



A network approach to modeling population aggregation and genetic control of pest insects

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ABSTRACT

Historically, models of the invasion and biological control of insect pests have omitted heterogeneities in the spatial structure of the targeted populations. In this study, we use stochastic network simulations to examine explicitly population heterogeneity as a function of landscape structure and insect behavior. We show that when insects are distributed non-randomly across a heterogeneous landscape, control can be significantly hindered. However, when insect populations are clustered as a result of limited dispersal, genetic control efficiency can be enhanced. In developing the model, we relax a key assumption of previous theoretical studies of genetic control: that released genetic control insects remain homogeneously distributed irrespective of the spatial structure of the wild type populations. Here, this behavior (termed the ‘coverage proportion’) is parameterized and its properties are explored. We show that landscape heterogeneity and limited dispersal have little effect on the critical coverage proportion necessary for control.

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1. Introduction

The Sterile Insect Technique (SIT) involves the repeated release of radiation-sterilized males into a wild type population in order to competitively inhibit productive mating (Knippling, 1955). It has been used effectively in the control of pests of both agriculture and public health (Dyck et al., 2005; Keng-Hong, 1998; Koyama et al., 2004; Krafur, 1998; Lindquist et al., 1992). Recent advances have been made to the SIT in the advent of transgenic technologies (Coleman and Alphey, 2002; Thomas et al., 2000), giving rise to a new wave of theoretical studies on genetic control (e.g. Boëte and Koella (2002), Gould and Schliekelman (2004) and Schliekelman and Gould (2000)). One underlying assumption in many of these models is that populations are a homogenous distribution of individuals, and resultantly, spatial structure is normally ignored.

A principal reason for the inclusion of space in population models is the existence of heterogeneity in the interactions between individuals. Heterogeneity in the local nature of interactions is well known to have counter-intuitive effects on ecological dynamics (DeAngelis and Gross, 1992; Tilman and Kareiva, 1997). The manner with which this is addressed by theoretical studies is seemingly field-specific. For example, in landscape ecology, heterogeneity is

often incorporated into computationally intensive fractal lattices (Gardner et al., 1987; Turner et al., 1989; With and King, 1999). In conservation biology, where the underlying issues involve the dynamics of local extinctions and re-colonizations in a connected system, metapopulation models have been developed (Colizza et al., 2007; Hanski, 1999; Levins, 1970). Epidemiological models have been used to explore the spread of infection over networks of connected individuals (Gupta et al., 1989; Keeling, 1999; Meyers et al., 2005; Newman, 2002). In these models, infection is seeded into a network of connected nodes, the structure of which can determine the rate of disease spread and the final epidemic size (Green et al., 2006). Albert and Barabasi (2002) recently reviewed the mechanics of complex networks and their broad-spectrum applications. In this paper, we develop a network approach to investigate the role of clustering on the population dynamics and management of an insect pest.

Insect aggregation is believed to be key to determining genetic control efficiency (Barclay, 2005). Despite this, most mathematical models of genetic control do not consider space in their projections. Two notable exceptions are a fractal landscape model (Wehrhahn, 1973) and a probability distribution model (Barclay, 1992). These studies concluded that spatial variability in pest densities will act to hinder a SIT program, because the more densely populated patches would not receive sufficient sterile males in order to be suppressed (Barclay, 1992; Wehrhahn, 1973). In addressing this important pest management issue, however, these analyses failed to take into consideration the

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significance of patch connectivity. The rate and distance to which insects migrate between patches might be expected to affect the influence of between-patch variability. We explore this issue using a network approach to create clustered and unclustered pest metapopulations, and determine the effect of the insect's migration rate and dispersal distance on projections of its control.

2. Methods

2.1. Network construction

A set of 500 subpopulations (nodes, N) was generated in 2-dimensional space, using a random number generator to ascribe their x and y coordinates (where $0 < x < \sqrt{N}$ and $0 < y < \sqrt{N}$). To generate a simple random network with a Poisson degree distribution and with an average number of connections per node, K , we simply connect any two nodes i and j with probability given by

$$P_{ij} = K/(N - 1), \quad i \neq j. \quad (1)$$

To generate random networks, the spatial locations of the nodes are not taken into consideration, and the network generation is completed by assigning a bidirectional connection between nodes i and j if $U(0, 1) < P_{ij}$, where $U(a, b)$ is defined as a function that returns a random number sampled uniformly from the interval $[a, b]$. Hence, if the probability of a connection between nodes i and j is 10% ($P_{ij} = 0.1$), a dispersal path is only created when the random number generator produces a number between 0 and 0.1 (from a possible range of 0–1). In this way, stochasticity is introduced into the connectivity of nodes.

