



Historical change in the outbreak dynamics of an invading forest insect

Andrew M. Liebhold · Ann E. Hajek · Jonathan A. Walter ·
Kyle J. Haynes · Joseph Elkinton · Rose-Marie Muzika

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Abstract The population dynamics and impacts of non-native species often change following their initial establishment, with impacts either increasing or decreasing over time. The reasons why the abundance of an invading species may change are varied but often reflect changes in the way in which populations interact with resident communities. Here we analyze changes in the outbreak dynamics of *Lymantria dispar* (formerly known to as the “gypsy moth”), a Eurasian foliage-feeding insect that has been established in N.

America for ca. 150 years. We find that during the course of this species’ presence in N. America, it has continually exhibited population dynamics in which populations reach outbreak levels, resulting in defoliation of large forested areas. However, there is evidence of some changes in both the periodicity and synchrony of these outbreaks. We hypothesize that the accidental introduction of an entomopathogenic nucleopolyhedrosis virus around 1906 resulted in populations shifting from a pattern of sustained

A. M. Liebhold (✉)
USDA Forest Service Northern Research Station,
Morgantown, WV 26505, USA
e-mail: Andrew.Liebhold@usda.gov

A. M. Liebhold
Faculty of Forestry and Wood Sciences, Czech University
of Life Sciences Prague, 165 21 Praha 6-Suchbát, Czech
Republic

A. E. Hajek
Department of Entomology, Cornell University, Ithaca,
NY 14853, USA

J. A. Walter
Department of Environmental Sciences, University of
Virginia, Charlottesville, VA 22904, USA

K. J. Haynes
The Blandy Experimental Farm, University of Virginia,
Boyce, VA 22620, USA

J. Elkinton
Department of Environmental Conservation, University of
Massachusetts, Amherst, MA 01003, USA

R.-M. Muzika
Carnegie Museum of Natural History, Pittsburgh,
PA 15213, USA

outbreaks to oscillatory dynamics with periodic outbreaks synchronized over large distances. We analyze historical *L. dispar* population data that provide some evidence in support of this hypothesis. There is also evidence that the more recent establishment of the fungal pathogen *Entomophaga maimaiga* has caused a decrease in the amplitude of *L. dispar* outbreaks since its emergence in 1989.

Keywords Gypsy moth · *Lymantria dispar* · Periodicity · Spatial synchrony · Natural enemy · Population dynamics

Introduction

While most non-native species are not particularly abundant, an exceptionally large number of non-native species escape from background population levels and dominate the landscape (Williamson 1996). These high population levels are often associated with a variety of impacts on other species through competition, herbivory, predation, disease transmission and other ecological interactions (Blackburn et al. 2014). Such effects can have cascading impacts on ecosystem processes and are responsible for much of the socio-economic impacts associated with biological invasions (Vilà and Hulme 2017).

Several theories have been proposed to explain the rapid population growth seen in some non-native species. First is the concept that non-native species are able to escape the limiting pressure of natural enemies present in their native range and this allows populations to grow to levels that would otherwise be impossible (Jeffries and Lawton 1984; Colautti et al. 2004). Another hypothesis is that the performance of non-native species is much greater when they encounter “naïve” hosts or competitors; because such hosts or competitors have no prior evolutionary contact with the invading species, they are often lacking in evolved defenses or competitive abilities (Gandhi and Herms 2010; Desurmont et al. 2011). In both concepts, exceptional population growth in the invading species is achieved by escaping from the effects of species in their native community that constrain their population growth. However, identifying the underlying cause of the exceptional success in individual non-native species is often difficult due to the complexity of

interactions of these species with other species in invaded communities.

Simberloff and Gibbons (2004) described a phenomenon observed in many different non-native organisms: populations increase to high levels following initial invasion but subsequently crash and the invading species becomes characteristically rare in the invaded community. They refer to this general phenomenon as “now you see them, now you don’t”. Simberloff and Gibbons (2004) noted that most of such population crashes are unexplained in that the causes for their declines are often unknown. However, there are at least some examples where such declines have been caused by either intentional or accidental introductions of natural enemy species (Hajek and Eilenberg 2018). In other systems, population crashes of invading species may result when native natural enemies switch to using the invading species as a host (e.g., Clifton et al. 2019). Though there are a few such cases where the mechanisms driving crashes in invader abundance are known, in most cases these events remain a mystery (Simberloff and Gibbons 2004). From a broader perspective, the field of invasion science generally lacks a clear framework for how the population dynamics of invading species changes following their establishment.

Here we explore post-invasion changes in population dynamics using *Lymantria dispar* (formerly known as the “gypsy moth”) in N. America as a model system. This species, native to most of temperate Eurasia and North Africa, has been established in N. America for > 150 years, thus providing a long history over which changes can be observed. *Lymantria dispar* is infamous, both in its native and invaded range, for exhibiting massive swings in abundance through several orders of magnitude, with outbreaks re-occurring at statistically regular intervals (Johnson et al. 2005). During these outbreaks, *L. dispar* larvae reach high population levels causing forest defoliation over large regions. These outbreaks have been well-studied and *L. dispar* population dynamics are characterized by both periodic oscillations and spatial synchrony across large spatial extents (Johnson et al. 2005, 2006; Allstadt et al. 2013, 2015; Haynes et al. 2019).

Because of the frequent occurrence of *L. dispar* outbreaks, this species is considered a pest and data have historically been collected to monitor populations and damage. Here, we analyze such historical

data from its invaded North American range with the goal of quantifying changes in population dynamics and drawing inferences about the processes driving these shifts. Specifically, we evaluate evidence for the hypotheses that over time there have been (a) changes in the fraction of susceptible forests damaged by *L. dispar* across its invaded range, (b) changes in spatial synchrony in *L. dispar* population dynamics and (c) shifts in the oscillatory dynamics of *L. dispar* populations. These questions are important since such changes are closely related to regional-scale impacts of forest pests (Liebhold et al. 2012).

