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Estimating Spread Rates of Non-native Species: The Gypsy Moth as a Case Study

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Abstract

Estimating rates of spread and generating projections of future range expansion for invasive alien species is a key process in the development of management guidelines and policy. Critical needs to estimate spread rates include the availability of surveys to characterize the spatial distribution of an invading species and the application of analytical methods to interpret survey data. In this chapter, we demonstrate the use of three methods, (i) square-root area regression, (ii) distance regression and (iii) boundary displacement, to estimate the rate of spread in the gypsy moth, *Lymantria dispar*, in the USA. The gypsy moth is a non-native species currently invading North America. An extensive amount of spatial and temporal distributional data exists for this invader. Consequently, it provides an ideal case study to demonstrate the use of methods to estimate spread rates. We rely on two sources of data: (i) polygonal data obtained from county quarantine records describing the geographical extent of gypsy moth establishment; and (ii) point data consisting of counts of male gypsy moths captured in pheromone-baited traps used to detect and monitor newly established gypsy moth populations. Both

data sources were compiled during the gypsy moth's invasion of the Lower Peninsula of Michigan, USA. We show that even with spatially crude county records of infestation, spread rates can still be estimated using relatively simple mathematical approaches. We also demonstrate how the boundary displacement method can be used to characterize the spatial and temporal dynamics of spread.

The Importance of Spread Rates and Patterns

Spread of a non-native species is the process by which an organism expands its range from geographical areas it currently occupies into ones it does not. The rate of spread is most often expressed as the rate of change in the distributional range per unit of time, and can vary considerably among species (Elton, 1958; Shigesada and Kawasaki, 1997; Liebhold and Tobin, 2008) and across spatial and temporal scales within a species (Tobin *et al.*, 2007c). In nearly all biological invasions, spread results from the coupling of local dispersal with population growth (Fisher, 1937; Skellam, 1951). However, in most cases, the spread of an invading alien species includes long-distance 'jumps' in

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which new colonies arise far from the established range. The combined process of short- and long-range dispersal is referred to as stratified dispersal (Shigesada *et al.*, 1995). Under stratified dispersal, colonies that successfully establish ahead of the expanding range can grow and eventually coalesce with the established area, greatly increasing the rate of spread over what would be expected in the absence of long-distance jumps (Hengeveld, 1989; Shigesada and Kawasaki, 1997). The ramifications of stratified dispersal have been documented for several non-native species, including the Africanized honeybee (*Apis mellifera scutellata*; Winston, 1992), Argentine ant (*Linepithema humile*; Suarez *et al.*, 2001), emerald ash borer (*Agrilus planipennis*; Muirhead *et al.*, 2006), horse-chestnut leaf miner (*Cameraria ohridella*; Gilbert *et al.*, 2004) and the gypsy moth (*Lymantria dispar*; Liebhold *et al.*, 1992).

Several methods exist to estimate the rate of spread of an invading species (Andow *et al.*, 1990; Sharov *et al.*, 1997; Tobin *et al.*, 2007b; Gilbert and Liebhold, 2010) and the ability to estimate spread rates can be a crucial step in the development of pest risk maps and management strategies. For example, before an invader spreads into a new area, several information needs must be addressed. These include determining susceptible habitats that are most vulnerable to invasion, estimating the time before a new invader spreads to these susceptible areas and predicting the eventual economic and ecological impacts. Spread rate estimates can be used to project future range boundaries and, in some cases, allow management tactics to mitigate expected impacts prior to arrival (Waring and O'Hara, 2005). Thus, it is not surprising that much past work has focused on estimating rates of spread of invading species, including very early studies that were published before the widespread recognition of the importance of biological invasions (Cooke, 1928; Elton, 1958). In this chapter, we describe three analytical methods that can be used to estimate the rate of spread of invading species using data on the spread of the gypsy moth.

Context for a Case Study: Gypsy Moth

One of the more widely studied and documented biological invasions is that of the gypsy moth in the USA. Despite the fact that many non-native pest species are currently invading the USA (Pimentel *et al.*, 2000; Aukema *et al.*, 2010), the gypsy moth is somewhat unique among invaders in that we know when it was introduced (1869), approximately from where it originated (France or Germany), where it was introduced (27 Myrtle Street, Medford, Massachusetts, USA) and by whom (Etienne Léopold Trouvelot; Riley and Vasey, 1870; Forbush and Fernald, 1896; Liebhold *et al.*, 1989). The gypsy moth is univoltine and its larvae are polyphagous folivores that can feed on over 300 host plants including the preferred genera of *Betula* (birch), *Crataegus* (hawthorn), *Larix* (larch), *Populus* (aspen), *Quercus* (oak), *Salix* (willow) and *Tilia* (basswood) (Elkinton and Liebhold, 1990; Liebhold *et al.*, 1995).

Larvae hatch from overwintering egg masses in spring and undergo five (male) or six (female) instars over approximately 8 weeks. The pupal period is approximately 2 weeks, followed by adult emergence. Females of the European strain, which is the strain established in North America, are not capable of sustained flight (Keena *et al.*, 2008). Males locate calling females through a sex pheromone and mate; females oviposit a single egg mass containing 250–500 eggs. Although gypsy moth populations are innocuous and barely noticed in most years, populations can periodically erupt in spatially widespread outbreaks that occur over 2–3 years (Haynes *et al.*, 2009). Ramifications of gypsy moth outbreaks include host tree mortality, loss of ecosystem services, detrimental effects to native species and public nuisance (Gansner and Herrick, 1984; Leuschner *et al.*, 1996; Redman and Scriber, 2000). Since 1924, over 360,000 km² of forests in the USA have been defoliated by the gypsy moth (USDA Forest Service, 2013).

Since its introduction in 1869 in Medford, Massachusetts, the gypsy moth

has slowly expanded its range in North America such that it now occupies a range from Nova Scotia to Wisconsin, and Ontario to Virginia (Tobin *et al.*, 2007b). Spread can be facilitated by larval ballooning and adult male flight, both of which are considered to occur over short distances (Mason and McManus, 1981; Elkinton and Liebhold, 1990). Longer-distance dispersal is believed to occur primarily through the anthropogenic movement of life stages (Lippitt *et al.*, 2008; Hajek and Tobin, 2009; Bigsby *et al.*, 2011). Despite the fact the gypsy moth has been established in North America for over 140 years and currently occupies >900,000 km², almost three-quarters of forested areas considered to be susceptible to gypsy moth outbreaks remain uninfested (Morin *et al.*, 2005). Thus, efforts to estimate the rate of gypsy moth spread remain of critical importance. Moreover, this species provides an ideal example for demonstrating methods of estimating invasion spread due to the extensive amount of spatial and temporal data collected on it. In this chapter, we estimate gypsy moth spread using both point data and polygonal data.

