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The role of Allee effects in gypsy moth, *Lymantria dispar* (L.), invasions

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Abstract Allee effects have been applied historically in efforts to understand the low-density population dynamics of rare and endangered species. Many biological invasions likewise experience the phenomenon of decreasing population growth rates at low population densities because most founding populations of introduced nonnative species occur at low densities. In range expansion of established species, the initial colonizers of habitat beyond the organism's current range are usually at low density, and thus could be subject to Allee dynamics. There has been consistent empirical and theoretical evidence demonstrating, and in some cases quantifying, the role of Allee dynamics in the gypsy moth, *Lymantria dispar* (L.), invasion of North America. In this review, we examine the potential causes of the Allee effect in the gypsy moth and highlight the importance of mate-finding failure as a primary mechanism behind an Allee effect, while the degree to which generalist predators induce an Allee effect remains unclear. We then explore the role of Allee effects in the establishment and spread dynamics of the gypsy moth system, which conceptually could serve as a model system for understanding how Allee effects manifest themselves in the dynamics of biological invasions.

Keywords Biological invasions · Establishment · Invasion dynamics · Nonindigenous species · Spread

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Introduction

In 1869, a French lithographer, Etienne Léopold Trouvelot (1827–1895), brought to North America egg masses of the gypsy moth, *Lymantria dispar* (L.) (Riley and Vasey 1870; Forbush and Fernald 1896; Liebhold et al. 1989). It is believed that life stages escaped from Trouvelot's home in Medford, Massachusetts, where he was rearing them under netting in his backyard (Forbush and Fernald 1896) when storm winds tore the netting and allowed larvae to escape (Kirkland 1906). Consequently, North American forests and occupants were to be greatly affected by the gypsy moth as over 36 million ha of forests in the USA alone have been defoliated since 1924 (Gypsy Moth Digest 2008). The negative ecological (e.g., Campbell and Sloan 1977; Doane and McManus 1981; Herrick and Gansner 1987; Thurber et al. 1994; Redman and Scriber 2000) and socioeconomic (e.g., McCay and White 1973; Payne et al. 1973; Moeller et al. 1977; Gansner et al. 1978; Herrick 1981; Gansner and Herrick 1987; Leuschner et al. 1996) impacts associated with gypsy moth are well documented.

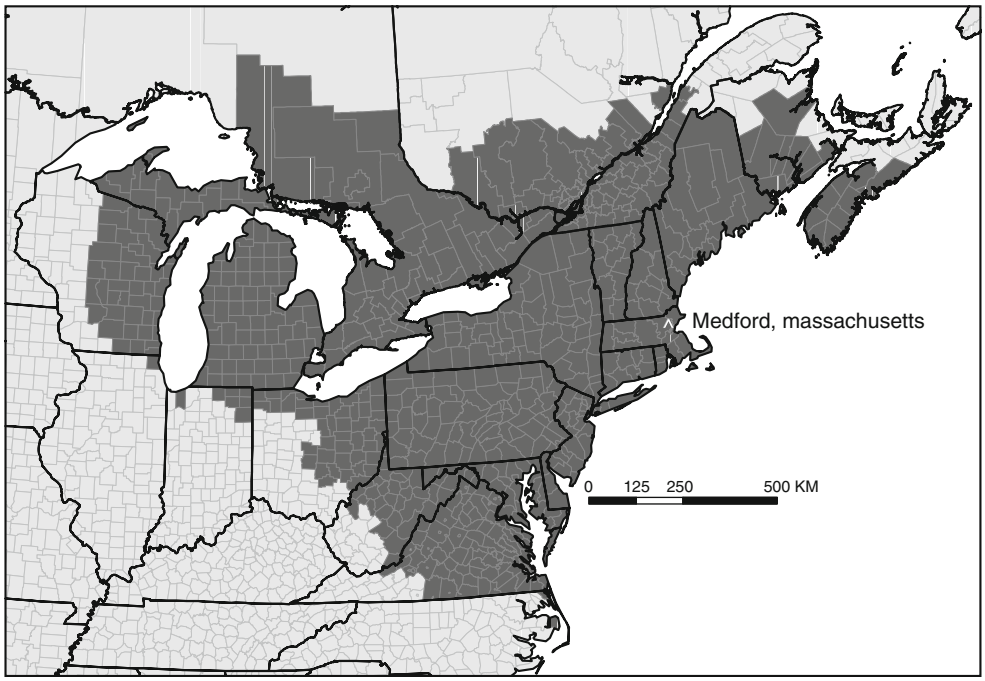

Fig. 1 Distribution of gypsy moth in North America, 2007. The initial site of introduction was Medford, Massachusetts, in 1869

