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Field margins provide a refuge for pest genes beneficial to resistance management

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Abstract
Fencelines and field margins in broad-acre cropping systems are commonly a refuge for weeds, diseases and invertebrates because they avoid many cropping and pest management regimes applied inside fields. As such, fenceline refuges are often managed separately with the goal to reduce pest reinfestation of fields from the margins. However, the implications of these pest control strategies are poorly understood in terms of their impact on pest genes beneficial to pesticide resistance management. Fenceline management, such as selectively reducing pest populations through insecticides, or non-selectively modifying habitat quality by removing host weeds with herbicides, might increase or decrease resistance evolution rates. Indeed, the potential to perform selective and non-selective control of pests separates management of field margins from structured in-field susceptible refuges (e.g. *Bt* crops). Here, a simulation approach was used to explore the effect of different fenceline management strategies, cropping characteristics and pest genetics on resistance evolution. The analysis was applied to a major crop pest, the mite *Halotydeus destructor*, for which fenceline treatments of herbicides and insecticides may be applied. Spraying fencelines with an insecticide decreased reinfestation and the overall abundance of mites, compared with not applying insecticides to fencelines. However, in all scenarios tested, resistance evolution was delayed by leaving fenceline refuges unsprayed with insecticides or herbicides. Just as field margins may provide a reservoir for invertebrates beneficial to pest management (e.g. predators and parasitoids), they may also serve as an important refuge for genes beneficial to resistance management.

Keywords Integrated pest management · Insecticide · Pesticide · Resistance · Evolution · Dispersal · Acari · Spatially explicit

Key message

- Field margins may provide a source of pests for crop reinfestation but may also act as reservoirs for genes beneficial to resistance management.
- Here, we test how management of field margins impacts their function as a reservoir for genes beneficial to resistance management.
- Using a simulation approach informed by biological data for a mite pest, we show that both selective and non-selective control of fenceline populations reduced reinfestation rates, but accelerated resistance evolution.

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Introduction

In broad-acre cropping systems, fenceline areas, which typically extend several metres either side of a fence, cannot be easily accessed by farm machinery used for sowing or chemical applications, and consequently become a refuge for non-crop plants and invertebrates (Wilson and Aebischer 1995). In some cases, fenceline biodiversity may pose little direct threat or may even be viewed as beneficial to crop growth (Marshall and Moonen 2002; Karp et al. 2018). For pests, this is particularly so when the species is slow moving, or population sizes are relatively small, and thus unlikely to move into fields to a large degree. The avoidance of unnecessary insecticide applications to fencelines can reduce operating costs, environmental impacts and harm to beneficial invertebrate populations. On the other hand, fencelines may provide habitat for invertebrate pests whose long-term persistence and risk of reinfestation from field margins can compromise production activities (Frank 1998; Karp et al. 2018). This is also true for pest genes or biotypes that make management more difficult—a rare event like a resistance mutation is more likely to occur when population sizes are large.

Fenceline management through the applications of insecticides and/or herbicides has been proposed as a means to help manage invertebrate crop pests, by decreasing population numbers and the habitat suitability of non-crop areas and thus rates of crop infestation (e.g. Umina et al. 2016). It is plausible that chemical sprays can be reduced to limit the selection pressure for resistant biotypes, without incurring economic losses, particularly when fenceline suitability is low and resistance tends to recessiveness (Georghiou and Taylor 1977). However, the implications of these interacting pest management strategies have not been formally investigated in terms of their impacts on resistance evolution, particularly for invertebrate pests, where resistance issues commonly result from short-term pest management priorities (i.e. excessive insecticide usage that reduces pest populations in the short-term tends to accelerate resistance evolution and cause long-term pest problems). Non-selective reduction in fenceline pest populations can theoretically reduce or increase resistance evolution; smaller populations lead to fewer mutation events but, due to genetic drift, smaller populations also increase the establishment potential any immigrating alleles (Roush and Tabashnik 1990). Untreated field margins can provide a pool of susceptible individuals, which may be important in delaying the evolution of resistance (Storer et al. 2003). At the same time, untreated field margins can act as a reservoir of pests that may increase reinfestation rates and the requirement for

in-field pest management, such as insecticide applications (Karp et al. 2018).

The importance of refuges as a reservoir of susceptible biotypes forms the mainstay of resistance management in transgenic *Bt* crops such that deliberately planted and untreated refuges are required as part of product licensing (Bourguet et al. 2005; Tabashnik et al. 2008). While sharing similarities with respect to resistance evolution, field margins depart from the refuge concept in some key areas. Reinfestation of the crop from *Bt* refuges is not a concern with respect to pest damage and does not increase the requirement for in-field pest controls that interact with resistance. For field margins, there is the option to manage pest populations both selectively (e.g. insecticides) and non-selectively (e.g. removal of host weeds) to reduce reinfestation and the requirement for in-field controls. Thus, the interaction between the genetics of resistance and the management options available in field margins are different to refuges.