Resources to Estimate Spread Rates

There are two broad data types that can be used to estimate the rate of spread in an invading species: (i) point data; and (ii) polygonal data. Point data can include the number of individuals collected from sampling devices, such as traps baited with semiochemical attractants and placed at a specific point in space. Point data can also include a record of the observed presence of the species. In addition to such records historically collected by regulatory officials or the scientific community, citizen scientists have contributed, more recently, to observation records (Ingwell and Preisser, 2011). In fact, in New Zealand, approximately half of new plant pest detections are first reported by the general public (Froud *et al.*, 2008). It is also believed that every known Asian longhorned beetle (*Anoplophora glabripennis*) infestation in the USA was first discovered by a citizen. In some cases, the

species need not be observed directly but rather its presence implied by a specific indication of damage. For example, in the case of wood and subcortical phloem feeders, the architecture of larval tunnelling and associated symbionts are often species-specific (Paine *et al.*, 1997), which can reveal the presence of a specific invasive alien pest even if the pest is absent; in some cases, feeding injury can reveal when the invasive alien species was first present when analysed through dendroecological techniques (Siegert *et al.*, 2010).

In contrast to point data where a species is considered to be present at a specific point in space, polygonal data encompass an area considered to be infested by a non-native species. Among the more common examples of polygonal data are those that are defined by geopolitical boundaries, such as county, state or territory boundaries. In many countries, species that are regulated under domestic quarantines have their range boundaries defined by polygonal data. In most cases, point data are essentially used in the construction of polygonal data with the assumption that a species detected through, for example, a trapping device at a specific point in space is, in actuality, distributed over a larger area. Geopolitical boundaries are often used to define this larger area because they facilitate regulatory responses, such as the restriction of potentially infested material from being transported from an infested county or state without proper phytosanitary measures.

Many data resources and repositories exist that contain point and polygonal data on the presence of a non-native species. Many governments maintain quarantines against established non-native species to limit their movement to uninfested areas and publish these records in government documents. In the USA, for example, quarantine regulations are codified by the USA Code of Federal Regulations, Title 7, Chapter III, Part 301, which is divided into subparts by species, and includes non-native insects, plants, nematodes and pathogens (Table 9.1). Within each subpart is a section on 'generally infested areas' that lists states (in whole), or specific counties or townships,

Table 9.1. Non-native species in the USA currently included in subparts of the USA Code of Federal Regulations, Title 7, Chapter III, Part 301.

Name	Species	Subpart
Fruit flies	Several	301.32
Black stem rust	<i>Puccinia graminis</i>	301.38
Gypsy moth	<i>Lymantria dispar</i>	301.45
Japanese beetle	<i>Popillia japonica</i>	301.48
Pine shoot beetle	<i>Tomicus piniperda</i>	301.50
Asian longhorned beetle	<i>Anoplophora glabripennis</i>	301.51
Pink bollworm	<i>Pectinophora gossypiella</i>	301.52
Emerald ash borer	<i>Agrilus planipennis</i>	301.53
South America cactus moth	<i>Cactoblastis cactorum</i>	301.55
Plum pox	<i>Potyvirus</i> spp.	301.71
Citrus canker	<i>Xanthomonas axonopodis</i> pv. <i>citri</i>	301.75
Asian citrus psyllid	<i>Diaphorina citri</i>	301.76
Witchweed	<i>Striga</i> spp.	301.80
Imported fire ant	<i>Solenopsis invicta</i> and <i>Solenopsis richteri</i>	301.81
Golden nematode	<i>Globodera rostochiensis</i>	301.85
Pale cyst nematode	<i>Globodera pallida</i>	301.86
Sugarcane diseases	<i>Xanthomonas albilineans</i>	301.87
Karnal bunt	<i>Tilletia indica</i>	301.89
European larch canker	<i>Lachnellula willkommii</i>	301.91
Sudden oak death	<i>Phytophthora ramorum</i>	301.92

that are considered infested at the time of publication. By going through the various years in which USA Code of Federal Regulations has been published, beginning with its first publication in 1938, it is possible to generate a space–time series of the presence of a regulated non-native species (Fig. 9.1).

When using either point or polygonal data to estimate spread rates, the minimum required details are the spatial and temporal distribution of the data. In many cases, point or polygonal data are considered binary (i.e. presence only), but in some cases, estimates of density are available; regardless, binary and continuous measurements of the non-native species can be used to estimate rates of spread. Based upon where and when a species is detected, or when an area is considered to be infested, there are a number of quantitative methods available. Given these time–space data, all of the estimation methods can be accomplished through statistical packages such as SAS (SAS Institute, Inc., 1999) or R (R Core Team, 2013), and some methods can be accomplished using more basic software packages such as Microsoft® Excel.

In this chapter, we use both polygonal and point gypsy moth data collected from the Lower Peninsula of Michigan to demonstrate three methods in estimating spread rates. This region provides an ideal case study of gypsy moth spread for several reasons. First, the introduction of gypsy moth life stages in Michigan was spatially disjunct from the established area at the time. Although Michigan has a long history of management efforts against the gypsy moth (Hanna, 1982; Dreistadt, 1983), the first counties were declared to be infested and included in the USA Code of Federal Regulations in 1981; at this time, the closest infested areas were in western New York and Pennsylvania. Thus, the invasion dynamics of the gypsy moth in Michigan would be comparable to those expected in a new invasion. From 1981 to 1994, counties from the Lower Peninsula of Michigan were added to the regulated area, which allows for the construction of a time series based upon these polygonal data (Fig. 9.2a). Second, when Michigan initially became infested, standardized pheromone-baited traps, which are sensitive monitoring tools that are effective even at low population densities