Since its introduction, the gypsy moth has spread at varying rates, from 3 to 29 km/year, and is now established approximately 1600, 900, and 700 km to the west, south, and north, respectively, of its initial site of introduction (Fig. 1, Tobin et al. 2007a). The dynamics of established gypsy moth populations appear to be governed by several factors and cycle between low and high densities (Doane and McManus 1981; Elkinton and Liebhold 1990). Low-density populations are most strongly affected by predation from small mammals, such as *Peromyscus* spp. (Bess et al. 1947; Campbell et al. 1977; Elkinton et al. 2004), whose populations in turn are thought to be influenced by mast dynamics (Elkinton et al. 1996; Jones et al. 1998). High-density populations and especially outbreaking populations usually collapse after 1–3 years due to regulation by two host-specific entomopathogens: the fungus *Entomophaga maimaiga* (Hajek et al. 1995; Hajek 1999; Dwyer et al. 2004), and a nucleopolyhedrosis virus (*Ld*MNPV) (Doane and McManus 1981; Elkinton and Liebhold 1990). Gypsy moth is a highly polyphagous folivore that can exploit over 300 deciduous and coniferous host species (Elkinton and Liebhold 1990), including the highly preferred species of oak, willow, aspen, larch, birch, and apple (Liebhold et al. 1995a).

Information on and interest in the North American gypsy moth invasion has a long history (e.g., Riley and Vasey 1870; Forbush and Fernald 1896; Burgess 1917; Perry 1955; Doane and McManus 1981; Dreistadt 1983; Liebhold et al. 1992; Tobin and Blackburn 2007), and consequently there are historical records available that detail its distribution through time. Also, a cost-effective but highly sensitive monitoring tool, pheromone-baited traps (Bierl et al. 1970; Beroza and Knipling 1972; Elkinton and Cardé 1988), is available for sampling very low-density populations and thus has facilitated the acquisition of data during all three stages of the invasion process: arrival, establishment, and spread. Recent investigations have taken advantage of the exceptionally large quantity of trap catch data, as well as extensive demographic information collected in previous studies, to examine the role of Allee effects in gypsy moth invasion dynamics (Liebhold and Bascompte 2003; Johnson et al. 2006; Whitmire and Tobin 2006; Tobin et al. 2007b; Robinet et al. 2008). In this review, we will briefly examine the fundamental causes of Allee effects in insect biological invasions. We will then consider the role of Allee effects in the invasion dynamics of the gypsy moth.

The Allee effect

Allee effects refer to a positive relationship between individual fitness and population density (Allee 1932; Dennis 1989; Courchamp et al. 1999, 2008; Stephens et al. 1999; Berec et al. 2007). A consequence is that low-density populations could be driven to extinction if individuals are less likely to, for example, find mates or satiate natural enemies. Decreases in one or more fitness components with decreases in population density, known as component Allee effects (e.g., the failure of individuals to locate mates in sparse populations), could result in a decline in per-capita

population growth rates, known as a demographic Allee effect. Not all component Allee effects result in a demographic Allee effect if, for example, the advantages of being in a low-density population (e.g., reduced intraspecific competition) sufficiently compensate for the reduction in fitness (Stephens et al. 1999; Courchamp et al. 2008).

There are many reports that outline the causes of Allee effects and their role in biological invasions (Lewis and Kareiva 1993; Kot et al. 1996; Keitt et al. 2001; Taylor and Hastings 2005; Lockwood et al. 2007). Different species, depending on details of natural history, colonization behavior, trophic interactions, and other abiotic and biotic effects, could be subjected to vastly different mechanisms of an Allee effect; thus, the causes and implications of an Allee effect are likely species specific. In low-density populations of insect invaders, there are many potential causes of an Allee effect. Here, we will consider the following mechanisms of an Allee effect, and either discount their role or highlight their importance to invading and expanding populations of the gypsy moth: (1) inbreeding depression, (2) lack of cooperative feeding, (3) failure to satiate natural enemies, and (4) failure to find mates. We will then focus more comprehensively on the most likely cause of an Allee effect in low-density gypsy moth populations: mate-finding failure.

Inbreeding depression

Founder populations of introduced nonindigenous species are often small in abundance. Consequently, these initial populations may suffer from a lack of genetic diversity, and populations could be more prone to extinction from an Allee effect induced through inbreeding (through a reduction in heterozygosity) or genetic drift (through decreases in allelic diversity) (Lande 1998; Lynch et al. 1995; Lee 2002).

However, in the case of the gypsy moth, there is no evidence that lack of genetic diversity adversely affects low-density populations or that it influences their ongoing invasion of North America. It has been reported that the founding gypsy moth population consisted of only "some" (Forbush and Fernald 1896) to "few" (Burgess 1917) egg masses that were likely collected from a single population in either Trouvelot's native France or Germany (Forbush and Fernald 1896). The number of individuals that escaped captivity by Trouvelot was furthermore reduced by his own aggressive efforts to search for life stages and destroy them to limit establishment success (Burgess 1917). Such a small initial population size can be expected to have extremely limited genetic diversity. Indeed, a study conducted over 100 years after the initial introduction indicated that genetic variation among North American gypsy moth populations was still extremely low when compared with Eurasian populations (Harrison et al. 1983).

