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Long-term persistence of agricultural pest insects by risk-spreading dispersal

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Abstract Insects are the most diverse organisms on earth consisting of more than 900 thousand species. However, only few of them are considered agricultural pests. Life history traits such as high fecundity, fast population growth, and high dispersal ability have been used to characterize agricultural pest insects. However, many other non-pest insects also share these traits, which indicates that there has not been a decisive condition characterizing agricultural pest insects. Agricultural habitats are risky and ephemeral to pests because of pest

control and harvesting. The usual arithmetic mean fitness cannot be used to measure the persistence of these pests, because the maximal mean fitness is achieved only when they exhibit no dispersal, but that leads to immediate extinction. Using a geometric mean fitness model, we propose a quantitative measure of long-term reproductive success for agricultural pest insects. By using this approach, we can evaluate the trade-off between long-distance dispersal and high reproduction correctly and estimate the condition for the long-term persistence of pest insects in agricultural habitats. We discuss some general perspectives of pest control from the proposed characterization.

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Introduction

Insects are the most diverse among all organisms (Jana et al. 2015) and are known for being extremely adaptable to different types of habitats (Hoffmann and Frodsham 1993). Some insects provide numerous benefits to humans, for examples, pollination, weed killers and soil builders (Getanjaly et al. 2015). However, some of them have invaded or expanded into farmlands with increased human cultivation and become agricultural pests (Kim and McPheron 1993). According to Williams (1947), any insects that are in the wrong place, based on human perception, are identified as pest insects. Currently, insects are identified as agricultural pest insects if they cause damage to humans and to the economy or cause cosmetic damages in crops (Conway 1976; Dent 2000). Pest insects are relatively rare and represent less than 1% of the total number of insect species (Gillott 1995; Gupta 2009). Well-known characteristics of agricultural pests are high fecundity rates, short life cycles and long dispersal capabilities (Kim and Sappington 2013; Mazzi and Dorn 2012; Khaliq et al. 2014). However, many other non-pest insects also often share these

characteristics, such as dispersal (Denno 1994). Therefore, a stronger explanation why so few insects become agricultural pests need to be addressed.

The substantial advantage of farmlands to agricultural pest insects, compared to wild habitats, is the large quantity of food resources, i.e., host plants (Geiger et al. 2010). On the other hand, the uniformity of farmed land presents unavoidable and unpredictable disadvantages to agricultural pest insects, in that it correlates to the risk posed in such environments. Examples of risks in farm habitats are pest control and harvesting. These two examples will extinguish agricultural pests from their farm habitats. If a pest insect does not extensively disperse itself, then it will face the risk of being decimated, or even become extinct due to wide-ranging farm practices that are fatal to insects. From the perspective of pests, the only potential way to escape the catastrophic habitat crashes is to develop an effective strategy of risk-spreading dispersal (Dorhout et al. 2008). There are two forms of risk-spreading dispersal: (i) long-distance dispersal, where no substitute host plants other than crops are available and (ii) dispersal to substitute wild habitats (Yoshimura and Jansen 1996; Jansen and Yoshimura 1998). In this study, we investigate the condition for an insect being a pest in the former case. Based on the concept of risk-spreading dispersal, we propose a quantitative characterization of a pest without substitute wild host plants, that is, a pest that uses only agricultural crops as food plants. We will here call it a pure pest, to contrast with a pest that can use alternative wild host plants. Examples of pure pest insects include rice stem borers and corn stem borers (Sun et al. 1993; Hafez et al. 2009; Sarwar 2012; Calatayud et al. 2014).

Risk-spreading adaptations, such as bet-hedging, of insects and other species can be investigated by analyzing their population dynamics (Jansen and Yoshimura 1998; Hopper 1999; Chen et al. 2012; Rajon et al. 2014; Morita and Yoshimura 2012, 2015; Hidalgo et al. 2015; Maslov and Sneppen 2015a). Temporal or spatial risk spreading is performed in varying environments, which leads to the species diversifying their choice of habitats (Yoshimura and Jansen 1996; Childs et al. 2010; Simons 2011). Specifically, the dispersal of offspring in mixed environments is a potential response by the insect population to the dynamic condition of the habitats, e.g., threat of destruction and climate fluctuations (Childs et al. 2010). This allows the species to survive in adverse but stable environments, and their populations in sink habitats can persist when they distribute their offspring to other environments (Jansen and Yoshimura 1998). According to Jansen and Yoshimura (1998), sink habitats are habitats in which populations cannot survive when they are isolated from other populations.

We introduce a simple geometric-mean fitness model of risk-spreading dispersal for a pest insect using only farm habitats. Note that risk-spreading adaptation cannot be evaluated by the arithmetic mean fitness, but need the geometric mean fitness, because it deals with the extinction risks over generations. However, the arithmetic mean fit-

ness measures the average reproductive success of a single generation (Yoshimura and Clark 1991; Metz et al. 1992; Yoshimura and Jansen 1996). The main reason why we need the analyses of the geometric mean or long-term persistence is that farmlands are extremely risky habitats. Note that the maximal arithmetic mean fitness is achieved when insects exhibit no dispersal since dispersal is always costly for reproduction. But this solution means immediate extinction because of pest control and harvesting within a farmland habitat. Because of this risk, the traditional arithmetic mean fitness cannot evaluate the trade-off between dispersal and reproduction correctly to estimate the long-term persistence of pest insects (Yoshimura and Jansen 1996; Jansen and Yoshimura 1998).

