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LETTER

Invasion speed is affected by geographical variation in the strength of Allee effects

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Abstract

Allee effects can play a critical role in slowing or preventing the establishment of low density founder populations of non-indigenous species. Similarly, the spread of established invaders into new habitats can be influenced by the degree to which small founder populations ahead of the invasion front are suppressed through Allee effects. We develop an approach to use empirical data on the gypsy moth, a non-indigenous invader in North America, to quantify the Allee threshold across geographical regions, and we report that the strength of the Allee effect is subject to spatial and temporal variability. Moreover, we present what is to our knowledge the first empirical evidence that geographical regions with higher Allee thresholds are associated with slower speeds of invasion.

Keywords

Allee effects, biological invasions, invasion speed, *Lymantria dispar*, non-indigenous species, spatial and temporal heterogeneity.

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INTRODUCTION

The ever increasing trends in global trade and international travel have increased the likelihood of arrivals of exotic species, occasionally with inimical effects (Parker *et al.* 1999; Pimentel *et al.* 2000; Mooney & Cleland 2001). Previous studies of habitat invasibility have highlighted the importance of understanding and identifying components that increase or decrease the ability of an exotic species to successfully invade a particular ecosystem. Much of this research effort has focused on plant communities. For example, elevated availability of unused resources and disturbance generally increase the susceptibility to invasion by exotic plants (Burke & Grime 1996; Tilman 1997; Davis *et al.* 2000). Invasibility may also be attributed to local climate patterns, and the presence or absence of competitors, mutualists and regulators (Crawley 1987; D'Antonio 1993; Marler *et al.* 1999; Ohlemüller *et al.* 2006). A consequence is that certain habitats may be more invasible than others, although developing a general paradigm with broad application has proved elusive (Lonsdale 1999; Davis *et al.* 2000).

One important aspect of invasibility is the role that Allee effects play in the invasion dynamics of non-indigenous species (Taylor & Hastings 2005) and more generally in the restriction of ranges (Lewis & Kareiva 1993; Keitt *et al.* 2001). Allee effects collectively refer to decreases in population growth rate with decreases in population abundance, and causes include the inability to locate mates, inbreeding depression and failure to satiate predators (Courchamp *et al.* 1999). Understanding Allee effects can be critical in assessing extinction risks from the perspective of conservation biology (Stephens & Sutherland 1999), and there is growing recognition of their potentially important role during the establishment phase of biological invasions (Drake 2004; Leung *et al.* 2004; Lockwood *et al.* 2005), and in the speed at which invaders spread (Lewis & Kareiva 1993; Kot *et al.* 1996; Taylor *et al.* 2004; Taylor & Hastings 2005).

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The probability of establishment of new species generally appears to decline with the size of the initial population (MacArthur & Wilson 1967; Mollison *et al.* 1986; Lockwood *et al.* 2005), a relationship exemplified by historical records of introductions of natural enemies as part of biological control programmes (Fagan *et al.* 2002). The magnitude of Allee effects likely varies among species due to variation in life-history traits, although all sexually reproducing species may be expected to exhibit an Allee effect, at least at extremely low densities when mate location is difficult. Moreover, demographic stochasticity alone has been shown to induce an Allee-like effect (Lande 1998). This suggests that founder populations, which are typically small, are at great risk of extinction due to stochasticity and Allee effects. Thus, there could be a threshold density below which a founder population is unlikely to establish itself. Considering that population growth may depend on community interactions or environmental factors, this critical threshold could vary in space and time.

The role of Allee effects, as well as stochasticity, in biological invasions has received considerable attention in recent years due to their effects on the dynamics of low-density populations (Lande 1993, 1998; Lewis & Kareiva 1993; Nee 1994; Groom 1998; Keitt *et al.* 2001; Liebhold & Bascompte 2003; Taylor & Hastings 2005). Moreover, the rate of non-indigenous species spread can also be influenced by the presence of Allee effects, and theoretical models indicate that invasion speeds are inversely related to the strength of the Allee effect (Lewis & Kareiva 1993; Kot *et al.* 1996; Taylor & Hastings 2005). However, in most cases – including studies in conservation, invasion and biological control – quantifying the role of the Allee effect has been challenging and largely limited to the theoretical arena. In this study, we use spatially and temporally extensive records of the gypsy moth, *Lymantria dispar* (L.), invasion in the USA to detail geographical variation in the strength of the Allee effect, and to show that this variability can influence and induce geographical variation in the invasion speed of the gypsy moth.

