LETTERS

Allee effects and pulsed invasion by the gypsy moth

Derek M. Johnson[1], Andrew M. Liebhold[2], Patrick C. Tobin[2] & Ottar N. Bjørnstad[3]

Biological invasions pose considerable threats to the world's ecosystems[1] and cause substantial economic losses[2]. A prime example is the invasion of the gypsy moth in the United States, for which more than $194 million was spent on management and monitoring between 1985 and 2004 alone[3]. The spread of the gypsy moth across eastern North America is, perhaps, the most thoroughly studied biological invasion in the world, providing a unique opportunity to explore spatiotemporal variability in rates of spread. Here we describe evidence for periodic pulsed invasions, defined as regularly punctuated range expansions interspersed among periods of range stasis. We use a theoretical model with parameter values estimated from long-term monitoring data to show how an interaction between strong Allee effects (negative population growth at low densities)[4] and stratified diffusion (most individuals disperse locally, but a few seed new colonies by long-range movement)[5] can explain the invasion pulses. Our results indicate that suppressing population peaks along range borders might greatly slow invasion.

Since its accidental release near Boston, Massachusetts in 1869, the Eurasian gypsy moth (*Lymantria dispar*) has invaded more than 1,000,000 km² of the northeastern United States[5]. Despite an extensive containment programme, gypsy moth invasion continues, causing large-scale defoliation (700–50,000 km² annually) and, occasionally, extensive tree mortality in eastern deciduous forests[6]. Currently, the gypsy moth's North American range extends from Maine to North Carolina and west into Wisconsin[7,8] (Fig. 1). Gypsy moth outbreaks are cyclic in the United States, as they are in its native Eurasian range, and the population undergoes large fluctuations, usually with a 10-yr period[9,10]. The historical rate of gypsy moth invasion in the northeastern

United States averages around 21 km yr⁻¹ (ref 5). The temporal variations in invasion rates are spatially synchronized across distances of up to 600 km (Fig. 2). Since 1988, the US Department of Agriculture has implemented a containment programme to suppress nascent populations at the frontier of the gypsy moth's expanding range[7]. The programme seems to have slowed the spread, but the gypsy moth still threatens to establish itself throughout most of the United States[11].

Diffusion models provide a natural starting point for understanding invasions. Skellam's classic model[12] showed that the radial rate of range expansion (V) is a joint function of the intrinsic rate of population increase (r) and the dispersal rate (D), according to $V = 2(rD)^{0.5}$. The key insight of this model is that the velocity of invasion should be constant when r and D are constant. Recent theories have predicted that the presence of multiple dispersal modes can result in accelerated invasions[13], and that environmental fluctuations can cause variations in rates of spread[14].

Adult female gypsy moths are flightless, and ballooning of 1st instars usually occurs only over short distances. Long-range movement is most often due to anthropogenic transportation of life stages, providing a second mode of spread. This leads to stratified diffusion[15]. Our analyses of historical county-level quarantine data between 1960 and 2002 show periodically fluctuating rates of invasion at pulses with a significant 4-yr period ($P < 0.05$; Fig. 3). We propose that these invasion pulses are caused by an interaction between stratified diffusion and a strong Allee effect.

Strong Allee effects can influence species ranges by prohibiting range expansion, termed 'invasion pinning'[16]. In invasion pinning, dispersal into habitats beyond the range border is too low to inflate population densities above the Allee threshold; therefore, nascent populations beyond the established range fail and, consequently, so does range expansion. However, when the number of immigrants exceeds the Allee threshold—the minimum density required for a
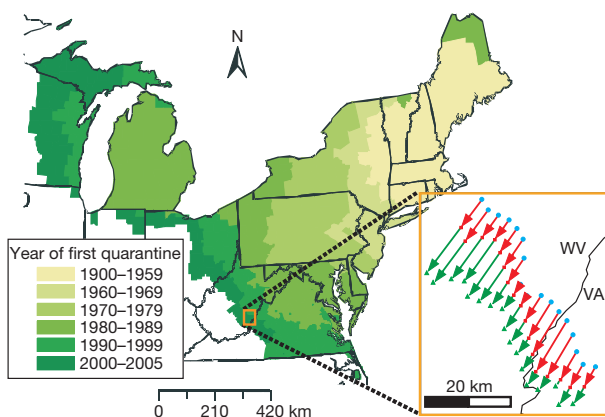