Computer simulations provide a powerful tool for understanding and predicting evolution of resistance to insecticides (Tabashnik 1990; Caprio and Tabashnik 1992; Alstad and Andow 1995; Caprio 1998; Onstad and Gould 1998; Bates et al. 2005; Tabashnik et al. 2008; Renton et al. 2014; Stratonovitch et al. 2014), particularly in situations where spatial heterogeneity is important and analytical approaches become intractable (DeAngelis et al. 1992; Storer et al. 2003; Somerville et al. 2017). Simulations have been used extensively to represent resistance evolution in invertebrate crop pests (Renton 2013) and to predict the effect of spatial refuges on the evolution of resistance to insecticides in mobile insects in high-dose/refuge resistance management strategies (Storer 2003; Storer et al. 2003). To our knowledge, no simulation studies have been conducted to explore the interaction of fenceline management (e.g. for disease, weeds or pests) with insecticide resistance evolution. This would be particularly informative for slow-moving and persistent crop pests like mites or Collembola, where a fine spatial resolution is required to capture spatial heterogeneity of management decisions as well as the large heterogeneity in population numbers that occurs through time.

Here, we developed a fine-scaled spatially explicit model to explore the impact of fenceline management on resistance evolution in slow-moving invertebrate crop pests. The model is parameterised with particular reference to the mite species *Halotydeus destructor* (Tucker), which is one of Australia's most economically important broad-acre crop pests. There has been a substantial amount of research on this pest, particularly following recent insecticide resistance evolution events, and findings can be used to parameterise model components and ensure relevance to field conditions. Like many other invertebrate pests living close to the soil surface, *H. destructor* is a largely resident pest that prefers cool, wet environments (Ridsill-Smith 1997). Pyrethroid

insecticides are routinely used to control crop pests, including *H. destructor*, which now possesses field-evolved resistance to pyrethroid pesticides in over 50 locations across southern Australia (Umina 2007; Maino et al. 2018a, b). A resistant population is ~ 200,000 times less susceptible to some pyrethroids than a non-resistant population (Umina 2007). The mechanism conferring pyrethroid resistance has been identified as a single-nucleotide polymorphism (*kdr*) in the para-sodium channel gene (Edwards et al. 2018). More recently, *H. destructor* has evolved moderate resistance (~ 40 times) to organophosphorus insecticides (Umina et al. 2017). In the present study, we only consider pyrethroid resistance, which has been studied and resolved in much greater depth; thus, 'resistance' hereafter is used with respect to pyrethroid resistance.

Specifically, we aimed to answer the following questions: (1) How does selectively reducing fenceline populations (i.e. through insecticide applications) affect the rate of resistance evolution across a field? (2) How does the non-selective reduction in the suitability of fencelines (e.g. host-weed removal) affect the rate of resistance evolution? and (3) How does the impact of fenceline management on resistance evolution rates depend on the recessiveness of resistance?

Methods

The following describes the design of a simulation model that captures the scenario in which resistance arises locally in a typical broad-acre field and has not yet spread (i.e. is in one grid cell). The model source code written in R is accessible in supplementary information. The behaviour of the model is explored to understand how the subsequent spread and evolution of resistance is impacted by different biological and management factors. This scenario was seen to be relevant for many practical situations including (1) when a small resistant population is introduced through human-mediated processes such as transported silage with resistant eggs attached, or contaminated soil attached to farm equipment, or (2) when a mutation arises and becomes established locally. In these cases, detection can occur before further spread, and thus containment or eradication may be possible. Human activities are increasingly appreciated as important in ecological dispersal processes (Capinha et al. 2015) and have been implicated in resistance spread in *H. destructor* using a phylogenetic approach (Hoffmann, unpublished). A model schematic is shown in Fig. 1, with model details provided in Table 1.