MATERIALS AND METHODS

Spatially referenced grids of pheromone-baited traps are deployed annually under a United States Department of Agriculture gypsy moth management programme (Tobin *et al.* 2004). These traps are very effective at attracting male gypsy moths even at very low abundance (Schwalbe 1981). Under this programme, *c.* 130 000–150 000 traps are deployed over an area of 344 000 km^2 from North Carolina to northeastern Minnesota to monitor gypsy moth spread and detect incipient colonies beyond the established range to be targeted for eradication (Fig. 1). The majority of traps are placed in an *c.* 2-km grid, though some are placed 3–8 km apart (Tobin *et al.* 2004). The trap area covers an *c.* 170- to 180-km-wide transition area that separates the portion of the USA that is currently invaded by the gypsy moth from areas that are not (Fig. 1).

The trap catch data were used to generate a continuous, interpolated surface of male gypsy moth abundance using median indicator kriging (Isaaks & Srivastava 1989) over a network of 5 × 5-km cells in a grid that encompassed the states of North Carolina, Virginia, West Virginia, Ohio, Indiana, Illinois and Wisconsin. Interpolated grids were generated for each year from 1996 to 2004. From the centre of each cell, we extracted the estimated number of male moths per trapping area for each of the years. To study Allee effects we subsequently paired each cell's estimate in successive years (i.e. year $t - 1$ with its corresponding value in year t). We omitted any pairs whose initial value was 0. Also, because some gypsy moth populations are targeted for eradication, we excluded any cells that were within 1.5 km of an area treated for gypsy moth. In practice, < 2% of the monitoring area were treated with pesticides.

All pairs of estimated abundances, from 1996/1997 to 2003/2004, were combined for each of three regions: (i) Wisconsin; (ii) Ohio, Indiana and Illinois; and (iii) West Virginia, Virginia and North Carolina, to form a single list of all pairs from the entire time interval (Fig. 1). These regions represent distinct climates, topography and associated forest types. Also, gypsy moth invasion dynamics have been previously shown to differ among these three regions (Whitmire & Tobin 2006). Across all years, a total of 29 822 (Wisconsin), 15 315 (Ohio, Indiana and Illinois) and 20 339

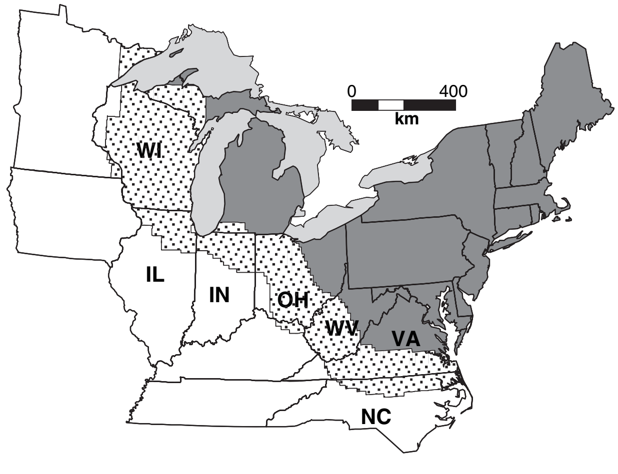

Figure 1 Areas of the USA where the gypsy moth is endemic (dark grey) or absent (white) in 2005. The dotted area between the two is the 'transition zone' that was monitored in 2005. Data from labelled states were used in this study (WI, Wisconsin; IL, Illinois; IN, Indiana; OH, Ohio, WV, West Virginia; VA, Virginia; NC, North Carolina).

(West Virginia, Virginia, and North Carolina) pairs were used in our analyses.