Methods

Lymantria dispar population data

Lymantria dispar is a univoltine insect and a standard method for estimating annual population densities is based on counting overwintering populations of egg masses, which are laid on tree trunks and branches as well as objects lying on the ground (Liebhold et al. 1994). From 1910 to 1934, staff from the US Dept. of Agriculture Gypsy Moth Laboratory (Melrose Highlands, Massachusetts) annually counted all egg masses in 264 circular plots (0.04 ha) located throughout eastern Massachusetts, southeastern New Hampshire and southern Maine in the Northeastern United States (See Campbell 1967 for more details on how these data were collected). We had access to data from 121 of the plots but dropped about half of the plots because they were missing observations for more than $\frac{1}{4}$ of the time series, thereby, leaving 62 plots. The precise locations of the egg mass plots are no longer known, and therefore, we used the centroids of the towns (municipalities) where plots were located as locations. We expect that this induced an error of no more than 8 km in position (most towns are no more than 8 km in diameter). Though the sampling spanned 1910–1934, we only had access to plot-level data from 1910 to 1931. Yearly means of all plots sampled in each year were published in Burgess and Baker (1938) so we used these data for analysis of mean population dynamics and the 1910–1931 individual plot data for more detailed analysis of spatial dynamics.

We also compiled historical records of annual area defoliated from the New England states of Massachusetts, Maine, New Hampshire, Vermont,

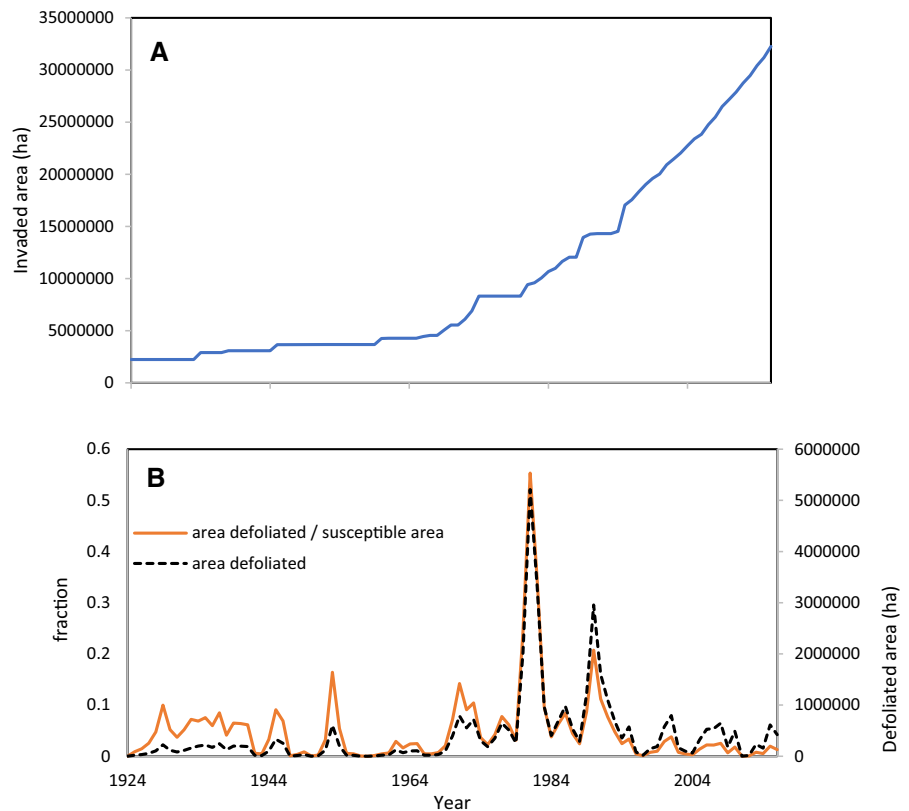
Connecticut and Rhode Island. Defoliated area is widely used as a proxy for *L. dispar* population densities (Williams et al. 1991; Liebhold et al. 1993). Prior to the 1960's, annual forest area defoliated by *L. dispar* was recorded by town "tree wardens" based upon observations made from the ground. Starting in the 1960's, defoliation surveys were conducted via aerial sketch mapping in which defoliated areas were mapped out directly on paper maps, and more recently using digital mapping technologies. We obtained annual area defoliated by *L. dispar* for each state from 1924 to 2016 from the US Forest Service "Gypsy Moth Digest" database (US Forest Service 2020).

In addition to state-wide defoliation records, we obtained historical records of annual area defoliated by *L. dispar* from 1931 to 1940 in individual towns in Massachusetts, Maine, New Hampshire, Vermont, Connecticut and Rhode Island from records found in the archives of the Harvard Forest, Petersham, Massachusetts. We also compiled comparable records of annual area defoliated in the same towns from 1975 to 2016 by extracting these data from annual aerial sketch mapping defoliation maps stored as map layers (Liebhold et al. 1997a, b) using the ArcGIS system.