Many differential equation models implicitly assume that every node can contact any other node and, as such, the mean field case is well approximated by a network model where all connections exist (e.g. $K = N - 1$). In many systems, however, nodes that share a common neighbor are themselves more likely to be connected, resulting in clusters regularly found in insect populations (Perry and Hewitt, 1991). Networks with clustering can be generated if the spatial proximity of the nodes is used when computing the probability of dispersal paths between subpopulations i.e. when the connection structure is no longer random. The spatial distance is incorporated into configuring non-random networks using the following rule:

$$P_{ij} = \begin{cases} 0, & \text{if } i = j \\ \frac{K}{2\pi D^2} \exp\left(\frac{-d_{ij}^2}{2D^2}\right), & \text{if } i \neq j \end{cases} \quad (2)$$

where D adjusts the average length of a connection, K the average number of connections per node, and $d_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$ is the Cartesian distance between nodes. Therefore, in addition to random mixing, we can also model the tendency for insects to disperse between close neighbors. This reflects the empirical patterns observed in numerous studies, where insect dispersal has been shown to be leptokurtic i.e. the vast majority of insects either remain where they are or move small distances, and the remaining dispersing proportion sharply decreases with distance (Dobzhansky and Wright, 1943; Kot et al., 1996; Makino et al., 1987; Taylor, 1978; Wolfenbarger, 1975). Importantly, and in contrast to the more traditionally used lattice approach, network models incorporate variability in the connection structure of subpopulations and include increased realism that is useful in simulating insect population dynamics.

Following Keeling (1999), the average number of connections per node is held constant, while the average length of connections between nodes is varied, in order to adjust the level of population

Table 1

Input parameter values required for desired output parameter values, and clustering coefficients (ϕ), in constructed networks for $N = 500$

| Input | | Output | | ϕ |
|-------|------|-----------|-------------|--------|
| K | D | K | D | |
| 3.58 | 2.54 | 3 (0.015) | 3 (0.009) | 0.02 |
| 3.2 | 0.83 | 3 (0.013) | 1 (0.002) | 0.2 |
| 3.8 | 0.5 | 3 (0.008) | 0.7 (0.001) | 0.4 |

Standard errors of the parameters are shown in brackets ($n = 50$).

Table 2

The parameter symbols used in the models and their definitions

| Symbol | Parameter definition |
|-----------|--|
| K | Average number of connections per subpopulation |
| D | Average distance between connected subpopulations |
| d_{ij} | Distance between subpopulation 'i' and 'j' |
| ϕ | Clustering coefficient |
| λ | Population growth rate |
| g | Scaling factor for subpopulation carrying capacity |
| A | Number of adults |
| F | Number of females |
| M | Number of males |
| S | Number of sterile males |

clustering. Smaller values of D result in more frequent short distance connections and these in turn lead to increased levels of clustering. This means that the connectivity of the network captures the average dispersal distance that is now proportional to D (see Eq. (2)). The parameter D is decreased in order to model an insect with more limited dispersal, generating a more clustered population. Again, the connections in the generated networks represent links across which dispersal occurs. As N approaches infinity, Eq. (2) will result in a network with number of connections per node K and average connection length D (Read and Keeling, 2003). As in our analysis N is maintained at 500, iterative adjustments of K and D are necessary until they match the desired values (Read and Keeling, 2003). Table 1 shows the true input values required to get the appropriate (desired) output values. The spatial coordinates of the nodes were held constant throughout, as changing them has no effect on the general properties of the network. However, the connections are randomly altered with each new network realization. No two simulated networks are the same at the local level, due to the stochastic nature of connection generation. However, the global properties of K and D in the individual realizations of the networks are the same.

The sole measure of population clustering is the clustering coefficient, ϕ , which is defined as the probability of two nodes with a common neighbor being themselves connected (e.g. if nodes B and C are both connected to node A then ϕ gives the probability that B and C are also connected). If nodes A , B and C are all connected, a triangle is formed; any triangle missing a single connection leads to a triple. Hence, the clustering coefficient of a network is the ratio of the number of triangles of connected nodes to the number of connected triples (Watts and Strogatz, 1998). Table 2 summarizes all parameters and their definitions. The presented results show the average of 50 network realizations.

2.2. Population dynamics

Each node within the network is a subpopulation, and exhibits simple density-dependent growth described by Bellows (1981):

$$A_{t+1} = \lambda A_t \exp(-gA_t), \quad (3)$$

where A_t is the adult pest population size at time t (an equal sex ratio is assumed); g adjusts the strength of density dependence and is inversely proportional to the carrying capacity, and λ is the maximum per capita population growth rate. The dynamical

properties of this model for density dependence are well known (May et al., 1974). Briefly, the mortality rate increases linearly with density. Subpopulations have a growth rate of five ($\lambda = 5$), and g is adjusted to maintain a carrying capacity of ten, unless stated otherwise. An invasion is simulated by randomly seeding the wild type pests into a set proportion of nodes and allowing them to spread through the network across the stochastic connections. An established pest population is initiated whereby all subpopulations are at carrying capacity at the start of simulations. A proportion of adult pests migrate each time step, and disperse to all connected subpopulations. In the absence of control, all subpopulations persist. Migration is set at a constant rate (0.1 unless stated otherwise) of adult insects emigrating to all linked subpopulations. We begin by examining the role of an insect's average dispersal distance, and the resultant level of clustering on the establishment of a network population.

