Habitat fragmentation and eradication of invading insect herbivores

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Abstract

1. Invasions by non-native pests and diseases represent serious threats to biodiversity, agriculture and human health. Under current border arrival rates associated with international trade not all such invasions can be prevented, so early detection and eradication (forced extinction) are important strategies for preventing establishment and long-term impacts. Removal of host plants has historically been a common tool used alone and in concert with other tools for eradication of plant pests but there is little scientific theory specific to the management of invasive species to guide the application of this eradication strategy.

2. We drew upon extensive conservation biology literature documenting the effect of habitat destruction or fragmentation driving extinction. We applied a previously developed spatially explicit model of gypsy moth, *Lymantria dispar*, spatial dynamics to explore how fragmentation affects population persistence. This model accounts for a component Allee effect driven by mate-finding failure that interacts with dispersal.

3. We observed a nonlinear dependency of population persistence on the fraction of habitat cover and the level of habitat fragmentation. Simulation of active habitat fragmentation via the removal of habitat in swaths of varying widths or the application of pesticide in varying swaths showed that removal of hosts or pesticide application in narrow swaths (i.e., 40 m wide) caused the greatest probabilities of extinction. Generally, habitat removal was more effective than one-off pesticide treatments at causing extinction.

4. Synthesis and applications. Spatially explicit modelling of Allee dynamics in invading gypsy moth populations showed that host removal can be an effective method to eradicate invasive plant-feeding insects especially when habitat fragmentation is applied at a desirable level. Furthermore, this can be used as an alternative to, or in conjunction with, pesticide treatments, to provide more options for carrying out eradications and to increase the probability of eradication success.

Keywords: eradication; extinction; host removal; invasion; *Lymantria dispar*; pesticide; simulation; swath width

Introduction

Biological invasions of insects and other taxa remain a major threat to agriculture, forests, the environment and human health, partly due to the increasing globalization of international trade (Brockerhoff & Liebhold, 2017; Seebens et al., 2018). Prevention of transport and movement of unwanted species is often identified as the most efficient strategy for mitigating the problem (Leung et al., 2002). However, current levels of international trade and travel make it impossible to prevent all transport and introduction of non-native potentially invasive species. Consequently, surveillance and eradication are crucial options for preventing establishment of newly founded populations. Eradication can be difficult and expensive, particularly if populations are not discovered early during their colonization period (Tobin et al., 2014; Liebhold et al., 2016). While many eradication attempts have been successful (Tobin et al., 2014; Suckling et al., 2016), others have failed and there continues to be a need to develop and integrate more effective strategies for eradicating newly founded populations (Liebhold et al., 2016).

Many different control tools and tactics have been applied to achieve insect eradication, including application of pesticides, mating disruption, sterile insect releases and male annihilation (Brockerhoff, Liebhold, Richardson, & Suckling, 2010; Suckling et al., 2014). One method commonly applied for eradication of herbivorous insects and plant pathogens, often in conjunction with other methods, is removal of host plants (e.g., Sosnowski, Fletcher, Daly, Rodoni, & Viljanen-Rollinson, 2009; Haack, Hérard, Sun, & Turgeon, 2010). Around 42% of recorded arthropod and plant pathogen eradications have utilised host removal, slightly more than the proportion using pesticides or biopesticides (Fig. 1). While the underlying logic that removal of hosts could contribute to eradication is intuitively obvious, the science behind this strategy has not been widely developed. For example, it is not clear how much host plant removal in the vicinity of an incursion is necessary and how fragmentation of host patches may be used advantageously, depending on an invader's population dynamics and dispersal ability. Here we explore the population ecology behind strategies for using host plant removal as an eradication strategy.

Managing invasions is somewhat related to conserving endangered species in that both activities involve management of low-density populations. However, while species conservation focuses on preventing extinction, eradication aims to generate extinction of the target species. One concept that is pervasive in conservation ecology is that habitat fragmentation can lead to extinction and thus management of habitat connectivity may be crucial to metapopulation persistence (With & King,

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1999; Hanski & Ovaskainen, 2003; Fischer & Lindenmayer, 2007). It follows that habitat fragmentation might also be exploited for eradication although the population ecology behind this concept has not previously been addressed.

The dynamics of many low-density populations are subject to Allee effects which are defined as decreasing per capita growth with decreasing population density (Courchamp, Berec, & Gascoigne, 2008). Allee effects may play a critical role in the extinction of low-density populations (Stephens, Sutherland, & Freckleton, 1999), and strong Allee effects create thresholds below which populations will tend to decline to extinction. Similarly, Allee effects can be important during the early stages of invasions, as populations arriving at levels below Allee thresholds are likely to go extinct (Taylor & Hastings, 2005; Liebhold & Tobin, 2008).

Allee effects, dispersal and habitat fragmentation interact in ways that affect extinction. In fragmented habitats, dispersal of populations away from habitat patches acts as a net drain on populations (Kean & Barlow, 2000) and can thus contribute to extinction of low-density populations (Courchamp, Berec, & Gascoigne, 2008; Kanarek, Webb, Barfield, & Holt, 2013). In a key theoretical study, Lewis and Kareiva (1993) demonstrated that in the presence of Allee dynamics there exists a minimum habitat patch size necessary for establishment of invading populations; below that threshold, the drain of emigration is so great that populations cannot persist. Similarly, Etienne, Wertheim, Hemerik, Schneider, and Powell (2002) explored how inter-patch distance in complex landscapes plays a crucial role in limiting establishment; dispersal in populations governed by Allee dynamics prevents populations from establishing when inter-patch distances are too large.