One generation is simulated each time step with no overlapping generations. [There are approximately three generations per year (Ridsdill-Smith 1997).] Populations of each biallelic resistance genotype (SS, RS, RR) for each sex (male and female) are tracked in each 10 m cell in the
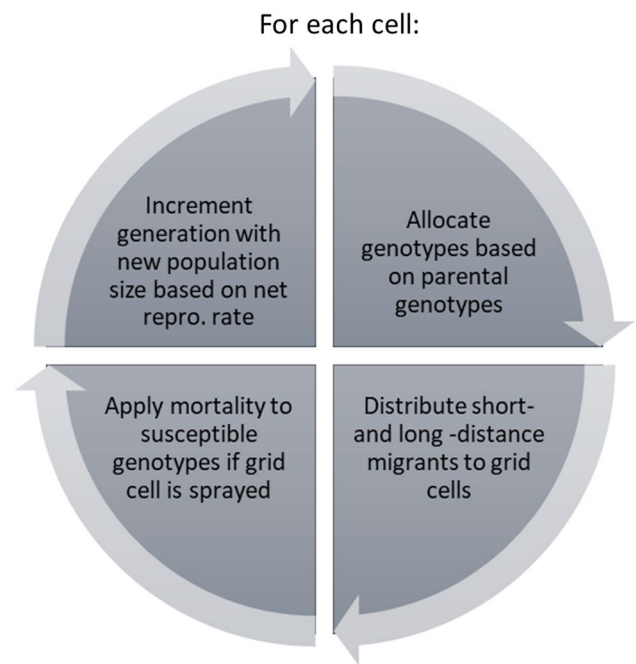
Fig. 1 Schematic of the simulation framework outlining how the grid of mite populations is updated with each generation time step

120 × 120 grid. Each grid cell can either represent a fenceline or field, each of which has a fixed mite suitability level (*S*) from 0 to 1.0 that directly scales the maximum net reproduction rate (*R*) rate and maximum population (*K*) in each cell. For each generation, dispersal, mating, reproduction and selective mortality (if insecticide is applied) are simulated as described below.

Dispersal is implemented as short-distance and long-distance migration events. Short-distance migration events represent individual mites walking across soil and vegetation (Weeks et al. 2000), while long-distance dispersal events represent passive and more stochastic dispersal process, such as eggs laid on vegetation or cadavers with viable eggs inside that are moved around the landscape by wind or contaminated farm equipment (Ridsdill-Smith 1997). In long-distance dispersal events, multiple individuals disperse from an origin to a destination, in contrast to short-distance dispersal in which individual mites actively move throughout the landscape.

Short-distance migration into the eight immediately adjacent cells occurs first. The probability of short-distance dispersal at each dispersal step is mr and migration into each of the eight neighbour cells scales inversely with distance (i.e. bordering cells are $\sqrt{1^2 + 1^2}$ more likely as a destination than diagonals cells). The number of dispersal steps per generation is msteps where a maximum of msteps cells can be traversed via short-distance dispersal per generation. The dispersal parameters for short-distance

Table 1 Description, units and justification of fixed and varied model parameter values used in simulations

