

Which traits promote persistence of feral GM crops? Part 2: implications of metapopulation structure

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Claessen, D., Gilligan, C. A. and van den Bosch, F. 2005. Which traits promote persistence of feral GM crops? Part 2: implications of metapopulation structure. – *Oikos* 110: 30–42.

Transgenes may spread from crops into the environment via the establishment of feral populations, often initiated by seed spill from transport lorries or farm machinery. Locally, such populations are often subject to large environmental variability and usually do not persist longer than a few years. Because secondary feral populations may arise from seed dispersal to adjacent sites, the dynamics of such populations should be studied in a metapopulation context. We study a structured metapopulation model with local dispersal, mimicking a string of roadside subpopulations of a feral crop. Population growth is assumed to be subject to local disturbances, introducing spatially random environmental stochasticity. Our aim is to understand the role of dispersal and environmental variability in the dynamics of such ephemeral populations. We determine the effect of dispersal on the extinction boundary and on the distribution of persistence times, and investigate the influence of spatially correlated disturbances as opposed to spatially random disturbances. We find that, given spatially random disturbances, dispersal slows down the decline of the metapopulation and results in the occurrence of long-lasting local populations which remain more or less static in space. We identify which life history traits, if changed by genetic modification, have the largest impact on the population growth rate and persistence times. For oilseed rape, these are seed bank survival and dormancy. Combining our findings with literature data on transgene-induced life history changes, we predict that persistence is promoted by transgenes for oil-modifications (high stearate or high laurate) and, possibly, for insect resistance (Bt). Transgenic tolerance to glufosinate herbicide is predicted to reduce persistence.

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Feral populations of transgenic crops may serve as sources or stepping stones of gene flow of transgenes from crops to wild relatives. Because genetic modification of plants has direct and indirect effects on life history traits such as germination, dormancy, seed survival and seed production (Crawley et al. 1993, 2001, Parker and Kareiva 1996, Hails et al. 1997, Wolfenbarger and Phifer 2000, Snow et al. 2003) it is important to know which of these changes are likely to

increase or decrease the persistence of feral populations. This gives insight in whether the feral crop populations are likely to cause problems such as gene flow to wild relatives, becoming persistent weeds in arable fields or becoming dominant plants in wild vegetation with consequences for native plants or herbivorous insects.

A commonly used approach for assessing the risk of spread of feral, transgenic crops is to estimate the population growth rate, often referred to as λ or its

Accepted 7 March 2005

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ISSN 0030-1299

logarithm, $\log \lambda$, of the plants in (semi) natural habitats (Crawley et al. 1993, 2001, Parker and Kareiva 1996). Positive population growth and persistence of the population are predicted if the condition $\log \lambda > 0$ is satisfied, while the population is expected to go extinct if $\log \lambda < 0$. Matrix population models are a useful tool to compute $\log \lambda$ based on empirical data of life history processes (Caswell 2001), as well as the sensitivity or elasticity of the population growth rate to changes in life history parameters (de Kroon et al. 1986). Elasticity analysis has been used to determine which traits, if changed by genetic modification, are likely to have a large impact on the population growth rate (Bullock 1999, Claessen et al. 2005).

For the case of oilseed rape both empirical and modelling studies predict that single populations are likely to become extinct. Crawley et al. (1993, 2001) found that experimentally established populations of oilseed rape do not persist for more than a few years, which is consistent with empirical observations of shortlived roadside populations of the same species (Crawley and Brown 1995, 2004). In a recent study of a stochastic matrix population model we have predicted a negative population growth rate unless the habitat is disturbed very frequently (Claessen et al. 2005), reflecting the poor ability of oilseed rape to compete with existing vegetation (Crawley et al. 2001, Walker et al. 2004). Moreover we showed that allowance for environmental stochasticity changed the relative importance of life history traits for the population growth rate when compared with a deterministic model (Claessen 2005, Claessen et al. 2005).

With the exception of Crawley and Brown (1995, 2004), previous analyses of invasion and persistence of feral crop populations have been constrained by focusing on a single, isolated population. The theory of metapopulation dynamics predicts that by ignoring spatial structure and dispersal one underestimates the potential of a spatially subdivided population to persist (Hanski and Gilpin 1997). The best example is the classical metapopulation model of Levins (1969, 1970), which shows that a collection of local subpopulations, each of which will go extinct with certainty, can persist if the rate of recolonisation of unoccupied sites exceeds the rate of local extinctions. Here we extend our original model (Claessen et al. 2005) to allow for metapopulation dynamics.

Many roadside feral populations of oilseed rape originate from seed spillage from lorries that transport harvested seeds to seed crushing plants (Crawley and Brown 1995, Pessel et al. 2001). A typical scenario we study is where a certain (e.g. transgenic) cultivar is being used for a number of years such that seed spills from lorries result in the emergence of patches of oilseed rape along a network of roads, initialising the metapopulation. When the use of the cultivar is stopped the

dynamics of the metapopulation are determined by local dynamics and seed dispersal only. Here we study the effect of dispersal on the population growth rate, on the predicted extinction boundary and on the expected time to extinction of the oilseed rape populations.

Noting that longterm persistence was possible only with a high disturbance rate in our model for an isolated, single population (Claessen et al. 2005), we now ask the following questions. Will sufficient dispersal enable the metapopulation to persist indefinitely? Does the relative importance of life history traits for population growth and persistence time change with metapopulation structure and hence what are the implications of genetic modification? In other words, how robust is the analysis of the stochastic matrix model (Claessen et al. 2005) to the introduction of density dependence and metapopulation structure? Of particular interest is the interaction between environmental variability and dispersal, previously investigated in the simpler context of only two patches by Wiener and Tuljapurkar (1994). They found that dispersal may increase the population growth rate by providing "insurance" against unfavourable conditions. Should we expect this "insurance effect" to be important for feral oilseed rape? In our model the number of sites is very large and dispersal is local, as opposed to the simple two-patch model of Wiener and Tuljapurkar (1994). Does the insurance effect result in the emergence of characteristic spatial patterns and, if so, can they help us detect the presence of this effect?

The model

We extend a stochastic matrix population model for a population in a single site as studied by Claessen et al. (2005) in two directions, to include metapopulation structure and density dependence. Our model incorporates (i) population structure in terms of a seed bank and flowering plants; (ii) dispersal between neighbouring sites; (iii) environmental stochasticity at two spatial scales (local site and whole metapopulation) affecting life history processes. Each local population is characterised in terms of abundance (not merely presence or absence) so our model may be classified as a spatially explicit, structured metapopulation model. We assume that habitat quality is high if the site is disturbed, since this favours the survival of seedlings, and low otherwise, while disturbances are assumed to be random and relatively rare. The chain of sites can hence be seen as a dynamic landscape in which the focus population lives. Yet our model differs from other dynamic landscape models in that we do not consider catastrophic extinctions of sites. For example, in the models of Keymer et al. (2000) and Johst and Drechsler (2003) a local population cannot survive beyond the life span of the habitat. By contrast, in our model a local population

may survive a run of unfavourable years in between disturbances, most likely in the seed bank. Local extinctions may occur if insufficient seed immigration and infrequent disturbances result in local population decline.