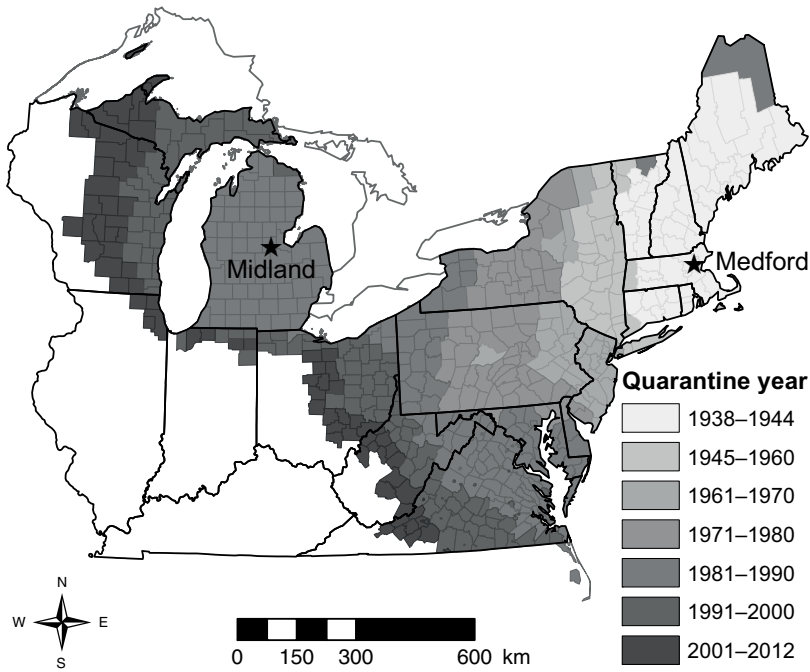


Fig. 9.1. Distribution of the gypsy moth in the USA, 1938–2012, based upon county quarantine records. Medford, Massachusetts and Midland, Michigan represent the initial and a subsequent site of introduction, respectively.

(Mastro *et al.*, 1977; Elkinton and Childs, 1983; Thorpe *et al.*, 1993), were available and allowed for the collection of point data (Tobin *et al.*, 2012). From 1985 to 1996, the entire Lower Peninsula of Michigan was trapped each year, with traps set ~5 km apart (Fig. 9.2b; Gage *et al.*, 1990; Yang *et al.*, 1998). Last, the initial infestation was considered to be in Midland County, Michigan, which is centrally located in the Lower Peninsula of Michigan. Thus, the gypsy moth had the opportunity to spread radially from this centralized point.

Data Analysis

There are three analytical methods that can be used with both point and polygonal data to estimate spread rates: (i) square-root area regression; (ii) distance regression; and (iii) boundary displacement.

Square-root area regression

This method is based on the analysis of distance-to-time and uses successive measurements of the invaded area. For each year, the square root of the total infested area is considered according to:

$$\sqrt{\frac{\text{total infested area}}{\pi}} \tag{9.1}$$

The values for each year are then regressed as a function of time to estimate the radial rate of spread, which is ascertained by the estimate of the regression slope (Shigesada and Kawasaki, 1997; Gilbert and Liebhold, 2010).

When applying the square-root area regression method to polygonal data from Michigan (Fig. 9.3a; see colour plate section), 1981 is considered as year 1 at which time six counties, encompassing an area of

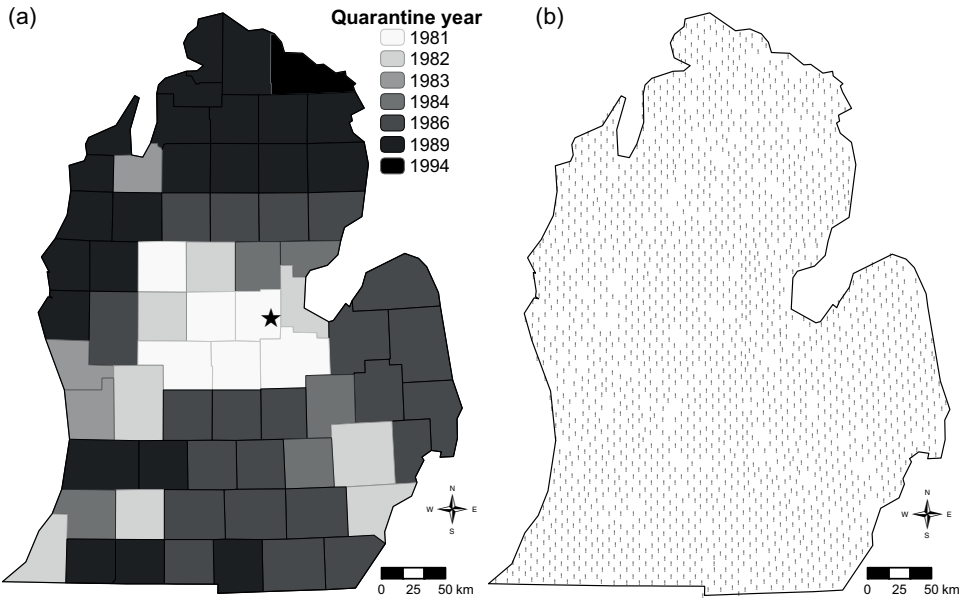


Fig. 9.2. (a) Distribution of the gypsy moth in the Lower Peninsula of Michigan, USA, based upon county quarantine records, 1981–1994; the star indicates Midland, Michigan, which is considered to be the site of the initial introduction into Michigan. (b) Spatial representation of the trapping grid used to record gypsy moth densities, 1985–1996.

9786 km², were regarded as infested with the gypsy moth. In 1982, eight additional counties were added to the infested area for a cumulative total infested area of 23,226 km². The last county was considered to be infested in 1994, bringing the total infested area to 106,887 km². However, by 1989, the infested area was 105,151 km² and no additional counties were added to the quarantine until 1994. Thus, when restricting the regression analysis from the initial year of introduction (1981) to the year at which the entire Lower Peninsula was nearly completely infested (1989), the annual rate of spread (as ascertained from the slope estimate) is 17.1 km/year (Fig. 9.4a). The standard error associated with the slope estimate from the linear regression provides an estimate of the variability associated with the spread rate, which in this case is 1.9.

