

How topography induces reproductive asynchrony and alters gypsy moth invasion dynamics

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Summary

1. Reproductive asynchrony, a temporal mismatch in reproductive maturation between an individual and potential mates, may contribute to mate-finding failure and Allee effects that influence the establishment and spread of invasive species. Variation in elevation is likely to promote variability in maturation times for species with temperature-dependent development, but it is not known how strongly this influences reproductive asynchrony or the population growth of invasive species.

2. We examined whether spatial variation in reproductive asynchrony, due to differences in elevation and local heterogeneity in elevation (hilliness), can explain spatial heterogeneity in the population growth rate of the gypsy moth, *Lymantria dispar* (L.), along its invasion front in Virginia and West Virginia, USA.

3. We used a spatially explicit model of the effects of reproductive asynchrony on mating success to develop predictions of the influences of elevation and elevational heterogeneity on local population growth rates. Population growth rates declined with increased elevation and more modestly with increased elevational heterogeneity. As in earlier work, we found a positive relationship between the population growth rate and the number of introduced egg masses, indicating a demographic Allee effect. At high elevations and high heterogeneity in elevation, the population growth rate was lowest and the density at which the population tended to replace itself (i.e. the Allee threshold) was highest.

4. An analysis of 22 years of field data also showed decreases in population growth rates with elevation and heterogeneity in elevation that were largely consistent with the model predictions.

5. These results highlight how topographic characteristics can affect reproductive asynchrony and influence mate-finding Allee effects in an invading non-native insect population. Given the dependence of developmental rates on temperature in poikilotherms, topographic effects on reproductive success could potentially be important to the population dynamics of many organisms.

Key-words: critical threshold, mating failure, phenology, positive density dependence, protandry

Introduction

Invasions by non-native species are significant threats to biodiversity and ecosystem function (Mack *et al.* 2000; Pimentel, Zuniga & Morrison 2005). One factor influencing

the establishment and spread of introduced species is the Allee effect (Lewis & Kareiva 1993; Fagan *et al.* 2002; Taylor & Hastings 2005). A demographic Allee effect describes a positive relationship between population growth rate and population size (Stephens, Sutherland & Freckleton 1999). Underlying mechanisms of Allee effects include inbreeding depression, failure to satiate predators, inability to acquire prey and failure to locate mates at

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low population densities (Kramer *et al.* 2009). In the case of a strong Allee effect, the population is unable to replace itself when below some minimum population density, termed the Allee threshold (Courchamp, Clutton-Brock & Grenfell 1999; Stephens, Sutherland & Freckleton 1999). Recent studies have detected spatiotemporal variability in the Allee threshold due to heterogeneity in biotic and abiotic conditions (Tobin *et al.* 2007b; Kramer, Sarnelle & Yen 2011). Variability in the strength of Allee effects may appear as changes in the Allee threshold density or in the slope of the relationship between population growth rate and population density. Despite the importance of this phenomenon to invasion ecology, there are relatively few empirical studies concerning Allee effects in biological invasions (Veit & Lewis 1996; Leung, Drake & Lodge 2004; Tobin *et al.* 2007b), partly due to the challenges of measuring low-density populations in which Allee effects occur.

One common cause of Allee effects is mate-finding failure (Gascoigne *et al.* 2009), which can be influenced by reproductive asynchrony (Calabrese & Fagan 2004; Robinet *et al.* 2008). Reproductive asynchrony describes a temporal mismatch in reproductive maturity between an individual and potential mates, which – though potentially adaptive in higher-density populations as it may promote outbreeding (Morbey & Ydenberg 2001), decrease female waiting (Morbey & Ydenberg 2001) and hedge against environmental stochasticity (Post *et al.* 2001) – could limit mating opportunities in low-density populations (Calabrese & Fagan 2004). Considering the population-level temporal distribution of reproductive activity, reproductive asynchrony may reduce fitness in low-density populations if the temporal distribution of reproductive activity for either sex is wide or if males and females tend to mature at different times (i.e. protandry or protogyny) (Calabrese & Fagan 2004; Calabrese *et al.* 2008; Larsen *et al.* 2013).

The degree of reproductive asynchrony in a population may show trends with elevation and latitude (Robinet, Liebhold & Gray 2007; Larsen *et al.* 2013), and another factor that would increase temporal dispersion in reproductive activity is if individuals from different locations – near enough to be linked by dispersal – developed at different times due to differences in microclimate. Consequently, factors leading to variability in phenology across spatial gradients could influence mating success. In taxa with temperature-dependent developmental rates (e.g. poikilotherms), heterogeneity in elevation could affect mating success by promoting spatial variability in the emergence of sexually mature adults, but this hypothesis has not been explored.

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is an ideal model organism for examining the influence of topography on mating success and the consequences for invasion dynamics. Introduced to North America outside Boston, MA, in 1869, its current North American range stretches from Nova Scotia to Wisconsin

and Ontario to Virginia (Tobin *et al.* 2012a), and range expansion continues at variable rates (Tobin, Liebhold & Anderson Roberts 2007a). Under the gypsy moth Slow-the-Spread programme, >100 000 pheromone-baited traps are deployed annually over >200 000 km² along the invasion front (Tobin *et al.* 2012a). Data from this programme are currently available from the Central Appalachian region from 1988 to 2012, providing a unique opportunity to study the population dynamics governing this invasion within a topographically diverse region.