To investigate thresholds in dynamics we initially collated the data pairs into a sequence of abundance categories (bins) with estimates for year $t - 1$ falling into intervals of five moths/trapping area (i.e. 1–5, 6–10, etc.). We excluded areas with estimates greater than 700 because of the diminished efficiency of pheromone-baited traps as they become saturated with moths (Elkinton 1987). Within each bin, we calculated a population replacement rate as the proportion of pairs in which moth abundance either increased or stayed the same from year $t - 1$ to year t. We then analysed this population replacement rate as a function of the bin value, using the midpoint value as a surrogate (i.e. 3.0 for the abundance category 1–5, 8.0 for the abundance category 6–10, etc.), using locally weighted polynomial regression to estimate region-specific Allee thresholds (and 'carrying capacities'). We calculated 95% confidence intervals based upon the 2.5 and 97.5 percentiles of a bootstrap distribution resampled 500 times (Efron & Tibshirani 1993).

Although the above analysis provided a broad understanding of Allee thresholds and carrying capacities over a range of values of the initial population abundance, we also sought to refine our estimates of the Allee threshold by specifically focusing our attention on low-density populations. We still calculated a population replacement rate (from year $t - 1$ to year t) within each population bin; however, in this case, the bins were in increments of 1 (i.e. 1, 2, 3, etc.) and we only included pairs of cells for which the initial population (in year t) was ≤ 30 moths/trapping area. We used data across years to pinpoint region-specific Allee thresholds, and also used data from each pair of years (i.e. 1996–1997, 2003–2004) to examine whether the Allee effect varied in time.

We also studied the relationship between spatiotemporal variation in Allee effects and the speed of gypsy moth invasion. Annual rates of gypsy moth spread were estimated by measuring the spatial displacement of population isoclines (derived from the trap catch data) between successive years along a transect perpendicular to the advancing front (Tobin *et al.* 2006). Annual average displacements were calculated for each region. The lack of autocorrelation in the time series of spread rates was ascertained using partial autocorrelation functions. For each pair of years (i.e. 1996–1997 and 2003–2004), we used the y-intercept from the locally weighted polynomial regression of the population replacement rate against abundance as a surrogate of the strength of the Allee effect. As larger y-intercepts reflect a higher rate of replacement at low densities, we subtracted the intercepts from 1 so that larger values would correspond to stronger Allee effects (and hence lower replacement rates). For each region, we then calculated the correlation coefficient between gypsy moth invasion speed and the strength of the Allee effect.

We defined the Allee threshold as the lowest abundance in year $t - 1$ at which a local population is equally likely to replace itself in the next year, below which it is more likely to decrease, and above which it is more likely to increase. We have found this operational definition to be more useful than the more traditional measure of Allee effects based on the year-to-year ratio of abundance (i.e. per capita growth rate) because population growth rates are very sensitive to the inevitable observation error at low population density. In parallel, we defined the 'carrying capacity' as the highest abundance at which the replacement probability decreases below 0.5, although this parameter was of less interest in this study because our main aim was to pinpoint the Allee threshold.

We tested the utility of our novel definition of the Allee threshold with synthetic data generated with a known Allee threshold and carrying capacity. Data were simulated using a discrete time logistic growth model (Keitt *et al.* 2001; Liebhold & Bascompte 2003):

$$N_{i,t} = N_{i,t-1} \exp\left(r_i \left(1 - \frac{N_{i,t-1}}{K} \right) \left(\frac{N_{i,t-1} - C}{K} \right) \right), \qquad (1)$$

where N is the local population density at location i in space at either time step t or $t - 1$, K is the carrying capacity, and C is the Allee threshold. Fifty local populations were each assumed to be governed by a growth rate, r_i that was sampled independently from a Gaussian distribution with mean = 0.1 and SD = 0.5. The Allee threshold and carrying capacity were arbitrarily set at 30 and 150 respectively. The population replacement rate, as defined above, was calculated for initial population densities from 1 to 200 in increments of 1. The relationship between initial population size and replacement at the next time step is shown in Fig. 2, which illustrates that our approach correctly pinpoints the thresholds. All analyses were performed in R (R Development Core Team 2005).