Parameter	Value	Description	Justification
Parameters fixed in sensitivity analysis			
C	10	Linear dimension in metres of each grid cell	See Fig. 2
mr	0.10	Migration rate, probability of leaving cell (into adjacent cell) each local migration step	See Fig. 2
msteps	4	Number of local migration steps per generation	See Fig. 2
lmr	1.0×10^{-7}	Long-distance migration probability	See Fig. 2
S(field)	0.50	Suitability in a field cell is taken as half the theoretical maximum (i.e. an idealised weedy fenceline). This is used to proportionally reflect lower reproduction rate and carrying capacity in field cells compared with weedy fencelines	(Maclennan et al. 1998; Umina and Hoffmann 2004; Cheng et al. 2018)
K	40,000	Carrying capacity, individuals per m^2 at maximum suitability	(Ridsdill-Smith 1997)
R	20	Net reproductive rate, N/individual/generation	(Ridsdill-Smith 1997)
M	0.999	Generational mortality rate when sprayed	(Gower et al. 2008)
ET	5000	Threshold density of mites per cell that triggers spraying	(Umina and McDonald 2015)
Parameters varied in sensitivity analysis			
sprayfences	TRUE, FALSE	Binary variable; when TRUE, fences are sprayed with insecticide sprays	
h	0, 0.01, 0.05, 0.25, 1	Genetic dominance of resistance; survival rate of heterozygotes compared to homozygous resistant individuals	
S(fenceline)	1.0,0.1	Fenceline suitability is directly proportional to net reproductive rate and carrying capacity in fenceline cells (maximum reproduction when $S=1$).	
apply.ET	TRUE, FALSE	Binary variable; when TRUE, simulate spraying once population averaged across all cells reaches ET density, otherwise spray every three generations irrespective of population size	
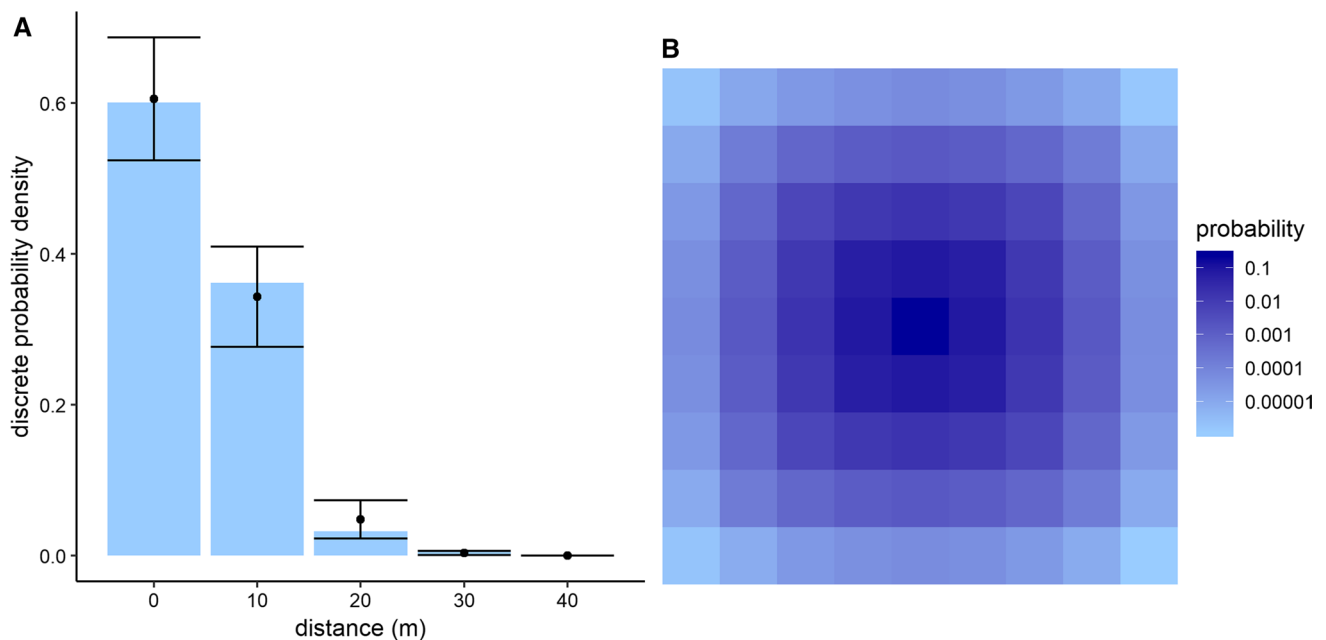
Fig. 2 a Discrete dispersal kernel used in current simulation (bars) for 10-m grid cells plotted against means (circles) and standard errors of discretised dispersal kernels measured by Weeks et al. (2000), for seven *H. destructor* populations after one generation (8 weeks). **b** Discrete two-dimensional dispersal kernel where the legend represents the probability of moving from the centre cell to each surrounding cell with each generational timestep

migration were calibrated against empirical spread data for *H. destructor* in Weeks et al. (2000) (Fig. 2).

Long-distance dispersal is simulated as a separate binomial trial for each cell where the probability of long-distance dispersal is lmr followed by randomly choosing the single shared location for all long-distance migration individuals from that cell. As migration is typically the most computationally expensive step in spatially explicit models, dividing dispersal into short distance and long distance is one method to achieve computational efficiencies, while capturing realistic features of dispersal in *H. destructor*.

Mating in *H. destructor* is dioecious (Ridsdill-Smith 1997) and assumed to be random within each cell. Likewise, the sex of offspring is allocated randomly with equal probability. If males are present in a cell, females will produce a number of offspring that is randomly drawn from a Poisson distribution (mean = SR). Both males and females follow the same dispersal, mortality and survival functions. Only two alleles at one locus are considered in this model following characterisation of *kdr* pyrethroid resistance in *H. destructor* (Edwards et al. 2018). The expected population size in the next generation ($E(N_{t+1})$) depends on the current number of individuals in a cell (N_t), the net reproductive rate (R) and the cell suitability (S), such that $E(N_{t+1}) = SRN_t$ until the maximum population for the cell (SC^2K) is reached. At this point, the net reproduction of each individual is reduced such that the size of the next generation is set equal to the maximum.

Insecticide-induced mortality was applied as a binomial trial to sprayed populations, with homozygous susceptible individuals dying at a rate of M and heterozygous resistant individuals at a rate of $M(1 - h)$. Homozygous resistant genotypes suffered no insecticide-induced mortality (as *kdr* resistant mites are up to 200,000 times less susceptible to pyrethroids, far greater than required to survive field exposure).