Manipulative studies of the effects of genetic diversity on the growth of small gypsy moth populations are lacking. However, the fact that North American gypsy moth populations are capable of high growth rates in the presence of low genetic diversity suggests that inbreeding and genetic drift are not important factors affecting their population growth. Thus, there is little evidence to suggest that inbreeding depression would contribute significantly to a component Allee effect in the gypsy moth.

Cooperative feeding behaviors

Several insect species use cooperative feeding behaviors, such as mass attacks on host plants to overcome host defensive strategies (Raffa and Berryman 1983). Thus, failure to overcome plant defenses can induce an Allee effect in low-density populations. This mechanism is likely important to the establishment process of certain invaders, such as the mass-attacking spruce bark beetle, *Ips typographus* (L.), which has been intercepted by US port inspectors 286 times from 1985–2001 but has yet to become established in North America (Haack 2001).

However, this mechanism is unlikely to contribute to an Allee effect in the gypsy moth because larvae are not cooperative feeders and do not need to rely on mass-attack mechanisms to overcome host tree defenses. Although there is evidence of plant compounds that adversely affect larval development and subsequent fecundity, especially when feeding on secondary hosts (Barbosa and Greenblatt 1979; Lechowicz and Jobin 1983; Rossiter et al. 1988; Barbosa et al. 1990), these lesser preferred species, such as pine, maple, and beech (Liebhold et al. 1995a), are generally exploited during outbreaks when preferred host tree species have been defoliated. Therefore, these fitness costs would affect primarily high-density populations not subject to Allee dynamics.

Interaction with natural enemies

Most insect species tend to reproduce prolifically and thus interact with natural enemies without necessarily going extinct in the process. Other insect species use group antipredatory behaviors that are likely more effective in deterring natural enemy attack at higher densities. A notable example is larvae of the gregarious pine sawfly *Neodiprion sertifer* (Geoffroy), which regurgitate host plant resin when disturbed (Eisner et al. 1974). Thus, at low densities, insect populations could be subject to an Allee effect due to an inability to satiate, or otherwise deter, natural enemies.

In the gypsy moth, entomopathogens such as *E. maimaiga* and *Ld*MNPV are often the primary cause of collapse in outbreak populations but cause little mortality in low-density populations (Elkinton and Liebhold 1990) because transmission tends to be density dependent (Dwyer et al. 2004). In contrast, pupal predation by native small mammals (Bess et al. 1947; Campbell et al. 1977; Liebhold et al. 2005) as well as the plethora of natural enemies introduced into the USA during the early 1900s (Howard and Fiske 1911; Burgess and Crossman 1929; Doane and McManus 1981; Gould et al. 1990) are primary sources of mortality in established low-density gypsy moth populations (Bess et al. 1947; Campbell et al. 1977; Elkinton and Liebhold 1990; Elkinton et al. 2004). Predation by small mammals on the gypsy moth follows a type II functional response (Elkinton et al. 2004), which can induce an Allee effect in other systems (Gascoigne and Lipcius 2004; Berec et al. 2007). Because gypsy moth represents a small proportion of the diet of generalist predators, they apparently do not respond numerically to changes in gypsy moth populations (Elkinton et al. 1996).

In newly established colonies that arise ahead of the population front, the role of an Allee effect due to predation is unknown. Some evidence suggests that specialist invertebrate natural enemies (e.g., predators and parasitoids) often spatially lag behind invading gypsy moth populations, and that they only become established in gypsy moth populations behind the invasion front (Hastings et al. 2002a, 2002b; Liebhold et al. 2005) and are completely lacking in newly establishing colonies ahead of the invasion front (Werner and Raffa 2000; Tcheslavskaia et al. 2002; Gray et al. 2008).

On the other hand, populations of the native generalist predator *Peromyscus* spp., thought to be one of the more if not the most important predator of low-density gypsy moth populations, are widely distributed throughout the current gypsy moth range as well as adjacent areas most susceptible to gypsy moth invasion in the foreseeable future. Patterns of *Peromyscus* predation in Wisconsin, which has been invaded by gypsy moth relatively recently (i.e., Wisconsin counties were first placed under a gypsy moth quarantine in 1998, and as of 2008, only approximately half of the state is under quarantine, US Code of Federal Regulations, Title 7, Chapter III, Section 301.45), were not observed to be different from those areas where gypsy moth is well established (Liebhold et al. 2005). However, densities of *Peromyscus* are strongly influenced by mast dynamics, and in areas experiencing high mast production, predation rates by *Peromyscus* are diminished (Elkinton et al. 1996).