RESULTS

We found substantial geographical variation in population replacement rates over a range of initial population abundances (Fig. 3), and in the region-specific estimates of the Allee thresholds (Fig. 4). The Allee threshold was estimated as 2.2 moths/trap in Wisconsin, but 20.7 moths/trap in West Virginia, Virginia and North Carolina. The estimated carrying capacity also varied (Fig. 3), and was highest in West Virginia, Virginia, and North Carolina (673 moths/trap) and less in Wisconsin (283 moths/trap). In Illinois, Indiana, and Ohio, neither the Allee threshold nor the carrying capacity could be quantified based on our criteria of a 0.5 probability of replacement due to

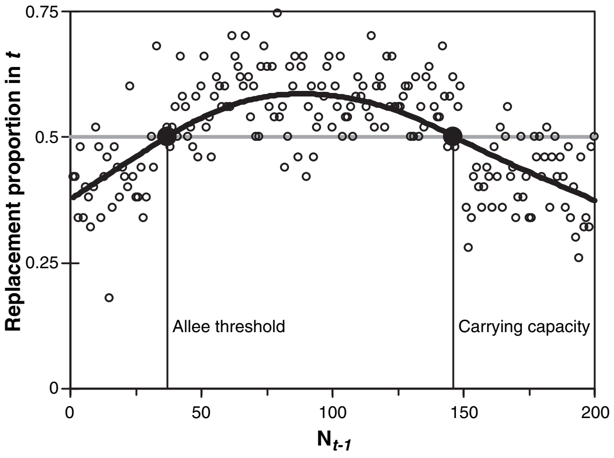

Figure 2 Theoretical representation, based on eqn 1, of the Allee effect and carrying capacity using the definition of population replacement from one time step to the next. When the initial density, N_{t-1}, is less than the Allee threshold or greater than the carrying capacity, populations are less likely to replace themselves, and hence decline in abundance, at the next time step.

consistently low replacement rates, even at high initial abundance (Fig. 3); therefore, the Allee effect would seem to be particularly strong in this region, and/or this region is generally suboptimal for the growth of gypsy moth populations.

We also observed considerable variability in the Allee threshold through time (Fig. 5). In some years, there was no or a diminished Allee effect, such as in 2002–2003 in Wisconsin during which replacement rates were very high regardless of the initial abundance (Fig. 5a). Outside of Wisconsin, replacement rates from 2001–2002 to 2003–2004 were very low even at high initial abundance (Fig. 5b,c), suggesting a strong Allee effect. One consistent pattern was observed in Wisconsin: although the strength of the Allee effect differentially affected very low-density populations (less than five moths/traps), there was very little interannual variation in populations exceeding 10 moths/trap (Fig. 5).

Despite temporal variability in the Allee effect, the invasion speed of the gypsy moth was significantly negatively correlated with the strength of the local Allee effect. Moreover, this was consistently observed in all regions: Wisconsin ($\rho = -0.74$, $P = 0.04$), Illinois, Indiana and Ohio ($\rho = -0.88$, $P = 0.02$), and West Virginia, Virginia and North Carolina ($\rho = -0.95$, $P < 0.01$) (Fig. 6).

DISCUSSION

Within the general context of invasion biology, the ability of an invader to establish initially in new areas and consequently spread can be affected by features of its natural