Spatial structure

To mimic a string of roadside populations we assume that the metapopulation consists of a chain of k sites, which initially are unoccupied by the focal cultivar. A site is assumed to stretch 100×1 m along a road. The model structure is summarised in Fig. 1 and the model parameters in Table 1. The state variables comprise, the number of plants and the number of seeds in the seed bank and are denoted by $a_i(t)$ and $b_i(t)$, respectively, where $i = 1 \dots k$ refers to the location of the site in the metapopulation. Dispersal is possible between neighbouring sites only. In addition, a site may receive seeds from spillage off lorries (Fig. 1b). We connect the first and last sites as if the string were circular, thus avoiding boundary effects. The structure of the metapopulation therefore resembles the geometry of the string of oilseed rape populations along the M25 motorway orbiting London, UK (Crawley and Brown 1995).

The following derived variables are used: the total abundance in site i , defined as $n_i(t) = a_i(t) + b_i(t)$; and the total fraction of occupied sites $m(t)$, defined as the fraction of sites with $n_i(t) > 0$.

Dynamics of plants and seeds

We describe the dynamics of $a_i(t)$ and $b_i(t)$ with difference equations, projecting the population at the

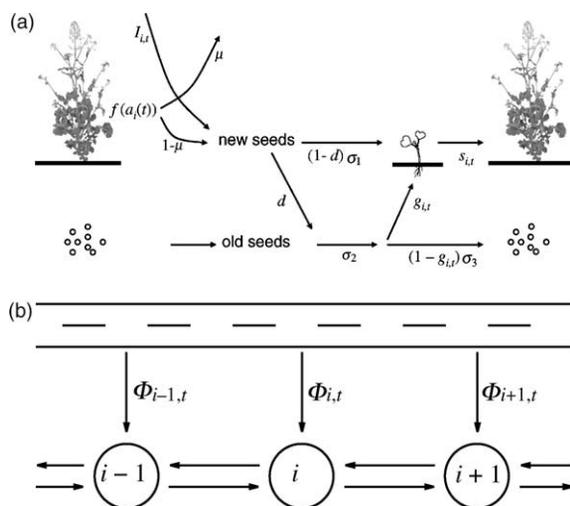


Fig. 1. (a) Life cycle within a single site. (b) The spatial configuration of sites and seed flux. Horizontal arrows indicate seed dispersal from site to site. The parameters are given in Table 1.

time of seed shed from year t to year $t+1$. The dynamics of $a_i(t)$ can be deduced from considering the number of seedlings that settle in site i . Seedlings may emerge from locally produced seed, from immigrating seed, or from the seed bank. Total local seed production is given by $a_i(t) f(a_i(t)) (1-\mu)$, where $f(a_i(t))$ is the density-dependent seed production per adult plant, discussed below, and $1-\mu$ is the fraction of seeds that do not disperse. The total number of seeds that immigrate into patch i , the sum of seed spillage and seed dispersal, is denoted by $I_{i,t}$ and will be specified later. Together, locally produced seeds and immigrating seeds are called new seeds (Fig. 1a), of which a fraction d will become dormant and enter the seed bank. Of the non-dormant fraction $1-d$, a proportion σ_1 survives the winter as seedlings. Finally, of the seeds in the seed bank, comprising both the old ones and the newly incorporated ones, a fraction $\sigma_2 g_{i,t}$ survives the winter and germinates in spring. Taking all these different pathways together, and multiplying with the seedling survival rate, denoted by $S_{i,t}$, we arrive at the equation for the number of flowering plants in year $t+1$ in site i :

$$a_i(t+1) = s_{i,t} [(a_i(t)f(a_i(t)) (1-\mu) + I_{i,t}) ((1-d)\sigma_1 + d \sigma_2 g_{i,t}) + b_i(t)\sigma_2 g_{i,t}] \quad (1)$$

The number of seeds in the seed bank next year equals the sum of the new seeds that are incorporated into the seed bank and the old seeds that do not germinate (Fig. 1a):

$$b_i(t+1) = [(a_i(t)f(a_i(t)) (1-\mu) + I_{i,t})d + b_i(t)] \sigma_2(1-g_{i,t})\sigma_3 \quad (2)$$

where σ_3 is the survival fraction in the seed bank in the summer.

Density dependence: fecundity

We assume that fecundity is density dependent owing to intra-specific competition. The number of viable seeds per flowering plant is assumed to follow

$$f(a_i(t)) = \frac{F_t}{1 + c_F a_i(t)} \quad (3)$$

where F_t is the maximum viable seed production in year t , reached only in the absence of intra-specific competition, and c_F a coefficient for the intensity of competition. The functional form of Eq. 3 provides a good fit to the data of Mendham et al. (1981) on arable oilseed rape. Viability of seeds incorporates the probability to find suitable habitat (i.e. to stay within the roadside verge) which is assumed to be high since most seeds will land close to the mother plant. Dispersal has no effect on viability since the distinction between dispersing and non-dispersing seeds is only made for the sake of bookkeeping: the total habitat (the roadside

Table 1. The model parameters and their default values for non-transgenic feral oilseed rape. Subscripts D and U refer to disturbed and undisturbed habitat, and G and B to good and bad years, respectively. Parameters are based on Claessen et al. (2005). Effect of GM indicates an increase (+) or decrease (-) relative to conventional variety. Transgenes are: OS =high stearate, OL =high laurate (both are oil modifications), Bt =Bt insecticide production, HT =herbicide tolerance (glufosinate).

Process	Symbol	Value	Effect of GM	Ref
Life history parameters				
max fecundity	F_G	3000	}+(Bt)	a
	F_B	1000		
fecundity d.d. parameter	c_F	0.001		
germination	g_D	0.8	}+(OS)	b
	g_U	0.5		
spring seedling survival	S_D	0.3	}+/- (HT)	d
	S_U	0.001		
winter survival of seedlings	σ_1	0.001		
winter survival in seed bank	σ_2	0.6	}+(OS)	e
summer survival in seed bank	σ_3	0.5		
emigration	μ	0.01 (varied)	}-(HT)	d, f
probability of dormancy	d	0.04		
			+ (OS), + (OL)	c
			- (OS), + (OL)	g
			- (HT)	h
Other parameters				
probability of disturbances	p	0.15 (varied)		
probability of seed spill	P_{spill}	0.01 (varied)		
probability of good year	q	0.5		
max size of seed spill	Φ	1000		
number of sites	k	1000 (varied)		
extinction threshold	χ	0.5		
number of time steps	T	1000 (varied)		

Refs: a Stewart et al. (1997); b Parker and Kareiva (1996); c Linder (1998); d Crawley et al. (2001); e Linder and Schmitt (1995); f Hails et al. (1997); g Walker et al. (2004) d = 1 – fraction initially germinated; h Gruber et al. (2004).

verge) is subdivided arbitrarily into sites, and crossing the border between sites has no particular consequences.