The square-root area regression method can also be applied to the point trapping data from Michigan (Fig. 9.3b; see colour

plate section). In this case, population thresholds can also be considered because trapping data provide a continuous measurement of density, as opposed to the presence/absence data that are generally available from polygonal data. We considered three population thresholds in this analysis: (i) an estimate of the area over which trapping records indicate gypsy moth presence (i.e. threshold = 1 moth); (ii) an estimate of the area where at least ten male moths are trapped; and (iii) an estimate of the area where at least 100 male moths are trapped. We chose these population thresholds arbitrarily to demonstrate the method. To estimate the area where populations exceeded these thresholds, we spatially interpolated the raw trapping data (latitude, longitude and male moths trapped at each trapping location) for each year to generate a continuous surface over a network of 1 km × 1 km cells using median indicator kriging (Isaaks and Srivastava, 1989; Deutsch and Journel, 1992). As with

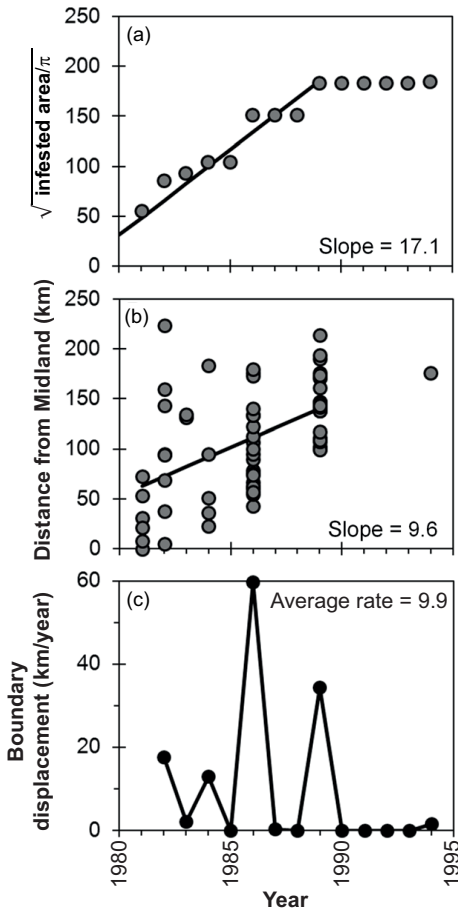


Fig. 9.4. Use of polygonal data to estimate gypsy moth rate of spread in the Lower Peninsula of Michigan using (a) the square-root area method; (b) the distance regression method; and (c) the boundary displacement method. Each circle in (a) represents the square root of the infested area for each year, while each circle in (b) represents the distance between each infested county (by year of infestation) and Midland, Michigan. The slope estimate from least-squares regression provides an estimate of the annual spread rate. The year-to-year boundary displacements in (c) can be averaged to estimate an annual rate of spread.

polygonal data, we then estimated the square root of each population threshold’s area $\div \pi$ for each year (Eqn 9.1) and next regressed this against the year. In this case, we also estimated an annual rate of spread for each population threshold based upon

the respective slope estimates for each population threshold (Fig. 9.5a). When applied to point data, and again restricting the regression analysis to 1981–1989 (i.e. estimates during the invasion of Michigan), this method estimates spread rates (\pm SE) of 13.5 (2.3), 21.2 (1.2) and 23.8 (2.2) km/year for the 1-, 10- and 100-moth thresholds, respectively. It is also possible to estimate a composite rate of spread by averaging over the estimates from all population thresholds, which yields a spread rate estimate (\pm SE) of 19.5 (3.1) km/year.

Distance regression

This method is based on regressing the distance of an infested location, either from polygonal or point data, from a reference point on the year it first became infested (Liebhold *et al.*, 1992; Tobin *et al.*, 2007b; Gilbert and Liebhold, 2010). The reference point can be an arbitrary location, but ideally it should reflect the initial site of introduction or simply the location at which a species was first detected. For the Michigan data, we used the city of Midland, the county seat of Midland County, as a proxy for the initial gypsy moth infestation in Michigan. Using the polygonal data, we first estimated the minimum distance between each infested county and Midland (Fig. 9.3c; see colour plate section). The distance for each county was then regressed on the year it was first infested, and the estimate of the slope of the regression line provided the estimated radial rate (\pm SE) of spread, which is 9.6 (2.0) km/year (Fig. 9.4b).

When applying the distance regression method to the point trapping data, we again used multiple population thresholds, such as the 1-, 10- and 100-moth thresholds, for each of the years in which trapping data exist (1985–1996). In this case, the distance between Midland, Michigan, and each trapping location that captured at least one, ten and 100 male moths is estimated (Fig. 9.3d; see colour plate section) and then regressed for each year. This method, when applied to point data, estimates spread rates (\pm SE) of 15.7 (0.3), 19.3 (0.5) and

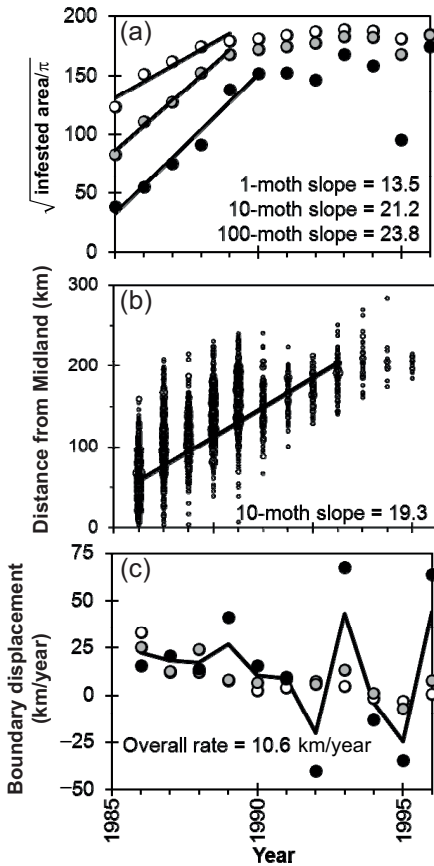


Fig. 9.5. Use of point data to estimate gypsy moth rate of spread in the Lower Peninsula of Michigan using (a) the square-root area method; (b) the distance regression method; and (c) the boundary displacement method. In (a), least-squares regression is fit against the linear portion of the relationship between the infested area and time when the infested area is based upon the 1-moth (open circles), 10-moth (grey circles) and 100-moth (solid circles) population thresholds. In (b), least-squares regression is fit against the linear portion of the relationship between the distance of the trap and Midland for each year when using the 10-moth threshold as an example; circles represent the distance between each trapping record by year and Midland, Michigan, and are proportional in size to the number of records. In (c), the year-to-year displacement for the 1-moth (open circles), 10-moth (grey circles) and 100-moth (solid circles) population thresholds is plotted over time. The solid line represents an average of the displacement across all three population thresholds at each year, which can be averaged across years and population threshold to estimate an overall average spread rate.