A prior analysis of Slow-the-Spread data revealed an Allee threshold below which populations declined to extinction and demonstrated how spatial variation in the Allee threshold influenced the rate of spread (Tobin *et al.* 2007b). Mate-finding failure is thought to be an important cause of Allee effects in this system (Tobin *et al.* 2009b). Gypsy moth females in North America are not capable of flight and attract flying males using a pheromone. Empirical studies have consistently documented that female mating success increases with male moth density (Sharov, Liebhold & Ravlin 1995; Tcheslavskaja, Brewster & Sharov 2002; Tobin, Onufrieva & Thorpe 2012b). Along the invasion front, females frequently go unmated (Contarini *et al.* 2009), and reproductive asynchrony is thought to be one potential cause of mate-finding failure (Robinet, Liebhold & Gray 2007; Robinet *et al.* 2008).

Across the range of the gypsy moth in North America, thermal gradients due to elevation and latitude produce variation in phenology (Regniere & Sharov 1998; Tobin, Klein & Leonard 2009a). Differences in protandry (the degree to which males tend to mature earlier than females) and the temporal dispersion of maturation times have been linked to geographic trends in mating success (Robinet, Liebhold & Gray 2007). While the authors do not explicitly discuss elevation, findings by Robinet, Liebhold & Gray (2007) indicate a reduction in mating success as elevation increases in the Central Appalachian region (see Fig. 4 in Robinet, Liebhold & Gray 2007). Mating success may decline with elevation if adult emergence becomes increasingly asynchronous, for instance because of increased day-to-day temperature variability at high elevations (Whiteman 2000). A pattern of increased phenological variability in mountainous areas has also been empirically observed (Regniere & Sharov 1998).

Despite the importance of Allee dynamics to the spatial spread of the gypsy moth (Johnson *et al.* 2006b), the underlying causes of geographic variation in the dynamics of low-density populations (Tobin *et al.* 2007b) remain unknown. We investigated the degree to which elevation and elevational heterogeneity, by influencing reproductive asynchrony, could affect geographic variability in the growth of gypsy moth populations. We extended a spatially explicit model to simulate phenology and mate finding in topographically variable landscapes and then connected these theoretical findings to an analysis of 22 years of field-collected population density data. We

made two hypotheses about the population growth rate of gypsy moths along the invasion front, where populations have not become fully established and densities are low. These are as follows: (i) population growth rates will decrease as elevation increases because gains in elevation increase reproductive asynchrony and (ii) population growth rates will decrease as local elevational heterogeneity (hilliness) increases because such heterogeneity causes potential mates from different elevations to become sexually mature at different times.

Materials and methods

STUDY SYSTEM

The gypsy moth is a polyphagous forest defoliating pest native to Eurasia. In North America, female gypsy moths are flightless; thus, natural population spread occurs mainly through passive wind-borne dispersal of neonates, during which larvae typically disperse tens to hundreds of metres (Mason & McManus 1981). Long-distance transport, over distances up to hundreds of kilometres, occurs mainly through accidental movement of gypsy moth life stages by humans (Liebhold & Tobin 2006). Because females are sessile, successful mating depends on a free-flying male locating a mature female. Consequently, rates of mating success are affected by local male moth density (Contarini *et al.* 2009; Tobin, Onufrieva & Thorpe 2012b). Adult males could disperse up to 1–3 km, but typical dispersal distances are on the order of tens to hundreds of metres (Mastro 1981). Prior research indicates that adult phenology can affect mating success, which is reduced by increases in protandry and temporal dispersion of reproductive maturation times (Robinet, Liebhold & Gray 2007; Robinet *et al.* 2008). Both of these phenological characteristics vary due to temperature gradients across the range of the gypsy moth, with temporal dispersion of reproductive maturation [measured as the standard deviation (SD) of the maturation distribution] ranging at least 2.3 to 4.5 days and protandry ranging at least 3–5 days (Robinet, Liebhold & Gray 2007).

STUDY AREA

We focused our study on a $\approx 100\,000\text{ km}^2$ area centred over Virginia and West Virginia, where elevation ranges from 95 to $>1900\text{ m}$ above sea level (Fig. 1). This area spans portions of the Piedmont, Blue Ridge, Northern Ridge and Valley, Central Appalachian and Western Allegheny Plateau ecoregions. Major forest-type groups include oak-hickory, maple-beech-birch, spruce-fir and oak-pine. The oak-hickory group covers the largest percentage (59%) of the study area (USDA Forest Service 2008). The mean gypsy moth spread rate in this area from the late 1980s to 2000s was $\approx 7\text{ km year}^{-1}$ (Tobin, Liebhold & Anderson Roberts 2007a). Continuous trapping records from the deployment of pheromone-baited traps, which attract adult males, from this area date to 1988.

POPULATION GROWTH MODEL

We extended the model of Robinet *et al.* (2008) to examine how elevation and heterogeneity in elevation influence gypsy moth mating success and population growth.

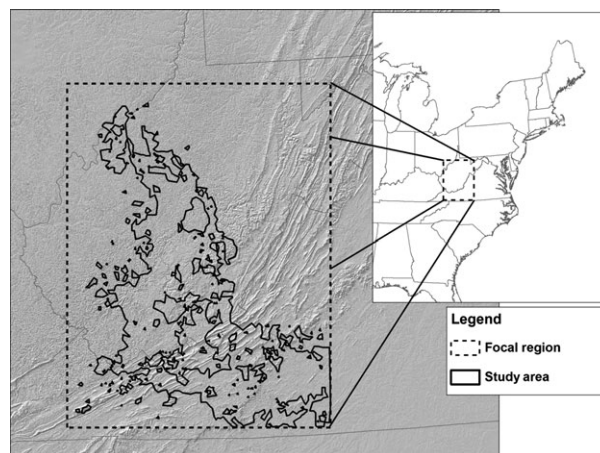


Fig. 1. Study area map. A hillshade layer illustrates topography. The ‘focal region’ defines the geographic area in which effects of topography on mating success were modelled. The ‘study area’ outlines grid cells retained for the empirical analysis after filtering to remove cells where the gypsy moth was present prior to the beginning of monitoring and where there were too few data (see ‘Growth Rates in Field Populations’ in Methods).