Knowledge of the interaction between multiple population control methods used in a given eradication programme is also of practical importance since multiple eradication tools may either interfere with each other or act synergistically (Blackwood et al., 2012; Suckling, Tobin, McCullough, & Herms, 2012). Furthermore, landscapes worldwide in which eradications are attempted are often complex urban environments with a diversity of land use and public interests. These factors may limit what control methods are permissible and where they can be applied. For example, although both the use of aerial application of pesticides and host plant removal during incursion responses can be controversial among stakeholders (McEntee, 2007; Meng, Hoover, & Keena, 2015), plant removal may be more acceptable (although when iconic or threatened trees are affected, for example, targeted pesticide application may be preferable). However, information is needed on how eradication success is influenced by spatial heterogeneity in application of eradication tactics such as host removal and pesticide treatments.

Here we use the gypsy moth, *Lymantria dispar* (L.), as a well-studied invasive species model system, for exploring how host removal and fragmentation of host resources can be exploited to eradicate invading populations. We also investigate how eradication success is affected by simultaneous applications of host removal and pesticides, including spatially heterogeneous pesticide applications. This analysis uses a model that incorporates a previously quantified component Allee effect and realistic insect dispersal rates.

Materials and Methods

MODEL DESCRIPTION

We developed a spatially explicit agent-based population model for the European strain of gypsy moth based on Robinet et al. (2008). The model captures an emergent mate-finding component Allee effect and was parameterized from field trials of mate location success with respect to distance between males and females as described in Robinet et al. (2008). Our lattice-based model landscape comprised a 60 × 60 matrix of grid cells where each cell represented a 20 m × 20 m area. We assumed periodic boundary conditions which were implemented in the model by calculating the distance between grid cells (used for larval dispersal and mating success functions described below) as if they were on a torus. Each cell was classified as either presence or absence of gypsy moth host plants. The model was coded in the R language (R Core Team, 2017), and the code is provided in Supplementary File S1 (in Supporting Information) and via the Dryad Digital Repository at https://doi.org/10.5061/dryad.rxwdbrv49 (Barron et al. 2019). The model parameters are described in Table 1.

Population change occurred on an annual time step (one generation per year) beginning with overwintering egg masses. We assumed a fixed egg survival rate of S_1=0.5. Survival of larvae and pupae was density dependent with a maximum of S_2=0.1. Together, these give the 5% maximum survival from egg hatch to adult emergence used by Robinet et al. (2008). Density dependence used a Ricker-type function:

$$S(N) = S_2 \cdot \exp(-c \cdot N)$$

where S_2 is the maximum stage survival, N is the larval density per ha in the cell, and c=0.000296 is a density-dependence coefficient. The value for c was estimated from a maximum larval density of 250,000 ha^{-1} (corresponding to 'outbreak' levels of fourth instar larvae; Campbell, 1981) and a maximum instantaneous rate of increase of r_m=3 per generation (=$\log_e(e \cdot S_1 \cdot S_2)$) (as per Robinet et al., 2008). Demographic

stochasticity was introduced by drawing the number of individuals surviving each stage from a binomial distribution.

First instar gypsy moth larvae disperse passively by ballooning. We modelled this movement by calculating the probability of a larva dispersing to another grid cell at distance, d using a Gaussian distribution:

$$g(d) = \frac{1}{H}\exp\left(\frac{d^2}{4D}\right)$$

where H is a normalizing constant (evaluated numerically), D is the diffusion coefficient set to 3000 m^2 per generation (Robinet et al., 2008) and distances between cells, d, were calculated between cell midpoints. The number of larvae dispersing from a focal cell to the surrounding cells was drawn from a multinomial draw according to the probabilities of dispersal as above. If larvae dispersed to a grid cell with no habitat then they were assumed to die at the next stage transition; otherwise, if habitat was present, they transitioned to the emerging adult stage according to $S(N)$ above. An even sex ratio was assumed for the emerging adults; the number of unmated females in each cell was drawn from a binomial distribution with a probability of 0.50.

Upon emergence, male gypsy moths must locate flightless females for mating; failure to find mates when they are scarce can contribute to Allee effects in low-density and/or fragmented populations (Tobin et al., 2009). We modelled the probability of males in a source grid cell locating females in a target cell based on the distance between cells d using the relationship derived by Robinet et al. (2008):

$$P(d) = a \cdot \exp(-b \cdot d)$$

where the distance scalar $b = 0.01$ was the mean of those authors' estimates and the maximum probability $a = 0.01$ was found by simulating a range of values for a and selecting the value that best reproduced the relationship between the number of egg masses and population growth rate depicted in Figure 2 of Robinet at al. (2008). We could not use the estimates of a directly from Robinet at al. (2008) because they were daily estimates based on asynchronous emergence times for adult males and females whereas we needed a generational estimate for parameter a that averaged over emergence times. The probability of a female in a target cell *not* being located and mated by males from a source cell was calculated as the complement of $P(d)$ raised to the power of the number of males in the source cell. The product of all source cell probabilities was used as an estimate of the probability of a female in a target cell *not* being mated by any males, and thus the complement of this was used as the probability of a female being mated by at least one male, p_m. Stochasticity in mating success was introduced by drawing the number of females mated per cell f from a binomial distribution governed by p_m. Each mated female was assumed to lay

a single egg mass with a mean of e = 400 eggs per mass. The number of eggs laid per cell was drawn from a Poisson distribution with a mean value of $\lambda = f \cdot e.$