2.3. Simulated control

Immediately following homogenous release across the target area, the tendency of released sterile males to mirror the spatial distribution of wild type insect patches appears to be variable (Hendricks et al., 1973; Knipling, 1979; Shiga, 1986). This behavior has been ignored by previous theoretical studies, and yet is likely to be vital to projections of genetic control. The 'coverage proportion' is the measure of the released insects' propensity to inhabit patches that are occupied by wild types. For example, a coverage proportion of 0.5 means that following their homogenous release across the target area, the modified males will subsequently only be found in half of the patches that are occupied by wild types. This can be simulated by randomly seeding the released males into 250 of the 500 patches. The sterile males will then be allowed to disperse across the stochastic connections. The dynamics of the subpopulations of pests receiving sterile males, S , is

$$A_{t+1} = \lambda F_t \frac{M_t}{M_t + S_t} \exp\left(-g \lambda F_t \frac{M_t}{M_t + S_t}\right), \quad (4)$$

where F_t and M_t are the densities of pest females and males, respectively. Hence, only the offspring of wild type females mating with wild type males ($\lambda F_t \frac{M_t}{M_t + S_t}$) contribute to density dependent survival. These dynamics hold provided the density dependence occurs in pre-adult stages, and an equal sex ratio (males, $M =$ females, $F = A/2$) is assumed (Barclay, 2001). In the terminology of Prout (1978), a 'hard release' is simulated, whereby the number of sterile males released each generation remains constant at a ratio to the numbers of wild type insects in an uncontrolled pest population at equilibrium, and is thus termed the 'release ratio'.

The coverage proportion required to control established pest populations is investigated. Intuitively, when fewer subpopulations are seeded with sterile males, a greater release ratio would be expected necessary for control. The absolute numbers of sterile males released is held constant to allow comparison between differing levels of coverage. The significance of population clustering on the relationship between the coverage proportion and the release ratio necessary for control is examined. Clustered and unclustered systems are then compared with a fully connected network that approximates the mean field. This latter comparison is used to determine the importance of including spatial structure. The significance of clustering, and pest surveillance, on the control of an invading pest (rather than suppressing an established pest) is then assessed.

Within a finite network, some nodes will have an above average number of connections (see Fig. 1). We will therefore determine the importance of being able to detect these well connected 'hub' subpopulations in optimizing control efforts with the SIT.

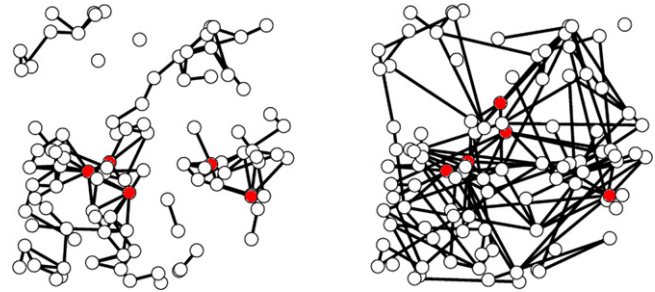


Fig. 1. Examples of a network of 100 nodes, with an average of three connections per node. Each node represents a subpopulation, and the gray nodes (red in the web version) constitute the top five hubs of the network. Left to right, the figures represent a clustered network (clustering coefficient of 0.2) and an unclustered/random network (clustering coefficient of 0.02).

In addition, some variability between the insect densities of each subpopulation is likely to arise due to heterogeneities in the landscape structure. This variability will be incorporated by assuming that the carrying capacity of the subpopulations is a random variable following a Poisson distribution, with a mean equal to that of the homogenous-node networks. This distribution is selected, because it plays a central role in the analyses of count data in ecology (Elston et al., 2001). If n insects occur at random across N patches, then the distribution of the numbers of insects per patch will be approximately Poisson (with mean n/N), and as such this distribution does not require any additional parameter to describe its variability (c.f. Gaussian and Binomial distributions). Preferential targeting of subpopulations with the highest carrying capacities will also be simulated. The idea of focusing efforts on such hubs has been mentioned before (Barclay, 1992), but no formal analysis of its significance has been undertaken for spatially-structured populations. To explore this issue, we assume that the top 25 or 50 hubs (with respect to connectivity or carrying capacity) of a network of 500 nodes have been identified and are preferentially targeted. This might be achieved in practice by performing ground releases of sterile insects into the identified hubs in conjunction with the more traditional aerial releases. Results will be compared to the completely random release approach.