The model represents a square 1-km field surrounded by a 10-m-wide fenceline area with a 100-m buffer outside the field. This arrangement would not be unusual in a broad-acre cropping situation in Australia. Almost all cells were assumed to start with an initial population of fully homozygous susceptible mites at a density of SK. Resistance was initialised by setting a density of 500 homozygous resistant individuals per m² in the single grid cell closest to the bottom-right fenceline intersection but inside the field. This scenario aimed to simulate a situation whereby resistance had entered the field through human-mediated processes (e.g. transported silage with resistant eggs attached, or contaminated soil attached to farm equipment). Simulations were conducted under a variety of scenarios given in Table 1. Each combination of parameter values in Table 1 was tested in order to evaluate the sensitivity of predicted time to resistance to different combinations

model parameter values (resulting in $2 \times 5 \times 2 \times 2 = 40$ unique parameter combinations).

Fencelines were either sprayed with an insecticide (sprayfence = TRUE) or not sprayed (sprayfence = FALSE) each time an insecticide was applied to a field, where generational mortality was implemented in the same way as described above. Timing of insecticide applications was decided dynamically (apply.ET = TRUE) after the average mite density across all field cells exceeded a predetermined economic threshold density (ET), with sprays capped at no more than once in three generations, while for calendar spraying (apply.ET = FALSE) timing was fixed at once every three generations, corresponding to about once a year, which is common practice for *H. destructor* control in Australia (Gower et al. 2008).

Non-selective fenceline management was simulated by lowering the habitat suitability of fenceline grid cells (fence. suit = 0.1) from its default maximum suitability (fence. suit = 1.0). For *H. destructor*, this could include the removal of broadleaf weeds through herbicide applications to fencelines (which reduces food availability), or minimising overall vegetation cover to decrease microclimate suitability (lower moisture and higher temperatures) through, for example, heavy grazing (Ridsdill-Smith and Annells 1997; Micic and Lord 2018).

To quantify the impact of each scenario on resistance, we compared the time to 50% resistance (defined to be when more than half the mite population (N) were no longer susceptible to the insecticide or equivalently when (h $N_{RS} + N_{RR}$)/$N_{total} > 0.50$ where h is the level of dominance). This was used instead of resistance allele frequencies, which must be considered in the context of the dominance of resistance and frequencies of heterozygotes. To smooth spikes in resistance frequencies that occur immediately after a spray, we used a moving average across three consecutive generations to determine time to resistance. As the simulations were stochastic rather than deterministic, we replicated each simulation five times to estimate the variability, which was small, even with this low number of replicates (as demonstrated by the nearly invisible error bars in Fig. 3).

To address some secondary questions, as well as further test the robustness of model assumptions, we performed additional simulations (see supplementary information) that explore the effect of initial resistance conditions, crop-host suitability, fitness costs, long-distance migration and application concentration of insecticide. These additional results are briefly summarised at the end of the results section.
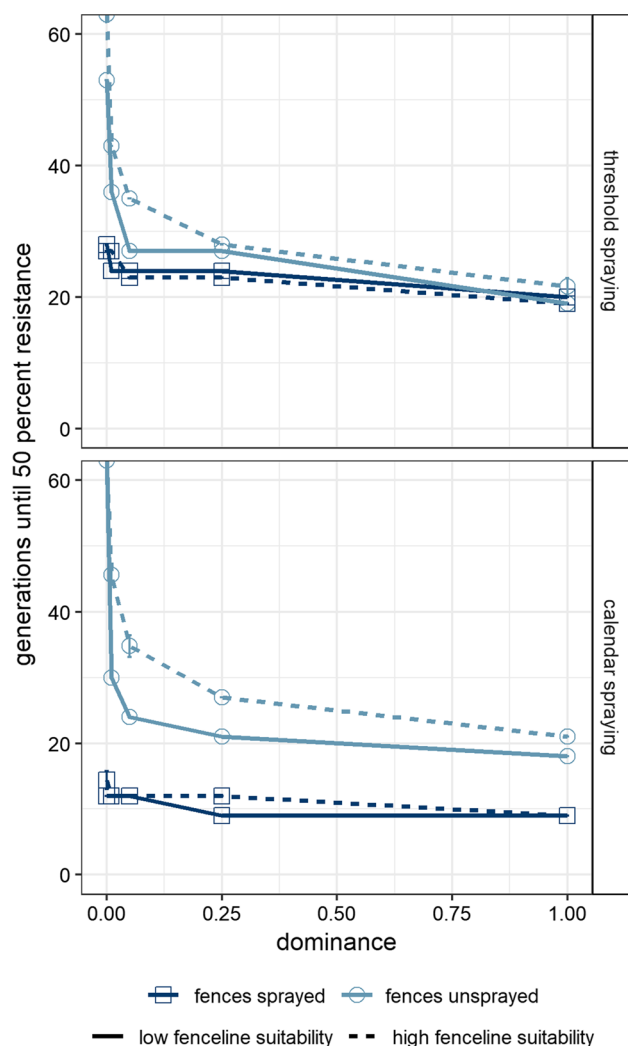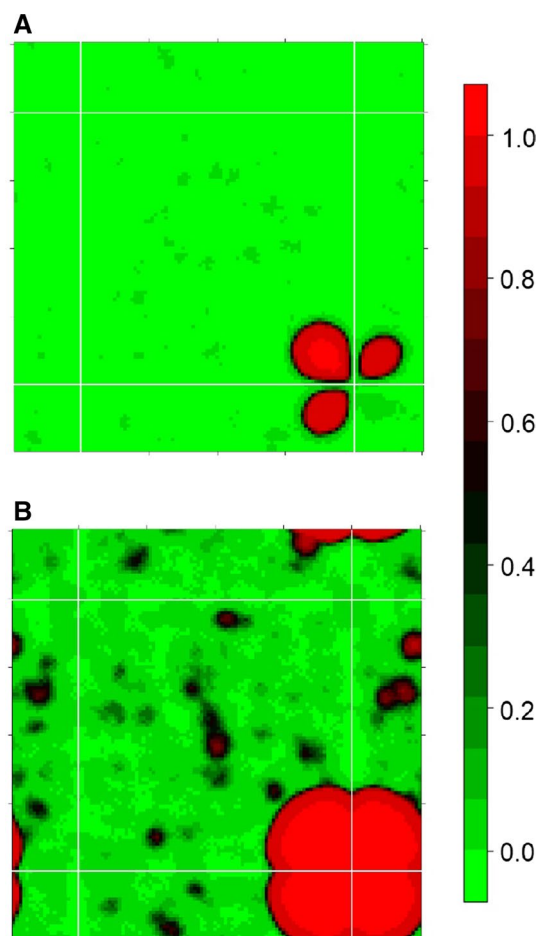
Fig. 3 Time to resistance in *H. destructor* predicted for different simulation settings where the spray regime, dominance of resistance, fenceline suitability and spraying of fencelines with insecticides was varied. Spray regimes included threshold spraying whereby control was implemented after average population density exceeded an economic threshold, or calendar spraying, where control was implemented every three generations regardless of population levels. Low fenceline suitability reflected the case where reproduction rate and carrying capacity in fenceline cells were 10% of the high fenceline suitability. Bars show standard deviations resulting from five replicates, which was often near zero