Their model was developed to study the effects of reproductive asynchrony (protandry and temporal dispersion of adult maturation) on gypsy moth mating success. In the model’s original form, N egg masses were introduced at the centre of a $0.5 \times 0.5\text{ km}$ region devoid of the species. Then, neonates of both sexes dispersed in two spatial dimensions (x and y) at time t based on the simple diffusion equation:

$$\frac{\partial U}{\partial t}(x, y, t) = D \left(\frac{\partial^2 U}{\partial x^2}(x, y, t) + \frac{\partial^2 U}{\partial y^2}(x, y, t) \right), \quad \text{eqn 1}$$

where the diffusion coefficient $D = 0.003\text{ km}^2$ (Liebhold & Tobin 2006) and U is the standardized population density. Individuals were assigned to locations based on probabilities generated by the diffusion equation. Egg-to-adult mortality was implemented by randomly choosing surviving individuals at a realistic survivorship rate of 0.05 (Elkinton & Liebhold 1990). The timing of reproductive maturation was simulated using Gaussian functions with peak male maturation fixed at an arbitrary day. Both the temporal dispersion of the maturation period and the amount of protandry were varied to assess their effects. Mating success depended on spatial and temporal overlap of potential mates. The probability of a female attracting a given male (p_i) at a given distance (x) and time lag between male and female maturation ($i = 0, 1$ or 2 days) was estimated using the negative exponential equation:

$$p_i(x) = a_i \exp(-b_i x), \quad \text{eqn 2}$$

where a_i and b_i are parameters fitted based on release–recapture experiments simulating mate finding (Robinet *et al.* 2008). Mortality of adult males was implicitly accounted for in the mate attraction function. Mate finding at lags ≥ 3 days was ignored given the short life spans of adult males. Females were assumed to be reproductively active only on the day of their emergence due to high rates of mortality (Sharov, Liebhold & Ravlin 1995). Robinet, Liebhold & Gray (2007) showed that the effect of variation in female longevity on mating success was small. The model

was run for a single generation, and mating success was measured in terms of the population growth rate, which was defined as the number of fertilized egg masses produced after 1 generation divided by the number of introduced egg masses.

To predict spatial variation in population growth resulting from differences in topography across our study region, we made three adjustments to the Robinet *et al.*'s (2008) model. We expanded the size of the model landscape to 1×1 km to match the spatial grain of gypsy moth pheromone-baited trap records (see 'Growth Rates in Field Populations' below), we introduced egg masses at locations selected randomly from a uniform distribution rather than a fixed point to mimic human-mediated long-distance transport (Liebhold & Tobin 2006), and we prescribed gypsy moth phenology to vary as a function of elevation and latitude, rather than controlling these parameters directly.

Relationships between elevation and latitude and three aspects of gypsy moth phenology – the day of peak male maturation, the SD (temporal dispersion) of the male maturation period and the degree of protandry – were determined based on predictions from the gypsy moth life stage model (GLS) (Gray 2004). GLS is a composite of phenology models for the egg (Gray, Ravlin & Braine 2001), early larval (Logan, Casagrande & Liebhold 1991) and late larval to adult stages (Sheehan 1992). GLS predicts developmental timing using stage-specific and, where applicable, sex-specific developmental responses to temperature. One key feature of GLS is that, rather than specifying egg mass fertilization at an arbitrary date, it uses an optimization procedure to estimate fertilization dates that are realistic to that particular climate (Gray 2004).

For the day of peak male maturation and temporal dispersion of male maturation, predictions for 2001–2011 were generated by applying the GLS model to meteorological records interpolated over the network of 1×1 km lattice cells using BioSIM software (Regniere & Saint-Amant 2008). BioSIM interpolates meteorological records, adjusting for latitude, longitude and elevation. As phenological predictions vary according to annual weather variations, we calculated the average day of peak maturation and average temporal dispersion over the 12-year period. These mean predictions were regressed against the mean elevation and northing (analogous to latitude) of the lattice cell. We considered linear, quadratic and exponential relationships, and the model having the lowest AIC value was selected. To quantify effects of elevation and latitude on protandry, we obtained GLS model predictions used by Robinet, Liebhold & Gray (2007) for 77 weather stations in our study area and estimated the mean amount of protandry (days from peak male to peak female abundance) for 1961–2000 at each weather station. We applied the same criterion as above to determine the equation that best described the effects of elevation and latitude on protandry. As in Robinet *et al.* (2008), we assumed that the temporal dispersion in maturation follows a normal distribution, and the female distribution has the same SD as the males', but is shifted in time due to protandry.

To model variation in population growth rate, we divided the study region into 1×1 km lattice cells and represented the topography present in each cell using a 10-m-resolution digital elevation model (DEM) (United States Geologic Survey 2009). The phenologies of introduced egg masses were determined based on relationships with elevation and latitude determined above, with elevation taken from the 10-m-resolution DEM at the location of the egg mass and using the mean latitude of the lattice cell. Our model was run on a stratified random sample of 2200

out of 106 928 lattice cells to improve computational tractability. We randomly selected 200 cells from each of 11 intervals of heterogeneity in elevation, which was computed as the SD of elevation (represented by the 10-m-resolution DEM) within each lattice cell. The 11 intervals were as follows: 0–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90, 90–100 and >100 m. Standard deviation of elevation in selected lattice cells ranged from 0 to 158 m, and mean elevation ranged from 129 to 1508 m.

