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Using delimiting surveys to characterize the spatiotemporal dynamics facilitates the management of an invasive non-native insect

Patrick C. Tobin · Laura M. Blackburn ·
Rebecca H. Gray · Christopher T. Lettau ·
Andrew M. Liebhold · Kenneth F. Raffa

Abstract The ability to ascertain abundance and spatial extent of a nascent population of a non-native species can inform management decisions. Following initial detection, delimiting surveys, which involve the use of a finer network of samples around the focal point of a newly detected colony, are often used to quantify colony size, spatial extent, and the location of the population core. Despite the widespread use of pheromone-baited traps in delimitation surveys to manage invading populations of *Lymantria dispar* (L.) in North America, there has been no prior comprehensive attempt to analytically determine the adequacy of these surveys. We used data from 2,190 delimiting grids collected from 2000 to 2010 in the United States to quantify the information gained from delimiting surveys. The use of delimiting surveys revealed that ≈ 53 % of populations of low initial abundance persisted as detectable populations in the following year; however, when trap data from delimiting surveys were excluded, only ≈ 16 % of these low density populations were detected in the following year. Measurements of abundance and spatial extent of a detected population were affected by the increased use of delimiting traps after accounting for initial abundance, the distance from an infested area, and colony area. The use of delimiting traps had a lesser effect on the estimation of the spatial location of the population core, indicating that initial detection of a population often reflects the population core. The need to prioritize resources in efforts to manage non-native species is paramount, and early detection is a key in invasive species management.

Keywords Biological invasions · Delimitation · Detection · Invasive species management · *Lymantria dispar* · Trap grid density

Introduction

Detection of nascent populations of non-native species in a novel habitat represents a critical component to the management of biological invasions. In response to increases in global trade and travel through which most non-native species arrive to a new area (Levine and D'Antonio 2003; Work et al. 2005; Lockwood et al. 2007; Hulme et al. 2008), efforts are made to minimize accidental introduction through the establishment of quarantine measures and inspections of incoming material. However, given the sheer volume of global trade relative to the small fraction of cargo, packaging material, ballast water and ship hulls that can be practically inspected, new invasions continue to occur (Brockerhoff et al. 2006; Liebhold et al. 2012). For those species that are not successfully excluded, subsequent efforts to detect and delineate their populations are often critical in both eradication and containment programs (Sharov and Liebhold 1998; Rejmánek and Pitcairn 2002; Panetta and Lawes 2005).

Among insects, initial detection can be realized through semiochemical monitoring tools, such as pheromone-baited traps (Mitchell 1981; El-Sayed 2012), as well as other

P. C. Tobin (✉) · L. M. Blackburn · A. M. Liebhold
Forest Service, United States Department of Agriculture,
Northern Research Station, Morgantown, WV 26505, USA
e-mail: ptobin@fs.fed.us

R. H. Gray · C. T. Lettau
Wisconsin Department of Agriculture, Trade and Consumer
Protection, 2811 Agriculture Drive, Madison, WI 53718, USA

K. F. Raffa
Department of Entomology, University of Wisconsin—Madison,
345 Russell Laboratories, 1630 Linden Drive,
Madison, WI 53706, USA

methods, such as visual surveys. Upon detection, the consequent management decision could differ depending on the situation, including the size and spatial pattern of the population. Generally, a higher priority is placed upon eradication of those species that are detected through monitoring efforts but are not considered to be established; thus, even the detection of a few individuals can trigger an aggressive eradication treatment. For example, New Zealand responded to the capture of one *Lymantria umbrosa* (Butler) moth male from survey traps in 2003 with weekly aerial applications of the biopesticide *Bacillus thuringiensis* variety *kurstaki* (*Btk*) over 8 weeks, encompassing 12.5 km^2 (Brockerhoff et al. 2010). In other cases, delimiting trapping grids can be deployed following initial detection (Tobin et al. 2004; Liebhold and Tobin 2006; Rabaglia et al. 2008; Guichard et al. 2012; McCullough and Mercader 2012).

In a delimiting grid, traps are deployed at a higher spatial resolution than in detection surveys, and are focused around the area of initial detection in an attempt to characterize the population size, the spatial location of the population core and the spatial extent of the population. This information is then used to help select an appropriate management decision. For example, higher-density infestations may require higher insecticidal doses and/or an increased number of applications relative to lower density ones. Knowledge of the spatial extent of the infestation allows for more precise spatial targeting of treatment tactics, which reduces non-target effects and the overall costs of treatment. Moreover, data from delimiting grids following initial detection could reveal that the population went extinct and hence no treatment is necessary (Liebhold and Bascompte 2003; Whitmire and Tobin 2006). Deployment of delimiting grids is also generally less expensive than treatments, which include the direct costs of application, the indirect costs of pre-treatment environment assessments, public outreach and public meetings, and intangible costs such as detrimental effects to non-target species and disruptions in ecosystem services.

In this study, we analyzed trapping records from delimiting surveys used to monitor and manage invading *Lymantria dispar* (L.) populations in the eastern United States to evaluate the applicability of the information gained through traps deployed in these delimiting grids. *Lymantria dispar*, which was introduced to North America from Europe in 1869, is a polyphagous folivore that can exploit over 300 species of deciduous and coniferous hosts, causing considerable ecological and economic damage (Elkinton and Liebhold 1990; Tobin et al. 2012). Because delimitation surveys are used in management efforts against non-native species across several taxa (e.g., Panetta and Lawes 2005; Holdich et al. 2009; Holder et al. 2010; Gormley et al. 2011; Kilroy and Unwin 2011), the concepts explored here could have broad applicability.

A practical consideration in optimizing the use of delimiting grids is the spatial resolution at which they should be deployed. Although *L. dispar* now has a long history in the United States, it continues to expand its range as the majority of the forested area considered to be susceptible to invasion by *L. dispar* remains uninfested (Tobin et al. 2012). Under the *L. dispar* Slow-the-Spread containment program in the eastern United States, colonies detected ahead of a moving population front are monitored initially using pheromone-baited traps deployed approximately 2–3 km apart (Tobin et al. 2004; Roberts and Ziegler 2007). Because these traps are effective at relatively low population densities (Schwalbe 1981), colonies are generally detected before they grow to the medium-to-high densities that are more challenging to eliminate. Following initial detection, delimiting grids with traps ≈250–1,000 m apart are typically deployed. Traps are not set closer than ≈250 m to avoid any potential of trap-to-trap interference, which is estimated to occur up to 80 m (Elkinton and Cardé 1988). Such programs face an inherent challenge in optimizing limited resources, namely the trade-off between deploying traps at wider spacing despite the biological and meteorological factors that limit a male moth's response to ≈80 m from a pheromone source in the field (Aylor et al. 1976; Elkinton et al. 1987; Elkinton and Cardé 1988), versus the cost-saving benefits that arise from the earlier detection achieved with a finer network of traps (Bogich et al. 2008; Epanchin-Niell et al. 2012).