Long-term trend in defoliated area

In order to test for an overall downward trend in the fraction of susceptible forests damaged by *L. dispar* across its invaded range over time, we analyzed historical records of total defoliation in all invaded US states from 1924 to 2016 (Fig. 1b). This series was adjusted by the annual area of susceptible forest that was invaded (Fig. 1a). Records of historical *L. dispar* range expansion are published in the annual county-level records of the *L. dispar* quarantine area historically designated by the US Dept. of Agriculture (US Code of Federal Regulations Title 7, Chapter III, Sect. 301.45). Only a fraction of invaded land area is covered by forests that are susceptible to *L. dispar* defoliation. Therefore, we multiplied the area of each invaded county by the proportion of the land area containing forests with > 20% basal area in preferred tree species (Liebhold et al. 1997a, b) to quantify land area susceptible to defoliation. This was used to calculate a time series of cumulative susceptible land area invaded in each year. The time series of annual defoliation over all states was divided by this susceptible land area to generate a time series of proportion

Fig. 1 Expansion of the *L. dispar* invaded range in the USA and time series of defoliated area across the entire invaded portion of the USA. **a** Increase in cumulative susceptible forest land area invaded over time. **b** Time series of annual defoliation in the USA, expressed as land area defoliated and proportion of susceptible land area defoliated



of invaded susceptible forest defoliated in each year (Fig. 1b). To test for a temporal trend in adjusted defoliated area, we used a modified Mann–Kendall test, a nonparametric test that is suitable for time series data in which autocorrelation occurs at one or more time lags (Hamed and Rao 1998) using the ‘modifiedmk’ R library (Patakamuri and O’Brien 2019).

Spatial synchrony

Spatial synchrony in defoliation among the five New England states (Massachusetts, Maine, New Hampshire, Vermont, Connecticut and Rhode Island) (Fig. 2a, b) was quantified in 10 yr moving windows, starting with 1924–1933 and ending with 2007–2016. Synchrony was measured as the average of all pairwise Pearson correlations of annual area defoliated in each of the five states. Defoliated area was $\log_{10}(-x + 1)$ transformed to normalize values prior to calculating correlation coefficients.

Spatial synchrony among time series of annual egg mass densities in plots (Fig. 3a) and annual defoliation levels in towns (Fig. 4a) was quantified using the

spatial covariance function, calculated using the ‘sncf’ function in the ‘ncf’ R library (Bjørnstad and Falck 2001). These calculations are performed by computing the correlation between time series at each paired combination of locations and then fitting a spline function to the relationship of correlation with distance between points. Confidence intervals were estimated using 500 replicate bootstrap samples for each correlogram. From these correlograms we extracted estimates of the y intercept and regional (mean correlation among of all pairs of points) synchrony. We calculated separate spatial covariance functions using the egg mass density time series for 1910–1921 and 1922–1932. We calculated spatial covariance functions for defoliation area time series (towns in Massachusetts, Maine, New Hampshire, Vermont, Connecticut and Rhode Island) from 1931–1940, 1975–1984, 1985–1994, 1995–2004 and 2005–2014.

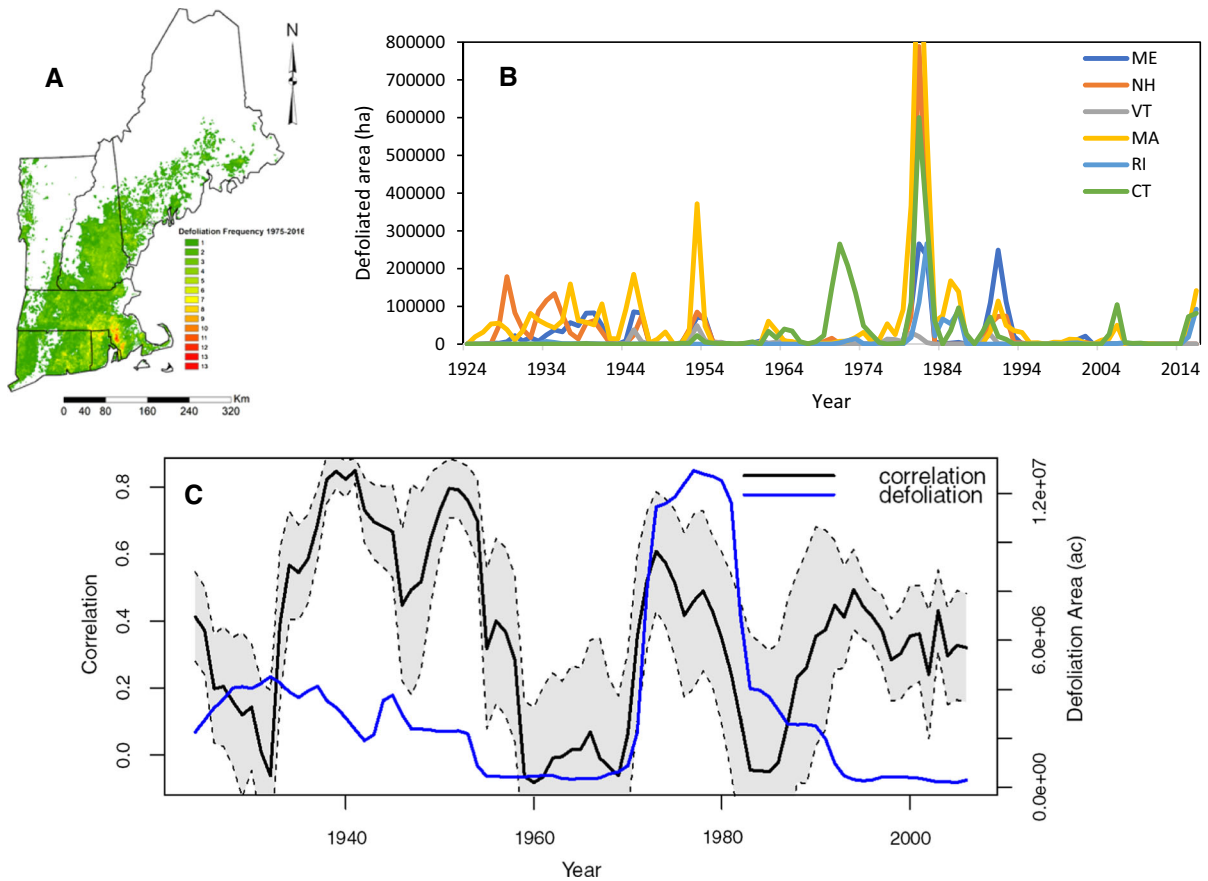


Fig. 2 Historical *L. dispar* defoliation in 5 New England states (Massachusetts, Maine, New Hampshire, Vermont, Connecticut and Rhode Island). **a** Map showing defoliation 1975–2016. **b** Annual defoliation in each state 1924–2016. **c** Mean

correlation in defoliation between states (i.e., spatial synchrony) using 10-yr moving windows (1924–1933 to 2007–2016); shaded area represents 95% confidence interval

