Krause et al. 1994). Such a mechanism does not require phenological synchrony with host plants, as would be the case for neonate dispersal, and local temperatures would not affect immature development, as would be the case for introduced egg masses. A previous study that examined the invasion of *L. dispar* into Wisconsin furthermore highlighted that the weather events that would facilitate the atmospheric movement of *L. dispar* life stages was more likely to coincide with the timing of adults as opposed to larvae (Frank et al. 2013). Moreover, moth wing lengths, which we used as a proxy for adult size, can be affected by population density with smaller male moths originating from high density populations (Carter et al. 1991), which could be a result from faster larval development that has been observed at outbreak densities (Lance et al. 1987). Since high density populations are more likely to serve as a source of immigrating adults, this could

Table 1 Estimates (±bootstrapped 95 % confidence intervals) of the local spatial autocorrelation function of the number of male moths per trap from St. Louis, Cook, and Lake Counties, Minnesota, 2000–2012

Significant spatial autocorrelation is present in years in which the confidence intervals do not include 0, and was detected in each year from 2007 to 2012

Year	Local spatial autocorrelation	95 % confidence intervals	
		Lower (2.5 %)	Upper (97.5 %)
2000	−0.17	−0.65	0.12
2001	−0.12	−0.44	0.05
2002	−0.06	−0.36	0.45
2003	−0.16	−0.50	0.17
2004	−0.02	−0.13	0.12
2005	0.08	−0.05	0.19
2006	0.01	−0.03	0.06
2007	0.73	0.56	0.94
2008	0.57	0.32	0.81
2009	0.42	0.31	0.58
2010	0.29	0.05	0.84
2011	0.61	0.37	0.87
2012	0.22	0.14	0.34

explain the significantly smaller moths that were trapped prior to the predicted flight season for northeastern Minnesota (Fig. 5). We also note that in 2009, which was the year of the highest number of male moths recorded from sentinel traps, a significantly negative association in wing size through time, which was the same pattern we observed from long established population in New York (Fig. 5).

The relationship between trap catch data and wing size in both northern Minnesota and New York (Fig. 5) presents an interesting phenomenon. In New York, where *L. dispar* has been established for >50 years, a strong negative association in wing size through time was observed in both 2012 and 2013. Results from northern Minnesota were less consistent, perhaps due to its more recent introduction; regardless, we observed a significantly negative association between date and wing size in the early season moths in 2008 and the late season moths in 2009 (Fig. 5). As for a possible mechanism for this phenomenon, the degree of synchrony between egg hatch in spring feeding herbivorous insects and host plant bud burst has been shown to affect insect developmental rate, survivorship, pupation weight, and fecundity (Parry et al. 1998; van Asch and Visser 2007). For example, in a geometrid species, larvae that fed on more mature leaves, such as those that would emerge later in the spring and after bud burst, were observed to develop more slowly and weigh less as pupae, in part due to the role of induced phenolics as plant defensive compounds (Haukioja et al. 2002). In *L. dispar*, past research has also shown a reduction in pupal size and fecundity with increases in the date of hatch in the spring; in addition to the possible role of plant defensive compounds, later hatching larvae also could consume less nutritious foliage (Hunter and Elkinton 1999, 2000).

Global trade and travel pathways continue to lead to the establishment of non-native insects in new continents and countries. Consequently, it remains important to understand and appreciate the complexities of the invasion process, and the role that stochastic immigration, which may or may not lead to successful establishment, affects the interpretation of invasive species monitoring data and the practical assessment of an established population. Although *L. dispar* is somewhat unique among invasive species given the robust spatial and temporal monitoring data available along its invasion front, the processes underlying its spatial spread are unlikely to be unique. As with all invasive species, new *L. dispar* populations in a novel environment face the same challenges all species face with regard to locating suitable hosts and surviving under potentially different climates. This paper sheds new light on the invasion dynamics of a non-native insect species with both biological and management implications.

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