Little is known regarding the contribution of natural enemies to Allee effects in gypsy moth populations. O. N. Bjørnstad et al. (personal communication) investigated Allee effects in a theoretical model of gypsy moth dynamics that incorporated generalist predators and entomopathogens. They found that, in the absence of entomopathogens (typical in low-density populations), generalist predators contributed a weak component Allee effect, and that the strength of the Allee effect was positively related to predator density. However, it remains unclear how this interacts with other component Allee effects, and whether it would contribute to an overall demographic Allee effect that would limit gypsy moth invasion success.

Mate-finding failure

Most insects reproduce sexually. Thus males and females must locate each other and occasionally do so over fragmented landscapes often replete with microclimatic variation and varying wind trajectories that could, for example, affect a male's ability to successfully track a sex pheromone emitted from a female. Thus, at low densities, the challenge for males and females to locate each other can be considerable, even though insects have highly evolved mate location systems. This problem could be particularly acute in founding populations during an invasion because they are surrounded by a vast void without conspecifics. Males emigrating from the founding colony are thus unlikely to be replaced by immigrating adults as would be expected in a widely established population (Robinet et al. 2008). Consequently, an important driver of a component Allee effect in invading gypsy moth populations is likely to be failure to locate mates at low densities.

One of the earliest observations on mate-finding failure in gypsy moth populations was by Sharov et al. (1995), who tethered virgin females to trees across a range of background male moth densities and, after 24 h, recorded whether or not they had been successfully located by males and mated. This experiment has since been repeated with similar results (Tcheslavskaia et al. 2002). At low male moth densities, females are not likely to be mated, while at higher densities females are almost always successfully mated (Fig. 2). An important management ramification from this mate-finding failure is that any tactic that reduces mate-finding probabilities, such as mating disruption, can be an effective means of reducing or even eradicating low-density populations. In certain gypsy moth management programs in the USA, plastic flakes impregnated with synthetic pheromone (Disrupt® II, Hercon® Environmental, Emigsville, Pennsylvania) are aerially applied to foliage in areas with low-density gypsy moth populations. This floods the area with pheromone and consequently chemically inhibits the male moth's ability to locate females (Tcheslavskaia et al. 2005; Thorpe et al. 2006). This tactic has been shown to be effective in eradicating low-density populations, even

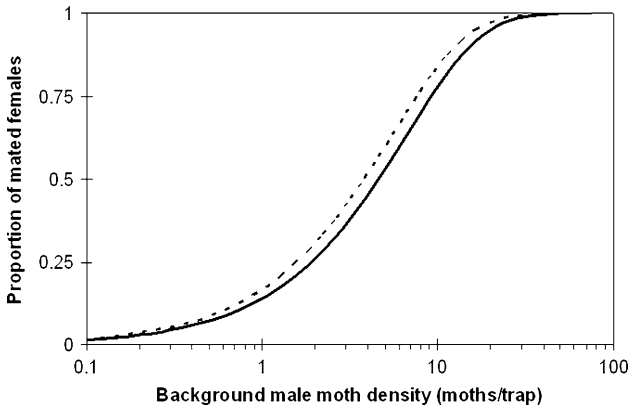

Fig. 2 Proportion of females successfully located by males and mated based upon the background male moth density in central West Virginia and Virginia, 1993–1994 (*solid line*, Sharov et al. 1995), and Wisconsin, 2000 (*dashed line*, Tcheslavskaia et al. 2002)

though no individuals are actually killed (Thorpe et al. 2000; Tobin and Blackburn 2007).

There are biological characteristics in North American gypsy moth populations that could influence the degree to which an Allee effect due to mate-finding failure drives invasion dynamics. First, in the North American population, females are incapable of flight, while females from Asian strains are capable of sustained flight (Koshio 1996; Reineke and Zebitz 1998; Keena et al. 2007). It is possible that this inability of females to fly could lessen the strength of an Allee effect because males need only locate a point source of pheromones as opposed to a potential moving target, and the lack of dispersal could diminish rates of emigration from low-density populations (Hopper and Roush 1993, South and Kenward 2001, Liebhold and Tobin 2008). The ability to fly has many evolutionary advantages, such as locating suitable ovipositional sites and evading natural enemies, as well as enhancing the rate of spread. However, it could also be a hindrance to low-density population establishment. Although there is little evidence on pre-ovipositional dispersal in female Asian gypsy moths under natural conditions, it has been inferred that most female flight, at least within a mixed-use landscape (urban, forest, and agricultural), occurs within 1 km of host forests (Liebhold et al. 2008). Nevertheless, theoretical work examining the influence of gypsy moth dispersal ability on mating success and population growth showed a reduced Allee effect in populations with nondispersing individuals, suggesting that establishment success is enhanced in these populations (C. Robinet and A.M. Liebhold, unpublished data).