For each selected 1×1 km lattice cell, we estimated mating success in terms of the population growth rate over 1 generation. Following Robinet *et al.* (2008), we estimated the finite rate of population growth (λ) according to $\lambda = E_t/E_{t-1}$, where E_t is the number of fertilized egg masses after one generation (gypsy moth females oviposit 1 egg mass each) and E_{t-1} is the number of introduced egg masses. To assess dependence between initial egg mass density and the population growth rate, landscapes were initially seeded with 3, 5, 7, 9, 11, 13, 15, 20, 25, 30, 35 or 40 egg masses. Each egg mass was assumed to contain 300 eggs with a 1 : 1 sex ratio (Robinet *et al.* 2008). Model simulations and analysis were conducted in R version 3.0.1 (R Core Team 2013). See Appendix S1 (Supporting information) for model code.

GROWTH RATES IN FIELD POPULATIONS

We also examined the influences of elevation and local heterogeneity in elevation on growth rates in field-collected data across the network of 1×1 km lattice cells described above. Growth rates were estimated using spatially referenced trap data from the gypsy moth Slow-the-Spread programme. The pheromone-baited traps used in this programme are effective at collecting males at very low densities (Schwalbe 1981), providing a means to identify the earliest stages of an invading gypsy moth colony. We used trap catch data collected in Virginia and West Virginia annually from 1988 to 2009 as a proxy for the true population density. The number of traps in the study area averaged 11,150 per year. Most traps were placed ≈ 2 km apart, although some are placed as much as 3–8 km apart or as little as 0.25 km apart (Tobin, Liebhold & Anderson Roberts 2007a). Because the exact location of traps changed from year to year, median indicator kriging (Isaaks & Srivastava 1989) was used to interpolate a continuous surface of gypsy moth abundance over the network of 1×1 km lattice cells using GSLIB software (Deutsch & Journel 1992). From the centre of each lattice cell, we extracted the estimated number of male moths per trapping area for each year. Because some gypsy moth populations are treated under the Slow-the-Spread programme in an effort to eliminate newly formed colonies (Tobin *et al.* 2012a), trap catch data within 1.5 km of a treated area were excluded. Generally, $\leq 2\%$ of the area was treated each year.

We determined the population growth rate in each lattice cell by fitting the geometric population growth equation $N_t = \lambda_m N_{t-1}$ to a time series of trap catch densities using ordinary least squares regression. The population growth rate λ_m describes the proportional change in the number of gypsy moth males (N) captured between time $t-1$ and time t . We limited our analysis to estimated densities between 0 and 50 moths per trapping area to focus on growth of low-density populations. Fifty moths are below this region's mean carrying capacity of 673 moths per trap, yet above the region-wide Allee threshold of 21 moths per trap (Tobin *et al.* 2007b). We used values greater than the 21-moth-per-trap threshold to allow for the possibility that the Allee

threshold might vary locally. Some lattice cells had very low estimated trap catch in one or more years before a gypsy moth was actually captured in the cell, which is an artefact of the interpolation method. Thus, N values <0.1 were considered to be 0. We ignored data prior to the last year in which $N = 0$ because N commonly fluctuated between 0 and very low densities (<2 moths) for ≈ 3 – 5 years prior to gypsy moths consistently being present in a lattice cell. Exploratory analyses, including data in which N fluctuated between 0 and non-zero values, resulted in poor fits of the population growth equation. Furthermore, the geometric growth model precludes population growth following a generation with zero individuals. We further excluded grid cells meeting certain non-mutually exclusive criteria, primarily removing cells in which gypsy moth was present at the beginning of our study period or cells with too little data (see Appendix S2 (Supporting information) for details).

We used generalized additive models (GAMs) to assess the influence of elevation, elevational heterogeneity and density of preferred host trees on population growth rates. GAMs combine properties of generalized linear models and additive models, allowing the replacement of linear regression coefficients with nonparametric smooth functions such as splines (Hastie & Tibshirani 1986). Using smoothed estimates for covariates is advantageous because it allows detection of nonlinear relationships, such as those between environmental covariates and aspects of gypsy moth population dynamics (Sharov, Liebhold & Anderson 1997; Haynes, Liebhold & Johnson 2012). In GAMs, smooth functions are penalized for increased nonlinearity to balance model fit and complexity. To further guard against overfitting, we increased the penalty for increasing spline degrees of freedom to 1.4 (Kim & Gu 2004). We specified the gamma distribution for the dependent variable and the log link function to improve normality of the model residuals. We also examined measures of concurvity (i.e. a generalized case of collinearity allowing for curvilinear relationships) between predictor variables to ensure that the analysis did not suffer from severe model identifiability issues. Concurvity statistics are bounded between 0 and 1, with 0 indicating no concurvity and 1 indicating complete lack of model identifiability.