TREATMENT SIMULATIONS

The first set of simulations explored the relationship between probability of gypsy moth population persistence and the amount and fragmentation of habitat available. Habitat was defined as the presence of gypsy moth hosts in a given cell. We created habitat maps spanning a range of percentage cover by habitat and habitat fragmentation levels using the modified random clusters method (Saura & Martínez-Millán, 2000). The controlling parameters for habitat map generation of A, the proportion of area assigned to habitat, and q, the initial probability of being assigned to a habitat patch (as opposed to a patch of non-habitat), took the values A = (0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1) and q= (0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50), respectively. See Saura and Martínez- Millán (2000, page 664) for an expanded definition of q (referred to as p in their model). An 8-neighbourhood rule was used to define if grid cells belonged to the same habitat patch, and patches were either habitat or empty (i.e., there was only one landscape type). Generally, increasing parameter q leads to increased patch aggregation (i.e., reduced fragmentation) (Figs 2a, b, c, d, see also Supplementary Tables S1-S2). We generated 500 habitat maps for each of the 100 habitat abundance and habitat fragmentation combinations. The model was initiated with 5 egg masses located in the central grid cell with habitat. We monitored the proportion of cells occupied and the number of mated females per cell over time. The proportion of populations persisting (at least one occupied cell) for 10 generations for each habitat configuration was estimated from the number of populations still present out of 500 replicate simulations.

The second set of simulations investigated the effects of applying host removal or pesticide treatment in different spatial configurations to areas supporting a newly founded gypsy moth population and assessing the impact on population persistence. In these simulations 75% of the grid cells were selected for host removal in a pattern of one swath removed, one swath left intact in both (x & y) dimensions, creating a plaid-like or Tartan-like pattern (e.g., Figs 2f, 2g, 2h). The width of the swaths (w) removed varied as: w=(1, 2, 3, 5, 6, 10, 15, 30) grid cells. Increasing the swath width resulted in fewer, larger habitat patches with larger inter-patch distances, and increasing aggregation (less fragmentation) as indicated by adjacency, aggregation and patch cohesion indices (Table 2; Supplementary Table S3; McGarigal, Cushman, Neel, & Ene, 2002). For comparison we also simulated removal of 75% of grid cells at random with no spatial dependence between the grid cells selected for treatment; these grid cells were selected for treatment with a Bernoulli draw (Fig. 2e). For each scenario, we also calculated a range of other

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landscape metrics, including, total core area, proportion in core area, mean perimeter to area ratio, and others (see Supplementary Table S4).

We initialised the simulations with 100% habitat and with 5 egg masses located in the central grid cell, and then ran the population model for four time steps (i.e., four years with one generation per year) before applying treatments. This pattern of initial population growth in an undisturbed habitat simulated the typical lag between founding of an invading population and its discovery and initiation of eradication treatments. At time T = 4 (i.e., after four generations), one of two treatments was applied:

1) Habitat removal – Host destruction was also assumed to remove 100% of eggs present in the treated grid cell and meant any larvae subsequently dispersing into that cell suffered 100% mortality due to the absence of habitat.

2) Pesticide treatment - A single application was assumed by default to cause an average of 95% larval mortality in treated grid cells (based on Reardon, Dubois, & McLane, 1994), and the number surviving was drawn from a binomial distribution. Varying swath widths and random distribution of pesticide applications were simulated as described above for host plant removal.

Simulations were run for an additional 6 time steps (to T = 10) following treatment and the proportion of populations going extinct (no occupied cells) for each treatment and swath width combination was estimated as the fraction of populations going extinct out of 500 replicate simulations.

To illustrate the effects of beginning treatments later or starting with a greater number of egg masses, we also modelled these scenarios for beginning treatments at T = 6 (instead of T = 4) and 8 initial egg masses (instead of 5 egg masses), respectively.

The third set of simulations investigated the impact of combined treatments (habitat removal plus pesticide application) on the probability of gypsy moth population persistence across a range of habitat removal levels and pesticide efficacies. The range of habitat removal simulated was 0-90% of grid cells removed in increments of 5%. Habitat removal was followed by simulated pesticide application to the remaining habitat with a range of efficacies (percentage of larval population in each cell killed) as z = (0.80, 0.82, 0.84, 0.86, 0.88, 0.90, 0.92, 0.94, 0.96). The range for pesticide efficacy was more limited to reflect the reality of pesticide applications in eradication. Spray/application conditions and the structural complexity of the vegetation means that not all larvae are fully exposed to pesticide (e.g, Richardson & Kimberley, 2010) and therefore realized efficacy is

often considerably less than the label (Bryant, 1994). Simulations were initialised with 100% habitat coverage and with 5 egg masses located in the central grid cell. Populations were allowed to grow for 4 generations before applying the combined treatment. Host removal treatments were applied in a spatially random manner where grid cells were selected for removal using a Bernoulli trial. The proportion of populations going extinct for each percentage habitat removal and pesticide efficacy combination was estimated from the number of populations extinct 6 years after treatment out of 500 replicate simulations.

Results

Percentage habitat was the dominant determinant of the fraction of populations persisting, exhibiting a positive influence on persistence. But this was modified in a non-linear fashion by habitat patchiness with increasing habitat aggregation leading to higher probabilities of persistence over most ranges of percentage habitat (Fig. 3). Closer inspection of landscape metrics for the proportional habitat and fragmentation combinations showed patch size-related factors (i.e., mean patch area, total core area, proportion in core area, mean perimeter to area ratio; see Supplementary Tables S1-S2) appeared to be the main drivers of this relationship. Mean patch areas greater than 100 ha or landscapes with greater than 70% of habitat in core areas resulted in a greater than 70% probability of gypsy moth population persistence.