3. Results

3.1. Highly clustered populations are less readily established

First, we describe the invasion of a previously un-infested landscape. Fig. 2 shows that increasing the proportion of nodes that are initially invaded acts to increase the overall pest population, once the system approaches its stable equilibrium. This is the result of individual and groups of nodes being disconnected from the portion of the network that is initially seeded. This explains why more clustered populations have a lower carrying capacity of pests (Fig. 2). As the number of initially invaded nodes/subpopulations is lowered (the probability of excluding disconnected nodes is increased) this difference becomes more pronounced. In biological terms this equates to a reduced probability of colonization of more isolated patches when the insect has restricted dispersal ability.

Not only do clustered populations tend to equilibrate at lower levels, but it also takes these populations longer for the seeded invasion to spread throughout the network (Fig. 3). The networks with a low clustering coefficient ($\phi = 0.02$, simulating random dispersal) eventually equilibrate within 25 generations of invasion, irrespective of the rate of migration (Fig. 4). However, Fig. 4 shows that when the migration rate and invasion seed are low, highly clustered networks can take as long as 75 generations to become

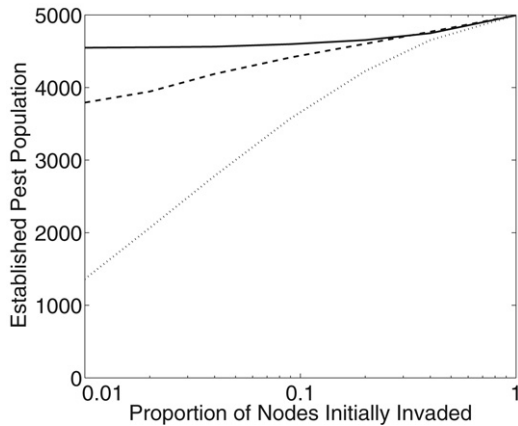


Fig. 2. The effect of clustering and the invasion seed on the equilibrium pest population. Results from simulations of networks with clustering coefficients of 0.02 (solid line), 0.2 (dashed line) and 0.4 (dotted line) are plotted. The average equilibrium population level is shown for 50 simulated networks. A maximum population of 5000 pests reflects the number of nodes (500) multiplied by the carrying capacity of the nodes (10).

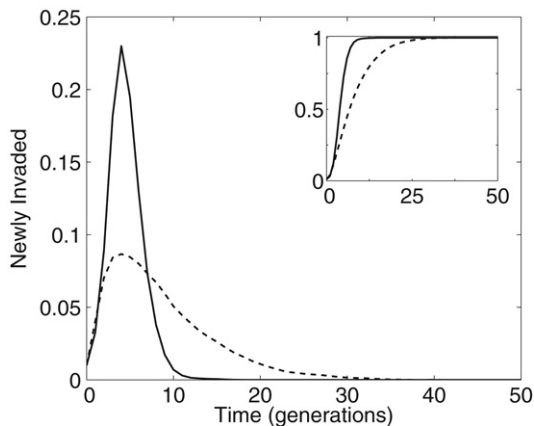


Fig. 3. The progression of pest invasion into a clustered and random network. Clustered ($\phi = 0.2$) and random ($\phi = 0.02$) networks are depicted by the broken and solid lines respectively. The inset plot shows the cumulative invasion of the nodes (y axis) over time (in generations, x axis) for both types of network. Each network had 500 subpopulations (nodes) with a carrying capacity of 10 and the pests had a growth rate of 5 and migration rate of 0.1.

fully established. This is because newly invaded subpopulations in a clustered network are more likely to have a greater proportion of connections with nodes that are infested already i.e. they have a smaller proportion of connections with uninfested nodes. More time is therefore required to spread to all habitat patches when an insect disperses shorter distances. No variation in the establishment times resulted when a range of carrying capacities was simulated (data not shown). Populations with lower growth rates showed an increased delay before full establishment (see Supplement Fig. 2). Hence, the pest's ability to colonize the simulated system is shown to be determined by its growth rate as well as its average dispersal distance.

3.2. Established populations with higher migration rates are more amenable to control

Due to the deterministic formulation of the population dynamics, a 95% reduction relative to the total pest numbers in an established population within 10 generations will be used as a proxy for control. Higher coverage proportions (i.e. a greater