Fig. 4 Resistance distribution in H. destructor (proportion of R alleles) after 30 generations for two simulations where resistance was initiated in the bottom right of the field closest to the fenceline corner. For panel A, sprayfence=FALSE, whereas for panel B sprayfence=TRUE. Other parameter values were the same for both simulations: mr=0.35, msteps=4, lmr=1e−07, apply.ET=TRUE, S(fenceline)=1, $h=0.01$

Results

Keeping fencelines unsprayed with insecticides slowed the time to resistance evolution in all scenarios (Figs. 3, 4). The reduction in time to resistance was particularly pronounced when fenceline suitability was high and dominance was low.

The use of economic thresholds generally reduced the total number of sprays used, particularly when fenceline suitability and dominance was low, and when fencelines were sprayed (Fig. 5). Under this scenario, it took longer

for mites to reinfest paddocks and subsequently fewer insecticide sprays were required to maintain low populations. Keeping fencelines unsprayed often increased the total number of sprays required in the field when applying economic thresholds; however, unsprayed fencelines always slowed resistance evolution, particularly when fenceline suitability was high (Figs. 3, 5). This pattern increased when the recessiveness of resistance increased (Fig. 3). The accelerating effect of spraying fencelines with insecticides on resistance is of particular significance in cases where economic thresholds were applied, which might be expected to result in fewer required insecticide sprays and consequently delay resistance evolution. Higher dominance accelerated resistance evolution, but resulted in slower times until fixation of resistance alleles due to the functional resistance of heterozygotes. Non-selective
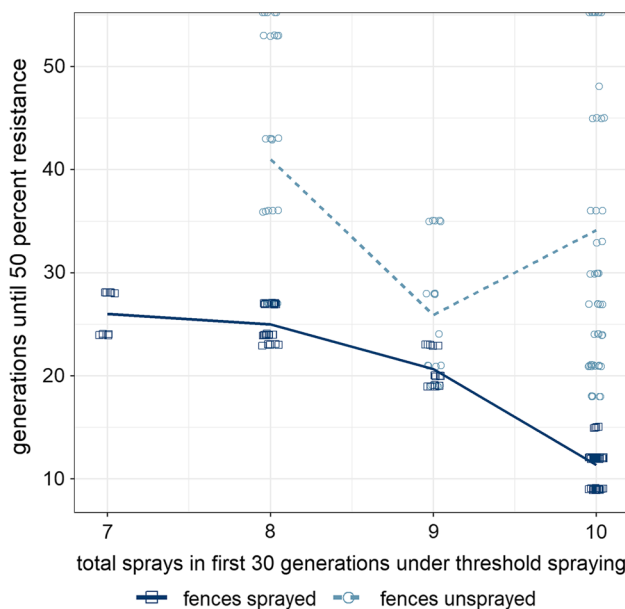
Fig. 5 Time to reach 50% loss of insecticide control efficacy for H. destructor plotted against the total number of insecticide applications applied under an economic threshold scenario across all parameter combinations and replicates. Means for each group shown by lines. Spraying fencelines can decrease the total number of insecticide applications required under an economic threshold scenario but nearly always accelerated the time to resistance

