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Spatiotemporal variability in Allee effects of invading gypsy moth populations

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Abstract

The Allee threshold, the critical population density separating growth from decline in populations experiencing strong Allee effects, can vary over space and time but few empirical studies have examined this variation. A lack of geographically extensive, long-term studies on low density population dynamics makes studying variability in Allee effects difficult. We used North American gypsy moth population data from 1996-2016 to quantify Allee thresholds in 11 regions of the invasion front. Allee thresholds spanned a continuum from being undetectable due to strong population growth at all densities, to being unmeasurable because populations declined across all densities. The lag-1 temporal autocorrelation in Allee thresholds tended to be negative and spatial synchrony in Allee thresholds extended no further than adjacent regions. This work furthers understanding of spatiotemporal variation in Allee effects using extensive empirical data at the range edge of an invasive insect.

Introduction

Demographic Allee effects play an important role in the establishment and spread of invasive species (Taylor and Hastings 2005; Courchamp et al. 2008). When strong Allee effects occur, the per-capita population growth rate becomes negative below a threshold population density—termed the Allee threshold or critical density—tending to lead to extinction (Courchamp et al. 1999). The strength of Allee effects can vary spatiotemporally (Tobin et al. 2007; Walter et al. 2017); however, the spatial and temporal structures of variation in Allee effects remain largely unknown. Allee effects have been demonstrated in North American populations of gypsy moth, *Lymantria dispar* (L.), a forest-defoliating pest introduced from Europe in 1868, and linked to mating failure in low-density populations (Contarini et al. 2009; Tobin et al. 2013). Tobin et al. (2007) introduced a method for estimating Allee thresholds from spatiotemporal abundance data, and applied it to gypsy moth. Based on available data at the time, Tobin and colleagues quantified Allee thresholds using three relatively large and ecologically heterogeneous regions over 8 years, 1996-2003 (Tobin et al. 2007). We used over a decade of additional data to examine 1) how the Allee threshold varied spatially over smaller, more homogenous regions; 2) the structure of temporal variability in Allee effects, and 3) whether Allee effects vary synchronously between regions.

Methods

We analyzed data from the Slow the Spread (STS) program, a gypsy moth management program that monitors range expansion and identifies incipient colonies ahead of the range edge for treatment (Tobin et al. 2004; Grayson and Johnson 2017). In this program, ≈100,000 georeferenced pheromone-baited traps are deployed annually across a ≈175 km-wide transition zone from North Carolina to Minnesota that separates the portion of the USA where gypsy moth is established from areas where it is not. Traps are placed on a ≈2 km grid in low gypsy moth density areas, with spacing increasing to 3-8 km towards the established range (Tobin et al. 2004). Traps catch only adult males, but are considered a valid index of population density and have been widely used as such (Grayson and Johnson 2017).

We used the method of Tobin et al. (2007) to pinpoint the Allee threshold. In brief, the trap catch data were used to generate interpolated surfaces for 1996-2017 over a grid of 5 × 5 km cells using indicator kriging. From each grid cell, we extracted the estimated number of male moths per trapping area for each year, $n_{i,t}$. and its estimate for the following year, $n_{i,t+1}$. We omitted any pairs whose initial value was 0, and any cells within 1.5 km of an area treated for gypsy moth. In practice, <2% of the monitoring area was treated in any given year. We binned the data into a sequence of density categories based on the estimated abundance in year t. The width of each bin was 1 moth (i.e., $0 < n_{i,t} \leq 1$, $1 < n_{i,t} \leq 2$, etc.). The population replacement proportion (i.e., the proportion of pairs with $n_{i,t+1} \geq n_{i,t}$) was calculated for each density bin. We used local polynomial regression (Fan and Gijbels 1996) to analyze how the replacement proportion changed as a function of density. The polynomials had degree = 1 with a smoothing parameter of 0.5. The Allee threshold was defined as the lowest abundance in year t at which the replacement proportion equaled or exceeded 0.5. This approach is suited to quantifying Allee thresholds in cases where there are data on many populations through time because taking the replacement proportion helps to identify signal in noisy data, while also minimizing the effect of stochastic changes in low-density populations that can be extreme on a $n_{i,t+1}/n_{i,t}$ basis. Further details are given in Supplementary Material S1.