Elevation and elevational heterogeneity [$SD(\text{elevation})$] were calculated using the 10-m-resolution DEM as above. Because we found nonlinear effects of elevation on day of peak maturation and temporal dispersion (Fig. 2a,b), we also tested whether the effects of elevational heterogeneity on population growth could become stronger at high elevations by including an interaction effect between elevational heterogeneity and elevation. The density of gypsy moth preferred host trees, which includes 79 tree species, was obtained from Morin *et al.* (2005) and is expressed as the basal area of preferred species ($\text{m}^2 \text{ha}^{-1}$) at 1-km resolution. A correlogram indicated that population growth rates were positively autocorrelated over a distance of ≈ 58 km (Appendix S3, Supporting information). Spatial autocorrelation in population growth rate was accounted for in the GAM by including the distance-weighted mean of the growth rate as a term in the model. Here, points >58 km from the focal point were assigned a weight of zero. Otherwise, the weight (w_{ij}) was calculated based on the fitted relationship between autocorrelation and distance:

$$w_{ij} = (0.8608 - 1.175e^{-5}(d_{ij}))^2, \quad \text{eqn 3}$$

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

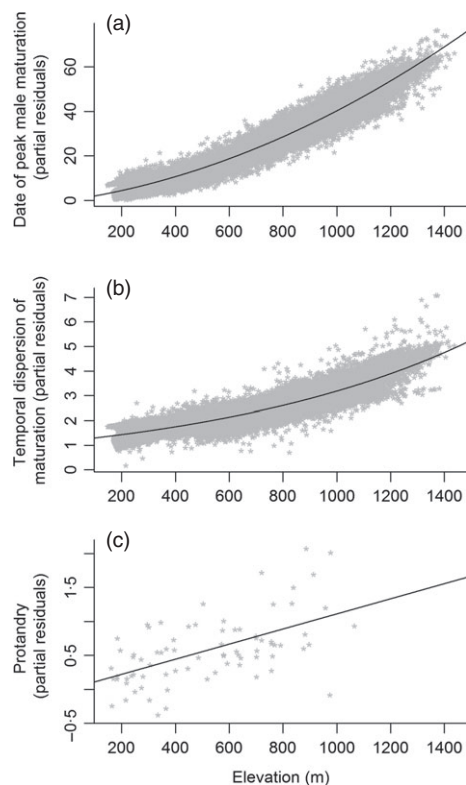


Fig. 2. Relationships between elevation and (a) day of peak male maturation, (b) dispersion (SD) of the population-wide distribution of male maturation and (c) protandry.

$$\bar{\lambda}_m = \frac{\sum_{j=1}^n w_{ij} \lambda_j}{\sum_{j=1}^n w_{ij}}. \quad \text{eqn 4}$$

Correlogram analyses were implemented using the ‘ncf’ package in R version 3.0.1 (R Core Team 2013).

Following Wood & Augustin (2002), we used a backward selection protocol to arrive at a parsimonious model. We began with the full model:

$$\lambda_m = s(\text{elev}) + s(\text{SD}(\text{elev})) + s(\text{hostba}) + s(\bar{\lambda}_m) + te(\text{elev}, \text{SD}(\text{elev})), \quad \text{eqn 5}$$

in which the growth rate was predicted by elevation, SD of elevation, density of preferred host trees, the distance-weighted mean growth rate and an interaction between elevation and SD of elevation. Here, s indicates smooth spline functions of the covariates and te indicates a tensor product smooth. Wood & Augustin (2002) suggested that a variable should be dropped from the model if it meets all of the following criteria: (i) the estimated degrees of freedom for that term are close to 1, (ii) the confidence region for the smooth function includes zero for all values of the independent variable, and (iii) the generalized cross-validation (GCV) score for the full model decreases if the term is removed. Because of the subjectivity of the first criterion, we removed terms based only on the second and third criteria. In practice, this method is more conservative than the one suggested by Wood & Augustin (2002) because it is less likely to retain variables. GAMs were implemented using the ‘mgcv’ package (Wood 2006) in R version 3.0.1 (R Core Team 2013).

Results

PARAMETERIZING THE POPULATION GROWTH MODEL

When analysing phenological predictions to parameterize our simulation model, we selected the candidate model with the lowest AIC value (Appendix S5, Supporting information). The most parsimonious relationship between the day of peak male maturation and elevation was $\text{peak} = 899.2 - 4.218e^{-4}[\text{northing (m)}] + 5.983e^{-11}[\text{northing(m)}]^2 + 1.766e^{-2}[\text{elevation (m)}] + 2.255e^{-5}[\text{elevation (m)}]^2$ ($R^2 = 0.953$) (Fig. 2a). Here, elevation is the DEM value at the coordinates where an egg mass is introduced and northing was measured at the centre of the 1×1 km landscape in a custom coordinate system (Appendix S4, Supporting information). The selected relationship ($R^2 = 0.870$) for the dispersion (SD) of the male maturation distribution was $\text{dispersion} = 23.09 - 1.358e^{-5}[\text{northing (m)}] + 2.067e^{-12}[\text{northing(m)}]^2 + 1.172\{\exp[\text{elevation (km)}]\}$ (Fig. 2b). The amount of protandry, in days, was estimated as $\text{protandry} = -3.639e^{-3} + 1.112e^{-3}[\text{elevation (m)}] + 8.401e^{-7}[\text{northing(m)}]$ ($R^2 = 0.318$) (Fig. 2c). Tables ranking each of the candidate models by AIC value are located in Appendix S5 (Supporting information). In the model, we allowed for variability from these relationships by adding to each estimate normally distributed random error, with SD determined from regression residuals. These values were 2.61, 0.224 and 0.406 days for the day of peak male maturation, the temporal dispersion of the maturation period and protandry, respectively.