Despite the widespread use of this and similar approaches, there has been little quantitative investigation of the benefits of delimiting grids. Specifically, we sought to understand how the conditions under which delimiting grids are deployed, such as *L. dispar* habitat quality, distance from an established range, and initial size of the detected infestation, influence the data obtained from these grids. The *L. dispar* Slow-the-Spread program has been implemented nationally since 2000, so there now are ample data across large spatial and temporal scales to examine the effectiveness of delimiting grids. We developed a quantitative relationship between trap catch in delimiting grids and initial *L. dispar* trap capture across a suite of potential explanatory variables that could influence the interpretation of trap catch data. The results illustrate how a strategy that integrates coarse grids for initial detection with detection-triggered deployment of finer delimiting surveys can enhance the management of an invading insect species.

Methods

Delimiting grids

Approximately 80,000–120,000 pheromone-baited traps are deployed and georeferenced annually under the

L. dispar Slow-the-Spread program, and traps are currently placed from North Carolina to Minnesota along the edge of the expanding *L. dispar* population front (Fig. 1). Under this program, pheromone-baited traps are deployed on a ≈ 2–3 km grid annually to detect new, and often isolated, *L. dispar* colonies that arise beyond the population front (Roberts and Ziegler 2007). After initial detection, delimiting grids (i.e., traps deployed at a higher density in the vicinity of the detected colony) are used in the following year. Individual delimiting grids can vary in spatial extent, from <1 to 1,200 km², as can the background male moth density that triggered the use of a delimiting grid, generally

from 1 to >100 male moths/trap. We considered those delimiting grids that were exclusively within the Slow-the-Spread monitoring area, which is ≈ 100 km in width and extends ≈ 120 km from the area considered to be generally infested by *L. dispar* (Fig. 1). From 2000 to 2010, there were a total of 2,190 delimiting grids used in this analysis, and the number per year ranged from 130 to 277 (Table 1).

Data compilation

We focused on four main objectives to quantify the information gained from the use of delimiting grids: (1) to

Fig. 1 Location of traps (*black*) deployed under the *L. dispar* Slow-the-Spread program, 2010, considered in this analysis. The infested area is shown in *grey*
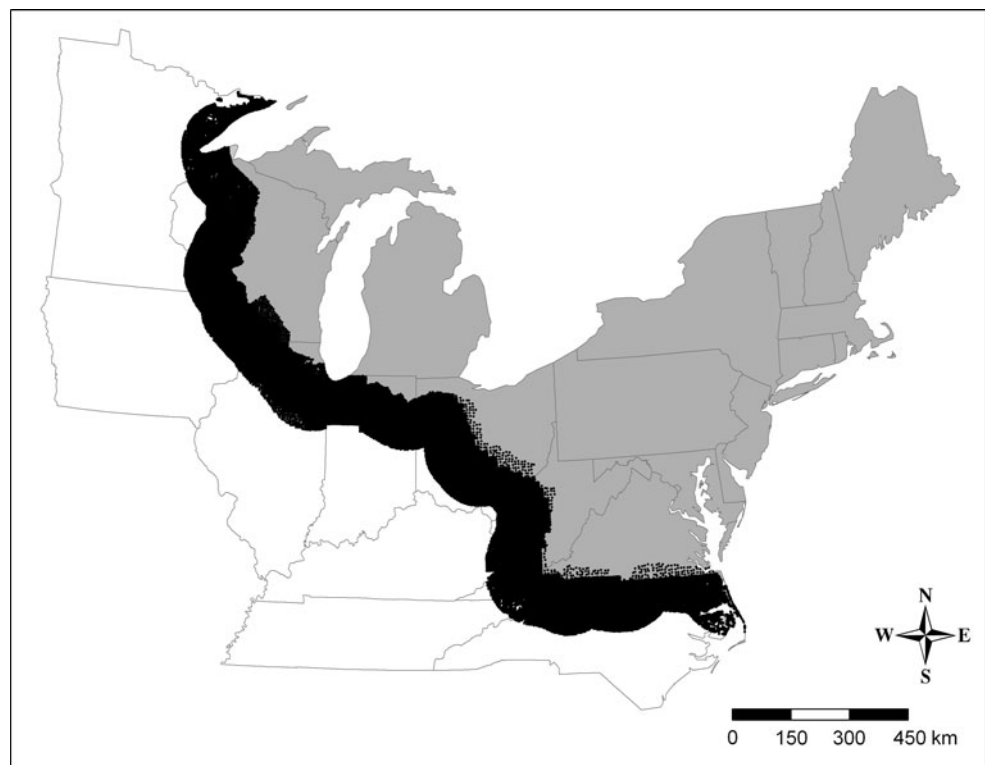
Table 1 Summary and characteristics of the delimiting grids used in this analysis

State	Number of delimiting grids	Median (range) of values across grids		
		Area (km²)	Distance from the established area (km)	Basal area of preferred host trees (m²/ha)
Iowa	5	7.6 (7.6–38.9)	88.1 (73.7–111.0)	16.1 (8.2–28.6)
Illinois	271	11.1 (1.2–70.1)	41.1 (0.0–118.2)	3.4 (0.0–25.8)
Indiana	258	6.3 (0.5–715.7)	25.9 (0.0–119.6)	2.4 (0.0–26.4)
Kentucky	2	5.3 (3.1–7.6)	89.4 (84.4–94.4)	28.9 (23.9–33.8)
Minnesota	111	3.1 (1.0–388.0)	97.0 (45.6–119.7)	27.3 (1.1–45.4)
North Carolina	180	5.1 (1.5–725.6)	68.3 (2.7–119.3)	18.8 (0.0–32.0)
Ohio	456	7.5 (1.4–440.9)	56.7 (0.0–119.1)	2.4 (0.0–48.5)
Virginia	278	5.3 (1.5–1,204.6)	38.3 (0.0–118.1)	23.6 (1.3–56.3)
Wisconsin	530	7.8 (1.0–326.1)	65.1 (0.0–118.8)	15.2 (0.0–39.6)
West Virginia	99	5.9 (1.4–932.5)	40.9 (0.0–110.9)	30.7 (8.1–58.1)

determine if the initially detected population had persisted in the following year; (2) to quantify *L. dispar* abundance in the delimiting grid, as ascertained by the total and maximum moth catch; (3) to identify the spatial location of the population core, as determined by the location of the maximum moth catch within the delimiting grid; and (4) to estimate the spatial extent of the population within the delimiting grid, as determined by the spatial interpolation of trap catch data within the delimiting grid. To determine the information gained from delimiting traps, we compiled, for each delimiting grid, two companion datasets: (1) a full trapping dataset that included trap catch data from the delimiting trap grids from year *t*, and (2) a subset trapping dataset that consisted of trap catch data from delimiting grids in year *t* but only from those traps that corresponded to the location of traps in year *t*−1; in this case, we sought to simulate trapping data that would have been obtained in year *t* if there were no additional delimiting traps (Fig. 2). In most cases, traps were not set in the exact location from year-to-year, and even if they were, variation in GPS accuracy from year-to-year could result in different recorded positions. Thus, we matched traps from year-to-year by considering the nearest neighboring trap (Fig. 2).