Another factor that can influence the strength of an Allee effect due to mate-finding failure could be its generalist feeding preferences. There are many advantages to being a generalist capable of feeding on the foliage of many different host trees. Most important relative to its invasion dynamics is the intuitive higher probability of locating a suitable host tree when invading new habitats. However, it is also possible that, as a generalist, newly establishing larval populations could be more spatially widespread, and even more temporally widespread due to microclimatic variation resulting in different rates of development. This could result in greater spatial and temporal separation between adults with a consequent increase in mate-finding failures (Figs. 3, 4; Robinet et al. 2008). In contrast, specialists would likely face greater challenges in locating suitable host trees and invading populations could fail due to a lack of hosts. However, if suitable host trees are located by a specialist invader, it is likely that their host trees would be spatially clustered. Even when a host tree is present singly in nature, this could still serve as a primary colonization point that attracts conspecifics over a large area. Thus, life stages would develop in closer space-time proximity. This presents somewhat of a paradox: although generalist insect invaders could be more likely to find a suitable host in new areas relative to specialists, they also could be less likely to find each other as adults, particularly if suitable host trees are spatially widespread.

Protandry, in which males emerge slightly before females, or more generally adult emergence asynchrony (Calabrese and Fagan 2004), also influences the degree to which males and females are temporally segregated (Figs. 3, 4; Robinet et al. 2007, 2008). This lag between male and female sexual maturation could lead to males "wandering away" from the colony center while searching for females and, by the time adult females finally emerge, many males could be located too far away to be attracted to the female sex pheromone; thus, females could go unmated. Moreover, immature development in poikilotherms is subject to climatic variability and could increase asynchrony in adult emergence times. In field experiments on gypsy moth mating, females, when mated, are generally located by males within 3 days (Robinet et al. 2008), so even subtle differences in emergence times are critical for mates to find each other.

Allee effects and gypsy moth establishment

The spread of the gypsy moth occurs through a combination of short- and long-range dispersal known as stratified dispersal (Hengeveld 1989; Andow et al. 1990; Shigesada et al. 1995; Shigesada and Kawasaki 1997). The gypsy moth currently occupies approximately one-third of its susceptible North American habitat, and both forms of dispersal are important in the continuing gypsy moth invasion. It is not known which populations serve as a source for newly established colonies and the relative

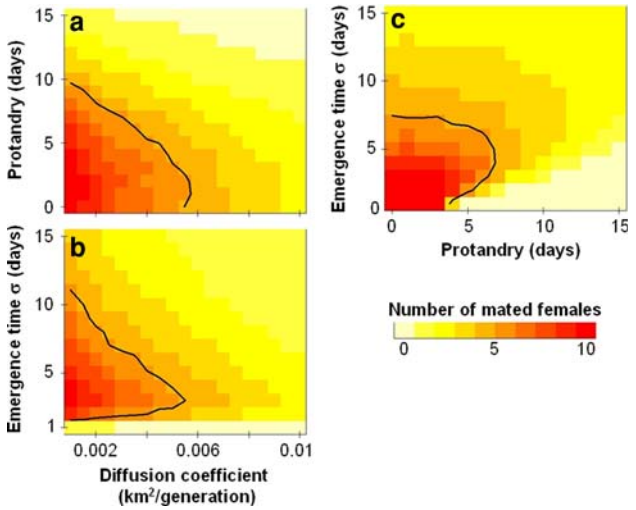

Fig. 3 Mating success as a function of spatial dispersion (diffusion coefficient) and temporal dispersion (σ of the Gaussian function representing the distribution of emergence dates, protandry). In these simulations, five egg masses (300 eggs/mass) were initially introduced at a single point. For each parameter combination, we calculated the mean number of mated females over 500 iterations, using the following fixed values: **a** emergence time $\sigma = 5$ days, **b** protandry = 5 days and **c** diffusion coefficient = 0.003 km^2/generation. The *bold line* corresponds to a population replacement rate of 1. Modified from Robinet et al. (2008)

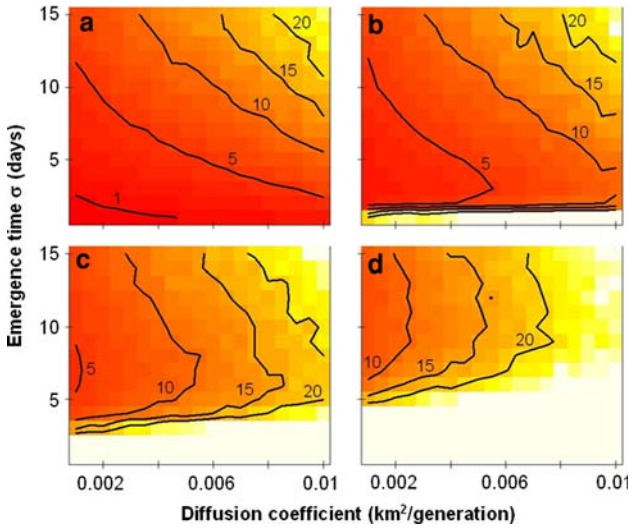

Fig. 4 Quantifying Allee thresholds when assuming protandry values of **a** 0 days, **b** 5 days, **c** 10 days, and **d** 15 days. For each parameter combination (diffusion coefficient and standard deviation of emergence), egg masses (1–5, 300 eggs/mass) were introduced at a single point. The mean Allee threshold (i.e., population replacement rates of 1) was then derived from 500 iterations. The contour lines indicate the Allee threshold across parameter values. In all simulations, the degree of spatial and temporal separation between males and females strongly influences the Allee threshold