We also develop a simulation model with/without density dependence to deal with more general cases where there are various numbers of habitat crashes. Based on the population growth rates, we evaluate the population persistence of pure pest insects for the combination of both dispersal and reproductive traits. Following our results, we present a quantitative characterization of pure pest insect: for an insect being a pest, a positive growth rate over generations has to be achieved by the combination of an optimal dispersal rate and sufficiently large reproduction. Sufficiently large reproduction means that the intrinsic growth rate is greater than 1, which is a common characteristic of pest populations. We also propose a more specific quantitative characterization of agricultural pest including pest insects using both farm and wild habitats. Finally, we discuss the implications for pest control.

Models and results

Suppose that the total population $N(t)$ of an insect at time t is distributed over n habitats (patches). All habitats are uniform farm habitats; and some of the habitats are simultaneously treated (or other agricultural management) but others not. We assume that at any season there are n_s untreated habitats and $n - n_s$ habitats that simultaneously undergo treatment. Let $N_i(t)$ be the population size in habitat $i = 1, 2, \dots, n$ at time t . The intrinsic growth rate, egg laying rate minus mortality rate, is represented by r . If the value of $r > 1$ then there is successful egg laying and birth in the population. Let K_i be the carrying capacity of habitat i . We denote the effect of the remaining portion of the carrying capacity of habitat i to the pest population growth as $r \left\{ 1 - \frac{(1-p)N_i(t) + \frac{pdN(t)}{n}}{K_i} \right\}$. Let $s_i(t)$ be the survival rate in habitat i at time t such that $s_i(t) = 0$ when habitat i undergoes pest control, harvesting or by planting varieties of crops that are resistant to pest; and $s_i(t) = 1$, otherwise. Moreover, let $0 \leq p \leq 1$ be the dispersal rate and $0 \leq c \leq 1$ be the rate of dispersal failure, where $d = 1 - c$ is the rate of dispersal success. Dispersal failure is the main cost of dispersal which affects the optimal dispersal strategy.

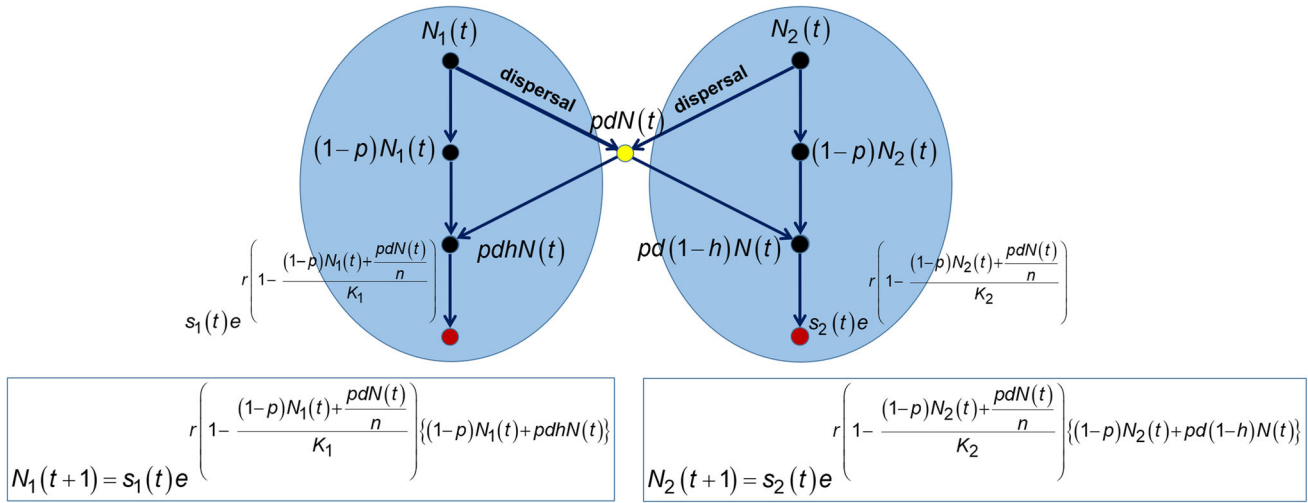


Fig. 1 Schematic diagram of the population dynamics of $N_1(t)$ and $N_2(t)$ where individuals disperse at a rate p with dispersal success rate d . For simplicity, we assume the portion $h = 1/2$. Two habitats ($n = 2$) were considered in this diagram but can be extended for $n > 2$ (where n is the number of habitats) following a similar migration pattern, resulting in Eqs. (1) and (2) in the main text.