We first determined whether or not *L. dispar* was detected in each delimiting grid in year *t* when using both datasets. We also estimated and compared the *L. dispar* abundance (total and maximum trap catch) in each delimiting grid based upon both datasets, and estimated the Euclidean distance between the trapping locations that recorded the maximum male moth trap catch when using both datasets to determine if the location of the detected population core differed between the two datasets. To compare the spatial extent of the population, we used the trap catch data from both

datasets to generate interpolated surfaces of male moths/trap over a network of 1×1 km cells using median indicator kriging (Isaaks and Srivastava 1989; Sharov et al. 1996) in GSLIB (Deutsch and Journel 1992). We then compared the number of 1×1 km cells interpolated as 0, 1–3, 4–9, 10–29, 30–99 and ≥ 100 moths/trap when using each dataset; these population thresholds were chosen based upon the distribution of male moth catch.

Data analysis

All statistical analyses were conducted in R (R Development Core Team 2012). When considering the differences between the two datasets, a primary explanatory variable was the ratio of the total number of traps between the full and subset datasets. This ratio ranged from 2 to 79, although in ≈ 94 % of cases the ratio was ≤ 20; thus, we restricted our analyses to ratios ranging from 2 to 20. We also extracted several potential explanatory variables for each delimiting grid that have been observed to influence the growth and dynamics of *L. dispar* populations (Liebhold and Tobin 2006; Whitmire and Tobin 2006). These variables included the area of the initial infestation as detected by the delimiting grid (km²) and the estimated mean basal area density (m²/ha) of preferred *L. dispar* host trees (Morin et al. 2005). We also considered the minimum distance (km) of delimiting grids from the area considered to be infested by *L. dispar*, which is generally delineated by a 10–moth population abundance threshold (Sharov et al. 1995; Tobin et al. 2007a). The range of these variables by state is listed in Table 1.

We first considered the presence or absence of moths detected from traps in year *t* when using both datasets, and
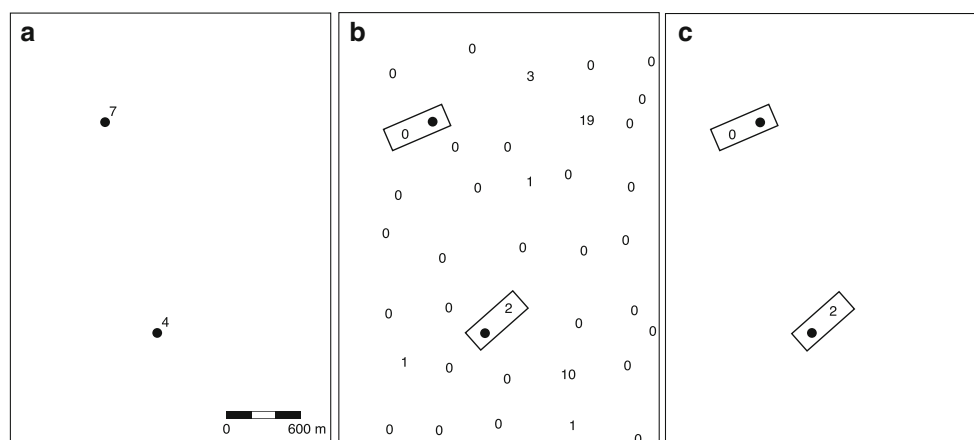

Fig. 2 Generation of the two datasets used in our analyses exemplified by a delimiting area in Ohio, 2010. **a** The trap locations (*solid circles*) and corresponding trap catches from detection surveys in year *t*−1 within an area delimited in year *t*. **b** The *numbers* represent the trap locations and number of males trapped in year *t* when using delimiting traps. The trap locations from year *t*−1 are shown as a

reference, and the nearest neighboring trap in year *t* from the locations of the traps in year *t*−1 are shown in the *boxed* area. **c** Trap catch values were extracted from traps set in year *t* but subset to only include traps most closely located to the traps set in year *t*−1. Thus, the trap data in **b** and **c** represent the two datasets with and without the use of delimiting traps, respectively

analyzed the relationship between this binary response variable and the initial abundance recorded in year $t-1$ using logistic regression. We then used the results from this logistic regression to examine specific ranges of initial abundance and the probability of detection in year t for these specific ranges based on the ratio between the total number of traps in the full and subset datasets, and the distance from the infested area, using logistic regression. Significance of effects was based on the likelihood ratio Chi squared, G^2.

For each delimiting grid, the difference in the total male moth trap catch, and the difference in the maximum trap catch between both datasets was transformed using $\log_{10+1}$, to correct for normality, and analyzed initially using least squares regression using the suite of explanatory variables. We also used this approach to determine the influence of the explanatory variables on the spatial distance between the population cores as ascertained by both datasets. To analyze the spatial extent of the delimiting area, we compared the number of 1 km^2 cells in each grid interpolated at each population threshold (0, 1–3, 4–9, 10–29, 30–99 and $\geq$100 male moths) based upon each dataset using least squares regression to determine the slope of the relationship (whereas a slope $= 1$ indicates congruence between the two datasets), and the R^2 value to determine the proportion of variation explained by the relationship. We also considered the percent error in spatial interpolation by comparing the two datasets.

When applicable, we also used locally polynomial quantile regression with the quantreg package (Koenker 2007) in R to better quantify the expected conditional response at different percentiles of the distribution instead of only the conditional mean response (Cade and Noon 2003). This was necessary due to the structure of the response variable. For example, in some cases, there was no difference between the two datasets, while in other cases, there were considerable differences, which greatly reduced the interpretative value of a conditional mean response obtained through standard least squares regression techniques. The quantile regression approach also is far more sensitive to outliers, which in our case were of paramount interest, as outliers are explicitly modeled in quantile regression.