Similarly, the level of fragmentation (controlled by swath width) in the spatial distribution of both control tools (habitat removal and pesticide treatments) strongly influenced the probability of population extinction. For both habitat removal and pesticide application, increasing the level of fragmentation, by using a smaller swath width, increased the probability of extinction (Fig. 3). However, the difference was more pronounced for habitat removal than it was for pesticide application (Fig. 4). The mean patch sizes created by using swath widths of 10, 15 and 30 grid cells were 4, 9, and 36 ha, respectively (Table 2; Supplementary Table S3) – with larger patches allowing some populations to persist. Spatially-random allocation of habitat removal resulted in similar probabilities of extinction to removing habitat in swaths 2 grid cell wide (i.e., 40 m wide) (Fig. 4), and these two types of fragmentation were also similar in terms of several landscape metrics and aggregation indices namely patch density, patch area, and the number of patches (Supplementary Table S4). Applying pesticide to 100% of the landscape had a similar impact to removing habitat in swaths 10 cell (= 200 m) wide (Fig. 4).

The timing of treatments had a considerable impact on the proportion of populations that went extinct. When fragmentation treatments began later, at T = 6 instead of T = 4, extinction occurred in only approximately 50% of cases even with the most effective treatment (Supplementary Fig. S1, Supplementary Table S5). Likewise, the number of initial egg masses affected the outcome of fragmentation treatments substantially. When populations began with a mean initial number of egg masses of eight (instead of five), the proportion of extinct populations dropped to less than approximately 50% (Supplementary Fig. S2, Supplementary Table S5).

Simulations performed using varying levels of habitat removal combined with pesticide applications of varying efficacy indicated that habitat removal had a consistent positive effect on population extinction with removal of over 40% of host cover resulting in a greater than 90% chance of eradication for all levels of pesticide efficacy (Fig. 5). Increasing pesticide efficacy on the remaining habitat also improved the chances of eradication; at the highest level of pesticide efficacy (96% kill) a 90% chance of eradication was achievable with only 5% of habitat removed (Fig. 5). There was no evidence of a synergistic effect between habitat removal and pesticide use (i.e., contours are approximately equal width).

Discussion

Our analysis of the effect of the spatial distribution of habitat on population persistence showed that different levels of habitat fragmentation can generate very different probabilities of population extinction in our model system. Increasing habitat fragmentation (i.e., smaller patch sizes and lower connectivity) resulted in a lower probability of persistence in a simulated gypsy moth population, even within the same level of habitat cover (Fig. 3). This occurred particularly at lower levels of habitat cover where fragmentation had a substantial effect on population persistence, but it had little effect at high levels of habitat cover.

Motivated primarily by species conservation problems, many studies have recognized that extinction can be driven by habitat loss and fragmentation. Early work grew out of island biogeography theory (e.g., Gilpin & Diamond, 1980), but a larger body of research applied metapopulation models to explore how habitat loss and fragmentation can lead to population decline and extinction (e.g., Lande, 1987; Nee & May, 1992). A common thread in these studies has been the identification of threshold levels of habitat cover or fragmentation below which populations cannot persist (e.g., Bascompte & Solé, 1996; With & King, 1999; Swift & Hannon, 2010).

Taking advantage of the observed effect of habitat fragmentation on population persistence, we simulated control (habitat removal or pesticide application) in a patchy fashion of a newly-founded gypsy moth population using varying swath widths to generate different levels of fragmentation. In these simulations, the amount of habitat 'treated' was the same (75%) for all treatments but the spatial allocation of control varied. High levels of habitat fragmentation could be generated with swath widths of less than 5 cells (= 100 m) or random allocation of cells for habitat removal. Both of these led to a high probability (> 90%) of population extinction. Smaller swath widths generated smaller habitat patches, causing high dispersal loss of ballooning gypsy larvae. The effects of random fragmentation were similar to small swath widths because in both cases, a large proportion of adjacent cells were non-habitat.

Our results were very sensitive to both the timing of treatments and the initial number of propagules that started the 'invasion'. When treatments occurred later, after six generations (T = 6), the proportion of extinct populations declined considerably, to approximately 50% or less in the most effective fragmentation treatment, compared with 100% of populations when T = 4 (see above). Similarly, when the invasion began with eight egg masses rather than five, fragmentation treatments became much less effective. This indicates that such larger populations have progressed too far beyond the Allee threshold, especially in our small model landscape, so that fragmentation alone is no longer a reliable treatment.

Compared with habitat removal, patchy pesticide application led to much lower probabilities of extinction and was less responsive to the level of fragmentation (Fig. 4). This difference in the strength of the fragmentation effect probably occurred because, contrary to habitat removal, pesticide effects are temporary and do not permanently disrupt dispersal success and mate finding. Provided a proportion of the population survives the initial pesticide application, it may persist unless it is so small that it falls below the Allee threshold. Even the least effective pesticide treatment (sw = 30) still nearly doubled the chances of extinction compared to conducting no control, suggesting that in the presence of Allee effects, modest population reduction alone can sometimes drive populations to extinction (Liebhold & Bascompte, 2003; Liebhold & Tobin, 2008).