Oscillatory dynamics

Temporal autocorrelation functions were used to characterize oscillatory dynamics of annual egg mass densities (Fig. 3a). Density series from 1911 to 1920 were compared with series from 1921 to 1934.

Results

Long-term trend in defoliated area

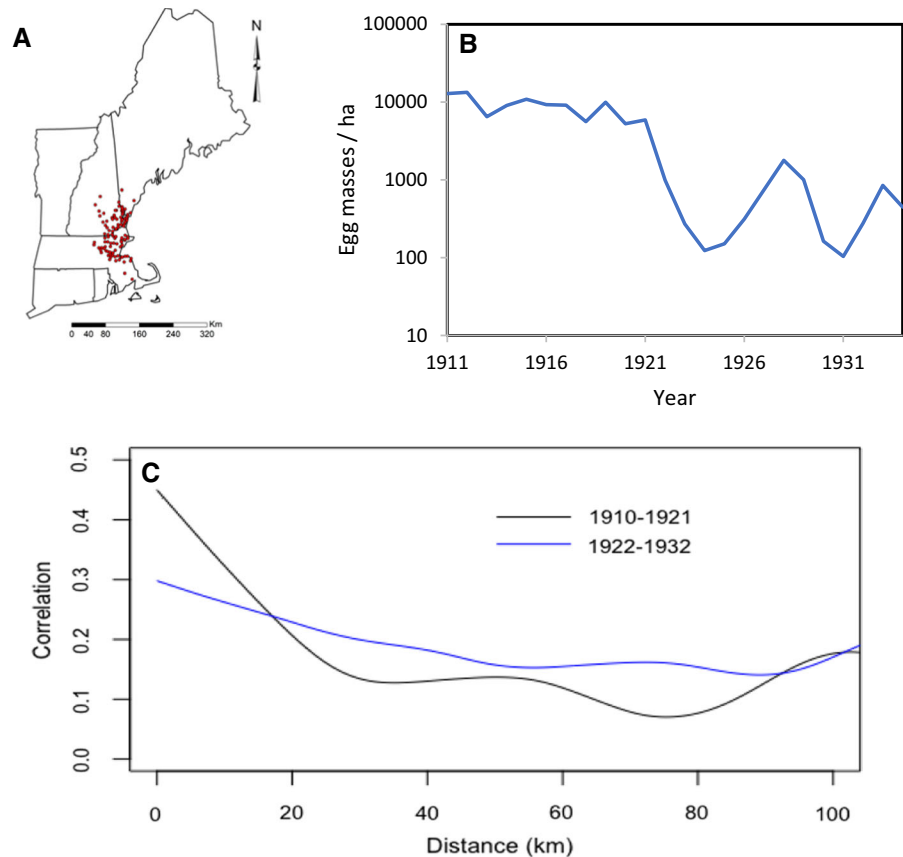
The time series of the yearly proportion of susceptible land area defoliated in the entire US showed considerable inter-annual variation reflecting the occurrence of regional outbreak episodes (Fig. 1b). However, regression analysis of the series from 1924 to 2016

indicated the lack of a significant temporal trend of increasing or decreasing defoliation (corrected $z = -9.56, P = 0.39$). However, a significant downward trend (Sen’s slope = -1.636 , corrected $z = -2.069, P = 0.039$) was detected when regressing proportion of area defoliated against time when the analysis was restricted to the period 1989–2016, which corresponds to the emergence of the pathogenic fungus *E. maimaiga* (Hajek et al. 1995).

Spatial synchrony

Visual comparison of time series of annual area defoliated in each of the 5 New England states indicates considerable spatial synchrony, with outbreaks mostly occurring simultaneously in multiple states (Fig. 2b) as previously quantified by Williams

Fig. 3 Historical egg mass data. **a** Location of historical US Dept. of Agriculture Gypsy Moth Laboratory egg mass plots in Massachusetts, New Hampshire and Maine. **b** Mean annual egg mass density over all plots 1910–1934 from Burgess and Baker (1938). **c** Spatial covariance functions of egg mass counts for 1910–1921 and 1922–1932



and Liebhold (1995). Synchrony among defoliation series was greatest ~ 1930 –1960 and ~ 1970 –1985 (Fig. 2c).

Spatial covariance functions based on annual egg mass density across all Melrose plots (Fig. 3c) suggest that local synchrony was greater during the 1910–1921 period than during the 1922–1932 period, but estimated regional synchrony and y-intercepts were not significantly different (Table 1).

More variation in patterns of synchrony among different time periods was observed in series of annual defoliation area in towns (Fig. 4b, Table 1). Regional synchrony was significantly lower in the 1931–1940 period than during later decades, though local synchrony (measured by y-intercept values) did not vary significantly among decades (Table 1).

Oscillatory dynamics

The time series of mean egg mass density across all Melrose plots (Fig. 3b) indicates very different

patterns from 1911–1920 versus 1921–1934. From 1911–1920, densities were consistently high and there was relatively little interannual variation. In contrast from 1921–1934 populations were generally lower and appeared to oscillate with two peaks separated by 5 years, with populations falling to very low levels in between. The autocorrelation function for the 1921–1934 series was characteristic of oscillatory dynamics (with a period of ca. 6 or 7 years) but for the 1911–1920 series, the autocorrelation function did not suggest any evidence of periodicity (Fig. 5).