Results and discussion

The probability that a population was detected in year t relative to the abundance in year $t-1$ was significantly different between the two datasets ($G^2 = 18.2$, $P < 0.01$). When analyzing each dataset separately, the probability of detecting a population in year t when using the full ($G^2 = 278.4$, $P < 0.01$) and subset ($G^2 = 619.5$,
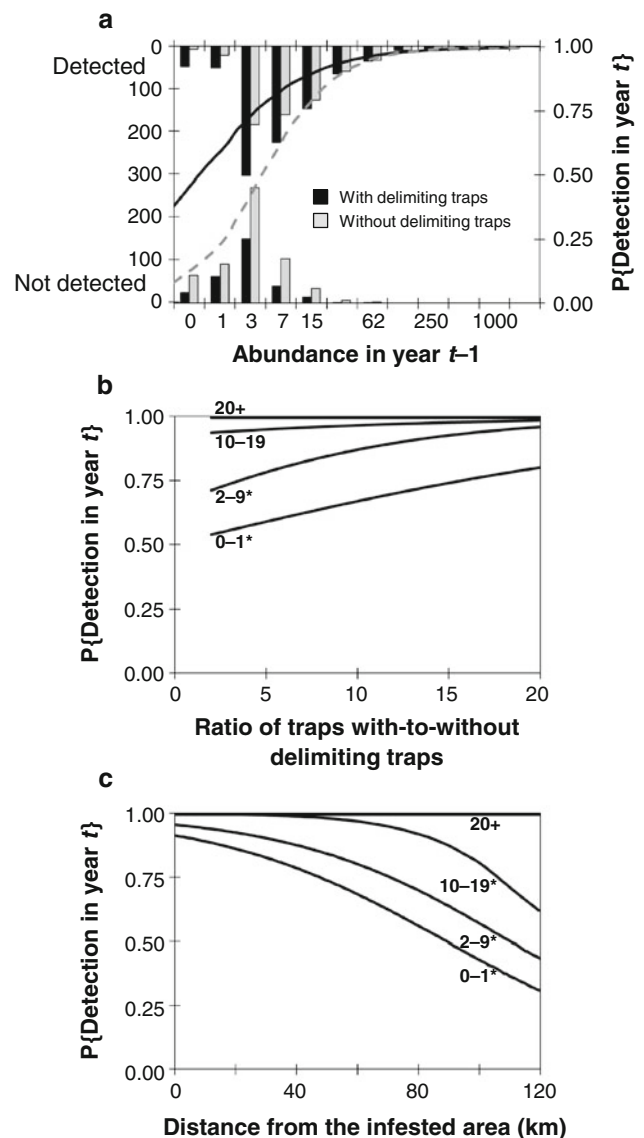

Fig. 3 a The probability of detection in year t based on the initial population abundance in year $t-1$ with (full dataset, *solid black line* and *bars*) or without (subset dataset, *dashed grey line* and *bars*) the use of delimiting traps. The histograms refer to the number, within an abundance bin, of delimiting areas where populations were detected or not in year t when using the full and subset datasets. The probability of detection in year t across the ratio of traps, **b** and distance from the infested area, **c** at specific initial abundances (as noted below the predicted probability *curves*). In **b** and **c**, significance of the predicted probability *curves* is noted by *asterisks*

$P > 0.01$) dataset was significantly affected by the initial abundance in $t-1$. Although at a high initial abundance, both datasets equally detected a population in year t, the lack of delimiting traps had a pronounced effect at lower initial abundances (Fig. 3a). When using delimiting traps, the predicted probability of detecting a population in year t as the initial abundance approached 0 was 0.38, while when excluding delimiting traps, the corresponding

predicted probability was 0.08. Based on these results, we partitioned the data by initial population abundance and examined the probability of detection when the initial abundance was 0–1, 2–9, 10–19 and ≥20 males/trap. The relationship for these ranges of abundance over the ratio of traps with-to-without delimiting traps, and the distance from the infested area are presented in Fig. 3b, c, respectively. The lower abundance ranges (0–1 and 2–9 males/trap) were both significantly affected by the ratio ($P < 0.01$) and distance to the infested area ($P < 0.01$), while the 10–19 males/trap range was significantly affected only by the distance ($P < 0.01$). Lower initial abundances were more likely to be detected with a greater resolution of delimiting traps (Fig. 3b). Specifically, within the lowest abundance range (0–1 males/trap), there were 376 delimiting areas of which 201 areas (53.5 %) were detected as populations in year t when using delimiting traps while only 60 (16.0 %) were detected in year t when not using delimiting traps. Also, populations, regardless of their initial abundance, were more likely to be detected closer to the invasion front (Fig. 3c).

This finding is particularly important in *L. dispar* eradication programs that target populations that are generally low in abundance and far from the infested area. Specifically, these results indicate that when initial population abundance is low, particularly in cases when <10 moths are trapped, it is important to deploy delimiting traps at higher densities to ascertain population persistence. Another implication is that when a very low population of *L. dispar* is initially detected in year $t-1$, immediate treatment may not be necessary because it may go extinct by year t without intervention (Liebhold and Bascompte 2003; Whitmire and Tobin 2006; Tobin et al. 2007b, 2009). Such a finding has important economic consequences in that it obviates the need to apply a treatment against the population.

An analysis to determine differences in the total and maximum *L. dispar* trap catch with and without delimiting traps posed a challenge because of the phenomenon described above in which for many cases, the initial detection of male moths from traps in year $t-1$ was followed by no moths being detected in the same area in year t. Consequently, quantile regression was used to determine the relationship between the ratio of traps in the full and subset datasets, and the difference in the total and maximum male moth catch between the two datasets (Fig. 4). When considering both the difference in the total and difference in the maximum catch, the 10th percentile response from quantile regression was 0, regardless of how many traps are deployed. In 49 % of these cases ($n = 988$), the lack of a difference was because no male moths were recorded in year t.

The area of the delimiting grid and the basal area of preferred *L. dispar* host trees in the delimiting grid affected the total and maximum *L. dispar* density with and without
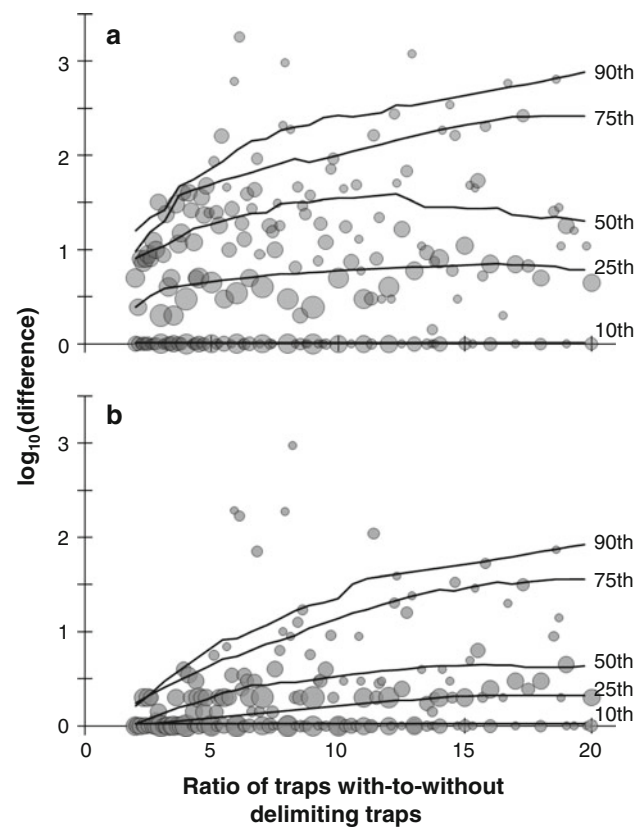