Figure 1 | Map showing the years of first quarantine of the gypsy moth in the eastern United States. The insert shows gypsy moth spread as measured by population isocline displacement from year to year (years represented by different colours) when measured along perpendicular transects spaced ∼6 km apart. Each arrow therefore represents the estimated range expansion from one year to the next at a specific location. VA, Virginia; WV, West Virginia.
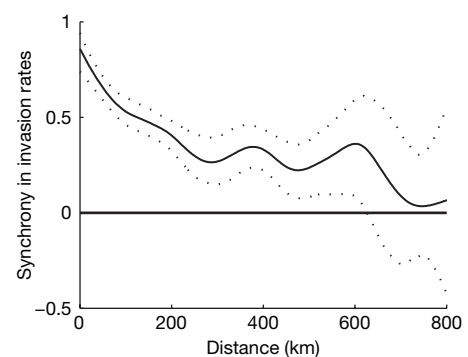

Figure 2 | Nonparametric spatial correlation function showing geographically synchronized rates of invasion out to a distance of 600 km. The full line represents the estimated distance-dependent synchrony and the dotted lines represent the 95% bootstrap confidence limits.

[1]Department of Biology, University of Louisiana, PO Box 42451, Lafayette, Louisiana 70504, USA. [2]United States Department of Agriculture, Forest Service, Northern Research Station, 180 Canfield Street, Morgantown, West Virginia 26505, USA. [3]501 ASI Building, Departments of Entomology and Biology, Pennsylvania State University, University Park, Pennsylvania 16802, USA.
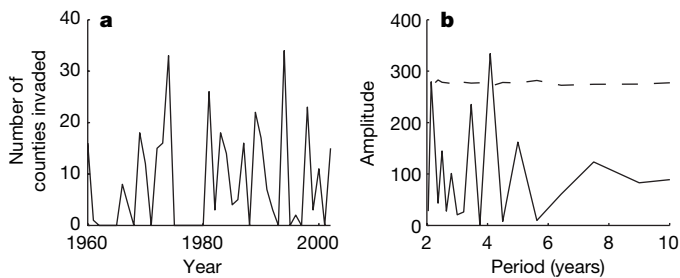
Figure 3 | Periodic invasion pulses in the gypsy moth. a, The number of counties quarantined for gypsy moth in each year from 1960 to 2002. **b**, The periodogram (solid line) reveals a significant 4-yr period in the rate of invasion by the gypsy moth. The dashed line represents the 95% null distribution from the randomization test.

Figure 4 | Simulation model. a, Time series of invasion rates (number of cells invaded) during a theoretical invasion in the model with an Allee effect and stratified diffusion. **b**, The power of periodicity, calculated from spectral analysis, of invasion pulses show a peak around 4 yr. The periodicity was smoothed by averaging moving windows of 10 periodicities.

population to grow—budding populations attain a positive growth rate and can establish.

Allee effects have been recognized as important in theoretical[16–18] and empirical[19,20] studies of invasions[21]. There are several studies that show Allee effects at low densities of gypsy moths[22–24], but estimates of the Allee threshold are usually approximate because most counts are zero, and high observation error and demographic stochasticities are inevitable consequences of low abundance. The current gypsy moth containment programme offers an exception because of its extensive grids of pheromone-baited traps (>100,000 traps per year), which are sensitive to extremely low moth densities along the invasion front. The result is what we believe to be the clearest illustration, and the most detailed quantification, of an Allee threshold in the gypsy moth (~17 moths per trap). The programme also allows us to estimate a 'carrying capacity'. The notion of a carrying capacity is nebulous for widely fluctuating species like the gypsy moth because it is unlikely to represent a stable attractor. However, with a working definition of carrying capacity as the upper threshold, below which populations are more likely to increase than decrease and above which the reverse is true, we pinpoint the 'carrying capacity' at around 687 moths per trap (the converse is our working definition of the Allee threshold; see Supplementary Information A), and were able to estimate the parameters of our model.

With stratified diffusion[15], large-scale range expansion is initiated by the seeding of nascent colonies that are isolated from the current range. These are usually of low abundance, particularly when the donor population is sparse. Without a strong Allee effect, these nascent populations will grow and, according to standard theory, invaders should establish—possibly with an allowance for resource fluctuations[25]—from any number of colonizers. When models lack an Allee effect or stratified diffusion, the simulated invasion rate also lacks periodicity (see Supplementary Information B). By contrast, strong Allee effects allow nascent populations to grow and invasion to progress only if the number of colonizers exceeds the Allee threshold. Thus, range expansion can resume only when the donor populations have grown large enough—the 'donor threshold'—to provide sufficient numbers of emigrants for further spread. Strong Allee effects, therefore, might induce donor thresholds and result in punctuated and pulsed invasions. The frequency of pulsing is determined by the time required for the population density in a newly colonized location to exceed the donor threshold.