Environmental stochasticity: fecundity, germination and seedling survival

We include two types of environmental stochasticity (Claessen et al. 2005); (i) good years and bad years for seed production resulting in variation in F_t ; and (ii) disturbance of the vegetation cover affecting germination and seedling survival. Good and bad years are common to the whole metapopulation and are assumed to occur with equal probability. The maximum fecundity F_t equals F_G in good years and F_B in bad ones, with $F_G > F_B$.

Disturbances are site specific. Each year, disturbances are assumed to occur in all sites independently with a probability p. The effect of spatially correlated disturbances is discussed later. Germination and seedling survival in spring are assumed to depend on disturbance of the existing vegetation cover. A disturbance is assumed to reduce interspecific competition by removing part of the competitively superior vegetation cover (mostly perennial grasses). We assume that both the germination rate $g_{i,t}$ and the fraction of seedlings that can reach the flowering stage, $s_{i,t}$, are high in disturbed habitat and low otherwise,

$$(g_{i,t}, s_{i,t}) = \begin{cases} (g_D, s_D) & \text{if site } i \text{ is disturbed} \\ (g_U, s_U) & \text{otherwise} \end{cases}$$

Migration: dispersal and seed spillage

Sites receive seeds that disperse from neighbouring sites (Fig. 1b). In addition, sites may receive seeds that are spilled from lorries. The number of seeds spilled into site i in year t is denoted $\phi_{i,t}$ and is assumed to be a stochastic variable. The total migration into site i is thus:

$$I_{i,t} = \phi_{i,t} + \frac{\mu}{2} [a_{i-1}(t)f(a_{i-1}(t)) + a_{i+1}(t)f(a_{i+1}(t))]$$

Seed spill occurs in a site with probability P_{spill} . If a spillage occurs, the number of seeds that enter the site is assumed to be a random number between zero and a maximum. Thus,

$$\phi_{i,t} = \begin{cases} \Phi z_t & \text{with probability } P_{spill} \\ 0 & \text{otherwise,} \end{cases}$$

where Φ is the maximum number of seeds per seed spillage and z_t is a random number between 0 and 1 drawn from a uniform distribution.

Extinction

We do not consider true extinction because we model population abundance in terms of density, i.e. a continuous variable not discrete individuals. Instead we use the quasi-extinction concept (Caswell 2001) and define a site extinct if the total abundance $n_i(t)$ falls below a trivial threshold χ , set to $\chi = 0.5$, after which the abundance remains zero until the site is recolonised. The metapopulation dynamics are hence governed by

Eq. 1, 2, for $i=1..k$, in combination with the rule for quasi-extinction, which resets $a_i(t)=0$ and $b_i(t)=0$ whenever the total density in that site falls below χ .

Spatially correlated disturbances

In simulations to study the effect of geographical correlation of disturbances, we assumed that the occurrence of disturbances is locally correlated. We implemented spatial autocorrelation by using a Markov chain with states ‘disturbed’ and ‘undisturbed’ and transition probabilities P_1 and P_2 such that if site i is disturbed, then site $i+1$ is undisturbed with probability P_1 . Conversely, if site i is undisturbed, then site $i+1$ is disturbed with probability P_2 . The process is characterised by the Markov chain transition matrix

$$P = \begin{pmatrix} 1-P_1 & P_2 \\ P_1 & 1-P_2 \end{pmatrix} \quad (4)$$

The expected frequencies of disturbed and undisturbed sites resulting from this Markov process equals the normalised right eigenvector w of P , while the correlation between the state in neighbouring sites, denoted r , equals the subdominant eigenvalue of P (Tuljapurkar and Orzack 1980, Caswell 2001). We define the transition matrix (Eq. 4) in terms of the required stationary frequency of disturbed sites p and the spatial autocorrelation r , by choosing $P_1=1-r-p(1-r)$ and $P_2=p(1-r)$, taking care that P_1 and P_2 remain within $(0, 1)$.

Parameter values

Standard values of the parameters are listed in Table 1. References for the parameterisation can be found in Claessen et al. (2005). The value of c_F is based on experiments in arable fields (Mendham et al. 1981). Our choice of $c_F=0.001$ slightly overestimates the effect of density dependence.

In the absence of reliable estimates for the disturbance rate p and the dispersal fraction μ we can obtain a rough estimate based on Crawley and Brown (1995). They recorded oilseed rape density (discretised into eight density classes) in each 100 by 1 m road verge along the M25 motorway (UK) in 1993 and 1994. They note that almost 20% of sites that were empty in 1993 were occupied in 1994. Assuming (i) that establishment requires disturbance and (ii) the presence of a seed bank (i.e. no seed limitation), then 20% of sites must have been disturbed and a first estimate is hence $p \approx 0.2$. A second and independent estimate can be made based on the assumptions that only sites which are occupied in 1993 and which are subject to a disturbance, will produce a higher density in 1994. Using Table 1 in Crawley and Brown (1995), by summing the probabilities of all transitions from density classes 1–7 in 1993 to a higher

density class in 1994, we obtain $p=0.11$. Based on these rough estimates, we assume $p=0.15$ in our calculations. Most results have, however, been checked for dependence on p . It appeared that the effect of μ on population growth and persistence responds to changes in p in the same way as found for the stochastic matrix model of a single isolated population studied in Claessen et al. (2005).

Since we have very little quantitative information for estimating the dispersal fraction μ , we choose to study the population dynamics for a wide range of μ . The sites in our model are assumed to represent adjacent sites of 100×1 m stretches of roadside verge. We assume that most seeds remain within a few meters of the mother plant. It hence follows that at most a few percent of all the seeds disperse to either neighbour. In analyses for a fixed dispersal rate we therefore choose $\mu=0.01$ as a default value or $\mu=0.05$ to illustrate the effect of high dispersal.

The habitat is assumed to be a spatially continuous strip, flanked by unsuitable habitat. Because new seeds are distributed up to a few meters from the mother plant, a fraction of seeds is likely to end up in unsuitable habitat. This form of seed mortality is included in the definition of “viability”, and its effect incorporated in the value of F_1 (Eq. 3). We assume the probability to end up in unsuitable habitat to be low (<0.2) since most oilseed rape seeds land close to the mother plant. This loss of seeds is equal for all mother plants: the borders that subdivide the habitat into sites are chosen arbitrarily, and therefore dispersal between sites imposes no additional mortality.

Methods of analysis

Simulation scenario

The results below were obtained from studying a scenario of using a cultivar for a number of years (10 unless stated otherwise), after which the use is terminated. Each simulation run hence consists of two phases; an initial phase with seed spills and a final phase without seed spills. Seed spillage during the initial phase results in the emergence of local populations in the roadside metapopulation. The resulting state of the metapopulation is random owing to the stochastic nature of seed spills, and mimics the relevant initial condition for practical questions related to the control of potentially unwanted feral crops. After the termination of seed spillage, the metapopulation persists for a number of years. During the final phase, we keep track of population growth rates and persistence times in the metapopulation, as described below. The length of simulation runs is denoted T and we use values between 200 to 10^4 to estimate the various measures of metapopulation dynamics. The number of

sites is also varied between $k = 200$ and 10^4 . The model was implemented and analysed with the software package `MATLAB`.