Fig. 4 Difference in the **a** total and **b** maximum moth catch based upon the ratio of traps. *Lines* are the predicted conditional responses from quantile regression at the *percentiles* indicated. The *circle* sizes are proportional to the number of delimiting grids

delimiting traps in a similar manner (Fig. 5a, c). In terms of the area of the delimiting grid, the results are intuitive in that more traps are deployed over larger areas, and hence are likely to record more moths. The increase in total moth catch with elevated basal area of host trees (Fig. 5c) could reflect the effect of more suitable habitat on population growth (Sharov et al. 1999). In contrast, we observed only slight differences in the variation of maximum trap catch by the area of the delimiting grid (Fig. 5b), and differences in the variation of maximum moth catch only at high levels of host basal area (Fig. 5d). These slight differences could reflect that the initial core of the population is often well indicated by the location of the trap catch in year $t-1$ that triggered the use of delimiting traps in year t.

The effect of the distance (km) from the *L. dispar* infested area on the differences in the total and maximum moth catch is presented in Fig. 6, and shows a similar relationship for both response variables. The differences detected in delimiting areas closer to the generally infested area tended to be greater than for those farther away; this observation could reflect dispersal from the infested area into these delimiting areas and that this immigration is supplementing local population growth. Moreover, the addition of immigrants

Fig. 5 Difference in the total, **a**, **c**, and maximum, **b**, **d**, moth catch based upon the area and density of *L. dispar* preferred host trees within the delimiting grid. The *circle* sizes are proportional to the number of delimiting grids
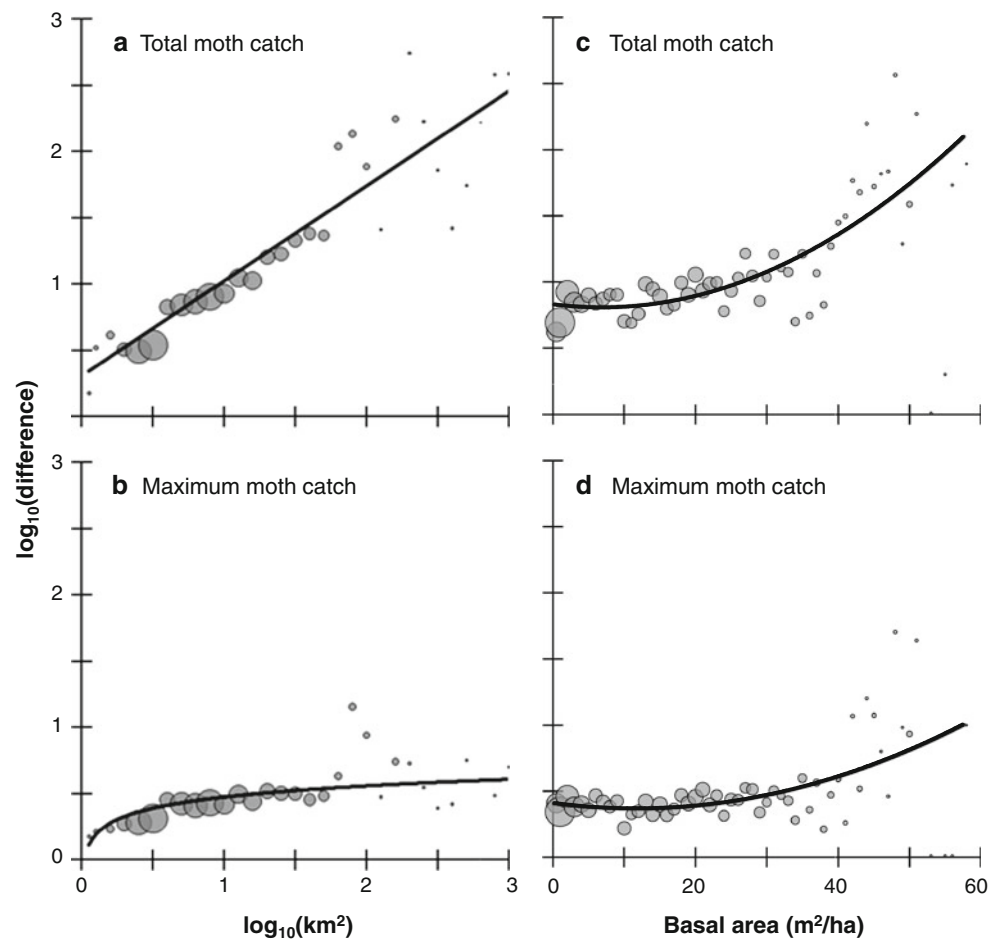
into these areas could also enable low-density populations to surpass an Allee threshold (Johnson et al. 2006; Tobin and Blackburn 2008; Contarini et al. 2009), which increases the likelihood of colony persistence and positive population growth in the following year.

Our third objective sought to quantify the relationship of the spatial location of the population core, as defined by the maximum catch, with and without the use of delimiting grids. We observed a non-significant relationship (i.e., a slope not significantly different from 0, $t = 1.01$; $P = 0.32$) when considering the distance between maximum trap catch as a function of the ratio of traps with-to-without delimiting traps (Fig. 7a). Thus, the initial detection of a new population in year $t-1$, around which delimiting traps are deployed in year t, could therefore reflect the core of the infestation. However, it is important to note that the y-intercept of the relationship presented in Fig. 7a was 1,008.8 m. Given that in the Slow-the-Spread program, delimiting traps are generally deployed 250–1,000 m apart, the use of some level of delimiting traps, especially in close proximity to the initial detected population, provides valuable information regarding the location of the population core. In addition, the area of the delimiting grid can significantly affect the estimate of

the spatial location of the population core ($t = 8.15$; $P < 0.01$; Fig. 7b); thus, the larger the area being delimited, the more important the delimiting grids are in determining the precise spatial location of the population core.

There were noticeable differences in the spatially interpolated values derived from the full and subset datasets (Fig. 8). When considering cells interpolated as 0, there was a slight tendency for more cells to be interpolated as 0 when not using delimiting traps than when using them. However, the high R^2 value (0.96) suggested that there was general congruence between the two datasets. In contrast, as population thresholds increased, the estimated values of the slope decreased because fewer cells were interpolated at these population thresholds in the absence of delimiting traps. Moreover, R^2 values also decreased with increasing population thresholds (Fig. 8). The lack of delimiting traps had the greatest consequence to areas of higher moth abundance, and it was rare for cells to be interpolated at values ≥ 100 moths without the use of delimiting traps.

