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Persistence of invading gypsy moth populations in the United States

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Abstract Exotic invasive species are a mounting threat to native biodiversity, and their effects are gaining more public attention as each new species is detected. Equally important are the dynamics of exotic invasives that are previously well established. While the literature reports many examples of the ability of a newly arrived exotic invader to persist prior to detection and population growth, we focused on the persistence dynamics of an established invader, the European gypsy moth (*Lymantria dispar*) in the United States. The spread of gypsy moth is largely thought to be the result of the growth and coalescence of isolated colonies in a transition zone ahead of the generally infested area. One important question is thus the ability of these isolated colonies to persist when subject to Allee effects and inimical stochastic events. We analyzed the US gypsy moth survey data and identified isolated colonies of gypsy moth using the local indicator of spatial autocorrelation. We then determined region-specific probabilities of colony persistence given the population abundance in the previous year and its relationship to a suite of ecological factors. We observed that colonies in Wisconsin, US, were significantly more likely to persist in the following year than in other geographic regions of the transition zone, and in all regions, the abundance of preferred host tree species and land use category did not appear to influence persistence. We propose that differences in region-specific rates of persistence may be attributed to Allee effects that are differentially expressed in space, and that

the inclusion of geographically varying Allee effects into colony-invasion models may provide an improved paradigm for addressing the establishment and spread of gypsy moth and other invasive exotic species.

Keywords Persistence · Biological invasions · Allee effects · Invasive species · Local indicator of spatial autocorrelation

Introduction

Persistence is the ability of a population to sustain itself in the environment subsequent to its arrival. Because of the role it plays in the continuity of populations, persistence is of central importance to studies in epidemiology, conservation biology, and invasion ecology (Shea 1998; Earn et al. 1998). In epidemiological and conservation biological investigations, much interest has been placed on the spatiotemporal dynamics of populations, in which persistence may or may not be enhanced depending on its relationship to population synchrony or asynchrony (Heino et al. 1997; Rohani et al. 1999). Due to the threat that invasive species pose to biological diversity, considerable research efforts and resources are devoted to documenting, predicting, and managing their effects (Pimentel et al. 2000). As such, the invasion dynamics of alien species in new habitats motivates key questions regarding persistence.

Biological invasions occur in three stages: arrival, establishment, and spread (Hengeveld 1988). Once an alien species is established in a new region, the prevention of local spread is often difficult, or logistically unrealistic (Krushelnycky et al. 2004). Population spread of an established invader can occur either by short-distance dispersal leading to continuous expansion of an established population, or by long-distance dispersal, which could be aided by human transport of propagules (Shigesada and Kawasaki 1997; Shigesada et al. 1995). Long-distance spread can result in the formation of isolated colonies ahead of areas that are

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generally infested. If these colonies are successful in persisting, then they can increase in abundance, coalesce, and eventually become incorporated into the range of the established population. In this manner, the overall spread of an invading organism can be accelerated (Sharov and Liebhold 1998b).

Low density, isolated colonies are often subject to Allee effects and stochasticity, both of which can inhibit the colonies' ability to persist (Liebhold and Bascombe 2003; Hastings 1996) and thus considered important factors when predicting the likelihood of the extinction of small colonies (Leung et al. 2004; Liebhold and Bascombe 2003). Allee effects collectively describe a decrease in fitness with a decrease in population abundance, and causes include the inability to locate mates, inbreeding depression, and failure to satiate predators (Allee et al. 1949; Stephens et al. 1999). Environmental stochasticity results in variable reproductive and mortality rates, causing population growth rates to vary. Laboratory experiments in which environmental variation was manipulated resulted in an increase in colony extinction and decrease of new colony establishment with increasing levels of stochastic variation (Drake and Lodge 2004). Stochastic events can have a strong influence on colony persistence, particularly for low density, isolated colonies.