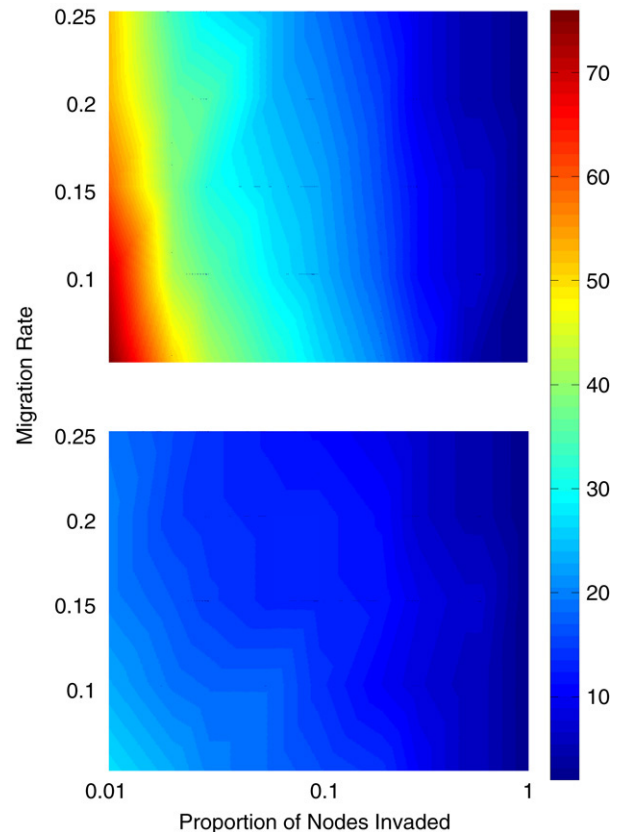


Fig. 4. Time (key units in generations) to establish pest equilibrium is dependent on aggregation (top to bottom, clustering coefficients are 0.2 and 0.02) as well as the proportion of nodes initially invaded and the migration rate. Each network had 500 subpopulations (nodes) with a carrying capacity of 10 and the pests had a growth rate of 5.

tendency for released males to assume the spatial structure of the wild types) enable control of an established population more effectively (Fig. 5). The pest population can always be controlled in a mean field approximation, provided a non-zero coverage proportion is simulated (Fig. 5). For both clustered and unclustered populations, however, there is a critical coverage proportion at which the pest can no longer be controlled. Biologically, this means that if the released sterile males do not have at least a moderate propensity to seek out the habitats of their wild type counterparts, they will fail to competitively inhibit wild type mating events and the pest population will persist.

Higher migration rates allow for the control of all three types of population (unclustered, clustered and mean field) at lower release ratios. Fig. 5 also shows that established clustered populations are more amenable to control than unclustered populations, irrespective of the coverage proportion. The exception is when coverage by the sterile male releases is complete i.e. the released insects perfectly match the spatial configuration of the wild type pests. Here, both the migration rate and level of subpopulation clustering lose their significance, and results are indistinguishable from the mean field approximation. Again, simulations were repeated using a range of carrying capacities and growth rates. Doubling the carrying capacity simply necessitated a release of double the numbers of sterile insects to control the pest population equivalently (data not shown). In accordance with the existing theoretical literature on the SIT and related genetic control e.g. Barclay (2005), Berryman (1967), Knippling (1955) and Schliekelman and Gould (2000), populations with higher growth rates require larger release ratios for control (Supplement Fig. 1).

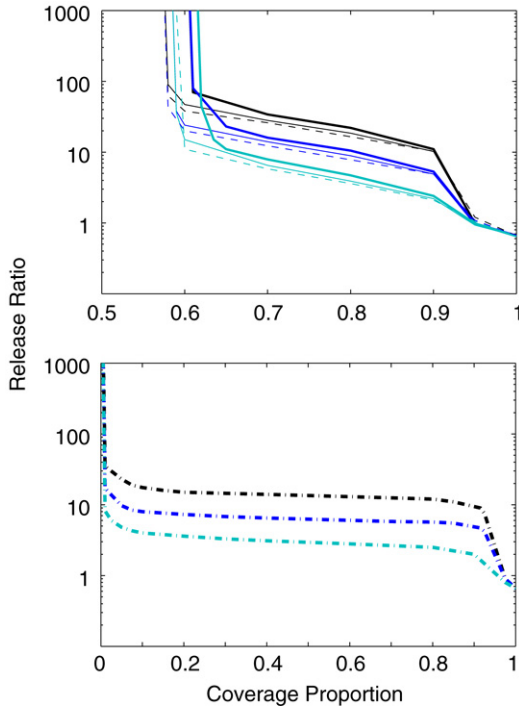


Fig. 5. The effect of the coverage proportion and the migration rate in reducing an established pest population by 95%, using the SIT. The solid, broken and dotted lines (thick, thin and broken lines in the web version) indicate unclustered ($\phi = 0.02$), clustered ($\phi = 0.2$) and highly clustered ($\phi = 0.4$) networks respectively (top panel). The mean field approximation is also illustrated (bottom panel). Migration rates of 0.05, 0.1 and 0.2 are depicted by the black, dark gray and light gray lines (black, dark blue and light blue lines in the web version) respectively. Each network had 500 subpopulations (nodes) with a carrying capacity of 10 and the pests had a growth rate of 5.