Discussion

The invasion of North America by *L. dispar* does not appear to be precisely an example of “now you see it, now you don’t” as seen in several other non-native species (Simberloff and Gibbons 2004). During the entire 150 years that this species has been established, it has continued to exhibit high density episodes and

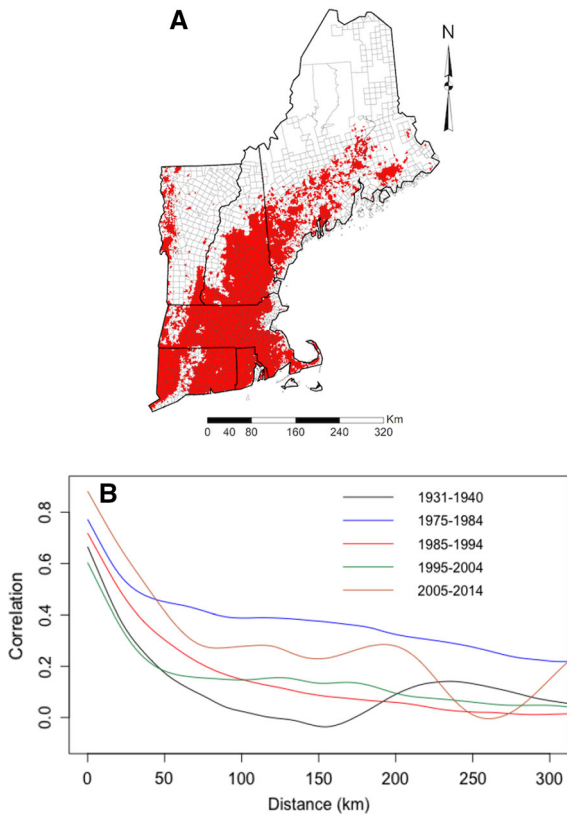


Fig. 4 Analysis of annual defoliated area in 1606 towns in Massachusetts, New Hampshire, Maine, Vermont, Rhode Island and Connecticut. **a** Location of town boundaries and cumulative area defoliated (red) 1975–2014. **b** Estimated spatial covariance functions for 1931–1940, 1975–1984, 1985–1994, 1995–2004 and 2005–2014

there is no clear evidence that these outbreaks are stopping (Fig. 1b). Many species native to North America are known to prey on this alien insect (Smith et al. 1981) and several predators and parasitoids that

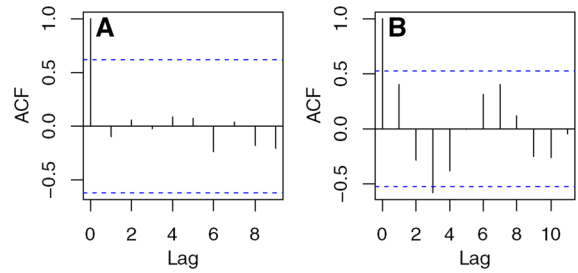


Fig. 5 Autocorrelation functions (dashed blue lines are 95% confidence levels) in of historical US Dept. of Agriculture Gypsy Moth Laboratory egg mass plots in Massachusetts, New Hampshire and Maine. Time series from **a** 1911–1920. **b** 1921–1934

use it as a host have been successfully introduced from its native range (Reardon 1981). The failure of biological control introductions to regulate populations at sub-outbreak levels can be partially explained by the fact that through much of its native range, *L. dispar* also exhibits similar patterns of periodic outbreaks (Johnson et al. 2005); therefore, in many areas where it is native it is not consistently controlled by natural enemies. Another factor that contributes to this insect’s sustained outbreak behavior is that even though outbreaks sometimes can elevate mortality of host trees, it has only a weak negative impact on the abundance of these hosts (Morin and Liebhold 2016), contrasting with certain other non-native forest pest species (e.g., chestnut blight invasion of N. America) which may cause severe declines in host abundance following establishment (Dalglish et al. 2015; Fei et al. 2019).

Even though *L. dispar* has continued to exhibit outbreak dynamics (with periods of extensive forest defoliation) throughout the 150 years of its presence

Table 1 Temporal variation in estimated parameters of spatial covariance functions of egg mass density in Massachusetts, New Hampshire, and Maine, and annual defoliation area in towns in these same states

Type of sampling	Years	Regional Synchrony	95% interval	Y intercept	95% interval
Egg mass density	1910–1921	0.143	0.095–0.205	0.450	0.269–0.673
	1922–1932	0.180	0.126–0.265	0.298	0.097–0.617
Defoliation area	1931–1940	0.081	0.067–0.098	0.666	0.604–0.731
	1975–1984	0.325	0.300–0.349	0.772	0.732–0.810
	1985–1994	0.115	0.0998–0.130	0.719	0.660–0.777
	1995–2004	0.142	0.102–0.184	0.604	0.475–0.778
	2005–2014	0.321	0.309–0.331	0.882	0.828–0.953