When considering the percent error in the spatial interpolation of population abundance, the error rate, when not using delimiting traps, was highest at the lower population thresholds (Fig. 9), mainly due to the larger volume of

interpolated cells at the lower population thresholds (Fig. 8). However, the error rate was still >1 % at population thresholds of 90 moths, and remained >0 % at threshold extending to 250 moths. Given that 2,190 delimiting grids were used in this analysis, an error rate as low as 1 % still represents ≈22 delimiting grids (or roughly 2 per year) where delimiting traps revealed considerably high population densities that would otherwise not have been detected. Because of the stochasticity associated with the year-to-year dynamics of an invading species and their eventual fate, including whether or not new colonies of *L. dispar* will successfully establish (Liebhold and Bascompte 2003; Whitmire and Tobin 2006), even a small error rate associated with the lack of delimiting traps could have important consequences in efforts to manage an invading species.
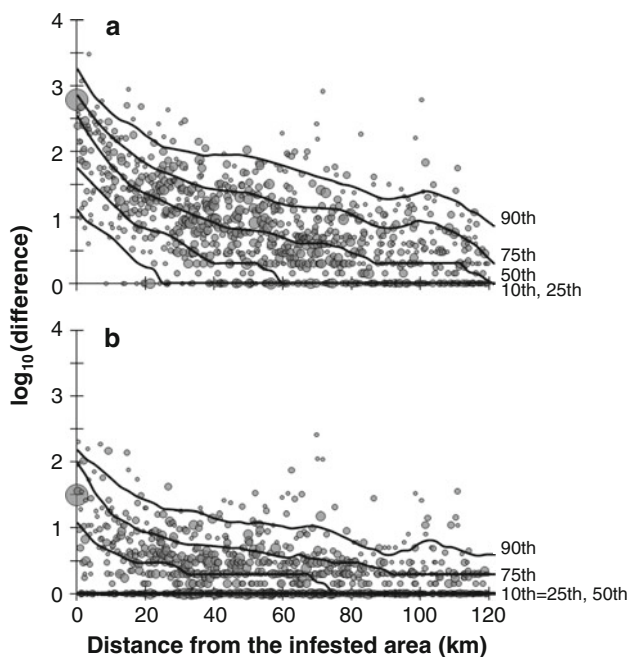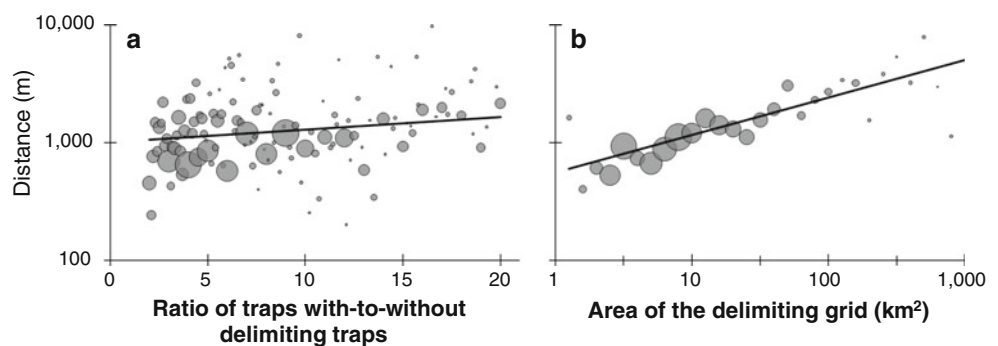

Fig. 6 Difference in the **a** total and **b** maximum moth catch based upon the distance from the infested area. *Lines* are the predicted conditional responses from quantile regression at the *percentiles* indicated. The *circle* sizes are proportional to the number of delimiting grids

The use of delimiting traps following the initial detection of an invading species can provide information crucial to effective management and ultimately be useful in attempts to prioritize treatment decisions (Tobin et al. 2004; Panetta and Lawes 2005; Suckling et al. 2005; Gust and Inglis 2006; Brockerhoff et al. 2010). Moreover, because some colonies could ultimately fail to establish after initial detection (Drake and Lodge 2006; Lockwood et al. 2007), delimiting traps could ascertain, with greater certainty, the lack of successful establishment, which would eliminate the need for unnecessary treatments. Because delimiting traps can also delineate the spatial extent of the population, the application of site-specific management tactics can be used. The more spatially precise allocation of population management efforts could increase the effectiveness of eradication programs, reduce treatment costs and minimize non-target effects. Whether the additional costs associated with delimitation surveys is offset by the benefits described above would likely vary among biological systems, which could vary with respect to sampling costs, sampling sensitivity and treatment costs. Knowledge of the spatial location and extent of the population core could facilitate the application of multiple tactics whose effectiveness can depend on the target population density (Blackwood et al. 2012; Suckling et al. 2012). For example, under the Slow-the-Spread program, some areas are managed using two tactics in the same year: (1) application of the biopesticide *Btk* against the larval stage at the high-density population core, and (2) application of synthetic pheromones to disrupt mating, which is less costly than *Btk* but not as effective against high-density populations.

In this study, we made use of extensive delimiting surveys that are operationally deployed to manage invading populations of *L. dispar*. Our examination of the effectiveness of delimiting traps through the quantification of the information lost in their absence and across a number of explanatory variables should be useful in future delimiting efforts against *L. dispar*. In parallel, the information presented in this paper could be useful as a general reference applied to other non-native invaders. Although life history strategies vary among invading species tremendously, the

Fig. 7 The distance from the population core when using or not using delimiting traps based upon the **a** trap ratio and **b** area of the delimiting grid. The *circle* sizes are proportional to the number of delimiting grids