Low-density colonies could persist as a result of metapopulation dynamics (Hanski 1999), in which metapopulations sustain themselves due to a balance between random extinction and recolonization of patches through dispersal (Levins 1969). Persistence of metapopulations has been shown to be influenced by population size within the patch (Berger 1990; Moilanen and Hanski 1998), age of the patch (Hastings 2003), spatial and landscape structure (With 2004; Hanski 1994; Moilanen and Hanski 1998), and environmental and demographic stochasticity (Fagan 1999). Moreover, populations governed by nonlinear dynamics, in which local population noise is amplified, may experience decrease in extinction rates due to increase in population asynchrony (Allen et al. 1993). There are numerous examples of invasions of exotic species where a small isolated colony persisted for some time prior to population expansion and consequent explosion (e.g., Shigesada and Kawasaki 1997, and examples therein). We sought to investigate the ability of isolated colonies of an established invasive species to persist ahead of a moving population front. We used the invasion of the European strain of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), in the United States as a model system for examining this type of persistence dynamics.

The gypsy moth was introduced into North America in the 1860s near Boston, MA, USA. Its current range includes southern Canada, west to Wisconsin, and south to North Carolina. The gypsy moth is a polyphagous herbivore with over 300 species of deciduous and coniferous hosts (Elkinton and Liebhold 1990). Since 1924, over 34.6 million hectares of US forests have been partially or completely defoliated by gypsy moth (Gypsy

Moth Digest 2004). The ecological and economic costs, both indirect and direct, have been well documented (e.g., Doane and McManus 1981; Thurber et al. 1994; Leuschner et al. 1996; Sample et al. 1996; Redman and Scriber 2000; Mayo et al. 2003).

Overwintering eggs hatch in the spring, and larvae feed on both young and fully developed foliage. Pupation occurs mainly on the trunks of trees, and adults emerge from mid to late summer. The gypsy moth is univoltine, and in the European strain of gypsy moth, females do not fly and usually oviposit within 1–2 m from the site of adult emergence (Odell and Mastro 1980). Forms of dispersal include ballooning early instars, and adult male flight. Gypsy moth population dynamics are complex (Campbell 1967, 1973; Doane and McManus 1981; Elkinton and Liebhold 1990; Williams and Liebhold 1995). Dwyer et al. (2004) recently suggested a host-pathogen-predator model, coupled with environmental stochasticity, to explain the gypsy moth outbreaks. In outbreak populations, viral epizootics can regulate gypsy moth populations though they impose little influence in low-density populations (Doane 1970; Elkinton and Liebhold 1990). Instead, low-density populations are most likely to be influenced by small mammals (Bess et al. 1947; Campbell et al. 1977; Elkinton et al. 1989, 2004; Elkinton and Liebhold 1990), such as the white-footed mouse, *Peromyscus leucopus*, whose populations in turn can be influenced by mast dynamics (Elkinton et al. 1996; Jones et al. 1998).

Regions of the US can be characterized as uninfested by the gypsy moth, generally infested, or within some transition zone between the two. In the transition zone, the gypsy moth invades previously uninfested habitat, initiates and establishes new colonies, which in turn can serve as a source for new infestations. Gypsy moth movement within this transition zone can vary from year-to-year and from area to area. For example, gypsy moth spread in the Appalachian states of West Virginia and Virginia has averaged roughly 2 km/year (SD = 20.9 km) since 1996, while the corresponding rate of spread in Wisconsin was 20 km/year (SD = 34.4 km), even though the management tactics in both regions were uniformly applied under the USDA Forest Service Slow-the-Spread program (Sharov et al. 2002; Tobin et al. 2004). Past analyses on gypsy moth spread and the factors that influence it have occasionally led to conflicting conclusions. For example, Liebhold et al. (1992) reported that in colder climates, such as those areas where minimum January temperatures were < 7°C, historical rates of spread in the Northeastern US were roughly three times slower than under the inverse condition. In contrast, Sharov et al. (1999) reported that in Michigan, rates of spread were actually higher in colder climates and instead linked the higher rates of spread to the increases in forest susceptibility.