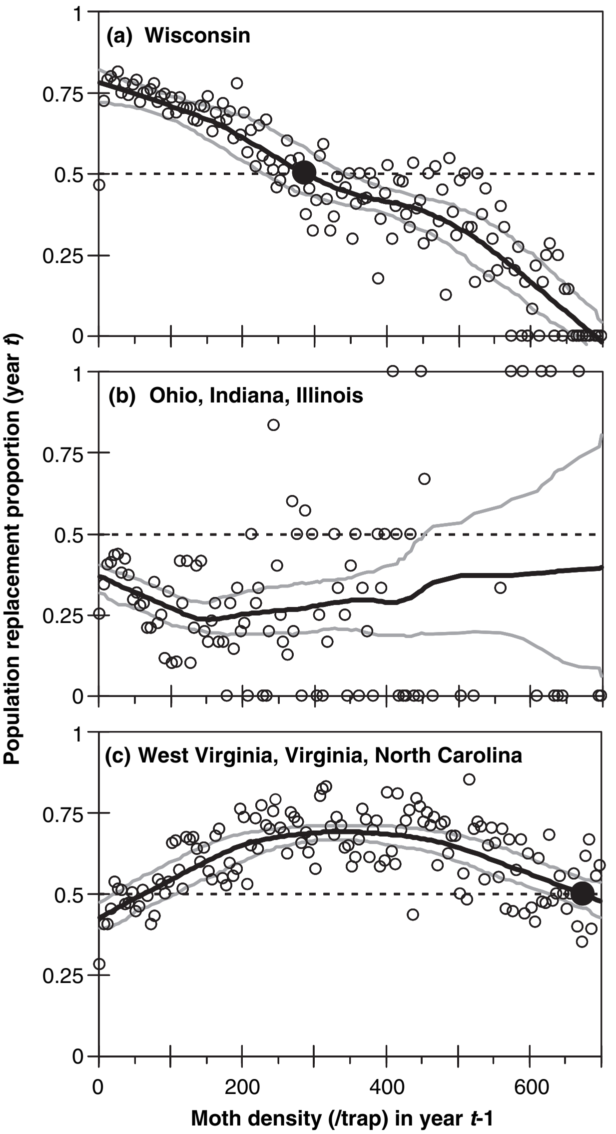

Figure 3 Region-specific relationships (mean, black line; 95% CI, grey lines) of population replacement rates and the respective population density in the prior year, pooled across 1996–2004. The carrying capacity (closed circle), as defined as the initial moth density estimate at which the replacement rate decreases to 0.5, is indicated in (a) and (c), but not in (b) due to replacement rates that were consistently < 0.5.

history that influence the ability of populations to persist at initially low levels (Crawley *et al.* 1986; Rejmánek & Richardson 1996; Kolar & Lodge 2001). For example, animals and plants that reproduce asexually could be considerably more invasive than sexually reproducing species because there is no need to locate mates, which could be a challenging endeavour in low-density populations. In this study, we show that for the gypsy moth, the

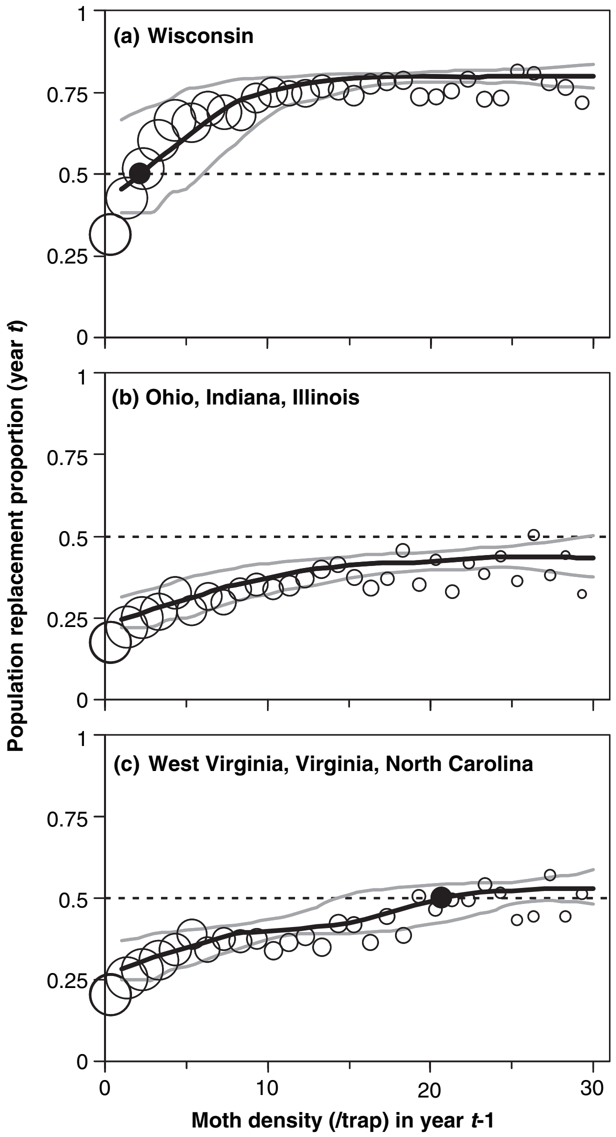

Figure 4 Region-specific relationships (mean, black line; 95% CI, grey lines) between population replacement rates and initial population densities ≤ 30 moths/trapping area (data pooled across 1996–2004). Estimates of the Allee thresholds (closed circle) is indicated in (a) and (c), but not in (b) due to replacement rates that were consistently < 0.5. The size of the observations (open circles) reflects the sample size in each population bin. For graphical purposes, the largest sized circle is for sample sizes > 1000. The range of sample sizes per bin is (a) 129–5838, (b) 63–3938 and (c) 93–4040.