proportion of colonies that arise through atmospheric versus anthropogenic transport mechanisms. However, in general, the majority of colonies arrive in close proximity to the leading edge (Sharov and Liebhold 1998; Tobin and Blackburn 2008). These colonies vary considerably in their initial size, and while some colonies successfully establish, the majority fail to persist. Despite regional and temporal variation in the rate of establishment success, a principle driver of establishment success is the initial population density (Table 1; Liebhold and Bascompte 2003; Whitmire and Tobin 2006).

A case study of the relationship between founding population size and rate of establishment success comes from western North America where gypsy moth is not currently established (Liebhold and Bascompte 2003). Occasionally, by way of domestic invasion pathways, such as the movement of contaminated goods through household moves or interstate commerce routes, gypsy moth life stages are transported from the established east coast region to the west coast. For example, in 2005 an automobile containing several gypsy moth egg masses was purchased from the east coast state of Connecticut, where the gypsy moth has been established since at least 1914 (Burgess 1930; Liebhold et al. 1992), through the auction web service eBay®, and then shipped roughly 4600 km to the west coast state of Oregon. Gypsy moth life stages can also enter western North America through international invasion pathways, as the west coast port cites of Long Beach, California (USA) and Vancouver, British Columbia (Canada) are common ports of entry for freight originating from Asia where gypsy moth is native.

Using data on the arrival of gypsy moth populations to Washington State (USA) and their subsequent fate, Liebhold and Bascompte (2003) observed that the rate of colony extinction following the initial detection of male moths in the prior year was inversely related to initial colony size (Table 1). They considered 192 potential gypsy moth colonies that were detected from 1974 to 1996, of which 162 went extinct without any management intervention, and 123 of these went extinct within 1 year after initial detection. Those colonies that failed to establish were overwhelmingly small in initial density, while those colonies from which >7 male moths were trapped almost always established. Based upon this evidence, they parameterized a model of invasion dynamics that incorporated Allee effects and stochasticity. They concluded that both could drive populations to extinction, thus defying the notion that eradication could only be achieved if all individuals were killed (Knipling 1966, 1979; Dahlsten et al. 1989; Myers et al. 1998).

Another case study that examined the role of Allee effects in gypsy moth establishment was conducted in front of the current leading edge and where new colonies are constantly being founded. Whitmire and Tobin (2006) examined gypsy moth trap data from 1996 to 2003 (>50,000 traps per year) and determined regional-specific

Table 1 Proportion of gypsy moth colonies failing to establish in Washington State (where gypsy moth is not established) and in three regions along the leading edge of the population front

Initial density (moths/trap)	Proportion of colonies failing to establish			
	Washington State; 1974–1996[a]	Wisconsin; 1996–2003[b]	Illinois, Indiana, Ohio; 1996–2003[b]	West Virginia, Virginia, North Carolina; 1996–2003[b]
≤2	0.80	0.21	0.49	0.36
3–4	0.75	0.18	0.44	0.32
5–6	0.50	0.15	0.38	0.29
7–8	0.00	0.13	0.33	0.26
9–10	0.00	0.11	0.28	0.23
>10	0.06	0.07	0.18	0.17

[a] Liebhold and Bascompte (2003)

[b] Whitmire and Tobin (2006)

rates of colony persistence and establishment. As with the findings from Liebhold and Bascompte (2003), lower-density colonies, especially those <5 moths/trap, usually went extinct in the next year without any management intervention, while higher-density colonies, such as those >10 moths, tended to persist into the following year (Table 1). Whitmire and Tobin (2006) also observed that the rate of colony persistence was greater in certain regions of the USA, and that other potential factors, such as the percentage of favorable host trees and land use, did little to explain these regional differences. Instead, they hypothesized that the differences in region-specific rates of colony persistence were attributed to geographic variation in the strength of the Allee effect.

Allee effects and gypsy moth spread

A major ramification of stratified dispersal is that spread does not necessarily follow a simple reaction-diffusion process (i.e., Skellam 1951), but rather the rate of spread could be dynamic over time; for example, an invading species could exhibit an accelerating range expansion-by-time relationship, whereby initial spread rates are low, followed by increasing rates of spread that then decline as the susceptible habitat becomes fully occupied (Hengeveld 1989; Andow et al. 1990; Shigesada et al. 1995; Shigesada and Kawasaki 1997). This is because newly founded colonies that do successfully establish then grow and eventually coalesce with the infested area, thus accelerating the rate of spread over that which is expected under diffusive dispersal. Allee effects, which act on the establishment of colonies, also influence nonindigenous species spread into uninfested areas. In the absence of an Allee effect, spatially disjunct colonies ahead of the established area are more likely to establish and thus more likely to accelerate rates of spread. This relationship has been observed in several theoretical studies, in which Allee dynamics negatively affected the growth and persistence of isolated colonies and consequently limited the rate of spread (Lewis and Kareiva 1993; Kot et al. 1996; Keitt et al. 2001).