3.3. Invasions are easier to combat when pest dispersal is limited

Invading pests that form clustered populations as a result of limited dispersal distance are generally more amenable to pre-emptive control (Fig. 6). Pre-emptive control is simulated by initiating sterile male releases at the same time step as the initial pest invasion. Intuitively, a lower seeded invasion whereby fewer subpopulations are initially colonized is more readily controlled. The transition between invasions that are controllable with a modest constant release of sterile males, to invasions that are uncontrollable is very abrupt (Fig. 6). Below a critical coverage proportion, control becomes impossible (Fig. 6). Significantly, this critical coverage proportion was similar for unclustered and clustered populations with high or low migration rates, but did not exist for the mean field approximation.

3.4. Earlier detection reduces the requirement for released sterile males to effectively disperse to patches of wild type pests

A reduced dispersal ability of the insects (higher clustering) facilitates control of an invading pest, irrespective of the coverage proportion (Figs. 6 and 7). Fig. 7 shows that increasing the delay between pest invasion and the implementation of the SIT program necessitates a greater release ratio. The absence of a delay (delay = 0 generations) simulates a pre-emptive release program. In a clustered population ($\phi = 0.2$), a release ratio of 25 and coverage proportion of 0.5 is sufficient to control the pest population, provided the sterile males are released no later than 5 generations after initial invasion (Fig. 7). If the time between invasion and implementation is delayed any further, the invasion cannot be reversed. Further, a reduced coverage proportion can,

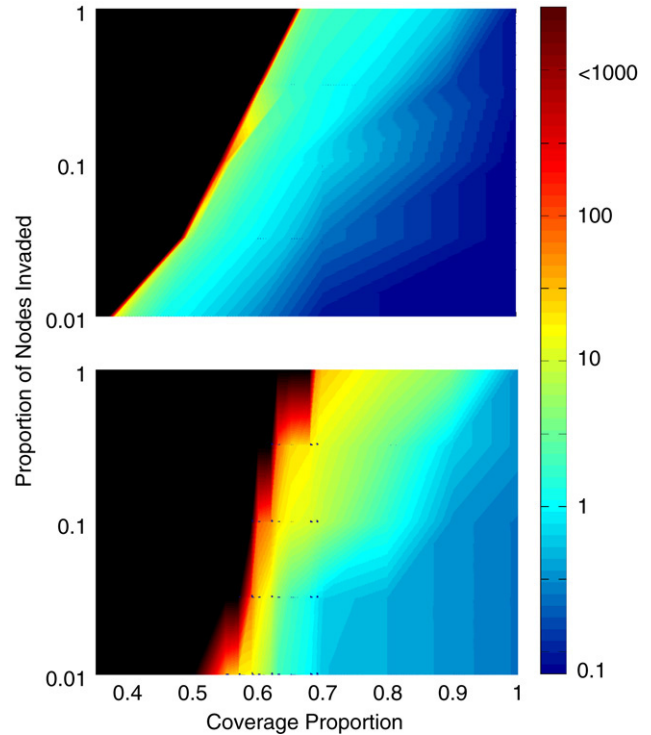


Fig. 6. The coverage proportion and proportion of nodes invaded affect the critical release ratio (see the key). The release ratios necessary for 95% pest suppression of (top to bottom) clustered ($\phi = 0.2$) and unclustered ($\phi = 0.02$) network populations are displayed. The release ratio is relative to the number of wild types inhabiting a fully established network. Each network had 500 subpopulations (nodes) with a carrying capacity of 10 and the pests had a growth rate of 5 and migration rate of 0.1.

to a certain extent, be compensated for by a reduced delay in SIT implementation (Fig. 7).

3.5. Targeting influential subpopulations provides limited improvements to control

Irrespective of the network structure, targeting the more highly connected subpopulations with simulated ground releases generally provides limited improvement in suppressing an established wild type pest population (Fig. 8). Targeting subpopulations with high connectivity increases the efficiency of the SIT only when the released sterile males approach the critical coverage proportion (Fig. 8). For example, an aerial release of sterile males with a coverage proportion of 0.6 in an unclustered population ($\phi = 0.02$) fails to control the pest. However, control is achievable for this population structure with a release ratio of 50, when the top 25 hubs are preferentially targeted with ground releases (Fig. 8).

When variability is incorporated into the carrying capacities of the subpopulations to simulate landscape heterogeneity, the established pest is significantly more resilient to control (Fig. 8). Across the range of coverage proportions for which 95% suppression is achievable, release ratios necessary for controlling a pest population in a heterogeneous network of subpopulation sizes are an order of magnitude greater than that required for networks where the subpopulations are of equal size (Fig. 8). This applies to both clustered and unclustered network structures. It is evident from these results, that there is little improvement with additional ground releases that target subpopulations with higher carrying capacities for the vast majority of the simulated parameter space. Again, the greatest benefit arises when the critical coverage proportion is approached (Fig. 8).