22.8 (0.6) km/year for the 1-, 10-, 100-moth thresholds, respectively, with an overall average (\pm SE), across the estimates from all three population thresholds, of 19.3 (2.0) km/year (Fig. 9.5b).

Boundary displacement

This method considers the displacement distances between pairs of consecutive invasion boundaries to estimate rates of spread. Typically, displacement is measured along axes radiating from a reference point, which could be the origin of the invasion or a point that falls along a line that is perpendicular to the main invasion front (Sharov *et al.*, 1995; Tobin *et al.*, 2007b; Gilbert and Liebhold, 2010). The first step in this method is to delimit spatially invasion boundaries. One simple approach for constructing boundaries is to use one of a variety of software packages to generate contour lines. Contour lines can be constructed for each year of data, from which the year-to-year displacements in the spatial location of contour lines can be quantified and used as an estimate of spread.

In this chapter, we used several steps to estimate spread from boundary displacements. First, we used indicator kriging to generate a spatially continuous surface using both polygonal and point data (Isaaks and Srivastava, 1989; Deutsch and Journel, 1992). When using polygonal data from Michigan, we overlaid a grid consisting of a network of 2 km \times 2 km cells across the state. For each year of polygonal data, we scored each cell by using the centre point of the cell as its spatial coordinates, as 1 or 0, where the former designation indicates that the centre of the cell was in an infested county while the latter indicates an absence of infestation. This resulted in a time series of spatially referenced binary point data based upon the polygonal data. We then used indicator kriging to generate a continuous surface from the spatially referenced binary point data (Fig. 9.3e; see colour plate section).

When using point data, we likewise used kriging (Isaaks and Srivastava, 1989; Deutsch and Journel, 1992) to interpolate a

spatially continuous surface for each year of trapping data (Fig. 9.3f; see colour plate section). Because point trapping data are a continuous measurement of density, it is also possible, as we have done in the previous methods using point data, to estimate a boundary that reflects the 1-, 10- and 100-moth threshold. Thus, for example, the 10-moth threshold boundary would delineate an area in which traps recorded ≥ 10 moths within the boundary and < 10 moths outside the boundary, much like a presence boundary delineates an area in which a species is present or absent.

We then applied an optimization approach to delimit the location of boundaries from the spatially interpolated surfaces generated from each data source (Sharov *et al.*, 1995). Population boundaries derived from spatially interpolated maps are often irregular, with 'islands', 'lakes' and 'folds' common within and outside the invading species' established area. Because irregular boundaries can be difficult to analyse, we used this optimization approach to construct boundaries that are more regular (Sharov *et al.*, 1995). This method connects populations of similar densities, such as presence or absence, to minimize the inclusion of populations within a boundary that do not satisfy a specific density, while also minimizing the exclusion of populations within a boundary that do.

The final step is to estimate the displacement of boundaries from year to year. To accomplish this step, we measured the distance from a fixed focal point in space to boundaries in consecutive years; in this case, we used transects radiating from the

focal point at 0.5° intervals. The year-to-year displacement (i.e. from 1981 to 1982) at each transect can then be measured and averaged to obtain a spread rate for each pair of successive years, which then in turn can be averaged to estimate an overall annual rate of spread across all years. When we used polygonal data from Michigan, annual rates of spread ranged from 0 to 59.7 km/year, while the overall average (\pm SE) rate of spread (1981–1994) was 9.9 (5.0) km/year (Fig. 9.4c; Table 9.2). When we used point data, estimates of the annual spread rates ranged from -3.1 to 33.2, -7.0 to 25.2 and -40.0 to 67.7 km/year for the 1-, 10- and 100-moth thresholds, respectively, while the overall (1985–1996) average rate of spread (\pm SE) was 10.6 (3.7) km/year (Fig. 9.5c; Table 9.2).

Discussion

A comparison of the spread rate estimates for all three methods and when using both polygonal and point data is presented in Table 9.2. All three methods provide similar estimates of spread when using polygonal data, which is not surprising given both the coarse nature of polygonal boundaries and the fact that a decision to regard a county as infested is generally never retracted. Point data, in contrast, generally provide greater spatial resolution in the determination of species presence. Moreover, point data can often consist of trapping devices from which a continuous estimate of abundance can be obtained as opposed to merely presence or absence.

Table 9.2. Estimates of gypsy moth spread from three analytical methods when based upon polygonal and point data.

Data source	Moth threshold	Spread rate estimate (\pm SE), km/year		
		Square-root area regression	Distance regression	Boundary displacement
Polygonal data	NA	17.1 (1.9)	9.6 (2.0)	9.9 (5.0)
Point data	1	13.5 (2.3)	15.7 (0.3)	7.3 (3.0)
	10	21.2 (1.2)	19.3 (0.5)	9.7 (2.8)
	100	23.8 (2.2)	22.8 (0.6)	14.7 (10.5)
	Overall	19.5 (3.1)	19.3 (2.0)	10.6 (3.7)

NA, not applicable.

The use of population thresholds (Fig. 9.5) based upon continuous measurements of abundance can also provide an estimate of spread rates for different population levels, such as in comparisons between the spread rate of initial populations (i.e. the 1-moth threshold) and high-density populations (i.e. the 100-moth threshold). This can be especially critical in management efforts because lower-density populations tend to be more amenable to control tactics than the higher-density populations at which the ecological and economic impacts are also the greatest. Spread rate estimates obtained from different population thresholds could also reflect the roles that other forces, such as stochasticity, abiotic factors and biotic factors, play in the biological invasion process (Hufbauer *et al.*, 2013; Miller and Inouye, 2013; Potapov and Rajakaruna, 2013). For example, low-density populations can be particularly prone to extinction after which reinvasion could occur and be successful; Sharov *et al.* (1997) revealed high variability in gypsy moth spread when measured by thresholds <10 moths, while intermediate population densities, as measured by the 10- and 30-moth thresholds, tended to be the most stable in space and time. Very-high-density populations can be affected by outbreak dynamics; in the gypsy moth system, outbreaks can be cyclical, and synchronously erupt and collapse across a large landscape due to biotic interactions (Elkinton *et al.*, 1996; Bjørnstad *et al.*, 2010).