Considering a situation of combined control treatments (e.g., random habitat removal and pesticide application to the remaining habitat), our simulation results (Fig. 5) showed that at lower levels of habitat removal, the insufficient habitat 'treatment' could be partly compensated with improved pesticide efficacy (and vice versa). We did not explore economic trade-offs in the cost-effectiveness of the

different control combinations. In some eradication programmes, the selection of control options may be driven more by externalities such as public perception and license to operate than purely by economic considerations. Our results suggest that in cases where a land owner refuses to grant permission to use a certain control on their property (e.g., they object to pesticide applications or plant removal), that this may not necessarily jeopardize the success of a wider eradication programme as it may be possible to compensate for one treatment with another (i.e., if pesticides are not allowed, it might still be possible to achieve eradication by removing more host material or vice-versa).

It is possible that the model system we chose, European gypsy moth, may be more amenable to disruption by habitat fragmentation than many other potential target pest species because of intrinsic biological and population attributes such as their mostly passive dispersal (larval ballooning) and strong Allee effects caused by mate-location failure (Tobin et al., 2009). However, other species that lack these vulnerabilities may still experience Allee effects due to these and other causes. For example, predation may cause Allee effects and is often an important factor in extinction in a conservation context (Gascoigne & Lipcius, 2004; Berec, Angulo, & Courchamp, 2007). For species that lack Allee effects or experience very weak Allee dynamics, we anticipate that partial host removal (as simulated here) will be much less effective at achieving eradication because very small residual populations are likely to persist.

Allee effects have been shown to play a key role in the dynamics of many low-density populations (Taylor & Hastings, 2005; Courchamp, Berec, & Gascoigne, 2008). The presence of an Allee effect can strengthen the effects of habitat loss and fragmentation on extinction (Lande, 1987; Amarasekare, 1998). Most invading populations founded at very small sizes are driven to extinction, and Allee effects often contribute to the low level of establishment success of invading populations (Brockerhoff & Liebhold, 2017). Lewis and Kareiva (1993) identified crucial interactions among dispersal loss, habitat patch size and Allee dynamics in invading populations, based on a theoretical modelling approach. In the presence of strong Allee effects, a minimum habitat patch size should exist below which establishment of invading populations is impossible.

Allee effects can be exploited to facilitate eradication of invading populations (Liebhold & Tobin, 2008, Liebhold et al., 2016). When a strong Allee effect exists, it may be possible to achieve eradication without direct removal of all individuals. Instead, populations can be suppressed below the Allee threshold and residual populations should subsequently decline toward extinction. In other situations, it

may be possible to achieve eradication by shifting the Allee threshold by applying a measure (e.g., mating disruption) which intensifies an existing component Allee effect (Liebhold et al., 2016). In this study, we have shown that moth dispersal and Allee effects can be exploited in efforts to eradicate invading species through habitat fragmentation alone and in combination with other (e.g., pesticide) treatments. As globalization drives additional invasions of potentially damaging non-native insect species, methods to eradicate invading populations while minimizing environmental impacts will be of increasing importance.

Authors' contributions

All authors contributed to conception, planning, model design and model parameterisation. MB, AL and JK carried out the model programming. All authors contributed to data analysis and interpretation, writing of the manuscript, and gave final approval for publication.

Acknowledgements

Data availability statement
All model input data are available in the main document of this paper. The model code and detailed model outputs are provided in the supporting information (online only) that accompanies this publication. The model code is also provided via the Dryad Digital Repository at https://doi.org/10.5061/dryad.rxwdbrv49 (Barron et al. 2019).

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Tables

Table 1. List of model parameters

Parameter	Description	Default value
	Grid cell size (m)	20 x 20
	Dimensions of habitat grid (cells)	60 x 60
S_1	egg to larva survival rate	0.5
S_2	Maximum larva to adult emergence survival rate	0.1
c	Density-dependence coefficient	0.000296
D	Diffusion coefficient (m² per generation)	3000
b	Distance scalar of mate-finding function	0.01
a	Maximum probability of mate-finding function	0.01
e	Fecundity (eggs / female)	400
N_0	Initial population size in center cell (egg masses)	5

Table 2. Patch size and fragmentation values of habitat fragmentation simulations

| **Fragmentation approach** (and illustration in Fig. 2 a-h)	q (initial probability of being habitat) or w (swath width, grid cells, removed)	**Percent habitat**	**Mean patch size** (m²)	**Inter-patch distance** (adjacency index)	**Aggregation** (aggregation index)	**Fragmentation** (patch cohesion index)
Random clusters (2a)	$q = 0.1$	25%	2,746	0.366	55.4	8.12
Random clusters (2b)	$q = 0.45$	25%	224,254	0.610	79.3	8.31
Random clusters (2c)	$q = 0.1$	75%	572,853	0.716	85.1	9.64
Random clusters (2d)	$q = 0.45$	75%	914,249	0.868	94.4	9.42
Swath removal (2f)	$w = 1$	25%	400	0.000	0.0	-
Swath removal (2g)	$w = 5$	25%	10,000	0.667	82.8	7.87
Swath removal (2h)	$w = 15$	25%	90,000	0.875	96.6	9.18