Characterising metapopulation dynamics

Persistence time: T_S and T_L

We use two different measure of persistence: site-level persistence (T_S) and the time until last occupancy of a site (T_L). The persistence time at site-level, denoted by T_S , is defined as the time elapsed between colonisation of a site and the first subsequent (quasi-) extinction of the local population in that site. Note that during a single simulation a site can be colonised and go extinct several times. We estimate the expected site-level persistence time $\varepsilon(T_S)$ as the average of all measured persistence times in a metapopulation of $k = 1000$ sites in 200 model runs with $T = 500$.

For each site in the metapopulation we record the last year in which it was occupied, denoted T_L . Unlike T_S , the value of T_L of a site is influenced by potential recolonisations. The expected time until last occupancy, denoted by $\varepsilon(T_L)$, we compute as the average of all non-zero T_L values in the metapopulation in a number of model runs. This is a more global measure of persistence than $\varepsilon(T_S)$, while still being practically independent of the number of sites k (unlike the global extinction time of the metapopulation). For an occupied site at the start of a run, $\varepsilon(T_L)$ is the expected time it takes before the population will not return to that site.

Fraction of occupied sites: $m(t)$

To characterise the steady state of the metapopulation we focus on the long-term average value of $m(t)$, the fraction of occupied sites. In the presence of density dependence (i.e. $c_F > 0$) the metapopulation is expected to converge either to global extinction ($m(t) = 0$) or to a steady state distribution with $0 < m(t) < 1$. To distinguish between extinction and persistence we compute the long-term average of $m(t)$ denoted $E(m(t))$, discarding transient dynamics. We estimate $E(m(t))$ as the average of the last 200 values of $m(t)$ in 100 model runs with $T = 1000$ and $k = 400$.

Local population growth rate: $\log \lambda_s$

We measure population growth at two levels: the local population growth rate (at site level) and the metapopulation growth rate. The former is defined by analogy with the theory of stochastic matrix models. If we simplify the metapopulation model by ignoring immigration of seeds from either dispersal or seed spillage (i.e. setting $I_{i,t} = 0$) and density dependence (i.e., $c_F = 0$), then the metapopulation reduces to a set of k independent sites. The dynamics of each population can then be described with a stochastic matrix population model.

The link with stochastic matrix models provides us with a well-studied measure of population growth: the stochastic population growth rate $\log \lambda_s$. Although this quantity was originally defined for simple stochastic matrices, we use it to characterise the local dynamics in the metapopulation.

The long-term, stochastic population growth rate of $n_i(t)$ is denoted $\log \lambda_s$ and is computed as

$$\log \lambda_s = \frac{1}{kT} \sum_{i=1}^k \sum_{t=1}^T \log \frac{n_i(t+1)}{n_i(t)} \quad (5)$$

with kT sufficiently large (Tuljapurkar 1990, Caswell 2001). We normally use $kT = 10^4$ and $T > 200$ which gives an accurate estimate.

In the metapopulation model the local population growth rate $\log \lambda_s$ (Eq. 5) is the expected growth rate that would normally be observed at any occupied site.

Metapopulation growth rate: $\log \lambda_m$

In analogy with the classical metapopulation models, which describe the dynamics of the fraction of occupied sites (Levins 1969, 1970), we measure the metapopulation growth rate $\log \lambda_m$,

$$\log \lambda_m = \frac{1}{T} \sum_{t=1}^T \log \frac{m(t+1)}{m(t)}, \quad (6)$$

which is the growth rate of the fraction of occupied sites. We estimate $\log \lambda_m$ from the dynamics during the initial 100 years (i.e. long before the steady state $m(t)$ has been reached), and averaged over 100 simulations.

Elasticity of population growth and persistence time

Elasticity is a popular measure of sensitivity of population-level quantities such as the population growth rate to individual-level parameters (de Kroon et al. 1986). The elasticity of the stochastic population growth rate λ_s to a life history parameter, denoted x , is defined as the proportional change in λ_s in response to a proportional change in x . It is computed as

$$e_x = \frac{\partial \log \lambda_s}{\partial \log x} \quad (7)$$

(Caswell 2001). Elasticities of λ_m , $\varepsilon(T_S)$ and $\varepsilon(T_L)$ are defined analogously.

We calculate the elasticities of λ_s , λ_m , $\varepsilon(T_S)$ and $\varepsilon(T_L)$ numerically by determining their relative change in response to a relative change in each parameter separately. For each parameter, we run the model 100 times (i) with the default parameters as in Table 1; (ii) with the focus parameter perturbed by a 10% increase; and (iii) with the focus parameter perturbed by a 10% decrease. If we denote the perturbed focus parameter by x' and the resulting population growth rate by $\log \lambda_{s'}$ then an approximation to the elasticity of λ_s to parameter x is

$$\epsilon_x = \frac{\log \lambda_s - \log \lambda'_s}{\log x - \log x'} \quad (8)$$

For each parameter, we use the two different perturbations to obtain two estimates of elasticity and use the mean of the two results as our estimate of elasticity for that parameter. The elasticities of λ_m , $\epsilon(T_S)$ and $\epsilon(T_L)$ are calculated analogously to Eq. 8, by replacing λ_s and λ'_s with the default and perturbed values of λ_m , $\epsilon(T_S)$ or $\epsilon(T_L)$. We determine the elasticities for $\mu = 0.01$ with $c_F = 0.001$. The effect of density dependence on elasticity is checked by repeating the calculations with $c_F = 0$.

Results

For an impression of the dynamics of our metapopulation model and the typical patterns that arise, two space–time plots obtained with different parameter settings are given in Fig. 2. Following a 10-year spell of seed spillage, most established local populations go extinct quickly, while a number of sites remain occupied for a considerable time. Persistent sub-populations typically occur in groups, or ‘patches’, which remain more or less fixed in space, possibly spanning

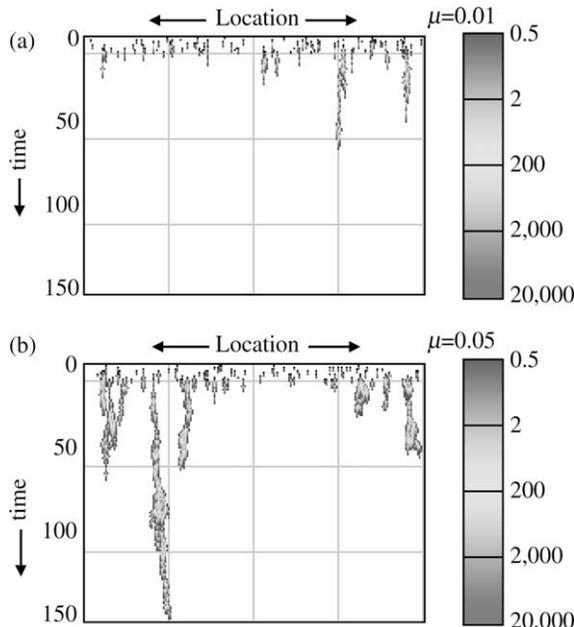


Fig. 2. Space–time plots of the metapopulation model with $k = 200$ sites, $T = 150$ years, $p = 0.15$ and two different values of the dispersal rate μ . Pixel colour represents local seed bank abundance $b_i(t)$; pixel co-ordinates represent location i (horizontal) and time t (vertical). Seed spillage (indicated by black pixels) lasts for 10 years with $P_{\text{spill}} = 0.05$. Horizontal grid lines mark 50 year intervals, starting from the end of seed spillage. Vertical grid lines are 50 sites apart. (a) Dispersal rate $\mu = 0.01$. (b) $\mu = 0.05$.

decades or even centuries (e.g. >140 years in Fig. 2b). The figure suggests that such patches persist longer with a high dispersal rate ($\mu = 0.05$) than with a low one ($\mu = 0.01$).