In the transition zone, the gypsy moth populations do not necessarily spread continuously along the population front. Rather, individual colonies become established beyond the expanding front. Adult dispersal is

limited, and ballooning instars are usually deposited within only a few hundred meters from the source (Mason and McManus 1981). Thus, the movement of gypsy moth beyond the infested zone is largely thought to be the result of the inadvertent transportation of life stages by humans (Schwalbe 1981; Mason and McManus 1981; Liebhold et al. 1992). Indeed, many new infestations have been positively associated with household moves from infested to uninfested zones (McFadden and McManus 1991). These patterns suggest that within the transition zone, colonies coalesce and contribute to the range expansion of gypsy moth (Sharov and Liebhold 1998b).

In support of this argument, Liebhold et al. (1992) modeled the gypsy moth range expansion and contended that if windborne instar movement was the only form of dispersal, then range expansion should occur at a rate of roughly 3 km/year. However, they estimated that the average spread rate was ≈ 21 km/year from 1965 to 1990, and they suggested that this greater rate of spread was due, in part, to the formation, growth, and coalescence of isolated populations ahead of the population front. However, it is unknown whether all isolated gypsy moth colonies, particularly low-density ones, persist from year-to-year within this transition zone, and if there is a regional effect to these invasion dynamics. We examined these questions by analyzing the persistence of isolated colonies from year-to-year over the spatial extent of the transition zone from 1996 to 2003 given the initial density of the colony and its relationship to a suite of ecological factors.

Materials and methods

Sampling regime

Gypsy moth populations within the transition zone are monitored through the USDA Forest Service Slow-the-Spread Program (Sharov et al. 2002; Tobin et al. 2004). One aspect of this program is to delineate population boundaries, as well as boundaries that delimit the transition zone (Sharov et al. 1995). The boundaries of the transition zone, which is roughly 100 km in width, are then delineated such that the boundary closest to the advancing population front is approximately 30–50 km from the 10-moth population boundary (Tobin et al. 2004). In the transition zone, pheromone-baited traps are placed at an intertrap distance of 2 km, which has been shown to be sufficient for detecting isolated colonies (Sharov and Liebhold 1998a). The traps are placed using handheld GPS units within a 500 m radius from target coordinates. From year-to-year, the number of traps placed in the transition zone varies, but generally exceeds 50,000. We used the gypsy moth pheromone trap data from 1996 to 2003 to test the spatial pattern of isolated gypsy moth colony persistence. During these years, traps within the transition zone were placed in

Wisconsin, Illinois, Indiana, Ohio, West Virginia, Virginia and North Carolina.

Identification of isolated colonies

We used Local Indicator of Spatial Autocorrelation methods to estimate the local Moran statistic (Anselin 1995; Getis and Ord 1996; Boots 2002) in R (R Development Core Team 2002) using the *spdep* package (Bivand 2004) to objectively identify spatially unique colonies of the gypsy moth. For each year, the transition zone was divided into $\approx 150 \times 150$ km² blocks. In each block, we estimated the local Moran statistic at each trap according to

$$\text{local Moran} = \frac{(z_i - \bar{Z})}{\text{var}(Z)} \sum_{j=1}^N w_{ij}(z_j - \bar{Z}) \quad (1)$$

where z_i is the number of moths recorded by the trap, z_j is the number of moths recorded by a trap within a local neighborhood around z_i , and \bar{Z} and $\text{var}(Z)$ refer to the block mean and variance, respectively. Prior to estimation, the moth counts were transformed using $\log_{10}(z+1)$. The weight function, w_{ij} , is binary and equal to 1 when a neighboring trap (i.e., z_j) is located within some a priori distance of z_i . Around each z_i , we used a radius of 3.1 km to capture these neighboring traps. Negative local Moran values represent traps that are locally spatially different from the value of their neighbors (i.e., “high–low” or “low–high” associations, cf. Anselin 1995). We considered traps across all years for which the local Moran statistic was significantly negative (Getis and Ord 1996). Because negative local Moran values can result from either “high–low” or “low–high” associations, we further partitioned the data by selecting the former association. Other traps were eliminated from further analysis if they were in an area treated for gypsy moth or if they fell outside the transition zone. Lastly, we considered only traps for which the initial moth abundance was ≥ 1 and ≤ 20 . This final subset of low-density, isolated colonies was then used in subsequent analyses.