These conclusions stem from a spatially explicit model on a one-dimensional discrete landscape of local populations that grow according to a 2nd-order Moran–Ricker model[26,27] (parameterized to reflect key features of gypsy moth dynamics), and spread according to an exponential dispersal kernel but with occasional long-range dispersal ('stratified diffusion'). With an Allee threshold and post-invasion fluctuations around the carrying capacity mirroring that observed in the data, and with stratified diffusion, invasion is predicted to be pulsed with a 4-yr period (Fig. 4). This matches the periodicity observed in the 1960–2002 quarantine records. We
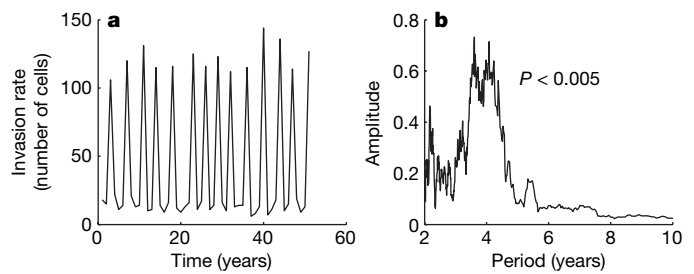
increased dispersal distance to more closely approximate continuous space, and showed that periodic pulses are not artefacts of the discrete-space model (see Supplementary Information C). Moreover, a simplified, continuous-space (point-process) model confirms periodic pulses of invasion in a model with an Allee effect (see Supplementary Information D). Sensitivity analyses show that the prediction of periodic invasion pulses is robust against moderate variation in the model parameters, and indicates that first- or second-order density dependence, the magnitude of environmental stochasticity, or the presence/absence of population cycles has no qualitative effects on the prediction (see Supplementary Information E). These results indicate that stratified diffusion might be a key ingredient in the production of invasion pulses, a conclusion that is consistent with the previously published models with Allee effects, but without stratified diffusion, that lack invasion pulses[18].

The time for a nascent population to increase to the donor threshold will depend on three factors: the magnitude of the Allee threshold, the growth rate of a population at low densities, and the emigration rate. The invasion period observed here (4–5 yr) is approximately half of the outbreak cycle (9–10 yr). Thus, the time for newly established populations to grow sufficiently large to serve as donor populations is similar to the time for a resident population to grow from low to outbreak levels, leading us to hypothesize that the donor threshold is crossed as populations near the expanding population front approach outbreak levels. In the model, invasion pulses are not synchronized with regional gypsy moth outbreaks because newly colonized populations are initially asynchronous with long-established populations. But invasion pulses are themselves spatially synchronous (Fig. 2), indicating that the growth of these populations is synchronized along the invasion front. The extensive data on gypsy moth populations might provide an excellent opportunity to test this prediction.

Understanding the processes that underlie observed patterns is key to devising successful management plans for invasive species. Slowing the spread of the gypsy moth is a priority in forest management in the United States. The current containment programme[7,8] aims to eradicate new populations beyond the established invasion front. Our results indicate that the invasion might also be slowed by suppressing outbreaks near the invasion front, to reduce the number of dispersers to below the donor threshold. The robustness of our model's prediction of periodic invasion pulses in the face of variation in most parameters except for the Allee effect is intriguing; if Allee effects and stratified diffusion are important in other invaders, it might be of interest to look for their footprint in patterns of pulsed invasion. Wherever they are found, suppression of donor population densities could be as important as extinguishing nascent foci to the control of a biological invasion.

METHODS

The data. The data are, in part, from the historical, county-level, gypsy moth quarantine status (US Code of Federal Regulations, Title 7, Chapter III, Section 301.45-3) as reported by the US Department of Agriculture (USDA) since 1934 and compiled in a geographical information system[5]. The spread has been

through expansion into contiguous counties with the exception of a disjunct population in central Michigan (excluded in our analysis).

As a part of the effort to slow the gypsy moth's spread across the United States, intensive monitoring efforts have been focused around the invasion front. Every year, around 150,000 pheromone-baited traps are deployed across an area that currently covers 344,000 km² (ref. 8). In central Virginia and West Virginia, data were collected annually from 1988 to 2004. Each year, more than 13,000 traps were placed at 2-, 3- or 8-km inter-trap distances up to 150 km from the border of the gypsy moth invasion front[8]. The trap data were transformed using $\log_{10} + 1$, and interpolated at a 1-km scale using median indicator kriging[28]. The resulting smoothed surface for each year was used to estimate isoclines of 1, 3, 10, 30 and 100 moths per trap. Local invasion rates were subsequently calculated by measuring the isocline displacements in consecutive years at fixed intervals[29] (Fig. 1) along the isoclines (see Supplementary Information A).