in North America, we present evidence here of changes in the dynamics of its populations. First, it appears that the dynamics of populations drastically changed sometime around 1920. Historical counts of egg masses from New England indicate that prior to 1921, populations fluctuated at very high densities sustained for at least a full decade (Fig. 3b). But in 1922 there was a synchronous population crash across the region (see Fig. 3 in Liebhold 1992) and from 1922–1934 populations fell into quasi-regular oscillations (Figs. 3b, 5). These oscillatory dynamics have continued through to the present (Figs. 1b, 2b); over the last 100 years, North American *L. dispar* populations have exhibited a dominant period of 8–10 years with a subharmonic period of 4–5 years though there has been some variation in the strength of this periodicity (Johnson et al. 2005; Bjørnstad et al. 2010; Allstadt et al. 2013). Specifically, Allstadt et al. (2013) analyzed historical *L. dispar* defoliation data from 1924–2009 and identified both intervals of periodic oscillations interspersed with intervals during which periodicity was lacking. However, in contrast to the 1911–1920 interval of sustained non-oscillatory high densities identified here (Fig. 3b), the intervals of non-periodic dynamics from 1924–2009 were entirely associated with low densities. Allstadt et al. (2013) used a multi-trophic model to show that intervals of sustained non-oscillatory low densities could be caused by the impacts of small mammal generalist predators. Predation by small mammals is known to have substantial impacts on low density *L. dispar* populations but has little impact on high density populations (Smith et al. 1981; Bjørnstad et al. 2010) and thus is unlikely to be a cause of the non-oscillatory interval of high densities seen from 1911 to 1920 (Fig. 3b).

The cause of the shift from sustained outbreaks to oscillatory dynamics around 1920 is uncertain. Most of the larval and pupal parasitoids that currently parasitize North American *L. dispar* populations were introduced from its native range in Europe and Asia between 1906 and 1912 (Reardon 1981). There is some uncertainty about the role that these parasitoids play, but parasitism rates are generally low compared with other host-parasitoid systems and there is little evidence that they play a major role in regulating populations or driving oscillations (Elkinton and Liebhold 1990). Instead, the dominant driver of *L. dispar* population oscillations is believed to be

pathogen epizootics. Specifically, the *Lymantria dispar multicapsid nuclear polyhedrosis virus* (LdMNPV) responds in a highly density-dependent fashion, contributing to the collapse of *L. dispar* outbreaks and is thereby thought to produce oscillations in *L. dispar* populations (Woods et al. 1991; Dwyer et al. 2004).

Despite the virus's ubiquity in present day *L. dispar* outbreaks, it appears to have been absent in North America from the time of initial arrival of *L. dispar* in 1868/1869 through at least 1900 (Glaser 1915); Forbush and Fernald (1896) reported detailed descriptions of *L. dispar* outbreaks but made no mention of larvae exhibiting symptoms typical of virus infections. The first records of widespread virus epizootics in North American *L. dispar* populations were reports of a "wilt disease" or "flacherie" causing extensive larval mortality in eastern Massachusetts in 1909 and 1910 (Jones 1910; Reiff 1911) though Rogers and Burgess (1910) and Howard and Fiske (1911) report the presence of the disease in isolated locations as early as 1907 and 1908. Glaser (1915) suggested the disease was introduced with imports of the tachinid parasitoid *Compsilura concinnata*. Though Howard and Fisk (1911) indicate *C. concinnata* was not introduced until 1907, Burgess (1944) records the release in Massachusetts in 1905 of 2000 t from *L. dispar* larvae and pupae collected in Europe. Thus, it is possible that LdMNPV initially arrived as early as 1905 with introduced parasitoids. This hypothesis is supported by Reardon and Podgwaite's (1976) finding that tachinid parasitoids that utilize *L. dispar* as a host are capable of vectoring LdMNPV.

Could the establishment of LdMNPV have caused the shift of *L. dispar* populations from sustained high levels to oscillatory dynamics ~ 15 years later in 1921 (Figs. 3b, 5)? It seems plausible that while LdMNPV was causing isolated epizootics initially, it was not sufficiently prevalent to cause a region-wide, synchronized epizootic and a synchronized population crash until 1921. Abbot and Dwyer (2008) demonstrated that a simple model of *L. dispar* host–pathogen dynamics incorporating regional stochasticity (synchronous meteorological impacts) can produce levels of spatial synchrony observed in North American *L. dispar* populations. Bjørnstad et al. (2008) found that the dynamics of *L. dispar* populations at the invasion front are often out of sync with populations in the rest of the range but fall into sync within 10–15 years. This

perhaps provides some insight into the dynamics of North American *L. dispar* populations from 1905 to 1921; it may have taken about the same amount of time for populations to become synchronized.

Unfortunately, no data were available prior to 1911 and using data from 1911 onward, we did not find significant changes in *L. dispar* synchrony following establishment of LdMNPV. Analysis of the historical egg mass data suggests a slight increase in local synchrony (Y intercept of covariance function) from 1910–1921 to 1922–1932 but this difference was not significant (Table 1). More substantial increases in spatial synchrony in *L. dispar* populations (based on analysis of annual area defoliated) occurred among populations after 1931–1940 (Table 1), suggesting that synchronization of *L. dispar* populations continued for several decades. A trend of increasing spatial synchrony following the shift to more regular pathogen-driven oscillations may reflect a general tendency predicted by mathematical models that periodicity promotes spatial synchrony (Bjørnstad 2000; Haynes et al. 2019). We note that the increase in synchrony from the 1931–1940 interval to the 1975–1984 interval could have arisen as an artefact of the change from mapping defoliation from ground to aerial surveys. Also, observed changes in *L. dispar* synchrony may reflect changes in the synchrony of weather (Allstadt et al. 2015), so it is difficult to identify the causes of these changes with certainty. Allstadt (2015) analyzed historical defoliation map data from across the *L. dispar* range from 1975 to 2009 aggregated to 64 km cells. This range of years overlapped with our analysis of synchrony in defoliation among New England states from 1924 to 2016 (Fig. 2c). However, their analysis is not directly comparable to ours because Allstadt et al. (2015) used 3 year moving time windows for calculating synchrony, but we used 10-year time windows and the analyses differed in their spatial extent and sample unit size.