Modeling persistence

For our response variable, we scored isolated colonies as extinct if in year $t+1$ the trap catch for the colony was 0, and persisting otherwise. Because exact trap locations can move from year-to-year, we matched the trap location in year t to its closest location in year $t+1$. [The mean distance between traps in successive years was within the 500 m buffer within which the traps were placed, and the distances did not differ significantly among regions in an analysis of variance ($F=1.6$, $df=2$, 873 , $P=0.2$)]. We used logistic regression (PROC LOGISTIC, SAS Institute 1999) to test the main effects of the (1) abundance of the colony in year t ; (2) the region

in which the colony was located; (3) abundance of moths recorded from neighboring traps within 3.1 km of the colony in year t ; (4) the distance of the colony to the generally infested area; (5) the basal area of the gypsy moth preferred host species associated with the colony; (6) USGS land cover category associated with the colony; and (7) interactions between main effects. We used Hosmer and Lemeshow (2001) model selection methods to determine the appropriate logistic regression model. The significance of main and interaction effects were based on the Wald χ^2 for Type 3 analysis. When appropriate, odds ratios and associated confidence intervals were estimated based on the Wald χ^2 .

Colonies were placed into region categories as follows: Wisconsin (WI); the Midwest United States (MW); traps in Illinois (IL), Indiana (IN), and Ohio (OH); the Appalachian region of the United States (AP); traps in West Virginia (WV), Virginia (VA), and North Carolina (NC). The basal area of the gypsy moth preferred host species was adjusted for forest density (Morin et al. 2005). Land cover data were obtained from the National Land Cover Data (USGS 2003) at a 30 m resolution. All forest types were collapsed into one forest category, as were all agricultural areas.

Additional analyses

To examine neighborhood effects on persistence, we modified our response variable to include moth captures from traps within a prespecified area around the isolated colony in year $t+1$. In this case, if the sum of moths caught at the isolated colony and in the traps in the neighborhood around the isolated colony was 0 in year $t+1$, then we considered the colony extinct; otherwise, the colony was considered to be persisting. We used two radii, 3.1 and 6.2 km, around the isolated colony to define these neighborhoods. Lastly, we examined the effect of elevation on isolated colony persistence in AP, where there are reasonable elevation differences. Elevation data were obtained from the North America digital elevation model, GTOPO30. GTOPO30 is a digital elevation model (DEM) with a horizontal grid spacing of 30 arc s (≈ 1 km) (USGS 2004).

Results

Across all years, the number of isolated colonies detected by the local Moran statistic in WI, MW, and AP were 321, 231, and 324, respectively. The local Moran method was successful in identifying the isolated colonies: across all regions; for example, over 50% of the colonies were surrounded by neighboring traps (i.e., those within 3.1 km radius of the colony) in which no moths were caught, and over 90% were surrounded by neighboring traps in which total moth counts were ≤ 2 .

We observed significant effects of the (1) abundance of the colony in year t ($\chi^2=6.9$, $df=1$, $P<0.01$, Figs. 1, 2)

region in which the colony was located ($\chi^2=39.2$, $df=2$, $P<0.01$, Fig. 1); (3) abundance of moths recorded from neighboring traps within 3.1 km of the colony in year t ($\chi^2=4.1$, $df=1$, $P=0.04$); and (4) the distance of the colony to the generally infested area ($\chi^2=24.4$, $df=1$, $P<0.01$, Fig. 2). No other main effects or interactions between main effects were significant (Hosmer and Lemeshow $\chi^2=4.3$, $df=8$, $P=0.83$). The isolated colonies in WI were 1.7 (95% CI, 1.2–2.3) and 2.5 (1.7–3.6) times more likely to persist than colonies in AP and MW, respectively, while the AP and MW were not significantly different (Fig. 1). Collapsing over initial abundance, the mean (variance) overall probability of persisting from year-to-year in WI, AP, and MW was 0.492 (0.250), 0.350 (0.228), and 0.268 (0.196), respectively.