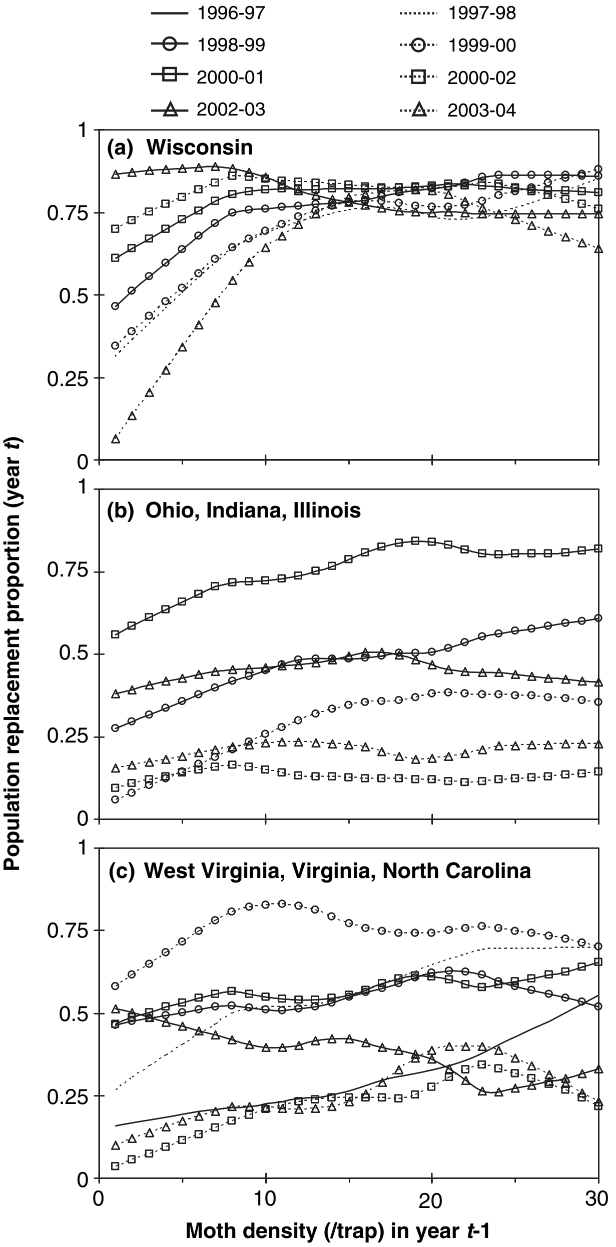

Figure 5 Temporal variation (year $t - 1$ to t) in the region-specific estimates of the Allee thresholds. Note that in Wisconsin, the Allee effect is consistently minimized or non-existent, while considerable year-to-year variation exists elsewhere (the estimates of the y-intercepts were used as a surrogate for the strength of the Allee effect, cf. Fig. 6).

strength of the Allee effect is variable in space and time (Figs 4 and 5), and that this variation has profound ramifications on the speed at which the gypsy moth invades (Fig. 6). This is particularly intriguing as these observations provide one of the first empirically derived examples of the relationship between the strength of Allee effects and the rate of spread of invading organisms. Although previous research has suggested that Allee effects can affect the spread and distribution of non-indigenous species (Lewis & Kareiva 1993; Kot *et al.* 1996; Keitt *et al.* 2001; Wang *et al.*