Figures
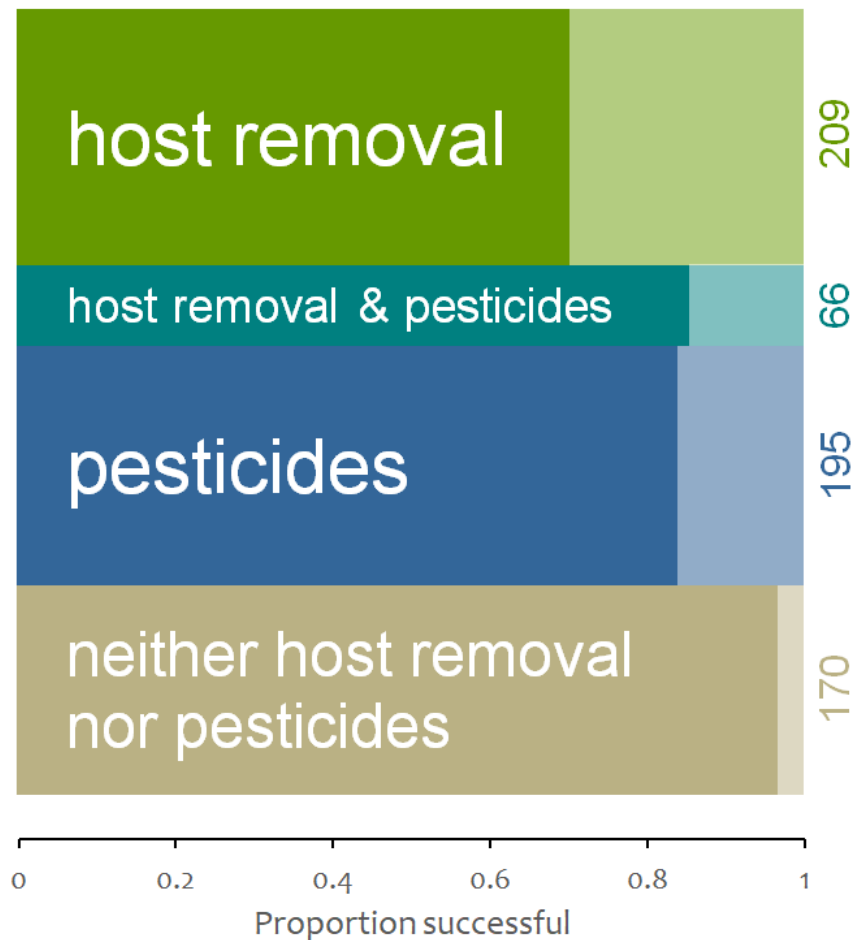
Figure 1. Number of insect and plant pathogen eradication programmes that have used host removal, pesticides, both, or other method. Bar height is proportional to the number of cases (shown on the right), including 499 herbivorous arthropods and molluscs, mostly insects, and 141 plant pathogens. Darker shaded areas indicate the proportion of programmes that were successful and lighter shaded areas correspond to failed eradications from the 534 programmes where the outcome was known. Data were sourced from the Global Eradication and Response Database (GERDA) on 27 November 2017 (Kean et al., 2017).
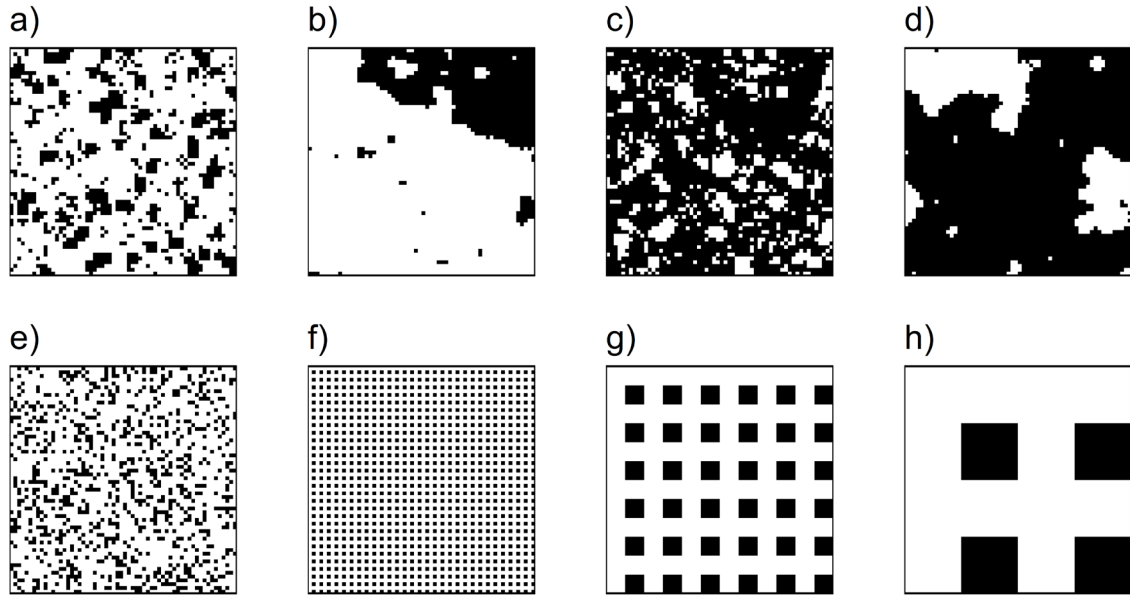
Figure 2. Examples of habitat maps used in simulations, white areas indicate non-habitat, black areas indicate habitat. Maps a-d were generated with the modified random clusters method (Saura & Martínez-Millán, 2000) with low (a,b) and high percentage habitat *A* (c,d) and high (a,c) and low (b, d) levels of fragmentation *q* (the values of *A* and *q* for maps a-d were as follows: a, *A*=25%, *q*=0.1, b, *A*=25%, *q*=0.45, c, *A*=75%, *q*=0.1, d, *A*=75%, *q*=0.45). Maps e-h all have 25% habitat and habitat patches were created randomly (e) or by using alternating swaths (f-h) of 20, 100 or 300 m respectively.
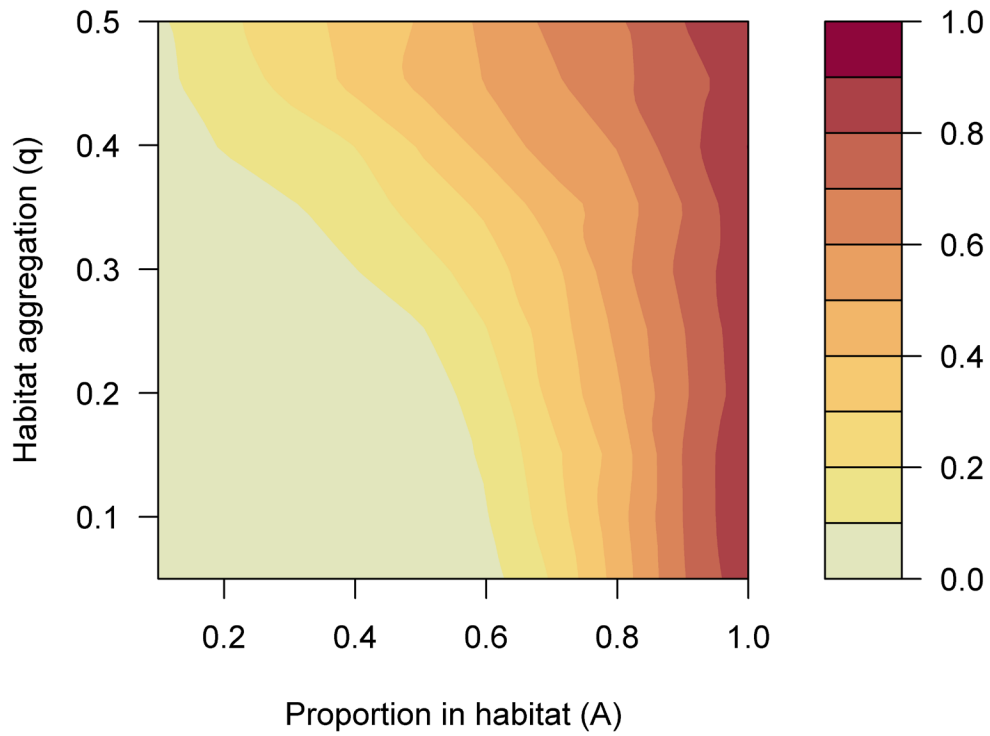
Figure 3. The proportion of simulated gypsy moth populations persisting (i.e., not going extinct) shown in coloured contours for at least six generations with varying percentage habitat and levels of habitat patch aggregation.
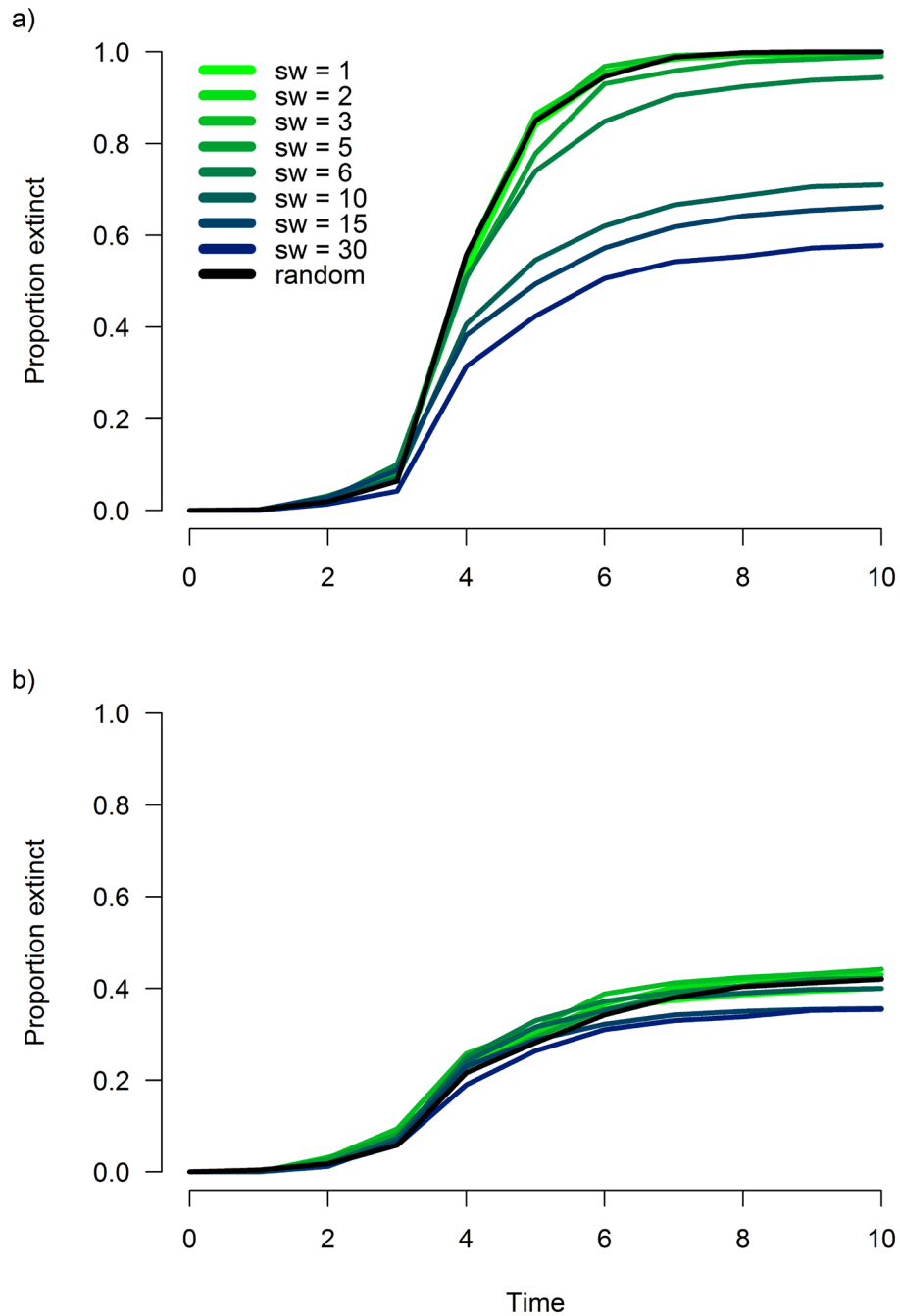
Figure 4. The proportion of simulated gypsy moth populations going extinct under varying swath widths ("sw") of a) host removal or b) pesticide application.
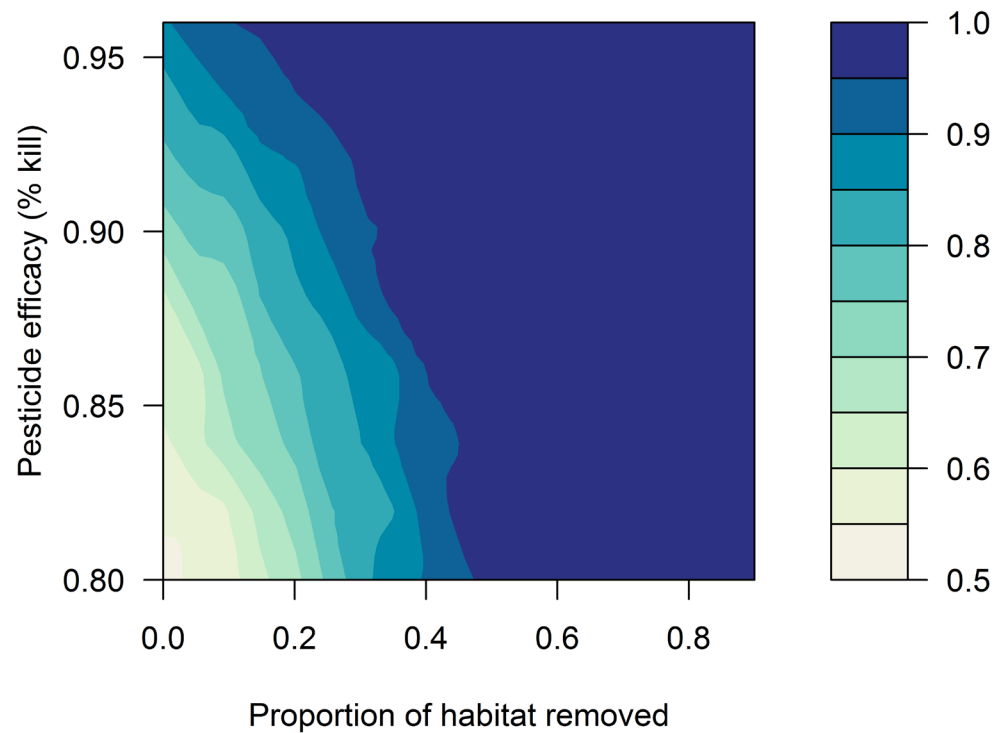
Figure 5. The proportion of gypsy moth populations going extinct (coloured contours) following application of simulated controls comprising varying levels of combined habitat removal and pesticide efficacy. Populations were assessed six generations after control was applied.