Isolated colonies were more likely to persist when closer to the generally infested area in all regions (Fig. 2). There was no interaction effect between the region and distance from the generally infested zone ($\chi^2=1.4$, $df=2$, $P=0.50$), suggesting slope homogeneity among regions. However, there was a significant region effect ($\chi^2=53.5$, $df=2$, $P<0.01$), such that at approximately 140 km from the generally infested area, the colonies in WI persisted roughly 50% of the time, while in AP and MW the corresponding rates were 30 and 20%, respectively.

The basal area of preferred host species and land use category did not explain differences in persistence rates among regions (Fig. 3). It was evident that even in areas of high host tree abundance, persistence of isolated gypsy moth colonies was not necessarily enhanced. Also, most of the colonies in all regions were located in areas classified as either forest or agricultural lands, with only a few colonies located in wetlands or urban areas (Table 1). In WI, isolated gypsy moth colonies still persisted roughly half of the time regardless of the land use category in which the colony was located (Table 1). In AP and MW, the colonies persisted approximately 35 and 20% of the time, respectively, and likewise regardless of the land use category (Table 1). However, it is important to note that there were differences in scale between the gypsy moth trap catch data, and in the scale used to interpolate the basal area of the gypsy moth preferred host species (Morin et al. 2005) and NLCD data (USGS 2003), which could render associations difficult to ascertain.

We observed that when the moths measured by neighboring traps in year $t+1$ are included in our criterion of colony persistence, persistence in all regions increased relative to their exclusion (Fig. 4). However, the regions remained significantly different from each other in the same fashion as previously observed. The results were similar when using either a 3.1 or 6.2 km radius. For a 3.1 km radius, isolated colonies in WI were 2.2 (95% CI, 1.5–3.3) and 3.6 (2.4–5.3) times more likely to persist than those in AP and MW, respectively, while colonies in AP were 1.6 (1.1–2.3) times more likely to persist than those in MW.

The range of elevation in AP was 0–1,132 m above sea level. In this region, 41% of the colonies at