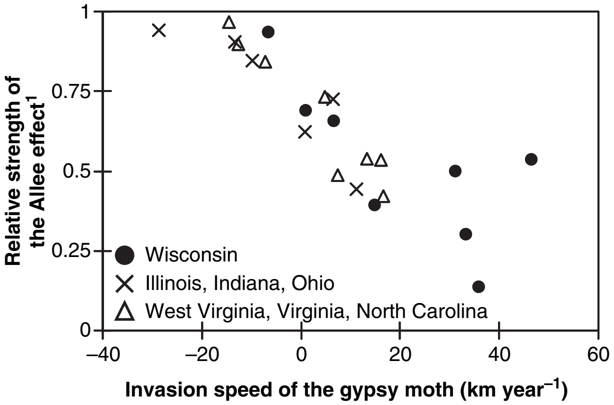

Figure 6 Invasion speed by the gypsy moth declines with an increase in the strength of the Allee effect in all regions of the USA. [1]Relative strength was estimated as 1 – the *y*-intercept estimates for each region and for each pair of consecutive years as shown in Fig. 5.

2002; Taylor *et al.* 2004; Taylor & Hastings 2005), quantifying this relationship has proved elusive due to the difficulty in estimating Allee effects. Moreover, geographical variation in the strength of the Allee effect may be a critical component to understanding habitat invasibility, and in particular, the speeds at which non-indigenous species invade new areas.

Low-density gypsy moth populations are strongly affected by predation from small mammals (Elkinton *et al.* 1996, 2004). However, the effects of small mammal predation do not appear to differ across large geographical regions in the USA (Liebhold *et al.* 2005), although interactions between mast production and small mammals (Elkinton *et al.* 1996) could cause temporal variability in the strength of the Allee effect. Liebhold & Bascompte (2003) proposed that for invading species, the Allee effect could be caused by decreased mating success extending from difficulties in mate finding at low densities. Empirical studies support this notion by documenting increases in gypsy moth mating success with increasing male moth abundance (Sharov *et al.* 1995), but this relationship likewise appears to be consistent across regions (Tcheslavskaia *et al.* 2002). The inability to locate mates at low densities is thus likely a universal cause of the Allee effect in gypsy moth, but it is unknown what factors or processes are responsible for spatial and temporal variability in its strength.

Gypsy moth is univoltine, and in North America, gypsy moth females are flightless and usually oviposit within 1–2 m from the site of adult emergence (Odell & Mastro 1980). Adult males are capable of flight, and early instars, which emerge from overwintering egg masses in Spring, can disperse through ballooning although generally they are deposited within a few 100 m (Mason & McManus 1981). Anthropogenic movement of life stages is the primary mechanism of long-range dispersal in the gypsy moth (Liebhold *et al.* 1992). Male and larval dispersal, as well as anthropogenic movement of life stages, could contribute to the diminution of Allee effects in both certain regions and years (Fig. 5). Dispersing immigrants or the accidental introduction of life stages from outbreak to newly invaded areas, which are generally colonized by low-density populations subject to Allee effects, could supplement the abundance of newly invading colonies, which in turn would enhance female mating success, and thereby diminish the Allee effect.

The relative strength of the Allee effect (Fig. 6) is consistently linked to the invasion speed of the gypsy moth in all regions, despite obvious differences among region-specific estimates of the Allee threshold (Fig. 4). The Allee effect is particularly strong in Ohio, Indiana and Illinois. Poor population replacement rates in this area could be due to the relatively limited distribution of preferred host tree species, whereas in West Virginia, Virginia, North Carolina and Wisconsin, gypsy moth preferred host species are far more abundant (Morin *et al.* 2005). Although the reasons for stronger Allee effects in Ohio, Indiana and Illinois, and weaker Allee effects in Wisconsin, require additional study, the planning and implementation of region-specific control tactics against the gypsy moth can be optimized through consideration of the region-specific Allee thresholds. Future studies could also attempt to compare invasion rates predicted by theoretical models, with and without an Allee effect, with observed rates of invasion by the gypsy moth to determine the factors and processes that drive its invasion dynamics.

This study detailed a novel approach to estimating Allee effects with empirical data. This method facilitated our observation that Allee effects can be subject to spatiotemporal variability over geographical scales. Furthermore, we present what is to our knowledge the first empirical evidence that geographical variation in Allee thresholds can affect the rate of spread of an invader. In many biological invasions, species-specific and geographically varying Allee effects could be strong components in defining habitat invasibility. Therefore, quantifying the Allee effect and its influence on invasion may be critical to determining where invasive species are more likely to establish.

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