Fig. 8 Scatterplot of the number of cells in each delimiting grid interpolated at various population thresholds when using delimiting traps and without using delimiting traps. The *dashed line* represents a 1:1 relationship, while the *solid line* represents the least squares regression fit. Note how the estimate of the slope and R^2 values decline with increasing population thresholds. The *circle* sizes are proportional to the number of delimiting grids
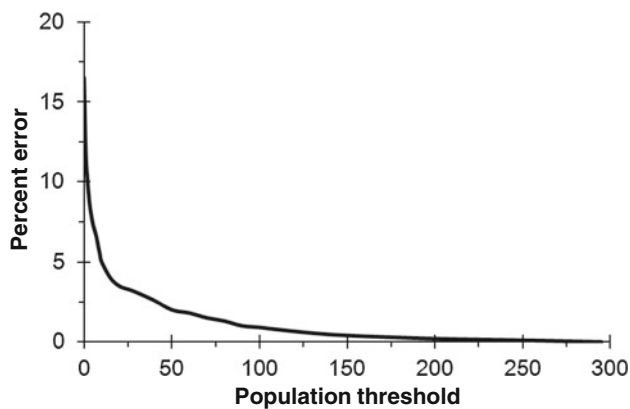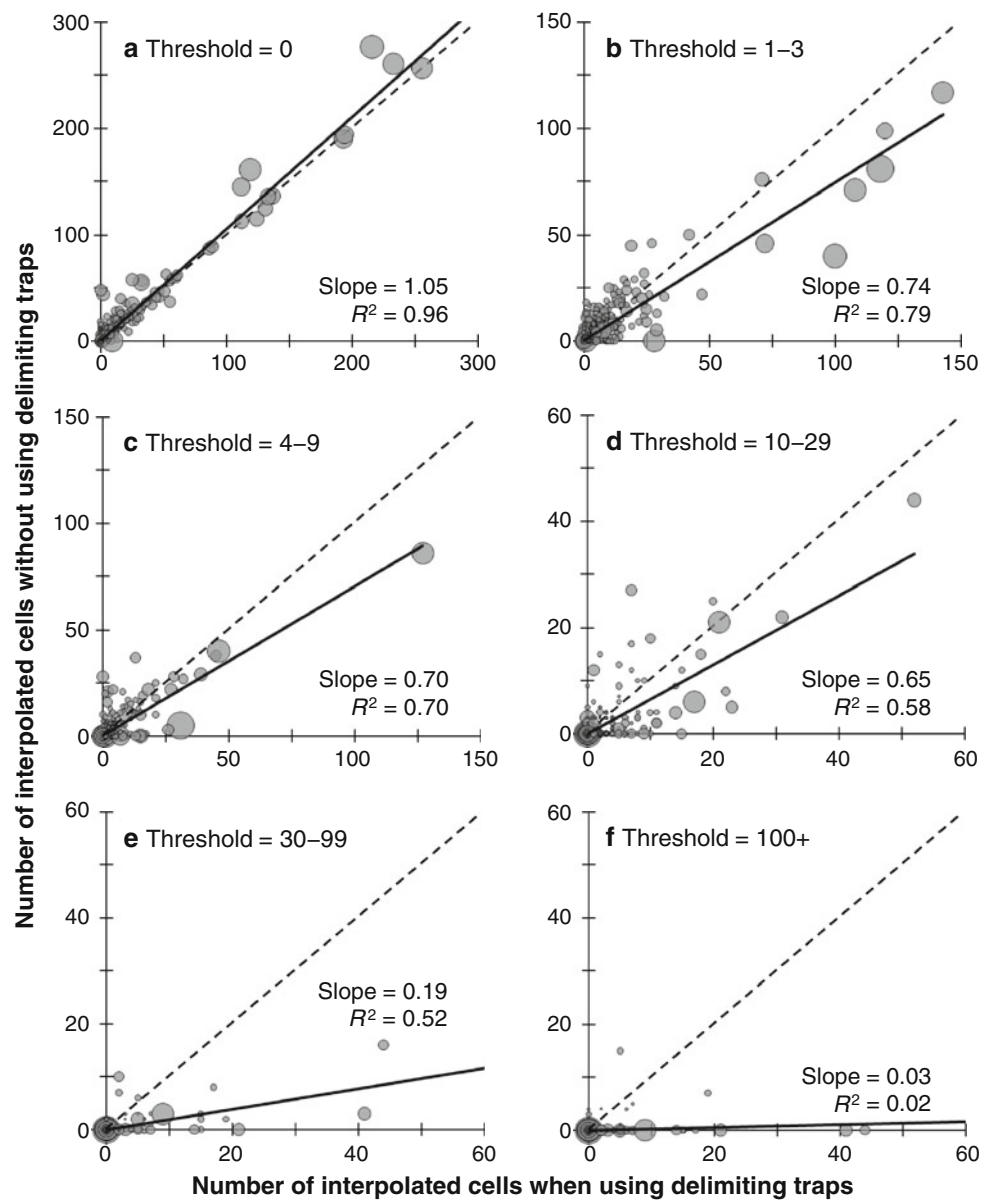

Fig. 9 Percent error associated with interpolating delimiting areas without the use of delimiting traps based upon the population density of delimiting area

stages of the biological invasion process are the same (Lockwood et al. 2007). Initial detection and subsequent delimitation surveys can be a particularly critical component in successful eradication programs (Myers et al. 2000; Rejmánek and Pitcairn 2002; Liebhold and Bascompte 2003; Panetta and Lawes 2005), as well as in barrier management programs aimed at long-term population suppression (Tobin and Blackburn 2007). An improved understanding of the underlying variables that influence the optimal use, interpretation, and efficacy of delimitation surveys could have broad applicability against a broad range of non-native invaders.

References

Aylor DE, Parlange J-Y, Granett J (1976) Turbulent dispersion of disparlure in the forest and male gypsy moth response. Environ Entomol 5:1026–1032

Blackwood JC, Berec L, Yamanaka T, Epanchin-Niell RS, Hastings A, Liebhold AM (2012) Bioeconomic synergy between tactics for insect eradication in the presence of Allee effects. Proc R Soc B 279:2807–2815

Bogich TL, Liebhold AM, Shea K (2008) To sample or eradicate? A cost minimization model for monitoring and managing an invasive species. J Appl Ecol 45:1134–1142

Brockerhoff EG, Bain J, Kimberley M, Knížek M (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Can J For Res 36:289–298

Brockerhoff EB, Liebhold AM, Richardson B, Suckling DM (2010) Eradication of invasive forest insects: concept, methods, costs and benefits. N Z J For 40(suppl.):S117–S135

Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. Front Ecol Environ 1:412–420

Contarini M, Onufrieva KS, Thorpe KW, Raffa KF, Tobin PC (2009) Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. Entomol Exp Appl 133:307–314

Deutsch CV, Journel AG (1992) GSLIB: geostatistical software library and user's guide. Oxford University Press, New York

Drake JA, Lodge DM (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. Biol Invasions 8:365–375

Elkinton JS, Cardé RT (1988) Effects of intertrap distance and wind direction on the interaction of gypsy moth (Lepidoptera: Lymantriidae) pheromone-baited traps. Environ Entomol 17:764–769

Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North America. Annu Rev Entomol 35:571–596

Elkinton JS, Schal C, Ono T, Cardé RT (1987) Pheromone puff trajectory and upwind flight of male gypsy moths in a forest. Physiol Entomol 12:399–406

El-Sayed AM (2012) The Pherobase: database of insect pheromones and semiochemicals http://www.pherobase.com

Epanchin-Niell RS, Haight RG, Berec L, Kean JM, Liebhold AM (2012) Optimal surveillance and eradication of invasive species in heterogeneous landscapes. Ecol Lett 15:803–812

Gormley AM, Forsyth DM, Griffioen P, Lindeman M, Ramsey DS, Scroggie MP, Woodford L (2011) Using presence–only and presence–absence data to estimate the current and potential distributions of established invasive species. J Appl Ecol 48:25–34