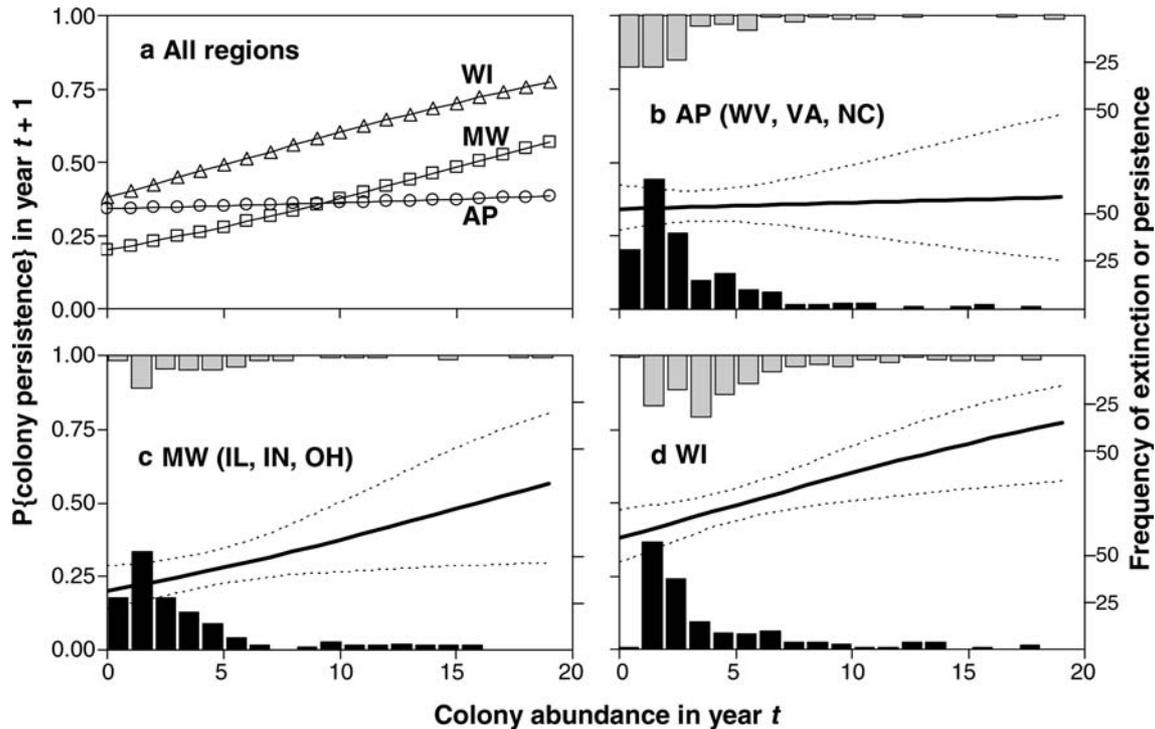


Fig. 1 Predicted probabilities of the gypsy moth (*Lymantria dispar*) colony persistence based on the abundance of the colony from the preceding year in **a** All regions, **b** Appalachia (AP), **c** Midwest (MW), and **d** Wisconsin (WI). The *histograms* represent the

observed frequency of colonies that became extinct (*black bars*) or persisted (*gray bars*) (cf. Smart et al. 2004). The model predictions (*solid line*) and 95% confidence intervals (*dashed lines*) are also shown for each region

Table 1 Percentage (and total number) of isolated gypsy moth colonies persisting (P) or not (E) by land use category and region

Land use Category	Region AP		Region MW		Region WI	
	P	E	P	E	P	E
Forest	33.3 (80)	66.7 (160)	23.4 (11)	76.6 (36)	46.7 (70)	53.3 (80)
Agriculture	39.3 (24)	60.7 (37)	28.5 (47)	71.5 (118)	49.6 (69)	50.4 (70)
Wetland	50.0 (5)	50.0 (5)	0.0 (0)	0.0 (0)	53.9 (14)	46.2 (12)
Urban	57.1 (4)	42.9 (3)	21.1 (4)	79.0 (15)	71.4 (5)	28.6 (2)

The consistency in persistence/extinction between forest and agricultural areas for each region. Data from wetland and urban areas are shown but were not analyzed due to insufficient sample sizes

elevations < 200 m persisted while only 25% at elevations 200–400 m persisted, and these rates were significantly different ($G^2 = 6.2$, $df = 1$, $P = 0.01$). Furthermore, most (72%) of the variation in the elevation effect was explained by the differences between colonies at elevations < 200 m and those at 200–400 m. Sharov et al. (1997) reported that in uninfested areas, higher colonization rates were higher at lower elevation, possibly due to increased human movement, and this study supports the notion of enhanced persistence at lower elevations.

Discussion

The difference in region-specific rates of the gypsy moth colony persistence within the transition zone has important consequences in the dynamics of gypsy moth

range expansion, and implications for the dynamics of other invading species. Low-density, isolated populations are generally subject to Allee effects, which can affect their ability to establish, spread, and persist (Lewis and Kareiva 1993; Hastings 1996; Keitt et al. 2001; Fagan et al. 2002; Liebhold and Bascompte 2003; Drake 2004; Drake and Lodge 2005). Indeed, the gypsy moth colonies in all regions that we explored generally had lower probabilities of persisting at lower densities (Fig. 1). Liebhold and Bascompte (2003) illustrated the importance of Allee effects in the isolated colonies of gypsy moth in an uninfested area of the United States. In this case, life stages were unintentionally introduced, and they contended that the failure of these colonies to persist and become established was due to a failure of finding mates. In our study, we propose that not only are Allee effects important in the gypsy moth persistence,