A recent study documented that Allee effects were related to the rate of gypsy moth spread (Tobin et al. 2007b). Monitoring data available on gypsy moth populations across the moving population front was used to quantify the Allee threshold in space and time, defined as the density at $t - 1$ for which it was expected that half of the populations would replace themselves in year t (Fig. 5). It was observed that Allee thresholds varied across space and time, and ranged between 2 and 21 male moths per trapping area. The spatial and temporal variation in the Allee thresholds was also strongly correlated to the year-to-year rate of gypsy moth spread (Fig. 6). Faster spread rates occurred when Allee thresholds were very low, while spread rates were low—and in some cases the gypsy moth range retracted—in years when the Allee threshold was high. These empirical findings supported prior theoretical predications of the negative impact of Allee dynamics on the spread of invading species (Lewis and Kareiva 1993; Kot et al. 1996; Kinlan and Hastings 2005).

In a companion study, Johnson et al. (2006) related Allee dynamics to long-term spread of the gypsy moth. Historical records of the gypsy moth quarantine designation on a US county level are available from 1934 to the present (US Code of Federal Regulations, Title 7, Chapter III, Section 301.45), which allows for temporally robust, though spatially crude, measures of spread (Tobin et al. 2007a). Johnson et al. (2006) observed an interesting phenomenon of periodically pulsed spread every 3–4 years based upon the historical records of gypsy moth range expansion, and proposed that this behavior was due to an interaction between stratified dispersal and Allee effects (Fig. 7). Specifically, they represented gypsy moth spread

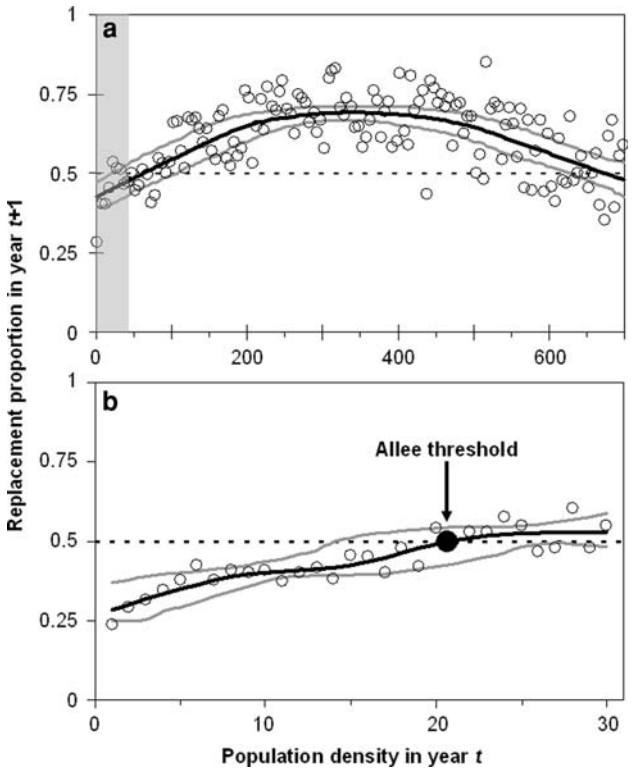

Fig. 5 Relationship between population density (moths/trap) in year t and population replacement rates in $t + 1$ (**a**) and the estimate of the Allee threshold (based upon data from the *shaded area* in **a**), for West Virginia, Virginia, and North Carolina, 1996–2004 (mean, *black line*; 95% confidence intervals, *grey lines*; reprinted from Tobin et al. 2007b)

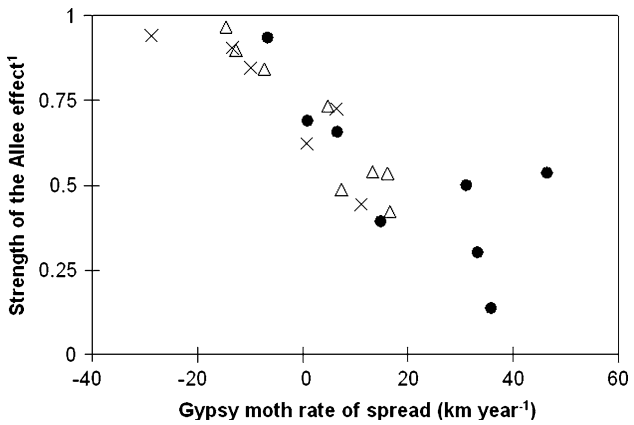

Fig. 6 Yearly rates of gypsy moth spread in Wisconsin (*circles*); Illinois, Indiana, and Ohio (*crosses*); and West Virginia, Virginia, and North Carolina (*triangles*) relative to the corresponding strength of the Allee effect. A strength of 0 would imply that the lowest density colonies (i.e., 1 moth/trap) still replaced themselves in the following year (reprinted from Tobin et al. 2007b)

in a one-dimensional model that simulated the formation of isolated colonies founded from long-distance dispersal but that failed to establish due to Allee effects. However, as populations at the leading edge of the advancing population