Even though we did not detect a temporal trend in the proportion of susceptible forest area defoliated from 1924 to 2016, we did detect a significant decline in defoliation levels from 1989 to 2016. The *L. dispar* fungal pathogen, *E. maimaiga*, was first discovered in North American *L. dispar* populations in 1989 and since then it has been observed to cause massive amounts of larval mortality, at levels that typically exceed those caused by LdMNPV (Hajek et al. 2015).

The pathway by which populations of *E. maimaiga* entered North America is not clear.

The pathogen was intentionally introduced in 1910–1911 but not considered to have established (Speare & Colley 1912). Analyses of weather data (Weseloh 1998) and world-wide genetic diversity of *E. maimaiga* (Nielsen et al. 2005) suggest an accidental introduction between 1971 and 1989. Allstadt (2013) quantified historical shifts in the periodicity of *L. dispar* outbreaks from 1924 to 2009 but did not find conclusive evidence of a change in the oscillation period associated with the emergence of *E. maimaiga*. Conclusive identification of changes in oscillation periods and the attribution of such changes is challenging, but our analysis indicates that the emergence of *E. maimaiga* is associated with a measurable decline in the amplitude of regional outbreaks.

The 150-year history of *L. dispar* in N. America provides a remarkable system for understanding how interactions of non-native species with other species, both native and non-native, can result in changes in their population dynamics and impacts over time. Temporal changes in the impacts of invasive species can be expected to cause concurrent changes in their economic impacts. Ultimately, understanding the causes of temporal variation in the impacts of invading species may be key to predicting the benefits of biosecurity efforts targeting arrival prevention or eradication (Epanchin-Niell and Liebhold 2015).

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Declarations

Conflicts of interest The authors that they have declare no conflict of interest.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Code used during the current study are available from the corresponding author on reasonable request.

References

- Abbott KC, Dwyer G (2008) Using mechanistic models to understand synchrony in forest insect populations: the North American gypsy moth as a case study. *Am Nat* 172:613–624
- Allstadt AJ, Haynes KJ, Liebhold AM, Johnson DM (2013) Long-term shifts in the cyclicality of outbreaks of a forest-defoliating insect. *Oecologia* 172:141–151
- Allstadt AJ, Liebhold AM, Johnson DM, Davis RE, Haynes KJ (2015) Temporal variation in the synchrony of weather and its consequences for spatiotemporal population dynamics. *Ecology* 96:2935–2946
- Bjørnstad ON (2000) Cycles and synchrony: two historical ‘experiments’ and one experience. *J Anim Ecol* 69:869–873
- Bjørnstad ON, Falck W (2001) Nonparametric spatial covariance functions: estimation and testing. *Environ Ecol Stat* 8:53–70
- Bjørnstad ON, Liebhold AM, Johnson DM (2008) Transient synchronization following invasion: revisiting Moran’s model and a case study. *Pop Ecol* 50:379–389
- Bjørnstad ON, Robinet C, Liebhold AM (2010) Geographic variation in the North American gypsy moth cycles: sub-harmonics, generalist predators and spatial coupling. *Ecology* 91:106–118
- Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biol* 12:e1001850
- Burgess AF, Baker WL (1938) The gypsy and brown-tail moths and their control. *US Dept Agric Circ* 464
- Burgess AF (1944) The gypsy moth and the brown-tail moth - history of the work for prevention of spread and extermination of these insects in North America. 343 p. online at <https://naldc.nal.usda.gov/catalog/6124364>
- Campbell RW (1967) The analysis of numerical change in gypsy moth populations. *For Sci Monogr* 33:1–34
- Clifton EH, Castrillo LA, Gryganskiy A, Hajek AE (2019) A pair of native fungal pathogens drives decline of a new invasive herbivore. *PNAS* 116:9178–9180
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecol Lett* 7:721–733
- Dalglish HJ, Nelson CD, Scrivani JA, Jacobs DF (2015) Consequences of shifts in abundance and distribution of American chestnut for restoration of a foundation forest tree. *Forests* 7:4
- Desurmont GA, Donoghue MJ, Clement WL, Agrawal AA (2011) Evolutionary history predicts plant defense against an invasive pest. *PNAS* 108:7070–7074
- Dwyer G, Dushoff J, Yee SH (2004) The combined effects of pathogens and predators on insect outbreaks. *Nature* 430:341–345
- Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North America. *Ann Rev Entomol* 35:571–596
- Epanchin-Niell RS, Liebhold AM (2015) Benefits of invasion prevention: effect of time lags, spread rates, and damage persistence. *Ecol Econ* 116:146–153
- Fei S, Morin RS, Oswald CM, Liebhold AM (2019) Biomass losses resulting from insect and disease invasions in US forests. *PNAS* 116:17371–17376
- Forbush EH, Fernald CH (1896) The gypsy moth. *Porthetria dispar* (Linn.). The gypsy moth. *Porthetria dispar* (Linn.). Wright & Potter, Boston
- Gandhi KJ, Herms DA (2010) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol Invas* 12:389–405
- Glaser RW (1915) Wilt of gypsy-moth caterpillar. *J Agric Res* 4:101–126
- Hajek AE, Eilenberg J (2018) Natural enemies: an introduction to biological control. Cambridge University Press, Cambridge
- Hajek AE, Humber RA, Elkinton JS (1995) Mysterious origin of *Entomophaga maimaiga* in North America. *Am Entomol* 41:31–43
- Hajek AE, Tobin PC, Haynes KJ (2015) Replacement of a dominant viral pathogen by a fungal pathogen does not alter the collapse of a regional forest insect outbreak. *Oecologia* 177:785–797
- Hamed KH, Rao RA (1998) A modified Mann-Kendall trend test for autocorrelated data. *J Hydrol* 204:182–196
- Haynes KJ, Walter JA, Liebhold AM (2019) Population spatial synchrony enhanced by periodicity and low detuning with environmental forcing. *Proc R Soc B* 286:20182828
- Howard LO, Fiske WF (1911) The importation into the United States of the parasites of the gypsy moth and the brown-tail moth: a report of progress, with some consideration of previous and concurrent efforts of this kind. *US Dept Agric Bull No. 91*. US Government Printing Office, Washington
- Jeffries MJ, Lawton JH (1984) Enemy free space and the structure of ecological communities. *Biol J Linn Soc* 23:269–286
- Johnson DM, Liebhold AM, Bjørnstad ON (2006) Geographical variation in the periodicity of gypsy moth outbreaks. *Ecography* 29:367–374
- Johnson DM, Liebhold AM, Bjørnstad ON, McManus ML (2005) Circumpolar variation in periodicity and synchrony among gypsy moth populations. *J Anim Ecol* 74:882–892
- Jones JN (1910) Further studies on the nature of the wilt disease of the gypsy moth Larvae. In: Rane FW (ed) *The State Forester of Massachusetts, Seventh Annual Report, 1910*. Boston, pp 100–105
- Liebhold AM (1992) Are North American populations of gypsy moth (Lepidoptera: Lymantriidae) bimodal? *Environ Entomol* 21:221–229
- Liebhold AM, Simons EE, Sior A, Unger JD (1993) Forecasting defoliation caused by the gypsy moth from field measurements. *Environ Entomol* 22:26–32
- Liebhold AM, Gottschalk KW, Mason DA, Bush RR (1997b) Evaluation of forest susceptibility to the gypsy moth across the conterminous United States. *J for* 95:20–24