To study the effect of dispersal on persistence more rigorously we plot the cumulative frequency distribution of site-level persistence times (T_S) for a range of dispersal rates (Fig. 3). The persistence times T_S are roughly exponentially distributed, except for the initial decline (first 5–10 years) which is steeper than the tail (result not shown). Figure 3 shows that sites tend to persist longer with a high dispersal rate than with a low one, as was illustrated in Fig. 2. Yet the distribution of T_S for $\mu = 0.05$ does not readily suggest the occurrence of very long-lived patches (i.e. groups of persisting sites) such as the ones observed in Fig. 2. The reason T_S is not a good

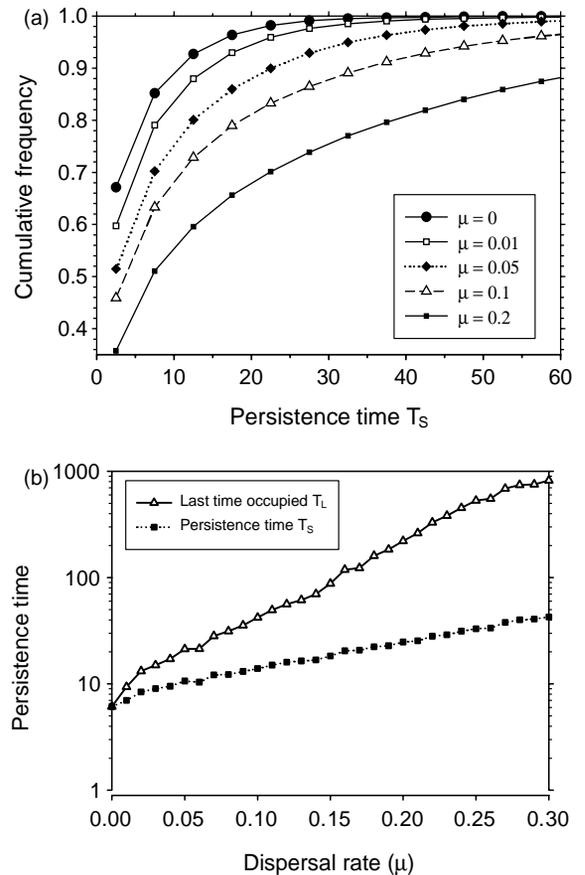


Fig. 3. (a) Cumulative frequency distributions of persistence time at site level, T_S , for a range of dispersal rates. Each data point gives the frequency of T_S being in the represented 5-year range (0–5, 5–10, etc). For each value of μ , data points are computed from 200 simulations with $k = 1000$ sites and $T = 500$. (b) The effect of the dispersal rate μ on the expected persistence time at site level $\epsilon(T_S)$ and on the expected time to last occupancy $\epsilon(T_L)$. Parameters are $k = 1000$ sites, $P_{\text{spill}} = 0.05$ during 5 years, disturbance rate $p = 0.15$, each point is the average of 50 runs with $T = 2000$.

predictor for the expected persistence times of such patches is that most of the individual sites that make up such a patch are much shorter lived than the patch as a whole.

The time until last occupancy, T_L , takes into account that sites can be recolonised, and hence is a better measure of the persistence of long-lived patches. The dependence on the dispersal rate of the expected time of last occupancy, $\varepsilon(T_L)$, is plotted in Fig. 3b, along with the expected persistence time $\varepsilon(T_S)$. In the absence of dispersal, empty sites cannot be recolonised which implies that for $\mu=0$ the values of T_S and T_L should coincide (Fig. 3b). Both quantities increase approximately exponentially with μ , albeit at very different rates: T_L is much more sensitive to changes in μ than T_S . For a wide range of μ , T_L is much larger than T_S which implies that long-term persistence is possible despite relatively short local persistence times. Visual inspection of space–time plots suggests that the long persistence times (T_L) are due to long-lived, static patches such as depicted in Fig. 2.

We have so far looked at dynamics for parameter values typical for oilseed rape (low p and μ) for which the metapopulation tends to go extinct. We now turn to answering the questions: will sufficient dispersal enable the metapopulation to persist indefinitely? Or is this possible only with a high disturbance rate (p), as was the case in the matrix model? The latter predicted persistence only if $p > 0.28$ (Claessen et al. 2005). For a fixed disturbance rate ($p=0.15$), Fig. 4 shows the steady-state, average fraction of occupied sites $m(t)$ without seed spillage plotted against the dispersal rate μ , as well as the population growth rates $\log \lambda_s$ and $\log \lambda_m$. Long-term persistence ($m(t) > 0$) is found only for unrealistically large dispersal rates ($\mu > 0.2$). The metapopulation growth rate $\log \lambda_m$ reaches positive values only for $\mu > 0.25$, implying that with smaller dispersal rates the number of occupied sites gradually declines. Interestingly, the metapopulation growth rate is considerably higher than the local population growth rate (i.e. $\log \lambda_m > \log \lambda_s$) throughout the range of μ . As in the classical metapopulation model, global persistence ($\log \lambda_m > 0$) is therefore possible despite sure local extinction ($\log \lambda_s < 0$), but it does require a very high dispersal rate.

Next, we determine the extinction boundary which separates the set of parameter values (μ , p) for which the metapopulation is expected to go extinct in the long run, from the parameter values for which it may persist indefinitely. The extinction boundary is defined by the condition $\log \lambda_m = 0$. In Fig. 4b we saw that the condition is fulfilled for the parameter values $\mu \approx 0.25$ and $p = 0.15$. The condition can be fulfilled with a low dispersal rate μ only by choosing a high disturbance rate (Fig. 5). For small μ , the critical p for persistence decreases roughly linearly with the logarithm of μ