POPULATION GROWTH MODEL PREDICTIONS

For all densities of introduced egg masses, the modelled mean population growth rate declined with increases in elevation (Fig. 3a, Appendix S6, Supporting information). The population growth rate declined more modestly with increases in elevational heterogeneity [SD(elevation)], and the effect was nearly imperceptible when <20 egg masses were introduced (Fig. 3b, Appendix S6, Supporting information) but grew as the number of introduced egg masses increased. We also found a positive effect of the number

of introduced egg masses on the population growth rate, indicating the presence of a demographic Allee effect. Increases in elevation and elevational heterogeneity increased the number of introduced egg masses at which population growth reaches the replacement rate of $\lambda = 1$ (Fig. 3). Additional plots showing trends and variability in the effects of elevation and elevational heterogeneity on population growth rates can be found in Appendix S6 (Supporting information).

GROWTH RATES IN FIELD POPULATIONS

Estimates of the growth rates of invading gypsy moth populations based on pheromone-baited trap catch data varied from $\lambda_m = 0.044$ to $\lambda_m = 23.0$, with a mean (\pm SD) of 1.16 ± 1.28 . Distance-weighted mean growth rate, density of preferred host trees, elevation and SD (elevation) met our model selection criteria and were retained in the GAM, but the interaction term between elevation and elevational heterogeneity was removed because the confidence intervals overlapped zero for all values of the covariates. Estimates of concavity between each term and the rest of the model were 0.278 for distance-weighted mean growth rate, 0.359 for density of preferred host trees, 0.546 for elevation and 0.289 for SD(elevation). The adjusted R^2 for the full model was 0.314. Population growth rates generally decreased with increases in elevation (Fig. 4a). The relationship between SD(elevation) and the growth rate was nonlinear, with the growth rate increasing with SD(elevation) in the flattest landscapes [$0 < \text{SD}(\text{elevation}) < 10$ m] and exhibiting little or no relationship across landscapes of intermediate hilliness [$10 \text{ m} < \text{SD}(\text{elevation}) < 100$ m; Fig. 4b]. The most sustained trend was a negative relationship between the growth rate and SD(elevation) in the hilliest landscapes [$\text{SD}(\text{elevation}) > 100$ m]. There was also a weak and generally negative relationship between the growth rate and basal area of preferred gypsy moth host trees (Fig. 4c). Inclusion of the distance-weighted mean growth rate term strongly reduced spatial autocorrelation in the GAM residuals (Appendix S3, Supporting information).

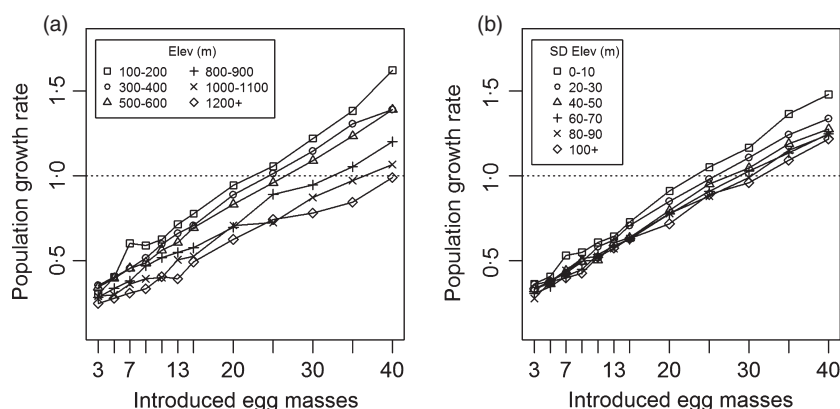


Fig. 3. The mean population growth rate increased as the number of introduced egg masses increased from 3 to 40, with the population growth rate increasing more slowly with increases in (a) elevation and (b) heterogeneity in elevation (SD of elevation). For visual clarity, a selection of ranges of elevation and elevational variability is shown, but the pattern remains consistent across all levels of elevation and elevational variability in the focal region.

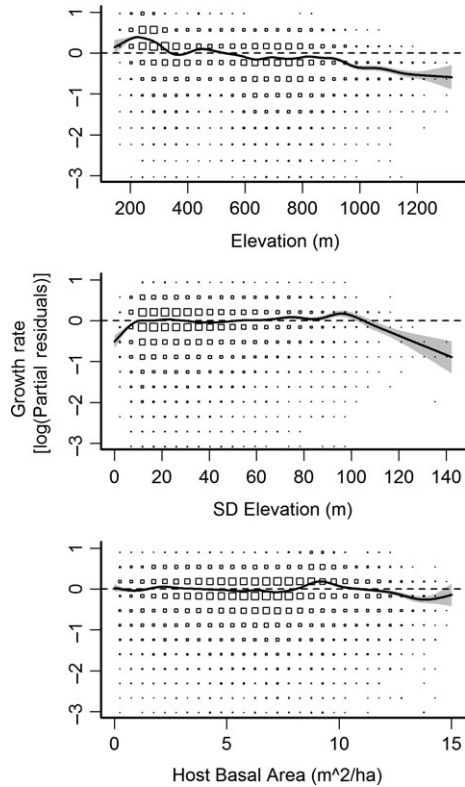


Fig. 4. Spline fit plots from GAM analysis describing relationships between growth rate and (top) elevation (spline with 18.8 d.f.), (middle) SD of elevation (spline with 16.1 d.f.) and (bottom) basal area of preferred host trees (spline with 15.8 d.f.). Grey regions are confidence bounds (± 2 standard errors). x -axes are scaled in units of the linear predictor. y -axes represent partial residuals on a logarithmic scale. Partial residuals were binned using equal-width intervals and are plotted using squares scaled according to the number of residuals in that bin. GAM, Generalized additive models.