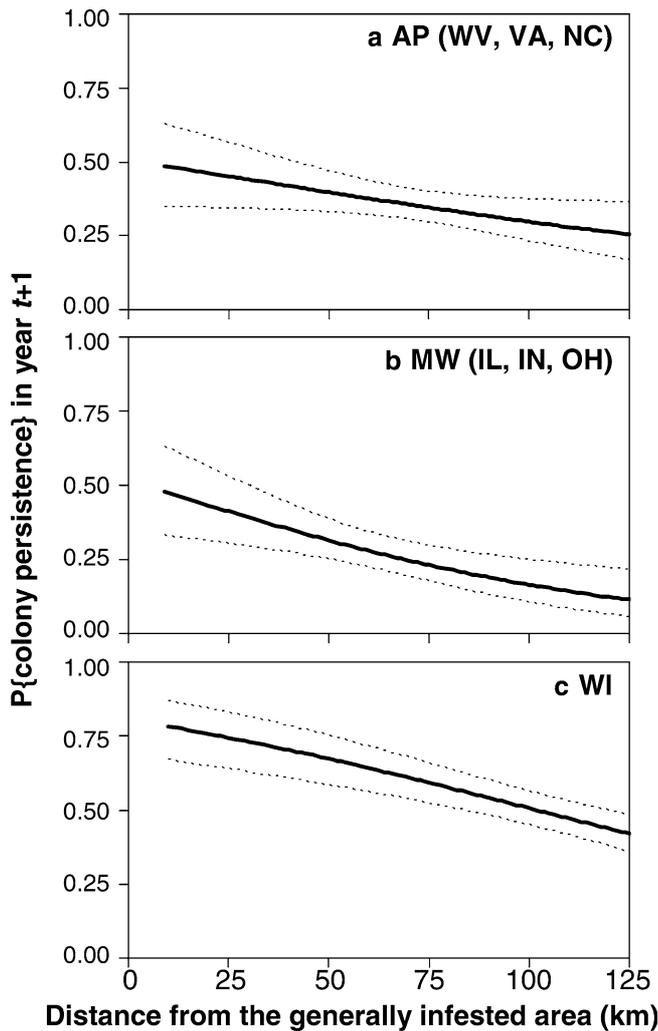


Fig. 2 Region-specific predicted probabilities ($\pm 95\%$ confidence intervals) of persistence in year $t+1$ of isolated colonies, regardless of their initial abundance in year t , over the distance between the colony and the gypsy moth generally infested area for **a** Appalachia (AP), **b** Midwest (MW), and **c** Wisconsin (WI)

but that the strength of the Allee effect appears to vary over geographic regions. This work shows how it thus may be important to consider region-specific Allee effects when addressing biological invasions.

In many invading species, dispersal from initial parent populations subsequent to invasion may be limited. The gradual range expansion generally follows a colony-invasion model in which spread can be accelerated by the coalescence of isolated colonies, or propagules, that establish away from the initial population (Shigesada and Kawasaki 1997). The inadvertent movement of life stages by humans is thought to be a key mechanism by which many species, including the gypsy moth (Schwalbe 1981; Mason and McManus 1981; Liebhold et al. 1992), traverse great distances. Moreover, recent work on the horse chestnut leafminer underscores the importance of the relationship between human population density and long-distance movement by an invading insect (Gilbert et al. 2004).