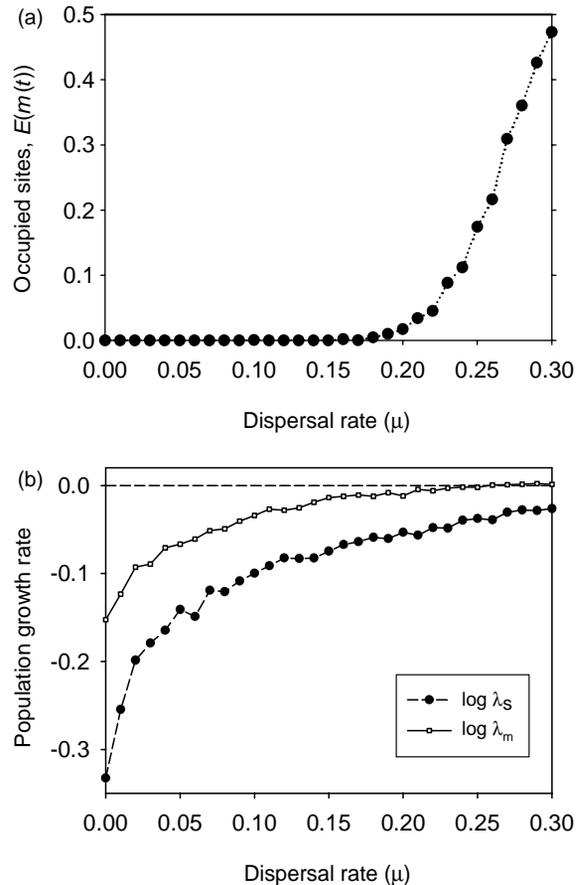


Fig. 4. (a) The effect of dispersal rate (μ) on the average fraction of occupied sites $\varepsilon(m(t))$, measured in the period from 800 to 1000 years after termination of seed spillage. $k=400$, $T=1000$, each point is the average of 100 runs. (b) The effect of dispersal rate (μ) on the local population growth rate $\log \lambda_s$, and on the metapopulation growth rate $\log \lambda_m$. $\log \lambda_m$ is estimated over the first 100 years, $\log \lambda_s$ over 1000 years. $k=1000$ sites, 100 runs per data point. In both panels, $P_{\text{spill}}=0.05$ during 5 years, $p=0.15$, $c_F=0.001$.

(Fig. 5a) and reaches a minimum around $\mu=0.8$. Close to the $\mu=0$ limit the metapopulation is highly sensitive to changes in μ ; even small values of μ have a major influence of the population growth rate. Overall, Fig. 5 shows that a larger dispersal ability allows the population to persist with a much lower disturbance rate. Yet there is a critical disturbance rate $p^* \approx 0.13$ below which long-term persistence is impossible irrespective of the dispersal rate.

The role of environmental unpredictability: spatial correlation

Here we study the effect of spatial correlation in the occurrence of disturbances on the population growth rates $\log \lambda_s$ and $\log \lambda_m$. Fig. 6 shows a gradual decrease

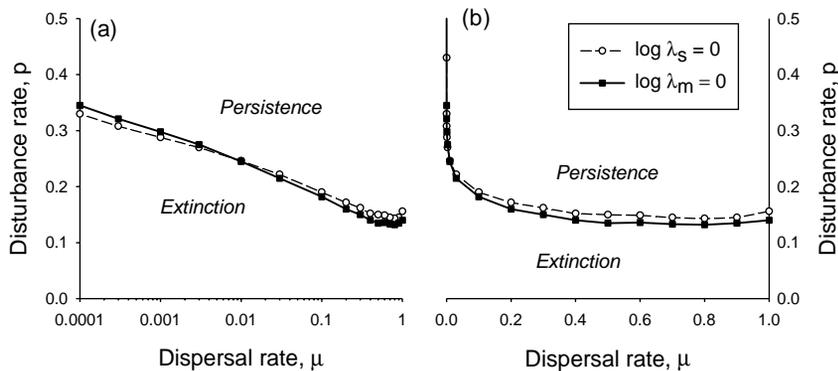


Fig. 5. (a) and (b) The extinction boundary as defined by the combinations of the parameters μ and p for which $\log \lambda_m = 0$. Also plotted is the condition for local persistence, $\log \lambda_s = 0$. (a) and (b) show the same data on different scales; (a) log-linear; (b) linear. Parameters: $k = 1000$, $T = 200$, $c_F = 0$, each point is determined from the average of 100 runs per parameter combination.

of the population growth rates with the spatial autocorrelation, r , up to $r \approx 0.9$, after which they decrease sharply with r . The same pattern is observed for $\mu = 0.01$ (results not shown) and hence does not depend on the specific value of μ . The beneficial effect of spreading risk by dispersal is hence robust to a large amount of spatial autocorrelation (up to $r \approx 0.9$), while negative autocorrelation between neighbouring sites enhances it.

The large difference in growth rate between the cases of complete correlation ($r = 1$) and little to mild correlation ($r < 0.9$) shows that the positive effect of dispersal on population growth depends on the asynchrony of disturbances in neighbouring sites. With $r = 1$ disturbances occur simultaneously throughout the metapopulation, while with $r < 1$ disturbances occur asynchronously. In the latter case, if a plant distributes its seeds over three sites, the probability that at least some of the seeds encounter favourable conditions (i.e. disturbed habitat) is larger than p . Thus, distributing seeds to neighbouring sites provides a degree of insurance against unfavourable conditions (Wiener and Tuljapurkar 1994). In a spatially random environment ($r < 1$), this insurance has a positive effect on population

growth, as has been shown for a two-patch model by Wiener and Tuljapurkar (1994), who called the phenomenon the 'insurance effect'. When disturbances occur synchronously ($r = 1$), long-lasting patches (i.e. groups of occupied adjacent sites) are not observed. The existence of patches thus depends on the insurance effect of dispersal in a spatially random environment.

Elasticity and the role of density dependence

Figure 7 summarizes the results of the elasticity analysis for both the density dependent case (black bars) and the density independent case (grey bars). In all panels the parameters are ranked according to the elasticity of the local population growth rate λ_s (Fig. 7a). In the density dependent case the local population growth rate λ_s responds most sensitively to changes in the winter survival rate in the seed bank, σ_2 , followed by the dormancy fraction d and spring seedling survival rate S_t (Fig. 7a, black bars). Seed production F_t , summer seed bank survival σ_3 and germination g_t appear to be less important. Also the dispersal rate μ turns out to have a low elasticity. The winter survival rate of early emerged seedlings, σ_1 , has negligible impact on metapopulation growth. The coefficient for density dependence, c_F , has a negative elasticity because increasing density dependence reduces seed production and hence population growth. The coefficient has a very low elasticity, though, suggesting that density dependence is not of major importance given these parameter values. This may not come as a surprise because the metapopulation is declining and heading for extinction, so densities are expected to be low.

The same Fig. 7a shows that removing density dependence by choosing $c_F = 0$ makes little difference to the ranking of the life history parameters in terms of their elasticity. The same three parameters (σ_2 , d and S_t) top the elasticity table and the overall pattern of elasticity is fairly robust to the presence or absence of density dependence. The only differences are that seed production (F_t) and germination (g_t) become slightly more important without density dependence, while

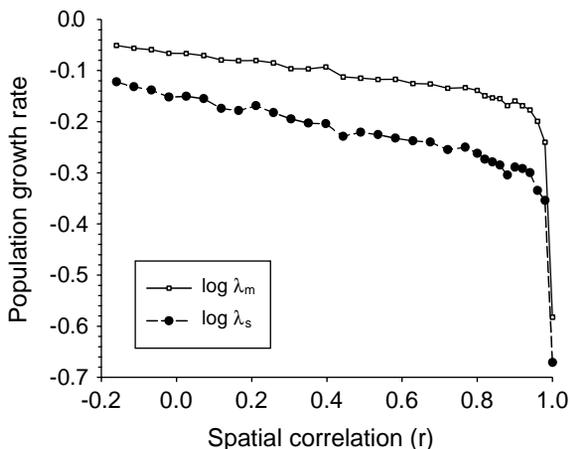


Fig. 6. The effect of spatial autocorrelation in disturbance, in the metapopulation model with Markov chain (Eq. 4). $\mu = 0.05$, $k = 500$ sites, $T = 200$, $P_{\text{spill}} = 0.05$ during 10 years, $p = 0.15$, $c_F = 0.001$. Each point is the average of 200 runs.