Discussion

In this study, a model simulating the effects of thermal regime on reproductive asynchrony predicted that increasing elevation and local heterogeneity in elevation (hilliness) negatively affect the growth rates of low-density gypsy moth populations. As in Robinet *et al.* (2008), our simulations predicted the existence of a demographic Allee effect and also supported our novel hypotheses, with populations in landscapes at the highest elevations and with the hilliest topographies suffering the lowest growth rates (Fig. 3). Consistent with these theoretical predictions, an analysis of field data collected near the invasion front showed that population growth rates declined with increasing elevation (Fig. 4a). High local elevational heterogeneity also tended to reduce population growth rates, though this relationship was not entirely consistent (Fig. 4b). The general agreement between theory and field data supports the hypothesis that topographic characteristics, acting through effects on reproductive asynchrony, influence the growth of gypsy moth populations along the margins of its range. Negative demographic consequences

of reproductive asynchrony have been documented for a variety of insect species (Calabrese *et al.* 2008; Régnière *et al.* 2013), and in the gypsy moth, there is a particularly clear link between reproductive asynchrony and the Allee effect (Robinet, Liebhold & Gray 2007; Robinet *et al.* 2008). Despite this, few studies have addressed specific causes of variability in Allee dynamics (but see Kramer, Sarnelle & Yen 2011), and we are not aware of any other studies addressing elevation or elevational heterogeneity as drivers of reproductive asynchrony and Allee effects.

The relatively strong decline in gypsy moth population growth rates with increasing elevation may be explained by increased protandry and temporal dispersion in maturation times (Fig. 2b,c), likely due to increased variability in temperature at high elevations (Whiteman 2000). Previously, Robinet, Liebhold & Gray (2007) and Robinet *et al.* (2008) showed that high levels of protandry and temporal dispersion of maturation times can reduce gypsy moth population growth rates by limiting mate finding. This study demonstrates how these phenological characteristics map onto real landscapes and shows clear implications for understanding the dynamics of gypsy moth spread.

We also hypothesized that elevational heterogeneity would negatively affect the population growth rate, given that, in steeply undulating landscapes, potential mates are exposed to different thermal conditions at different elevations. The resulting phenological differences lower mating success by locally increasing temporal dispersion in maturation times; in other words, these phenological differences effectively reduce the number of males available to mate with each female, ergo reducing mating success and the population growth rate. However, this effect was weak compared to the effect of elevation on population growth. Allowing different egg masses to develop under different thermal conditions effectively widens the population-level distribution of reproductive maturation, which others found to have less influence on mating success than protandry (Robinet, Liebhold & Gray 2007; Robinet *et al.* 2008). Here, phenological differences between egg masses caused by elevational heterogeneity were not large relative to the width of the maturation distribution of a single egg mass, weakening the resulting effect on population growth. We predict that elevational heterogeneity may more strongly influence population growth in species whose individual reproductive period is shorter relative to their ability to locate mates in space, whose phenology displays greater sensitivity to temperature or who inhabit landscapes with very high elevational heterogeneity.

In simulated populations, the slope of the relationship indicated a stronger decline in population growth rates with increases in elevation and elevational heterogeneity when more egg masses were introduced (Fig. 3, Appendix S6, Supporting information). For elevational heterogeneity, this is likely because the average distance between egg masses was so high that dispersal limitation largely prevented mating between individuals from different egg

masses. In other words, isolation in time was less significant when there was already substantial isolation in space. This effect may influence observed relationships between elevation and population growth rate, given that higher elevation sites tend also to have more elevational variability.

In field populations, the relationship between elevational heterogeneity and the population growth rate did not strictly conform to the predictions of the simulation model. The model predicted a linear decline in the population growth rate with increasing elevational variability, but in field populations, there was a positive relationship across a narrow range of the flattest landscapes, no relationship in landscapes of intermediate hilliness and a negative relationship in the hilliest landscapes. Although the decline in population growth rate in very heterogeneous landscapes is significant (Fig. 4b), it is based on <2% of the data set [124 grid cells with $SD(\text{elevation}) \geq 100$]. One possible explanation for the positive relationship between population growth rate and hilliness in the flattest landscapes is that a slight amount of reproductive asynchrony may be beneficial if it allows some individuals to escape episodic disturbances such as severe weather events (Post *et al.* 2001). Because the mortality rate was constant in the simulation model, we were not able to address this potential benefit of a small amount of asynchrony.

The basal area of preferred host tree species was expected to positively influence gypsy moth population growth rates because gypsy moths exhibit higher survivorship and fecundity when feeding on preferred hosts (Hamilton & Lechowicz 1991). Indeed, the development of gypsy moth outbreaks is strongly influenced by the density of preferred host tree species (Gottschalk 1993; Johnson, Liebhold & Bjørnstad 2006a). However, the relationship between host tree density and the dynamics of low-density populations is unclear. One study from the lower peninsula of Michigan observed a positive relationship between the rate of gypsy moth spread and the density of preferred host trees (Sharov *et al.* 1999). However, another study across the entire invasion front, from Wisconsin to North Carolina, showed no relationship between the persistence of low-density populations and host tree density (Whitmire & Tobin 2006). One possible explanation is that although population growth to outbreak densities is dependent upon the density of preferred hosts (Gottschalk 1993), population growth in low-density gypsy moth populations is more strongly influenced by drivers of Allee effects such as mate-finding failure because low-density populations require a relatively low abundance of resources.