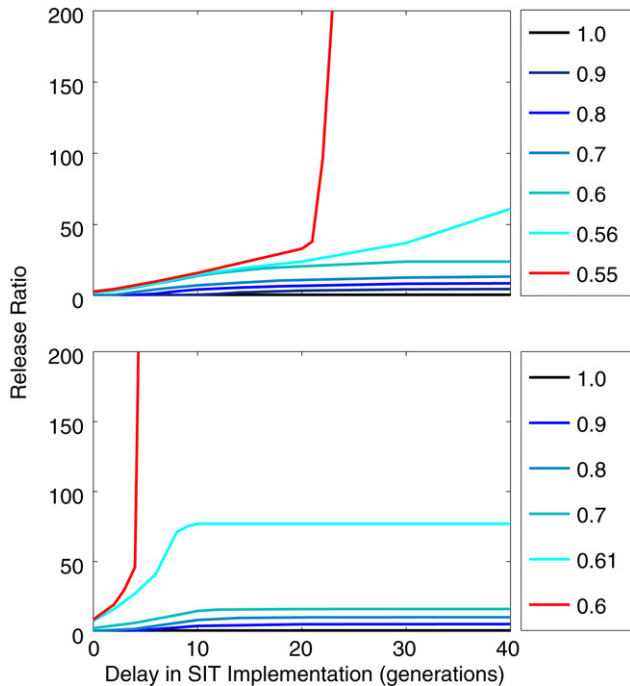


Fig. 7. The effect of a delay between pest invasion and SIT implementation on the release ratio necessary to prevent pest establishment. The key shows the coverage proportion i.e. the tendency of the released sterile males to assume the same spatial structure as the wild types. Results for clustered populations (top, $\phi = 0.2$) and randomly connected populations (bottom, $\phi = 0.02$) are shown. Each network had 500 subpopulations (nodes) with a carrying capacity of 10 and the pests had a growth rate of 5 and migration rate of 0.1.

4. Discussion

We have described a novel modeling framework for understanding insect population dynamics. A stochastic network model was used to assess the significance of population structure on the establishment of an invading pest, and its control with the SIT. Intuitively, when individuals are more limited in their dispersal, they will tend to form clusters, rather than mix homogeneously in a system. In general, we have shown that insects that tend to cluster are much slower to invade and equilibrate at lower overall densities once established. This is in agreement with Keeling (1999), who demonstrated that epidemiological invasions were similarly affected by local spatial structure. Yamamura (1989) analyzed empirical data on numerous insect species and reported a trend for more aggregated populations to equilibrate at lower densities. We show that as a result of limited dispersal, insect clustering tends to result in pest populations that are more amenable to control with the SIT. This is a result of the pest being less able to spread throughout the area and replenish depleted subpopulations when it has restricted dispersal.

In previous SIT models (Barclay, 1992; Wehrhahn, 1973), it was assumed that the density of sterile males remains homogenous following release, implying they disperse randomly, if at all, and fail to redistribute themselves amongst patches of wild types. The parameter, which we have termed the coverage proportion, was incorporated into the model to analyze the importance of this behavior. Traditionally, empirical studies have used the observed dispersal distances of released males as a proxy for their ability to spread effectively throughout the control zone (Miyahara and Kawai, 1979; Peck et al., 2005; Plant and Cunningham, 1991). We argue that there ought to be a distinction between the distance over which the insects disperse (the average connection distance), and the extent to which sterile males assume the same spatial structure as their wild type equivalents (the coverage proportion).