Depending on the data source and method used to estimate spread, there can be considerable differences in spread rate estimates (Table 9.2). Also, the estimation of spread rates of many species can be constrained by the lack of adequate survey data. Point data typically tend to be more robust than polygonal data because they are usually replicated at smaller spatial scales and can be used to estimate pest abundance at a specific point as opposed to simple presence or absence of a pest within a political boundary. However, point data are also greatly influenced by the sensitivity of the method used for making measurements.

Semiochemical-based traps that contain species-specific attractants (e.g. sex or aggregation pheromones) often provide a highly sensitive means to detect a species (Elkinton and Cardé, 1981; Suckling and Karg, 2000). However, for many invasive alien species, especially for those that are not economically important in their native range, research on pheromone identification has been insufficient and so sensitive monitoring tools may not be immediately available. For other species, attractants may be difficult to identify or produce synthetically for use in survey programmes (Crook *et al.*, 2008). Moreover, some species, such as the emerald ash borer (*A. planipennis*), may lack chemically mediated attraction behaviours that can be exploited with trapping systems to detect newly established, low-density populations (Crook and Mastro, 2010). In such cases, point data from poor trapping systems could, in fact, be misleading and provide either an underestimate of population density or the time of initial establishment. Thus, the mere availability of point data may not necessarily equate to a more accurate estimate of spread even when polygonal data are measured over a non-biological scale, such as a county or state boundary.

Regardless of the type of survey data available to estimate spread, 'true' rates of spread can still be challenging to ascertain (Gilbert and Liebhold, 2010). Part of this is due to stochastic processes that can affect spread, including the role of anthropogenic, atmospheric and hydrological transport mechanisms that facilitate long-distance dispersal (Venette and Ragsdale, 2004; Davidson *et al.*, 2005; Tobin and Blackburn, 2008; Bigsby *et al.*, 2011). The spread of invading organisms can also be affected by biological constraints, such as Allee effects, or positive-density dependence (Andow *et al.*, 1990; Lewis and Kareiva, 1993; Taylor *et al.*, 2004; Tobin *et al.*, 2007c). Gilbert and Liebhold (2010) generated synthetic data from simulations based upon a reaction-diffusion model with a known rate of spread and compared different methods for quantifying spread. They found that the

distance regression method provided the most reliable estimate of spread, particularly when sample size was limited (Gilbert and Liebhold, 2010). In cases where the invaded area is irregularly constrained, such as by lakes or other geographic barriers, previous work has shown that the square-root area regression method provided biased estimates of radial spread rates and thus would be an undesirable approach under such conditions (Shigesada and Kawasaki, 1997; Gilbert and Liebhold, 2010). As noted above and previously (Gilbert and Liebhold, 2010), an advantage of the boundary displacement method is that it can characterize temporal and spatial variation in spread rates.

We demonstrated three principal methods that are used for quantifying spread rates; however, there are additional methods that could be used to quantify invasion speed. For example, one additional method that has been used to estimate spread rates is the use of the 'Wombling' approach, which is a statistical technique for estimating vector gradients from spatially referenced data (Womble, 1951). This method can be used to estimate local rates of change from a map surface, such as the waiting time associated with the time of first establishment for an invading species. Consequently, these localized slope estimates provide a measure of local spread rate, and can be furthermore used to characterize the spatial and temporal variation in the rate of invasion spread (Fortin *et al.*, 2005; Fitzpatrick *et al.*, 2010). Regardless of the challenges associated with estimating rates of spread, and the limitations associated with various methods, even coarse estimates of spread can still provide guidance to managers, such as in efforts aimed at managing spread (Taylor and Hastings, 2004; Tobin *et al.*, 2007a; McCullough and Mercader, 2012). Estimates of spread can also be useful in identifying and quantifying the role of long-distance dispersal on the overall spread of invaders (Liebhold *et al.*, 1992), thereby providing a basis to formulate management guidelines (Sharov and Liebhold, 1998).

References

- Andow, D.A., Kareiva, P.M., Levin, S.A. and Okubo, A. (1990) Spread of invading organisms. *Landscape Ecology* 4, 177–188.
- Aukema, J.E., McCullough, D.G., Von Holle, B., Liebhold, A.M., Britton, K. and Frankel, S.J. (2010) Historical accumulation of nonindigenous forest pests in the continental US. *Bioscience* 60, 886–897.
- Bigsby, K.M., Tobin, P.C. and Sills, E.O. (2011) Anthropogenic drivers of gypsy moth spread. *Biological Invasions* 13, 2077–2090.
- Bjørnstad, O.N., Robinet, C. and Liebhold, A.M. (2010) Geographic variation in North American gypsy moth cycles: subharmonics, generalist predators, and spatial coupling. *Ecology* 91, 106–118.
- Cooke, M.T. (1928) *The Spread of the European Starling in North America (to 1928)*. Circular No. 40. US Department of Agriculture, Washington, DC.
- Crook, D.J. and Mastro, V.C. (2010) Chemical ecology of the emerald ash borer, *Agrilus planipennis*. *Journal of Chemical Ecology* 36, 101–112.
- Crook, D.J., Khimian, A., Francese, J.A., Fraser, I., Poland, T.M., Sawyer, A.J. and Mastro, V.C. (2008) Development of a host-based semiochemical lure for trapping emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae). *Environmental Entomology* 37, 356–365.
- Davidson, J., Wickland, A.C., Patterson, H.A., Falk, K.R. and Rizzo, D.M. (2005) Transmission of *Phytophthora ramorum* in mixed-evergreen forest in California. *Phytopathology* 95, 587–596.
- Deutsch, C.V. and Journel, A.G. (1992) *GSLIB: Geostatistical Software Library and User's Guide*. Oxford University Press, New York.
- Dreistadt, S.H. (1983) An assessment of gypsy moth eradication attempts in Michigan (Lepidoptera: Lymantriidae). *The Great Lakes Entomologist* 16, 143–148.
- Elkinton, J.S. and Cardé, R.T. (1981) The use of pheromone traps to monitor the distribution and population trends of the gypsy moth. In: Mitchell, E.R. (ed.) *Management of Insect Pests with Semiochemicals*. Plenum, New York, pp. 41–55.
- Elkinton, J.S. and Childs, R.D. (1983) Efficiency of two gypsy moth (Lepidoptera: Lymantriidae) pheromone-baited traps. *Environmental Entomology* 12, 1519–1525.
- Elkinton, J.S. and Liebhold, A.M. (1990) Population dynamics of gypsy moth in North America. *Annual Review of Entomology* 35, 571–596.