By definition, Allee effects occur in small populations, so we considered only relatively low density populations (Tobin et al. 2007). Earlier work operationally defined low densities as ≤ 30 moths trap^{-1}, but in some cases Allee thresholds were not estimated because population replacement proportions never exceeded 0.5 over this range (Tobin et al. 2007). To estimate Allee thresholds at higher densities, we applied the threshold estimation procedure to subsets of data with maximum trap catch densities beginning at 30 moths trap^{-1} and increasing sequentially by 10 moths trap^{-1} until an Allee threshold could be estimated or the maximum empirical trap catch density was reached.

Allee thresholds were estimated for 11 regions defined by the STS project to measure spread rates and plan treatments to eliminate nascent gypsy moth colonies (Fig. 1). These boundaries reflect geopolitical units and regional habitat. We estimated both a 1996-2016 time series of Allee thresholds and an overall Allee threshold combining data from all years. Allee thresholds were not estimated if there were data from fewer than 50 grid cells or fewer than 10 unique population density bins. Despite our new algorithm, we were unable to pinpoint an Allee threshold in regions and years where the replacement proportion never exceeded 0.5. In such cases, we used the maximum observed trap catch density as a surrogate for the Allee threshold. If the replacement proportion was ≥ 0.5 at all densities, the Allee threshold was considered 0.

We quantified temporal autocorrelation and spatial synchrony in annual variation in the Allee threshold to characterize changes over time and space. Temporal autocorrelation was described using the lag-1 Spearman autocorrelation for each region. We quantified spatial synchrony in Allee thresholds by measuring pairwise Spearman correlations between all regions and plotting synchrony as a function of distance between region pairs, measured in number of regions, with adjacent regions having distance = 1 and the most distant regions (1 and 11) having a distance = 10. Spearman rank correlation was deemed more appropriate than Pearson correlation given that we were not always able to quantitatively pinpoint the Allee threshold, and thus some values were best interpreted as relative, not absolute, estimates.

Results

Spatiotemporal variation in gypsy moth Allee thresholds was substantial (Fig. 2a-c, Table 1). Long-term average Allee thresholds tended to be smallest in Wisconsin and the Appalachian mountains of Virginia and West Virginia, and largest in the Midwest and eastern Virginia. However, all regions experienced years with no measurable Allee threshold (i.e., all densities had population replacement proportions ≥ 0.5), and all but two regions experienced years where the Allee threshold could not be quantified because for all recorded densities, up to >800 moths per trap, the replacement proportion was < 0.5. Estimated Allee thresholds were nearly identical when we excluded populations with trap catch densities >0.1 and >0.5 moths per trap. The lag-1 temporal autocorrelation ranged from -0.56 in region 8 to 0.10 in region 3 (Table 1), with a mean of -0.13. In adjacent regions the Allee threshold tended to fluctuate synchronously, but on average spatial synchrony did not extend beyond adjacent regions (Fig. 2d).

Discussion

By examining finer-scale geographic variation, we found differences in low-density population dynamics that were not apparent from earlier work (Tobin et al. 2007). In the Midwest (our regions 5-8), Tobin and colleagues found population replacement proportions rarely exceeded 0.5 at any trap catch density (Tobin et al. 2007), but in regions 5-6 (Illinois and Indiana) we found relatively modest Allee thresholds (Table 1). We also found that the earlier Allee threshold estimate for Virginia, West Virginia and North Carolina (our regions 9-11) was inflated by poor conditions for gypsy moth population growth and persistence in the Atlantic coastal plain (region 11) and that the Allee thresholds for southern mountainous areas were more similar to northern regions. Temperatures in the coastal plain regularly exceed the optimum for larval development and likely drive higher thresholds (Tobin et al. 2014).