Guichard S, Kriticos DJ, Leriche A, Kean JM, Worner SP (2012) Individual-based modelling of moth dispersal to improve biosecurity incursion response. J Appl Ecol 49:287–296

Gust N, Inglis GJ (2006) Adaptive multi-scale sampling to determine an invasive crab's habitat usage and range in New Zealand. Biol Invasions 8:339–353

Holder P, George S, Disbury M, Singe M, Kean JM, McFadden A (2010) A biosecurity response to Aedes albopictus (Diptera: Culicidae) in Auckland, New Zealand. J Med Entomol 47:600–609

Holdich DM, Reynolds JD, Souty-Grosset C, Sibley PJ (2009) A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. Knowl Manag Aquat Ecosyst 394–395:1–46

Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J Appl Ecol 45:403–414

Isaaks EH, Srivastava RM (1989) An introduction to applied geostatistics. Oxford University Press, Oxford

Johnson DM, Liebhold AM, Tobin PC, Bjørnstad ON (2006) Allee effects and pulsed invasion of the gypsy moth. Nature 444:361–363

Kilroy C, Unwin M (2011) The arrival and spread of the bloom-forming, freshwater diatom, Didymosphenia geminata, in New Zealand. Aquat Invasions 6:249–262

Koenker R (2007) Quantile regression http://cran.r-project.org/doc/packages/quantreg.pdf

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326

Liebhold AM, Bascompte J (2003) The Allee effect, stochastic dynamics and the eradication of alien species. Ecol Lett 6:133–140

Liebhold AM, Tobin PC (2006) Growth of newly established alien populations: comparison of North American gypsy moth colonies with invasion theory. Popul Ecol 48:253–262

Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO (2012) Live plant imports: the major pathway for forest insect and pathogen invasions of the United States. Front Ecol Environ 10:135–143

Lockwood JL, Hoopes M, Marchetti M (2007) Invasion ecology. Blackwell, Malden

McCullough DG, Mercader RJ (2012) Evaluation of potential strategies to SLow Ash Mortality (SLAM) caused by emerald ash borer (Agrilus planipennis): SLAM in an urban forest. Int J Pest Manag 58:9–23

Mitchell ER (ed) (1981) Management of insect pests with semiochemicals. Plenum, New York

Morin RS, Liebhold AM, Luzader ER, Lister AJ, Gottschalk KW, Twardus DB (2005) Mapping host-species abundance of three major exotic forest pests. Research Paper NE-726, USDA Forest Service, Newtown Square, Pennsylvania

Myers JH, Simberloff DS, Kuris AM, Carey JR (2000) Eradication revisited: dealing with exotic species. Trends Ecol Evol 15:316–320

Panetta FD, Lawes R (2005) Evaluation of weed eradication programs: the delimitation of extent. Divers Distrib 11:435–442

R Development Core Team (2012) The R project for statistical computing http://www.r-project.org

Rabaglia RJ, Duerr D, Acciavatti R, Ragenovich I (2008) Early detection and rapid response for non-native bark and ambrosia beetles. United States Department of Agriculture, Forest Service, Forest Health Protection http://www.fs.fed.us/foresthealth/publications/EDRRProjectReport.pdf, p 12

Rejmánek M, Pitcairn MJ (2002) When is eradication of exotic pest plants a realistic goal? In: Veitch CR, Clout MN (eds) Turning the tide: the eradication of invasive species. IUCN, Gland, Switzerland, pp 94–98

Roberts EA, Ziegler AH (2007) Gypsy moth population monitoring and data collection. In: Tobin PC, Blackburn LM (eds) Slow the spread: a national program to manage the gypsy moth. USDA Forest Service General Technical Report NRS-6, Newtown Square, pp 33–46

Schwalbe CP (1981) The use of attractants in traps. In: Doane CC, McManus ML (eds) The gypsy moth: research toward integrated

pest management. Technical Bulletin 1584, United States Department of Agriculture, Washington, DC, pp 542–548

Sharov AA, Liebhold AM (1998) Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. Ecol Appl 8:1170–1179

Sharov AA, Roberts EA, Liebhold AM, Ravlin FW (1995) Gypsy moth (Lepidoptera: Lymantriidae) spread in the central Appalachians: three methods for species boundary estimation. Environ Entomol 24:1529–1538

Sharov AA, Liebhold AM, Roberts EA (1996) Spatial variation among counts of gypsy moths (Lepidoptera: Lymantriidae) in pheromone-baited traps at expanding population fronts. Environ Entomol 25:1312–1320

Sharov AA, Pijanowski BC, Liebhold AM, Gage SH (1999) What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility. Agric For Entomol 1:37–45

Suckling DM, Gibb AR, Dentener PR, Seldon DS, Clare GK, Jamieson L, Baird D, Kriticos D, El-Sayed AM (2005) *Uraba lugens* (Lepidoptera: Nolidae) in New Zealand: pheromone trapping for delimitation and phenology. J Econ Entomol 98:1187–1192

Suckling DM, Tobin PC, McCullough DG, Herms DA (2012) Combining tactics to exploit Allee effects for eradication of alien insect populations. J Econ Entomol 105:1–13

Tobin PC, Blackburn LM (2007) Slow the spread: a national program to manage the gypsy moth. USDA Forest Service General Technical Report NRS-6, Newtown Square, PA

Tobin PC, Blackburn LM (2008) Long-distance dispersal of the gypsy moth (Lepidoptera: Lymantriidae) facilitated its initial invasion of Wisconsin. Environ Entomol 37:87–93

Tobin PC, Sharov AA, Liebhold AM, Leonard DS, Roberts EA, Learn MR (2004) Management of the gypsy moth through a decision algorithm under the Slow-the-Spread project. Am Entomol 50:200–209

Tobin PC, Liebhold AM, Roberts EA (2007a) Comparison of methods for estimating the spread of a non-indigenous species. J Biogeogr 34:305–312

Tobin PC, Whitmire SL, Johnson DM, Bjørnstad ON, Liebhold AM (2007b) Invasion speed is affected by geographic variation in the strength of Allee effects. Ecol Lett 10:36–43

Tobin PC, Robinet C, Johnson DM, Whitmire SL, Bjørnstad ON, Liebhold AM (2009) The role of Allee effects in gypsy moth, *Lymantria dispar* (L.), invasions. Popul Ecol 51:373–384

Tobin PC, Bai BB, Eggen DA, Leonard DS (2012) The ecology, geopolitics, and economics of managing *Lymantria dispar* in the United States. Int J Pest Manag 53:195–210

Whitmire SL, Tobin PC (2006) Persistence of invading gypsy moth populations in the United States. Oecologia 147:230–237

Work TT, McCullough DG, Cavey JF, Komsa R (2005) Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol Invasions 7:323–332