- Elkinton, J.S., Healy, W.M., Buonaccorsi, J.P., Boettner, G.H., Hazzard, A.M., Smith, H.R. and Liebhold, A.M. (1996) Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77, 2332–2342.
- Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen and Co., London.
- Fisher, R.A. (1937) The wave of advance of advantageous genes. *Annals of Eugenics* 7, 355–369.
- Fitzpatrick, M.C., Preisser, E.L., Porter, A., Elkinton, J., Waller, L.A., Carlin, B.P. and Ellison, A.M. (2010) Ecological boundary detection using Bayesian areal wombling. *Ecology* 91, 3448–3455.
- Forbush, E.H. and Fernald, C.H. (1896) *The Gypsy Moth*. Wright and Potter, Boston, Massachusetts.
- Fortin, M.-J., Keitt, T.H., Maurer, B.A., Taper, M.L., Kaufman, D.M. and Blackburn, T.M. (2005) Species' geographic ranges and distributional limits: pattern analysis and statistical issues. *Oikos* 108, 7–17.
- Froud, K.J., Oliver, T.M., Bingham, P.C., Flynn, A.R. and Rowswell, N.J. (2008) Passive surveillance of new exotic pests and diseases in New Zealand. In: Froud, K.J., Popay, I.A. and Zydenbos, S.M. (eds) *Surveillance for Biosecurity: Pre-border to Pest Management*. New Zealand Plant Protection Society, Christchurch, New Zealand, pp. 97–110.
- Gage, S.H., Wirth, T.M. and Simmons, G.A. (1990) Predicting regional gypsy moth (Lymantriidae) population trends in an expanding population using pheromone trap catch and spatial analysis. *Environmental Entomology* 19, 370–377.
- Gansner, D.A. and Herrick, O.W. (1984) Guides for estimating forest stand losses to gypsy moth. *Northern Journal of Applied Forestry* 1, 21–23.
- Gilbert, M. and Liebhold, A.M. (2010) Comparing methods for measuring the rate of spread of invading populations. *Ecography* 33, 809–817.
- Gilbert, M., Grégoire, J.-C., Freise, J.F. and Heitland, W. (2004) Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. *Journal of Animal Ecology* 73, 459–468.
- Hajek, A.E. and Tobin, P.C. (2009) North American eradications of Asian and European gypsy moth. In: Hajek, A.E., Glare, T.R. and O'Callaghan, M. (eds) *Use of Microbes for Control and Eradication of Invasive Arthropods*. Springer, New York, pp. 71–89.
- Hanna, M. (1982) Gypsy moth (Lepidoptera: Lymantriidae) history of eradication efforts in Michigan, 1954–1981. *The Great Lakes Entomologist* 15, 191–198.
- Haynes, K.J., Liebhold, A.M. and Johnson, D.M. (2009) Spatial analysis of harmonic oscillation of gypsy moth outbreak intensity. *Oecologia* 159, 249–256.
- Hengeveld, R. (1989) *Dynamics of Biological Invasions*. Chapman and Hall, London.
- Hufbauer, R.A., Rutschmann, A., Serrate, B., Vermeil de Conchard, H. and Facon, B. (2013) Role of propagule pressure in colonization success: disentangling the relative importance of demographic, genetic and habitat effects. *Journal of Evolutionary Biology* 26, 1691–1699.
- Ingwell, L.L. and Preisser, E.L. (2011) Using citizen science programs to identify host resistance in pest-invaded forests. *Conservation Biology* 25, 182–188.
- Isaaks, E.H. and Srivastava, R.M. (1989) *An Introduction to Applied Geostatistics*. Oxford University Press, Oxford.
- Keena, M.A., Côté, M.-J., Grinberg, P.S. and Wallner, W.E. (2008) World distribution of female flight and genetic variation in *Lymantria dispar* (Lepidoptera: Lymantriidae). *Environmental Entomology* 37, 636–649.
- Leuschner, W.A., Young, J.A., Waldon, S.A. and Ravlin, F.W. (1996) Potential benefits of slowing the gypsy moth's spread. *Southern Journal of Applied Forestry* 20, 65–73.
- Lewis, M.A. and Kareiva, P. (1993) Allee dynamics and the spread of invading organisms. *Theoretical Population Biology* 43, 141–158.
- Liebhold, A.M. and Tobin, P.C. (2008) Population ecology of insect invasions and their management. *Annual Review of Entomology* 53, 387–408.
- Liebhold, A., Mastro, V. and Schaefer, P.W. (1989) Learning from the legacy of Leopold Trouvelot. *Bulletin of the Entomological Society of America* 35, 20–22.
- Liebhold, A.M., Halverson, J.A. and Elmes, G.A. (1992) Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography* 19, 513–520.
- Liebhold, A.M., Gottschalk, K.W., Muzika, R.M., Montgomery, M.E., Young, R., O'Day, K. and Kelley, B. (1995) *Suitability of North American Tree Species to the Gypsy Moth: A Summary of Field and Laboratory Tests*. General Technical Report No. NE-211. US Department of Agriculture, Forest Service, Radnor, Pennsylvania.
- Lippitt, C.D., Rogan, J., Toledano, J., Sangermano, F., Eastman, J.R., Mastro, V. and Sawyer, A.J. (2008) Incorporating anthropogenic variables into a species distribution model to map gypsy moth risk. *Ecological Modelling* 210, 339–350.