reduction in fenceline populations accelerated resistance (Fig. 3).

To briefly summarise results of additional simulations (see supplementary information), moving initial resistance towards the paddock centre generally delayed resistance, decreasing crop-host suitability generally delayed resistance, fitness costs delayed resistance, increased long-distance migration accelerated resistance and lower insecticide-induced mortality delayed resistance. Importantly, none of these additional simulations changed key qualitative findings around the impacts of fenceline management on resistance.

Discussion

This work suggests the evolution of resistance in *H. destructor* is likely to be accelerated in paddocks where resistance is present in isolated patches if fencelines are sprayed with insecticides. This result held across all parameter combinations explored in our simulation study and highlights an example of when short-term management goals (reducing reinfestation of pests from fencelines) can conflict with long-term management goals (slowing resistance evolution).

In essence, our model considers a specific case of the 'high-dose/refuge strategy' for limiting resistance evolution (Comins 1977a, b; Gould 1998; Huang et al. 2011) where

heterozygotes are killed, resistance starts at a low frequency, and refuges provide a continual influx of susceptible alleles. However, the approach taken departs from previous genetic refuge studies in its consideration of multiple management objective (fencelines may be managed as a refuge for crop pests, weeds, and disease as well as beneficial genes) and the fine spatial scale (~ 10 m) required for studying dispersal processes in a slow-moving pest.

The inclusion of an economic threshold decision for chemical application ensured insecticides were applied before mite densities reached damaging levels, which avoided economic losses so long as the insecticide remained effective. Compared with calendar spraying, economic thresholds reduced the total number of field sprays required and generally delayed resistance evolution. Surprisingly, the total sprays required under a threshold approach were less if fencelines were also sprayed; however, in this context, the reduction in total sprays accelerated resistance. This suggests that while fewer insecticide applications generally delay resistance evolution, it depends on spatial heterogeneity in population numbers and resistance frequencies.

Non-selective reduction in pest populations along fencelines (e.g. host-weed removal, control from predators) also accelerated time to resistance by decreasing the size of the susceptible population that would mix with resistant individuals, thereby decreasing the influx of susceptible alleles. This parallels findings of high-dose/refuge strategies where larger susceptible refuges delayed resistance evolution in *Bt* crops (Storer et al. 2003). In the absence of resistance having evolved (*i.e.* if we had considered random mutations as the source of resistance), the non-selective reduction in population size might be expected to slow evolution through a reduction in total mutation events. However, in our simulation where resistance had established locally (i.e. in one grid cell) lowering fenceline population size had the opposite effect. Conversely, lowering field suitability (e.g. through a less-suitable crop host) decreased the field population size and increased the effect of the susceptible refuge population, delaying resistance (see supplementary information for additional simulations). Thus, even partially resistant plant varieties are an important tool in managing pesticide resistance.

The dominance (or recessiveness) of the resistance allele interacted with fenceline management to impact evolution of resistance, which would be expected from previous refuge studies (Gould 1998; Ives and Andow 2002; Sudo et al. 2018). Dominance also modulates the impact of refuge size on rates of resistance evolution (Takahashi et al. 2017). Results showed a highly nonlinear increase in time to resistance as resistance tended to recessiveness, although dominance had little impact when fencelines were sprayed with insecticides. The dominance of *kdr* resistance in *H. destructor* has not yet been quantified formally but several lines of evidence support the notion that resistance is