- Liebhold AM, Haynes KJ, Bjørnstad ON (2012) Spatial synchrony of insect outbreaks. pages. In: Barbosa P, LeTourneau DK, Agrawal AA (eds) *Insect outbreaks revisited*. Wiley, New York, pp 113–125
- Liebhold A, Thorpe K, Ghent J, Lyons DB (1994) Gypsy moth egg mass sampling for decision-making: a user's guide. US Dept Agric Forest Service NA-TP-04-94
- Liebhold AM, Gottschalk KW, Luzader ER, Bush R, Twardus DB (1997a) Gypsy moth in the United States: an atlas. US Dept Agric Forest Service Gen Tech Rep NE-233
- Morin RS, Liebhold AM (2016) Invasive forest defoliator contributes to the impending downward trend of oak dominance in eastern North America. *Forestry* 89:284–289
- Nielsen C, Milgroom MG, Hajek AE (2005) Genetic diversity in the gypsy moth fungal pathogen *Entomophaga maimaiga* from founder populations in North America and source populations in Asia. *Mycol Res* 109:941–950
- Patakamuri SK, O'Brien N (2019) modifiedmk: Modified Versions of Mann Kendall and Spearman's Rho Trend Tests. R package version 1.3.0. <https://CRAN.R-project.org/package=modifiedmk>
- Reardon RC, Podgwaite JD (1976) Disease-parasitoid relationships in natural populations of *Lymantria dispar* (Lep.: Lymantriidae) in the northeastern United States. *Entomophaga* 21:333–341
- Reardon RC (1981) Rearing, evaluating, and attempting to establish exotic species and redistributing established species, attempts before 1960. In: Doane CC, McManus ML (eds) *The gypsy moth: research toward integrated pest management*. US Dept Agric Tech Bull, Washington, pp 348–351
- Reiff W (1911) The "wilt disease" or "flacherie" of the gypsy moth. Wright & Potter, Boston
- Rogers DM, Burgess AF (1910) Report on the field work against the gypsy moth and the brown-tail moth. US Dept Agric Bur Entomol Bulletin No 87, Washington
- Simberloff D, Gibbons L (2004) Now you see them, now you don't!—population crashes of established introduced species. *Biol Invas* 6:161–172
- Smith HR, Lautenschlager RA, Doane CC, McManus ML (1981) Gypsy moth predators. In: Doane CC, McManus ML (eds) *The gypsy moth: research toward integrated pest management*. US Dept Agric Tech Bull, Washington, pp 96–125
- Speare AT, Colley RH (1912) The artificial use of the browntail fungus in Massachusetts, with practical suggestions for private experiment, and a brief note on a fungus disease of the gypsy caterpillar. Wright & Potter, Boston
- U.S. Forest Service (2020) Gypsy moth digest (online database). <https://www.fs.usda.gov/naspf/programs/forest-health-protection/gypsy-moth-digest>
- Vilà M, Hulme PE (eds) (2017) *Impact of biological invasions on ecosystem services*. Springer International Publishing, Cham
- Weseloh RM (1998) Possibility for recent origin of the gypsy moth (Lepidoptera: Lymantriidae) fungal pathogen *Entomophaga maimaiga* (Zygomycetes: Entomophthorales) in North America. *Environ Entomol* 27:171–177
- Williams DW, Liebhold AM (1995) Influence of weather on the synchrony of gypsy moth (Lepidoptera: Lymantriidae) outbreaks in New England. *Environ Entomol* 24:987–995
- Williams DW, Fuester RW, Metterhouse WW, Balaam RJ, Bullock RH, Chianesei RJ (1991) Oak defoliation and population density relationships for the gypsy moth (Lepidoptera: Lymantriidae). *J Econ Entomol* 84:1508–1514
- Williamson M (1996) *Biological Invasions*. Chapman & Hall, London
- Woods SA, Elkinton JS, Murray KD, Liebhold AM, Gould JR, Podgwaite JD (1991) Transmission dynamics of a nuclear polyhedrosis virus and predicting mortality in gypsy moth (Lepidoptera: Lymantriidae) populations. *J Econ Entomol* 84:423–430

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