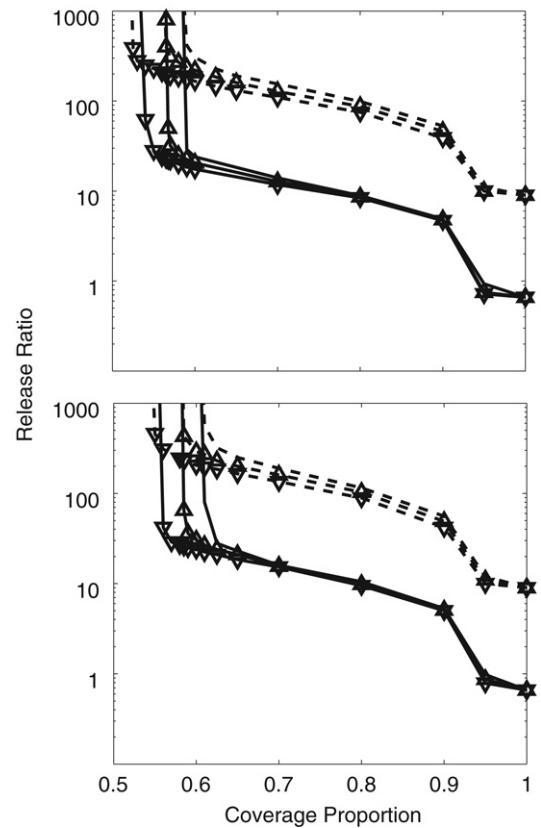


Fig. 8. The preferential targeting of subpopulations with high connectivity or carrying capacity. The release ratio necessary for a sustained 95% pest suppression of homogenous (solid lines) and heterogeneous (broken lines) subpopulations is plotted. Targeted release into the top 25 (face-up triangle) and top 50 (face-down triangle) hubs are shown for clustered (top, $\phi = 0.2$) and unclustered (bottom, $\phi = 0.02$) populations. Each network had 500 subpopulations (nodes) with a carrying capacity of 10 and the pests had a growth rate of 5 and migration rate of 0.1.

In analyzing the coverage proportion, we have determined the relationship it has with the control of both established and invading insect populations of differing levels of clustering. When the released sterile males perfectly match the spatial structure of the wild type insects, the connection structure of the subpopulations (i.e. the average dispersal distance of the adult insect) becomes irrelevant to control projections. However, in more realistic scenarios, where the sterile males are not located at each wild type patch, clustering can affect control efforts. In the mean field analysis, where the insects mix homogeneously, control is always possible with a sterile male release. Results clearly show, however, that when spatial structure is incorporated, control of established pest populations is impossible below a critical threshold coverage proportion. This threshold is similar when comparing clustered and unclustered populations. Importantly, the threshold is actually lower for populations that are more clustered. The limiting factor in the control of a spatially structured pest population is the ability of the wild types to spread through the system and re-colonize depleted patches. If it were the dispersal distance of the sterile males limiting control efforts, clustered populations would be less amenable to control. Following Vreysen (2005) and Weldon (2006), empirical information of the dispersal behavior of the wild type pests, as well as that of the sterile males, would therefore be prudent before an SIT program is initiated. Significantly, the critical coverage proportion threshold is not notably affected by incorporating heterogeneity into the simulated landscape (i.e. by allowing for between-habitat variation in the carrying capacities). Therefore,

once the parameters governing the growth and dispersal of a population are determined for a given pest, the critical coverage proportion can be estimated.

Three further general conclusions can be drawn from our analysis. First, prevention is better than control. A low release ratio utilized pre-emptively in a high-risk area could negate the need for a continuous and exhaustive release, once the invading pest population has a foothold. This type of preventative release is most beneficial when the sterile males have a limited tendency to inhabit patches of wild types (low coverage proportion). Therefore, a good understanding of this behavior might be important to policy-makers in determining the suitability of a preventative release program. Alternatively, vigilant surveillance would have a similar effect, albeit to a reduced extent. An efficiently executed active surveillance program is regarded as a primary attribute of the successful eradication of New World screwworm from Libya with the SIT (Lindquist et al., 1992). Depending on the coverage proportion, a delay between the initial invasion and the release of sterile males may render a population uncontrollable.

The second general conclusion of this analysis is that sterile male releases (or any related genetic control programs) ought to be adapted to the landscape structure of the target area. Variability in the carrying capacity of the nodes within a network resulted in pest populations that are ten-fold less amenable to control i.e. they require an order of magnitude greater release ratios for 95% suppression. Conclusions resembling those of Wehrhahn (1973) and Barclay (1992) are a result of variability in the landscape structure of the target area. By illustrating the effect that clustering has on pest management, our analysis emphasizes the importance of having a good knowledge of patch connectivity as well as landscape heterogeneity.

Third, the perceived wisdom of preferentially targeting the more connected patches (or the patches with higher carrying capacities) (Barclay, 2005) is not necessarily justified. Provided the hubs of an established population can be isolated, and the practicalities of preferential targeting overcome, the additional benefits in our analysis were generally found to be unimportant. To a large extent this result is likely attributable to the imposed limitation of variability in subpopulations' connectivity and/or carrying capacities. Conversely, the degree of connectivity in a scale-free network can vary greatly, resulting in a small proportion of nodes that can have several orders of magnitude more connections than other nodes (Reka and Barabasi, 2002). If evidence arose for such 'super-spreading' subpopulations occurring in insect ecology, scale-free networks might be a more appropriate approach, and the advantages of a partially targeted control would be expected to improve.

A formal assessment of a preferentially targeted strategy would be better left until the policy to control a particular pest in a precise location is determined. Only then, can species-specific parameters be included, and greater complexity incorporated into the network. In addition to expanding current understanding of controlling a spatially structured population with the SIT, we believe that our analysis provides a simplistic template for theoretical studies of genetic control in the advent of transgenic technologies. Finally, we have presented a novel way in which to incorporate different aspects of space into the dynamics of species interactions that has broader applications to ecological theory.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tpb.2008.09.003.

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