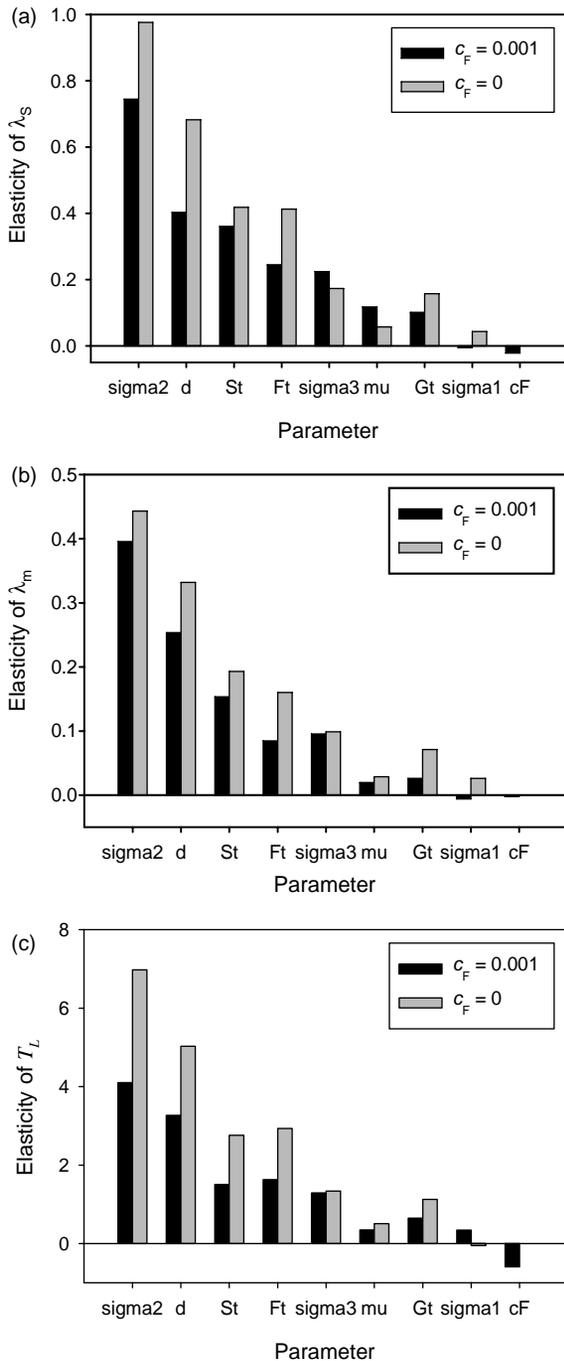


Fig. 7. Results of the elasticity analysis. (a) elasticities of the local population growth rate λ_s , (b) elasticities of the metapopulation growth rate λ_m , (c) elasticities of the mean time to last occupancy $\epsilon(T_L)$. Black bars: $c_F = 0.001$. Grey bars: $c_F = 0$. Parameters: Table 1 and $\mu = 0.01$, $k = 1000$ sites, $T = 200$, $P_{\text{spill}} = 0.2$ during 10 years, $p = 0.15$. Elasticity of each parameter is the average of 300 repetitions.

dispersal (μ) becomes less influential. The effect on the elasticity of F_t reflects that in our model density dependence works by reducing fecundity at higher

densities, thus reducing the influence of seed production on population growth.

In terms of the metapopulation growth rate λ_m the elasticities show a similar ranking (Fig. 7b). The main difference is that, in the density-dependent case, the elasticity of F_t is smaller than that of σ_3 . As in Fig. 7a, the main effect of density dependence is to reduce the elasticity of F_t and g_t . Overall Fig. 7a and b show good correspondence between the elasticity of λ_m and λ_s in terms of the ranking of parameters and the small effect of density dependence on elasticity.

The response of the expected time to last occupancy, $\epsilon(T_L)$, to changes in life history parameters reveals roughly the same ranking (Fig. 7c). Again seed bank survival (σ_2) and dormancy (d) are most important. Three parameters have intermediate elasticity: F_t , S_t and σ_3 , while the remaining parameters have little influence. The coefficient of density dependence c_F appears to have somewhat more influence on persistence time than on both population growth rates. This is also apparent from the large difference between the elasticities with and without density dependence.

Discussion

The aims of this article were: (i) to assess the importance of dispersal and metapopulation structure for the persistence and extinction of feral, roadside populations; (ii) to study the dynamics of a structured metapopulation subject to environmental stochasticity, with a focus on extinction; (iii) to evaluate the robustness of our previous approach of using a matrix population model by relaxing the assumptions of spatial homogeneity and density independence.

Concerning the importance of dispersal, we have found that including metapopulation structure can enhance persistence times considerably because adjacent sites can re-establish each other after local extinctions. This is manifested by the existence of small groups of occupied sites, or “patches”, which remain more or less fixed in space and which are likely to persist much longer than the expected, site-level persistence time. This conclusion is based on the result that with a positive dispersal rate, the time to last persistence is much larger than the site-level persistence time ($T_L \gg T_S$), implying that despite short expected local persistence times (e.g. 5–10 years), persistence over medium long term (e.g. 150 years) is likely to occur, albeit in just a few localised patches.

We have also found that in the case of roadside oilseed rape, dispersal is unlikely to result in permanent, global persistence at the metapopulation level, because this requires unrealistically high dispersal rates ($\mu \gg 0.1$), given that the disturbance rate is likely to be small ($p < 0.2$).

Concerning environmental stochasticity, we have found that the emergence of patches (i.e. groups of occupied sites) depends on the spatial asynchrony of disturbances. The results confirm the analysis by Wiener and Tuljapurkar (1994), who used an analytic approximation of the stochastic population growth rate to show that dispersal in a system of two patches and two life stages increases population growth provided that the cost of migration and the correlation between the sites are sufficiently small. They compared the effect of dispersal to an insurance against unfavourable conditions. Distributing seeds over a number of sites reduces the net variability experienced in the next generation. Environmental variability has a negative effect on population growth (Lewontin and Cohen 1969), and by reducing variability the insurance effect increases population growth. The positive effect of spreading risk, here attained by distributing offspring over a number of sites, is akin to the success of 'bet hedging' life history strategies which are often favourable in random environments (Cooper and Kaplan 1982). We have shown that the insurance effect works in a more complicated, metapopulation system and that when the metapopulation is declining to extinction the effect manifests itself as the occurrence of static, relatively long lasting patches (Fig. 2).