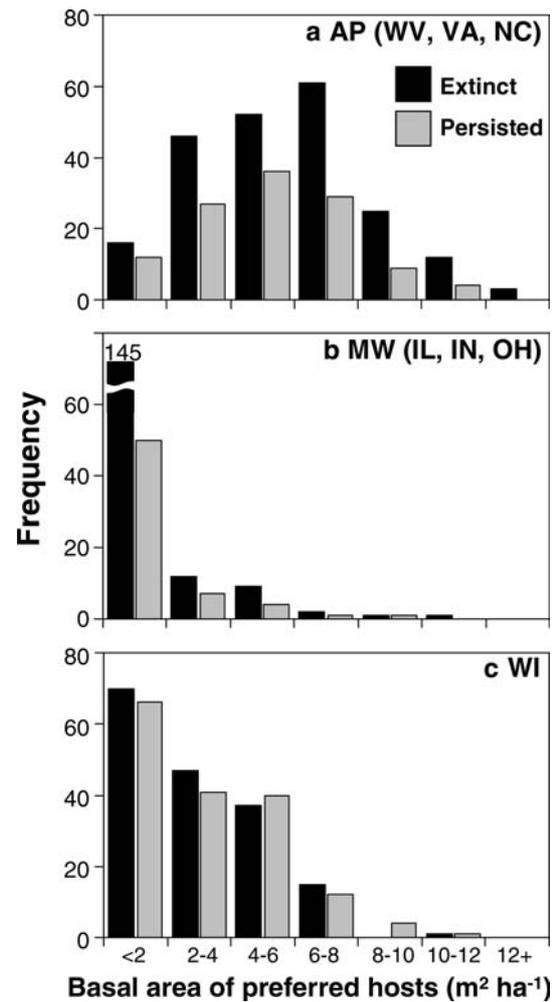


Fig. 3 Histogram of the frequency of isolated gypsy moth colonies that became extinct (*black bars*) or persisted (*gray bars*) over the quantity (*basal area*) of preferred gypsy moth host trees in which the colony was located for **a** Appalachia (AP), **b** Midwest (MW), and **c** Wisconsin (WI)

The inclusion of spatially explicit Allee effects into the colony-invasion models seems to be applicable for the gypsy moth, and may also be applicable for other invading species. One result of such a paradigm could be the development of irregular population spread boundaries from an initial infestation point, in which propagules in space are subject to varying Allee effects. Biological invasions with such corrugated boundaries have been hypothesized to increase their range expansion more rapidly than those with planer boundaries (Lewis and Kareiva 1993). The gypsy moth provides an example of this phenomenon. In WI, the spread of invading gypsy moth does often lead to the appearance of “bulges” in population boundaries, whereas in other regions, the spread follows a more planar boundary (Decision-Support System for the Slow-the-Spread Project 2005). In this study, we have observed regional differences in colony persistence, perhaps due to geographically varying Allee effects. If such Allee effects are

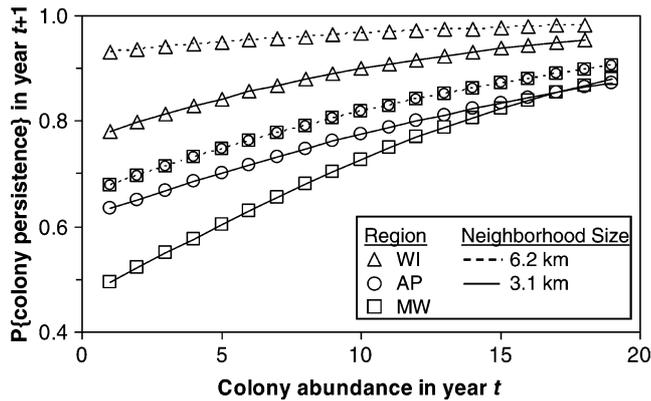


Fig. 4 Effect of the size of the local neighborhood to region-specific predicted probabilities of persistence of the colony and its neighborhood (within 3.1 or 6.2 km) given their abundance from the preceding year. In the AP and MW regions, this relationship did not differ significantly when using the 6.2 km neighborhood

occurring in the spread dynamics of the gypsy moth, then this may provide a plausible explanation for the more rapid rate of spread in WI relative to other regions of the United States (Decision-Support System for the Slow-the-Spread Project 2005). However, in the case of gypsy moth, it is still not clear which process, persistence or spread, is driving the other.

In this study, we demonstrated the potential for Allee effects to be differentially expressed in space. These findings have implications in the development of population dynamics and spread models in both established invaders and newly arrived invaders. There are also important implications in the overall management of invasive species, such as the importance of management protocols to be specific to the locality of infestation, as well as underscoring the uncertainty associated with management over regional scales.

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