Supplementary Information (on-line only)

Supplementary Table S1: Landscape statistics for varying fragmentation levels and proportions of habitat.
(Excel File: Suppl_Table_1-LandscapeStatsForVarFragnPropHab.xlsx)

Supplementary Table S2: Summary (pivot table) of landscape statistics for varying fragmentation levels and proportions of habitat.
(Excel File: Suppl_Table_2-LandscapeStatsForVarFragnPropHab-Summary.xlsx)

Supplementary Table S3: Landscape statistics for different swath widths.
(Excel File: Suppl_Table_3-LandscapeStatsForDiffSWs.xlsx)

Supplementary Table S4: Comparison of landscape statistics for swath widths vs random clusters (for 25% habitat).
(Excel File: Suppl_Table_4-LandscapeStats-Comparative-SwathsvsRandClust.xlsx)

Supplementary Table S5: Metapopulation model outcomes for later intervention (at T = 6) and for a larger number of initial egg masses (N = 8) across a range of swath widths.
(Excel File: Suppl_Table_5-SummarySimsDiffInterventTimesAndInitNumEggMasses.xlsx)

Supplementary Figure S1: The proportion of simulated gypsy moth populations going extinct under varying swath widths ("sw") of host removal with 5 initial egg masses and intervention beginning at T = 6 (instead of T = 4).
(Png File: SupplFigS1-HabRemSWsIntT5.png)

Supplementary Figure S2: The proportion of simulated gypsy moth populations going extinct under varying swath widths ("sw") of host removal with 8 initial egg masses (instead of 5 egg masses) and intervention beginning at T = 4.
(Png File: SupplFigS2_HabRemSWs8initEm.png)

Supplementary File S1: R code of the metapopulation model.
(Png File: SupplFileS1-R_code-MetaPopTidy.R)