Temporal variation in the Allee threshold exceeded spatial variation: every region experienced good and poor years for gypsy moth population growth, regardless of the long-term typical conditions (Fig. 2a-c). Ostensibly, year-to-year weather variation underpins some of this variability (Streifel et al.; Tobin et al. 2014). The lag-1 autocorrelation of Allee threshold time series was typically negative (Table 1), implying that successive years tend to have somewhat dissimilar Allee thresholds. Further research is needed to identify the drivers of temporal variation in gypsy moth Allee thresholds, which are likely to include both density-dependent and independent factors (Walter et al. 2017).

Spatial synchrony in Allee thresholds rarely extended past adjacent regions (Fig. 2d). The lack of spatial synchrony could assist efforts to restrict the spread of the gypsy moth in North America. Since different parts of the invasion front experience favorable conditions for gypsy moth population growth in different years, it could be possible to allocate resources to areas where nascent populations are proliferating while maintaining a consistent overall expenditure on management activities. Identifying factors associated with temporal variation in Allee thresholds would yield additional benefits in this regard.

This work contributes to a body of research on variation in Allee effects. Over 20 years and 11 regions, Allee thresholds often were absent for two diametrically opposed reasons: populations at all densities tended to replace themselves or grow in size, or populations at all densities tended to decline. Our findings highlight that spatiotemporal variability can dramatically alter conclusions about the strength of Allee effects. Further work on tools for quantifying Allee effects and relating variation to ecological mechanisms has the potential to vastly increase knowledge of low-density population dynamics and the factors that drive extinction or population growth, particularly in the context of biological invasions.

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Data availability: Data and analysis code are available at https://github.com/jonathan-walter/gmAlleeVar

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Tables and Figures

Table 1: Aggregate 1996-2016 Allee threshold and lag-1 temporal autocorrelation in annual Allee thresholds for STS regions 1-11 (Fig. 1). Values in brackets indicate that the maximum observed trap catch density was used as a surrogate for the Allee threshold.

Region	Allee threshold	Lag-1 autocorrelation
1	0	0.13
2	1.40	-0.25
3	0	0.10
4	2.25	-0.25
5	11.67	-0.37
6	6.75	-0.21
7	[380]	-0.02
8	[550]	-0.56
9	5.24	-0.04
10	2.42	-0.05
11	[550]	0.05

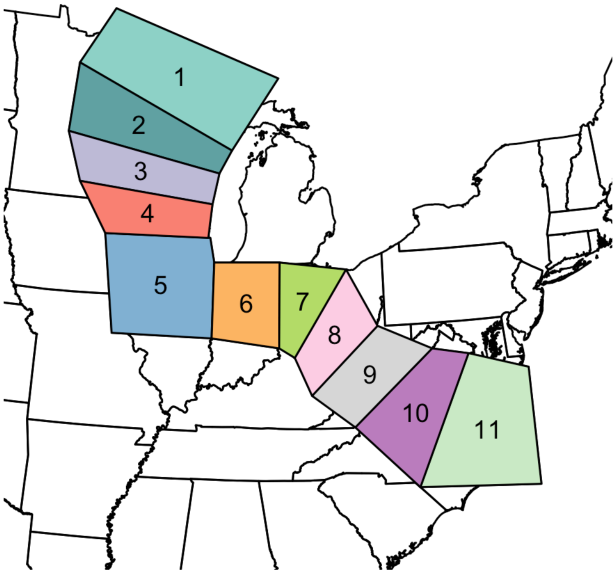

Fig. 1: Map of regions defined by the STS program.