In interpreting empirical relationships between growth rate, elevation, elevational heterogeneity and host tree basal area, potential relationships between these variables should be noted. In many landscapes, the greatest elevational variability may occur at the highest elevations, and due to patterns of human development, these may also be the most heavily forested sites. In this case, GAMs fitted using the procedures implemented in the R package 'mgcv'

have been shown to be robust to concurvity (Wood 2008), and concurvity metrics did not suggest severe model identifiability issues in our data. However, given that gypsy moths require some amount of suitable host, an increase in host tree density with elevation and elevational heterogeneity should make it more difficult to detect negative effects of elevation and elevational heterogeneity on population growth rates.

Other factors influencing gypsy moth survivorship or mating success may also confound or counter the relationships found in this study. For example, small mammals, which are important predators of gypsy moth pupae (Hoffman Gray *et al.* 2008), may be less abundant at high elevations (Yahner & Smith 1991; Brooks, Smith & Healey 1998). Similar to the effect of elevation on host tree basal area, this elevational gradient in predation pressure would make it more difficult to detect negative effects of elevation on population growth rates. In addition, topography may bias the movement of some insects (Pe'er *et al.* 2004), but whether this applies to the gypsy moth is unknown. Theory predicts that populations subject to strong Allee effects exhibit a critical occupied area, in addition to a critical density, for persistence (Lewis & Kareiva 1993). This prediction was empirically confirmed for the gypsy moth (Vercken *et al.* 2011). This finding could have implications for our results if factors such as topography or forest patchiness constrain the area of a population by limiting movement or if the size of favourable habitat patches tends to vary along topographic gradients. The extent to which these may occur is not known. The findings of Vercken *et al.* (2011) also underscore that the population dynamics of nearby grid cells may not be independent of each other, but our efforts to control for spatial autocorrelation minimized spatial non-independence.

One notable difference between the results of the simulation model and observed rates of population growth is that observed rates were generally above the replacement rate $\lambda = 1$, while growth rates in the model only exceeded $\lambda = 1$ at relatively high densities. This difference is due in part to data filtering in the empirical analysis removing unsuccessful colonization events; however, it may also result from the model considering isolated populations, whereas nascent populations near the gypsy moth invasion front receive immigrants from well-established populations behind the front (Tobin & Blackburn 2008). We also note that observations filtered for having too few years of usable data, or where trap catch was zero in 2009, were located ahead of the leading edge of the invasion, indicating that failure to establish was largely dependent on distance from the invasion front, not on local ecological factors.

Although we and others (Tobin *et al.* 2007b) have detected spatial variability in the strength of Allee effects in the gypsy moth, we interpret our results as indicating that gypsy moth reproductive biology could lead to an Allee threshold at a fixed 'effective density' of reproductive adults considering both space and time. Reproductive

asynchrony, then, relates total density over the entire reproductive period to effective density such that holding the total density over the entire reproductive period constant, increasing reproductive asynchrony decreases the effective density. Other factors, such as wind effects on pheromones or male flight, would operate in a similar manner, introducing error into the relationship between total density and effective density. Supporting this interpretation, Tobin *et al.* (2007b) detected regional variability in the Allee threshold using season-long pheromone-baited trap catch records, even though the relationship between daily male moth density and female mating success is broadly consistent across regions (Contarini *et al.* 2009). This apparent discrepancy may be explained by regional differences in weather that influence immigration rates (Tobin & Blackburn 2008; Frank *et al.* 2013), producing variations in the effective population density not reflected in density measures based on season-long trap catch records.

Understanding how and why spatiotemporally variable environmental characteristics influence the dynamics of populations subject to Allee effects may have broad implications for conserving threatened species and managing biological invasions (Courchamp, Berec & Gascoigne 2008; Tobin, Berec & Liebhold 2011). Specifically, our findings suggest that future rates of gypsy moth spread could be partially predicted based on topography. Considering the link between Allee effects and invasion rate (Lewis & Kareiva 1993), our findings indicate that, all else being equal, the areas at the highest risk of invasion by gypsy moths are at low elevations and have little elevational heterogeneity. Consistent with this prediction, unusually high invasion rates have been observed in Wisconsin (Tobin, Liebhold & Anderson Roberts 2007a), where elevation and elevational heterogeneity are low relative to the Central Appalachians, but other factors, particularly transport of gypsy moths, may differ between the two regions (Biggsby, Tobin & Sills 2011; Frank *et al.* 2013). Very low invasion rates have been observed in Ohio, Indiana and Illinois (Tobin *et al.* 2007b) where elevation and elevational heterogeneity are also low relative to our study area, but this is likely explained by much lower density of host trees in heavily agricultural areas (Morin *et al.* 2005). Thus, there could be a crucially important interplay between topography and resource availability in the invasion dynamics of the gypsy moth, which has immediate implications to management efforts seeking to reduce gypsy moth spread. More generally, the evidence presented by this study underscores that reproductive asynchrony may affect the invasion dynamics of poikilotherms, particularly other non-native insects that also can be subject to the challenges of mate-finding failure at low densities.

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Data Accessibility

R model scripts: uploaded as online supporting information.

Field population data: DRYAD entry doi: 10.5061/dryad.7k2d1.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Simulation model R code.

Appendix S2. Details of data filtering methods.

Appendix S3. Spatial autocorrelation in population growth rates.

Appendix S4. Details of custom geographic projection.

Appendix S5. Phenology candidate models ranked by AIC.

Appendix S6. Plots of population growth rate vs. elevation and elevational variability.