- Mason, C.J. and McManus, M.L. (1981) Larval dispersal of the gypsy moth. In: Doane, C.C. and McManus, M.L. (eds) *The Gypsy Moth: Research Toward Integrated Pest Management. Technical Bulletin No. 1584*. US Department of Agriculture, Washington, DC, pp. 161–202.
- Mastro, V.C., Richerson, J.V. and Cameron, E.A. (1977) An evaluation of gypsy moth pheromone-baited traps using behavioral observations as a measure of trap efficiency. *Environmental Entomology* 6, 128–132.
- McCullough, D.G. and Mercader, R.J. (2012) Evaluation of potential strategies to SLow Ash Mortality (SLAM) caused by emerald ash borer (*Agrilus planipennis*): SLAM in an urban forest. *International Journal of Pest Management* 58, 9–23.
- Miller, T.E.X. and Inouye, B.D. (2013) Sex and stochasticity affect range expansion of experimental invasions. *Ecology Letters* 16, 354–361.
- Morin, R.S., Liebhold, A.M., Luzader, E.R., Lister, A.J., Gottschalk, K.W. and Twardus, D.B. (2005) *Mapping Host-Species Abundance of Three Major Exotic Forest Pests. Research Paper No. NE-726*. US Department of Agriculture, Forest Service, Newtown Square, Pennsylvania.
- Muirhead, J.R., Leung, B., van Overdijk, C., Kelly, D.W., Nandakumar, K., Marchant, K.R. and MacIsaac, H.J. (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. *Diversity and Distributions* 12, 71–79.
- Paine, T.D., Raffa, K.F. and Harrington, T.C. (1997) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* 42, 179–206.
- Pimentel, D., Lach, L., Zuniga, R. and Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50, 53–65.
- Potapov, A. and Rajakaruna, H. (2013) Allee threshold and stochasticity in biological invasions: colonization time at low propagule pressure. *Journal of Theoretical Biology* 337, 1–14.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Redman, A.M. and Scriber, J.M. (2000) Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens, and parasitoids. *Oecologia* 125, 218–228.
- Riley, C.V. and Vasey, G. (1870) Imported insects and native American insects. *The American Entomologist* 2, 110–112.
- SAS Institute, Inc. (1999) *SAS/STAT® User's Guide, Version 8*. SAS Institute, Inc., Cary, North Carolina.
- Sharov, A.A. and Liebhold, A.M. (1998) Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecological Applications* 8, 833–845.
- Sharov, A.A., Roberts, E.A., Liebhold, A.M. and Ravlin, F.W. (1995) Gypsy moth (Lepidoptera: Lymantriidae) spread in the central Appalachians: three methods for species boundary estimation. *Environmental Entomology* 24, 1529–1538.
- Sharov, A.A., Liebhold, A.M. and Roberts, E.A. (1997) Methods for monitoring the spread of gypsy moth (Lepidoptera: Lymantriidae) populations in the Appalachian Mountains. *Journal of Economic Entomology* 90, 1259–1266.
- Shigesada, N. and Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, New York.
- Shigesada, N., Kawasaki, K. and Takeda, Y. (1995) Modelling stratified diffusion in biological invasions. *American Naturalist* 146, 229–251.
- Siegert, N.W., McCullough, D.G., Williams, D.W., Fraser, I., Poland, T.M. and Pierce, S.J. (2010) Dispersal of *Agrilus planipennis* (Coleoptera: Buprestidae) from discrete epicenters in two outlier sites. *Environmental Entomology* 39, 253–265.
- Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Suarez, A.V., Holway, D.A. and Case, T.J. (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of the National Academy of Sciences USA* 98, 1095–1100.
- Suckling, D.M. and Karg, G. (2000) Pheromones and other semiochemicals. In: Rechcigl, J.E. and Rechcigl, N.A. (eds) *Biological and Biotechnological Control of Insect Pests*. CRC Press, Boca Raton, Florida, pp. 63–100.
- Taylor, C.M. and Hastings, A. (2004) Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *Journal of Applied Ecology* 41, 1049–1057.
- Taylor, C.M., Davis, H.G., Cville, J.C., Grevstad, F.S. and Hastings, A. (2004) Consequences of an Allee effect on the invasion of a Pacific estuary by *Spartina alterniflora*. *Ecology* 85, 3254–3266.
- Thorpe, K.W., Ridgway, R.L. and Leonhardt, B.A. (1993) Relationship between gypsy moth (Lepidoptera: Lymantriidae) pheromone trap catch and population density: comparison of

- traps baited with 1 and 500 μg (+)-disparlure lures. *Journal of Economic Entomology* 86, 86–92.
- Tobin, P.C. and Blackburn, L.M. (2008) Long-distance dispersal of the gypsy moth (Lepidoptera: Lymantriidae) facilitated its initial invasion of Wisconsin. *Environmental Entomology* 37, 87–93.
- Tobin, P.C., Sharov, A.A., and Liebhold, A.M. (2007a) The decision algorithm: project evaluation. In: Tobin, P.C. and Blackburn, L.M. (eds) *Slow the Spread: A National Program to Manage the Gypsy Moth. General Technical Report No. NRS-6*. US Department of Agriculture, Forest Service, Newtown Square, Pennsylvania, pp. 61–76.
- Tobin, P.C., Liebhold, A.M. and Roberts, E.A. (2007b) Comparison of methods for estimating the spread of a non-indigenous species. *Journal of Biogeography* 34, 305–312.
- Tobin, P.C., Whitmire, S.L., Johnson, D.M., Bjørnstad, O.N. and Liebhold, A.M. (2007c) Invasion speed is affected by geographic variation in the strength of Allee effects. *Ecology Letters* 10, 36–43.
- Tobin, P.C., Bai, B.B., Eggen, D.A. and Leonard, D.S. (2012) The ecology, geopolitics, and economics of managing *Lymantria dispar* in the United States. *International Journal of Pest Management* 53, 195–210.
- USDA Forest Service (2013) *Gypsy Moth Digest – Defoliation*. US Department of Agriculture, Forest Service, Morgantown, West Virginia. Available at: <http://na.fs.fed.us/fhp/gm/defoliation/index.shtml> (accessed 20 December 2013).
- Venette, R.C. and Ragsdale, D.W. (2004) Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? *Annals of the Entomological Society of America* 97, 219–226.
- Waring, K.M. and O'Hara, K.L. (2005) Silvicultural strategies in forest ecosystems affected by introduced pests. *Forest Ecology and Management* 209, 27–41.
- Winston, M.L. (1992) The biology and management of Africanized honey bees. *Annual Review of Entomology* 37, 173–193.
- Womble, W.H. (1951) Differential systematics. *Science* 114, 315–355.
- Yang, D., Pijanowski, B.C. and Gage, S.H. (1998) Analysis of gypsy moth (Lepidoptera: Lymantriidae) population dynamics in Michigan using Geographic Information Systems. *Environmental Entomology* 27, 842–852.