The insurance effect is distinct from the 'rescue effect' which is defined as a reduced probability of extinction of small, local populations owing to immigration (Brown and Kodric-Brown 1977). The mechanism of the rescue effect is that (i) immigration increases local abundance and (ii) large populations are less likely to go extinct than small ones (Gyllenberg and Hanski 1997). The underlying mechanism may be deterministic or the relation between population size on the effect of within-site demographic stochasticity on extinction. In contrast to the insurance effect, the rescue effect does not require environmental variability. Thus, while the rescue effect works through the effect of immigrants on local population dynamics, the insurance effect works through the effect of distributing offspring over a number of sites which reduces the net variability. Both effects can be expected to be operational in metapopulations subject to environmental stochasticity.

Concerning spatial heterogeneity and density dependence, the elasticity analysis carried out in this study yields results very similar to the elasticity analysis of a spatially unstructured, density independent matrix model (Claessen et al. 2005). Both studies identify the survival rate of seeds in the seed bank as the life history trait with most impact on population growth, followed by the dormancy fraction d , followed by spring seedling survival S_t and seed production F_t . Both models predict that changes in germination fraction g_t , dispersal rate μ and winter seedling survival σ_1 have less impact on population growth. As in Claessen et al. (2005), we

found that life history traits that are critical to the population growth rate are also critical to persistence times: the elasticities of λ_s , λ_m and $\epsilon(T_L)$ display roughly the same ranking (cf. Fig. 7a–c). The added value of the present study is that we can assess the importance of the dispersal rate, which was impossible in the context of our previous model. We found that the elasticity of μ is small, both in terms of the (meta-) population growth rate and in terms of persistence time. Yet our analysis shows that close to $\mu = 0$ there is a strong non-linear effect of dispersal on the extinction boundary (Fig. 5). Close to $\mu = 0$ the population growth rate responds most sensitively to changes in μ , while the response flattens with increasing μ (Wiener and Tuljapurkar 1994). The non-linear effect of dispersal is also well illustrated by the effect of spatial correlation of disturbances. The case of $r = 1$ resembles the non-spatial matrix model, because there is no scope for spreading risk through the insurance effect. The drastic effect of even the slightest asynchrony on disturbances, and hence of dispersal in a spatially random environment, is apparent from Fig. 6. There is thus a large difference between $\mu = 0$ and $\mu > 0$, as well as between $r = 1$ and $r < 1$, but given that $\mu > 0$ and $r < 1$, the effect of changes in μ and r are relatively small.

Models that exclude dispersal and metapopulation structure underestimate both the population growth rate and persistence times. However, for oilseed rape we do not expect dispersal to allow for long term persistence, but it seems likely that isolated patches (i.e. groups of adjacent occupied sites) can persist for decades or possibly even centuries, despite most sites going extinct within 5 or 10 years.

There is anecdotal evidence for the existence of long-lasting patches of roadside oilseed rape, such as described by Crawley and Brown (1995) who report the occurrence a small number of "apparently permanent, dense rape populations" along the M25 motorway. The authors speculate that in these patches local seed production may be so high that it provides resistance to invasion by perennial grasses. Our theoretical study suggests that such patches may simply be the consequence of the interplay between dispersal and spatially random disturbances. The possibility that adjacent sites rescue each other from local extinction can explain the existence of quasi-permanent populations without the need to invoke additional mechanisms such as resistance against invasion or positive density dependence.

Implications of genetic modification

The context for this study is to assess the risks of transgenic crops spreading into the environment. Feral transgenic populations may serve as sources or stepping stones of transgene flow to wild relatives, or may be an ecological threat in themselves, if they

constitute persistent weeds in arable fields or dominate wild vegetation. It is therefore important to assess the consequences of genetic modification on population growth and persistence of feral populations.

One of the tools we have used to this end is elasticity analysis. It should be noted that elasticities express the effect on the population growth rate (or another population level quantity) resulting from a proportional change in the life history trait. Thus, by identifying the importance of a trait with its elasticity, as we do below, it is implicitly assumed that the effects of GM on different life history traits will have similar relative magnitude. To make a definitive assessment of which transgenes will have the biggest impact, it is necessary to have quantitative estimates of these proportional changes in life history traits. As many authors study the changes merely in terms of increase or decrease under laboratory conditions, such estimates are unfortunately rare. The quantitative estimates of changes in d as found by Gruber et al. (2004) are an exception. Thus, the discussion below necessarily has a more qualitative character; a more precise risk analysis will require more quantitative measurements of the effect of transgenes on life history traits.

In a previous study we linked observed transgene-induced life history changes in oilseed rape to predicted consequences for population growth and persistence (Claessen et al. 2005). Our present study shows that the conclusions from that paper are robust to the extension to metapopulation structure and density dependence. That is, transgenes that improve survival in the seed bank or the dormancy fraction are most likely to improve persistence of feral populations.

Our recommendation are hence that (i) GM seeds are tested for these life history traits, and (ii) that cultivars with low seedbank survival and low dormancy are used as parental lines whenever new transgenic crops are being developed. An example in which this has been done (perhaps inadvertently) is revealed by a recently published comparison of two transgenic oil-modified cultivars with their parental lines (Walker et al. 2004). The transgenic high-laurate cultivar LA002 was based on parental line cv. 212/86. Walker et al. (2004) claim this parental line displays an unusually poor ability to enter secondary dormancy (as measured by unusually high levels of initial germination). Owing to this poor performance of the parental line, even the oil-modified cultivar has a low dormancy compared to conventional cultivars despite the positive influence of the oil-modification on dormancy.

As we have pointed out previously (Claessen et al. 2005), comparison of our modelling results with known effects of transgenes on life history in oilseed rape (Table 1), leads to predictions on the effects of particular transgenic traits on feral persistence. High-stearate transgenes have been reported to increase seed

survival (Table 1). The role of dormancy in high-stearate transgenes is ambiguous, however, as both positive (Linder 1998) and negative (Walker et al. 2004) effects have been reported. For high-laurate cultivars the effect on seed survival is not known, but both known effects (increased dormancy and increased germination rate) promote persistence (Table 1). Although these effects of oil-modification have not been found under all experimental conditions (Linder 1998), we conclude that oil-modification at least has the potential to promote feral persistence. Bt transgenes increase performance through plant survival and fecundity (Table 1), which are predicted to have a relatively small impact on fitness. It will therefore depend to a large extent on the unintentional effects on seed survival and dormancy whether Bt transgenes increase or decrease persistence. To our knowledge, the effect of Bt transgenes on seed survival and dormancy is currently unknown, so the net effect on persistence cannot be assessed. A recent publication compares dormancy of transgenic, herbicide (glufosinate) tolerant cultivars with that of their near-isogenic conventional counterparts. It shows that the transgenic cultivars Lilly and Modull ($d=0.014, 0.009$, resp) have lower dormancy than the conventional ones Liberator and Falcon ($d=0.58, 0.05$, resp). In combination with a previously established negative effect on seed bank survival (Table 1) this confirms the expectation that, in absence of herbicide application, this transgene does not convey a fitness advantage.

Acknowledgements – Rothamsted Research is supported by the Biotechnology and Biological Sciences Research Council (BBSRC).

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Subject Editor: Tim Benton