The Allee threshold and 'carrying capacity' were estimated from the phero-mone-baited trap data by quantifying the patterns of increase and decrease in trap capture for each year (see Supplementary Information B).

The model. The model is a spatially extended, stochastic, second-order Moran–Ricker model[26,27]—represented here on the natural scale as opposed to the com-mon log-linear formulation[26]—with an Allee effect:

$$n_{i,t} = \sum_{j=i-50}^{i+50} \left[(an_{i,t-1})(e_i^\nu)(n_{i,t-1}^\alpha n_{i,t-2}^\beta) \left(\frac{n_{i,t-1}^2}{c^2 + n_{i,t-2}^2} \right) (d_{ij}^\tau) \right] + n_{i-k,t-1}\phi \quad (1)$$

Here, $n_{i,t}$ is the abundance at location i in generation t and a is the maximum population growth rate. We pinpoint this parameter at 26.3 because, along with the specific parameters of density-dependence (see below), this makes the model mirror the post-invasion fluctuations around 687 captures per trap that are seen in the historical data (see Supplementary Information A). The second term, e_i^ν, represents unit-mean, log-normally distributed environmental stochasticity in population growth. On the basis of the general understanding that such stochas-ticity arises from a combination of local (σ) and regional (ρ) processes, we model ν as the mixture $r\rho_{i,t} + (1-r)\sigma_t$, where $\rho_{i,t}$ and σ_t represent zero-mean random Gaussian variates each with a variance u, and r represents the relative importance of the local versus regional variability. In our analyses we set the regional versus local stochasticity at 75%:25%[27] and arbitrarily set u at 0.4. The parameters α and β represent the strength of first- and second-order density-dependence, respec-tively. These have previously been estimated at $\alpha = -0.1$ and $\beta = -0.4$ from gypsy moth time-series data[27], reflecting the noisy 10-yr cycle of gypsy moth outbreaks. The fourth term represents a sigmoid Allee effect, for which $c = 0$ denotes no Allee effect. We use the empirical value of $c = 39.4$, which produces an Allee threshold of 17 individuals in the model (see Supplementary Information A). In the simulation, we considered a one-dimensional landscape consisting of 1,000 locations. Each location cell was linked through dispersal according to an arbit-rarily scaled exponential kernel ($\tau = -0.19$) with a maximum local dispersal distance of 100 cells (d_{ij} is the distance between cells i and j). Jump dispersal, according to a stratified diffusion process[13,15], has a proportion of the population (ϕ)—arbitrarily set at 0.005—jump a distance (k) as randomly selected from a uniform distribution on the integers [100, …, 200]. Sensitivity analyses of all parameters are provided in Supplementary Information E.

Spatial analysis. Isocline displacements in all pairs of consecutive years, from 1988 to 2004, were used to quantify the spatial synchrony of invasion rates at stationary spatial locations (Fig. 1). The spatial correlation of invasion rates in the time series was analysed using a nonparametric spatial correlation function[30] in R. Confidence intervals were constructed using bootstrap resampling based on 500 iterations.

Spectral analysis. Periodograms were used to identify periodicity in both the empirical data and simulated models of invasion dynamics. With respect to the Allee effect, we defined an invasion pulse as when a nascent population beyond the invasion front first attains a positive growth rate (excluding migration). For the empirical data, significance levels for powers of periodicity were calculated through randomization tests using 10,000 permutations. Because the spectral analyses on the model (Fig. 4, Supplementary Information B) were calculated from a simulation with ~5,000 invasion pulses, the spectral powers were smoothed with moving averages across windows of 10 periods (the windows covered a very small periodicity range, especially at periodicities below 10 time steps). Significant periodicities were assessed by comparing the maximum power of periodicity to a distribution of maximum powers of periodicity from 10,000 resamplings of the time series with replacement.