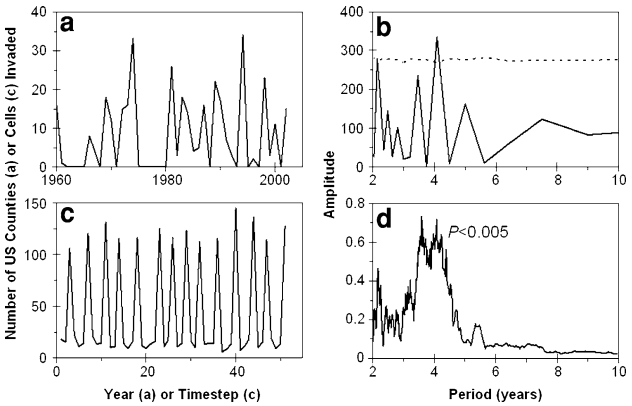

Fig. 7 The number of US counties quarantined for gypsy moth in each year from 1960 to 2002 (**a**), and the periodogram (**b**) that reveals a significant (as denoted by the *dashed line*) 4-year period in the empirical rate of gypsy moth invasion. **c**, **d** Corresponding number of invaded cells and significant 4-year periodicity from a simulation model that combines a stochastic, second-order Moran–Ricker model with an Allee effect (modified from Johnson et al. 2006)

front grew to sufficient densities, they could seed new colonies that were of sufficient densities to exceed Allee thresholds. When this occurred, the gypsy moth distribution would "pulse" forward, but then stop until donor populations again grew to sufficient levels.

Discussion

Biological invasions continue worldwide due to trends in world trade and travel (Vitousek et al. 1996; Work et al. 2005; Brockerhoff et al. 2006; Liebhold et al. 2006; McCullough et al. 2006). As a consequence of our increasingly global community, species are being relocated and many of these introductions result in the successful establishment of a species in its nonnative range (Liebhold et al. 1995b; Niemelä and Mattson 1996; Mattson et al. 2007). The ramifications can be profound ecological changes to native communities and biodiversity, as well as significant economic costs in efforts to mitigate their negative impacts (Parker et al. 1999; Mooney and Cleland 2001; Pimentel et al. 2005).

The gypsy moth provides a remarkable model system of the invasion dynamics of a nonindigenous species because there are detailed data on its initial distribution (Forbush and Fernald 1896; Liebhold and Tobin 2006), its distribution through time (Burgess 1917, 1930; Perry 1955; Liebhold et al. 1992; Tobin et al. 2007a), and its population biology and ecology (Bess et al. 1947; Campbell 1967; Elkinton and Liebhold 1990); thus, there exists a tremendous opportunity for understanding the pattern and process of a biological invasion. In recent years, the role of Allee effects in biological invasions has garnered much interest

(Taylor and Hastings 2005). Because of the feasibility and reliability of monitoring low-density gypsy moth populations to which Allee effects apply, the gypsy moth serves as an ideal model system for more precisely quantifying their role.

In this review, we have outlined possible causes of an Allee effect in insect invasions. Two possible causes of an Allee effect in low-density gypsy moth populations are the failure to satiate predators and find mates. The latter cause has been previously quantified to play an important role (Sharov et al. 1995; Tcheslavskaia et al. 2002; Robinet et al. 2007, 2008). The role of natural enemies in causing an Allee effect in the gypsy moth is unclear, and this should be considered as an important area of future study. Mate-finding failures detrimentally affect the ability of newly arriving, low-density populations to persist and successfully establish, and many founding populations are consequently driven to extinction without any management effort (Liebhold and Bascompte 2003; Whitmire and Tobin 2006). This phenomenon in turn influences the degree to which these new colonies contribute to gypsy moth spread through stratified dispersal (Johnson et al. 2006; Tobin et al. 2007b). In eradication efforts, management tactics currently exploit the Allee effect in the gypsy moth by using aerial applications of synthetic pheromones to chemically confuse males so that they are unable to locate females (Thorpe et al. 2006). Because of the likely, though still largely unknown, importance of Allee effects in the dynamics of biological invasions, it could be possible to exploit species-specific characteristics that influence the strength of the Allee effect, thus facilitating the development of improved management strategies and risk assessments.

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