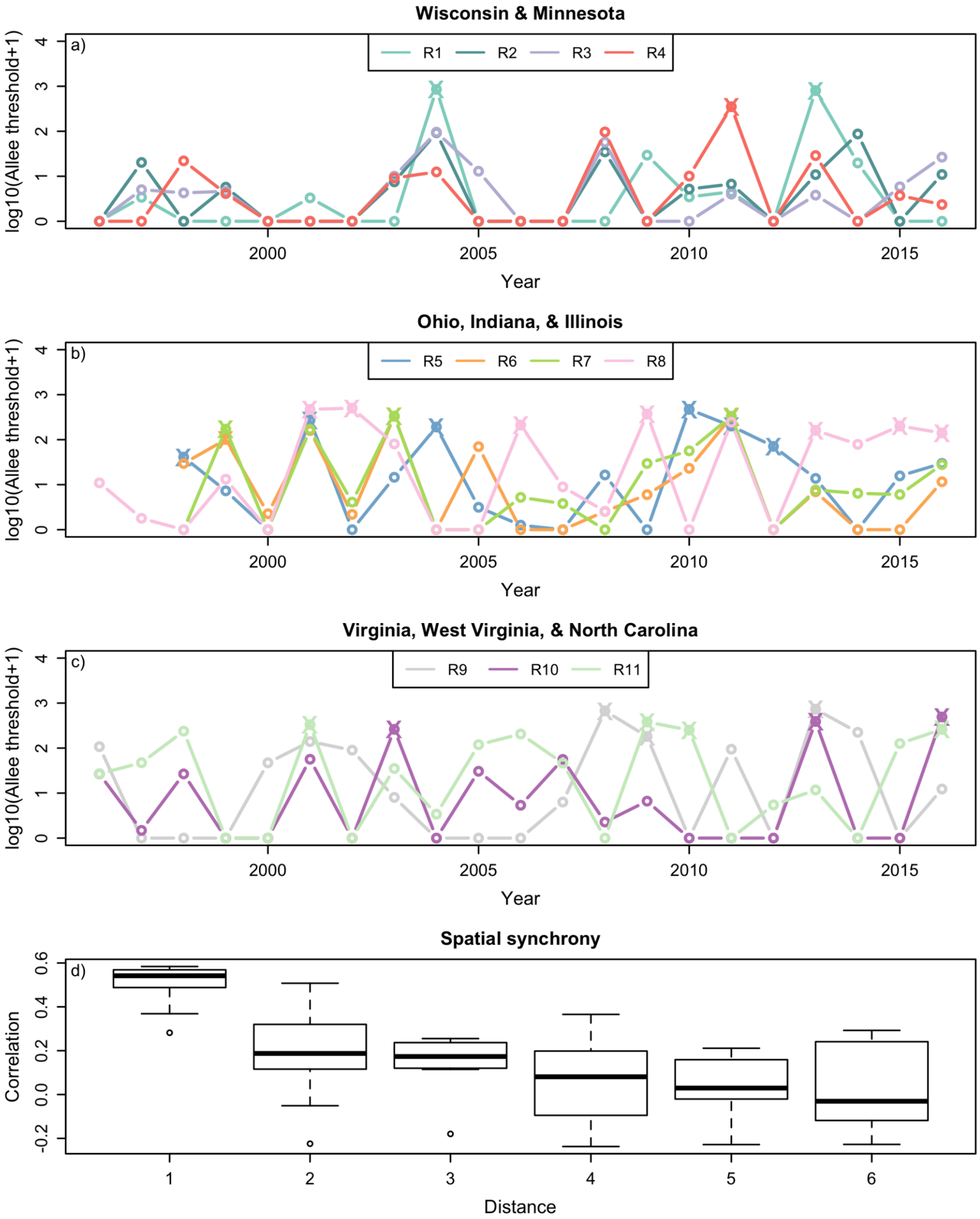

Fig. 2: Time series of Allee thresholds for by region in a) Wisconsin and Minnesota, b) Ohio, Indiana, and Illinois, and c) Virginia, West Virginia, and North Carolina; and d) spatial synchrony in Allee thresholds. Distance is measured in number of regions. In a-c, points marked with “x” indicate cases in which the maximum observed trap catch density was used as a surrogate for the Allee threshold.