1. Vitousek, P. M., D'Antonio, C. M., Loope, L. L. & Westbrooks, R. Biological invasions as global environmental change. *Am. Sci.* **84**, 468–478 (1996).
2. Barbier, E. B. A note on the economics of biological invasions. *Ecol. Econ.* **39**, 197–202 (2001).
3. Mayo, J. H., Straka, T. J. & Leonard, D. S. The cost of slowing the spread of the gypsy moth (Lepidoptera: Lymantriidae). *J. Econ. Entomol.* **96**, 1448–1454 (2003).
4. Allee, W. C. *The Social Life of Animals* (Norton, New York, 1938).
5. Liebhold, A. M., Halverson, J. A. & Elmes, G. A. Gypsy moth invasion in North America: a quantitative analysis. *J. Biogeogr.* **19**, 513–520 (1992).
6. Montgomery, M. E. & Wallner, W. E. in *Dynamics of Forest Insect Populations: Patterns, Causes, Implications* (ed. Berryman, A. A.) 253–375 (Plenum, New York, 1988).
7. Sharov, A. A., Leonard, D., Liebhold, A. M., Roberts, E. A. & Dickerson, W. "Slow the Spread": A national program to contain the gypsy moth. *J. For.* **100**, 30–35 (2002).
8. Tobin, P. C. *et al.* Management of the gypsy moth through a decision algorithm under the Slow-the-Spread project. *Am. Entomol.* **50**, 200–209 (2004).
9. Dwyer, G., Dushoff, J. & Yee, S. H. The combined effects of pathogens and predators on insect outbreaks. *Nature* **430**, 341–345 (2004).
10. Johnson, D. M., Liebhold, A. M. & Bjørnstad, O. N. Circumpolar variation in periodicity and synchrony among gypsy moth populations. *J. Anim. Ecol.* **74**, 882–892 (2005).
11. Sharov, A. A. & Liebhold, A. M. Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecol. Appl.* **8**, 833–845 (1998).
12. Skellam, J. G. Random dispersal in theoretical populations. *Biometrika* **38**, 196–218 (1951).
13. Shigesada, N., Kawasaki, K. & Takeda, Y. Modeling stratified diffusion in biological invasions. *Am. Nat.* **146**, 229–251 (1995).
14. Neubert, M. G., Kot, M. & Lewis, M. A. Invasion speeds in fluctuating environments. *Proc. R. Soc. Lond. B* **267**, 1603–1610 (2000).
15. Sharov, A. A. & Liebhold, A. M. Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecol. Appl.* **8**, 1170–1179 (1998).
16. Keitt, T. H., Lewis, M. A. & Holt, R. D. Allee effects, invasion pinning, and species' borders. *Am. Nat.* **157**, 203–216 (2001).
17. Wang, M. H. & Kot, M. Speeds of invasion in a model with strong or weak Allee effects. *Math. Biosci.* **171**, 83–97 (2001).
18. Lewis, M. A. & Kareiva, P. Allee dynamics and the spread of invading organisms. *Theor. Popul. Biol.* **43**, 141–158 (1993).
19. Taylor, C. M., Davis, H. G., Civille, J. C., Grevstad, F. S. & Hastings, A. Consequences of an Allee effect in the invasion of a Pacific estuary by *Spartina alterniflora. Ecology* **85**, 3254–3266 (2004).
20. Veit, R. R. & Lewis, M. A. Dispersal, population growth, and the Allee effect: Dynamics of the House Finch invasion of eastern North America. *Am. Nat.* **148**, 255–274 (1996).
21. Taylor, C. M. & Hastings, A. Allee effects in biological invasions. *Ecol. Lett.* **8**, 895–908 (2005).
22. Liebhold, A. & Bascompte, J. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecol. Lett.* **6**, 133–140 (2003).
23. Sharov, A. A., Liebhold, A. M. & Ravlin, F. W. Prediction of gypsy-moth (Lepidoptera, Lymantriidae) mating success from pheromone trap counts. *Environ. Entomol.* **24**, 1239–1244 (1995).
24. Whitmire, S. L. & Tobin, P. C. Persistence of invading gypsy moth colonies in the United States. *Oecologia* **147**, 230–237 (2006).
25. Dwyer, G. & Morris, W. F. Resource-dependent dispersal and the speed of biological invasions. *Am. Nat.* **167**, 165–176 (2006).
26. Royama, T. *Analytical Population Dynamics* (Chapman & Hall, London, 1992).
27. Peltonen, M., Liebhold, A. M., Bjørnstad, O. N. & Williams, D. W. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology* **83**, 3120–3129 (2002).
28. Deutsch, C. V. & Journel, A. G. *GSLIB: Geostatistical Software Library and User's Guide* (Oxford Univ. Press, New York, 1992).
29. Sharov, A. A., Roberts, E. A., Liebhold, A. M. & Ravlin, R. W. Gypsy moth (Lepidoptera: Lymantriidae) spread in the central Appalachians: three methods for species boundary estimation. *Environ. Entomol.* **24**, 1529–1538 (1995).
30. Bjørnstad, O. N. & Falck, W. Nonparametric spatial covariance functions: estimation and testing. *Ecol. Environ. Ecol. Stat.* **8**, 53–70 (2001).