largely recessive. As part of national resistance screening efforts, multiple resistant populations have been found with resistance allele frequencies near fixation (Umina, Maino, unpub. data). The time to fixation increases with the level of dominance; more intermediate resistant allele frequencies would be expected if resistance tended towards dominance. Edwards et al. (2018) found *kdr* allele frequencies in a range of resistant populations correlated linearly with bioassay survival, suggesting intermediate dominance (i.e. because the proportion of functional resistance scales approximately as $2hp + (1 − 2h)p^2$ or p when $h = 0.5$ where p is the resistance allele frequency). However, more recent and direct data on *kdr* dominance based on genotyping individual mites exposed to a range of doses of the pyrethroid bifenthrin (separated as alive or dead) has recently suggested *kdr* resistance is closer to recessive (Xuan Cheng pers. comm.). If resistance is confirmed to be recessive in *H. destructor*, our results demonstrate there are considerable opportunities to actively manage susceptible refuge populations. This could extend beyond fenceline management. For example, a strategy for heterogeneous insecticide applications in crops might encourage a level susceptibility in the field to reduce homozygous resistant individuals below problematic levels. This may be achieved by simply leaving patches of a field unsprayed, or by using a mixture of chemical groups in a mosaic (Roush 1998)—although some field studies have shown pesticide mosaics accelerate resistance evolution compared with chemical rotation (Zhao et al. 2010). Previous simulation studies have emphasised the importance of susceptible survivors in crops in retarding resistance evolution (Comins 1977a).

The nature of fitness costs associated with resistance can have important effects on evolutionary outcomes (Roush and McKenzie 1987; Hackett and Bonsall 2016), but these effects were not explored in great detail in our study as there is little evidence for large fitness costs of pyrethroid resistance in *H. destructor*. Resistance levels have remained at high levels in monitored field populations for a number of years, even after pyrethroid applications had been withdrawn (Maino, unpub. data). Nonetheless, the effects of fitness costs were explored through a reduction in net reproduction that scaled with resistant allele numbers (see supplementary information). Even with large fitness costs (50% reduction in net reproduction for RR individuals), there were only modest effects on the time to resistance. Fitness costs would play a larger role in cases where selection pressure is less intense, e.g. chemical controls are used rarely, or at lower concentrations.

As with any simulation study, necessary simplifying assumptions were made so that the model's behaviour could be transparently explored, while focussing on the key processes relevant to our research questions. In short, management practices, genetics, spatial heterogeneity and local dispersal processes were prioritised. Future studies might additionally include effects of age structure, or overlapping generations, to explore variable mortality through time (e.g. as a chemical degrades) or by life stage (e.g. eggs are not affected by insecticides). Similarly, inclusion of predator populations, which often rely on non-crop areas to persist, may interact in interesting ways with chemical controls and resistance evolution. Nevertheless, despite our model's simplicity it was parameterised using decades of cumulative scientific knowledge on the behavioural, ecological and genetic biology of *H. destructor* and our study produced some counter-intuitive, though logical, predictions. Such insights will be important to help guide future field studies that aim to explore these processes under realistic conditions. We suspect that these results can be generalised to other situations and species with similar characteristics.

Current recommendations around fenceline management may require rethinking in light of our findings. Farmers are often encouraged to control weeds with herbicides, cultivation or heavy grazing to decrease mite numbers, as a weed free area will have fewer mites and over-summering eggs to carry through to the following season (Micic and Lord 2018). Disease management practices in field margins can also inadvertently diminish the beneficial gene refuge through altering plant composition. For example, weed control is implemented to reduce sources of plant viruses and other pathogens that can be transmitted to healthy crop plants by vectors such as aphids (Jones et al. 1990). A more holistic solution might be direct sowing of desired host plants varieties in field margins to support multiple weed, pest and disease management objectives (Hatt et al. 2018). The tension between resistance management and pest and disease control is a constant concern, where the impact of management decisions is often difficult to extrapolate to timescales relevant to evolutionary processes. Similarly, the finding that unsprayed fencelines delayed resistance, but increased reinfestation rates, may nevertheless result in some farmers opting to spray fencelines when a higher value is placed on minimising spray frequency. If a susceptible refuge strategy can be demonstrated to be effective for *H. destructor*, incorporation into current resistance management strategies, which suffer from increasingly limited options due to insecticide resistance and regulatory pressures (Umina et al. 2018), would help to maintain control options into the future.

There is increasing evidence that non-crop habitats provide benefits to crop productivity in agricultural systems through their role as refugia or reservoirs for 'beneficial' species (Lee et al. 2001; Swinton et al. 2007; Gardiner and Neal 2009; Skellern and Cook 2018). Our findings suggest that the notion of refugia as a beneficial reservoir can be extended beyond species to include particular genotypes and phenotypes within species. A large reservoir of beneficial

genes in the context of a predatory species could lead to enhanced population fitness under a variety of challenging conditions and consequently enhance pest control or pollination services (Herrmann et al. 2007). Indeed, genetic diversity, as well as species diversity, has been found to positively relate to diversity of non-crop habitats (Shirk et al. 2010) but not in all cases (e.g. Herrmann et al. 2007). Conversely, in the context of a crop pest, a beneficial reservoir might include genes that maintain susceptibility to insecticides (i.e. conditions beneficial to their management).

Authors' contributions

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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