Note that the population size with/without density dependence is given by Eq. (1) and $N_i(t + 1) = s_i(t)e^r \left\{ (1 - p)N_i(t) + \frac{pdN(t)}{n} \right\}$, respectively, and $s_i(t)$ is the survival rate of habitat i , K_i is the carrying capacity of habitat i , Color figure online

We model the discrete generation dynamics of a population size N based on the Ricker logistic equation (Ricker 1954). In addition, we assume that density-dependence occurs after the dispersal of pest insects over n habitats. The computation is as follows (Fig. 1):

$$N_i(t + 1) = s_i(t)e^{r \left(1 - \frac{(1-p)N_i(t) + \frac{pdN(t)}{n}}{K_i} \right)} \left\{ (1 - p)N_i(t) + \frac{pdN(t)}{n} \right\}, \tag{1}$$

$$N(t) = \sum_{i=1}^n N_i(t). \tag{2}$$

We evaluate the geometric mean fitness of this model by mathematical induction for density-independent case and by simulation for more general cases where there are various numbers of habitat crashes (Fig. 2). We used the software Java 8 Update 101 for our simulation analysis. In general, it is not possible to calculate the geometric mean $G(p)$ of the population growth rate analytically. However, if there is no density dependence (i.e., $N_i(t + 1) = s_i(t)e^r \left\{ (1 - p)N_i(t) + \frac{pdN(t)}{n} \right\}$ and $n_s = 1$ then the geometric mean of population growth rate is derived analytically (Fig. 2a; refer to the supporting text in the supplementary materials):

$$G(p) = e^r \left(1 + \left(\frac{d}{n} - 1 \right) p \right)^{\frac{1}{n}} \left(\frac{dp}{n} \right)^{\frac{n-1}{n}}. \tag{3}$$

The value of p^* , dispersal rate that gives the unique maximum geometric mean, is

$$p^* = \frac{n - 1}{n - d} = \frac{n - 1}{n - 1 + c}. \tag{4}$$

In the derivation of Eq. (4), we consider the assumption that one out of n habitats is untreated (i.e., $n_s = 1$ and there are $n - 1$ simultaneously treated) to determine if the population can still persist for some period of time in this extreme condition. The case where there are n simultaneously treated habitats ($n_s = 0$) is trivial because the total population will become extinct with certainty and treating all habitats is unfeasible in reality. Moreover, from Eq. (4), the dispersal rate p^* decreases as the rate of dispersal failure c increases for any number of habitat n (Fig. 2c). The optimal value of $G(p)$ occurs for a higher value of p when c decreases.

Even though the optimal value of $G(p)$ cannot be solved analytically when $n_s \neq 1$, we can estimate it by simulations. Here, we assume agricultural management occurs at random for each habitat and for each timing. The optimal dispersal rate using simulation, denoted by p_s^* , is same with the analytical solution p^* when $n_s = 1$, i.e., $p_s^* = p^*$ (Fig. 2a, b). In addition, the geometric mean fitness increases but the optimal geometric mean shifts to a lower value of p as n_s approaches n (Fig. 2b). This shift in the optimal value of p implies that too much pest dispersal is a suboptimal risk-spreading strategy. However, the geometric mean decreases as n increases (Fig. 2a, b, $n_s = 1$) due to the assumption that there are $n - 1$ simultaneously treated habitats. These results indicate that the maximal geometric mean fitness is achieved when the value of dispersal rate is between 0 and 1, i.e., $0 < p_s^* < 1$.

In addition, we also consider the effect of density dependence to the population geometric mean GM when density dependence occurs before dispersal as shown in the following equations:

$$N_i(t + 1) = s_i(t) \left\{ (1 - p) \left(e^{r \left(1 - \frac{(1-p)N_i(t)}{K_i} \right)} N_i(t) \right) + \frac{pdN(t)}{n} \right\}, \tag{5}$$

$$N(t) = \sum_{i=1}^n N_i(t). \tag{6}$$

We also plotted the changes in the value of the geometric mean using the intrinsic growth rate r and dispersal rate p for the number of untreated habitats $n_s = 4, 10$ and 16 out of 20 habitats (Fig. 3 and electronic supplementary material, Fig. S1). Figure 3a, f shows the optimal value of geometric mean, with/without density dependence, based on the value of p, r and n_s . Figure 3d–f shows the optimal value of geometric mean as influenced by intrinsic growth rate r when density-dependent factor is equal to $\left(1 - \frac{(1-p)N_i(t) + \frac{pdN(t)}{n}}{K_i} \right)$. Note that the optimal value of the geometric mean will change when the representation of the density-dependent factor changes. Maximal geometric mean occurs at different value of p_s^* when we increase the value of the intrinsic growth rate r . (Figure 3g–i and electronic supplementary material, Fig. S1a–S1c). A positive geometric mean ($GM > 1$) can be achieved if the right combination of intrinsic growth rate r and optimal dispersal rate p is chosen (Fig. 3j–l and electronic supplementary material, Fig. S1). A population will become extinct if its intrinsic growth rate is below the threshold value (i.e., $r < r_{thres}$). In addition, it may also become extinct if it cannot acquire an optimal dispersal rate ($p \neq p_s^*$) despite it attains the minimal intrinsic growth rate (i.e., $r = r_{thres}$). Note that temporal dynamics for numerical

simulations are always different even if all the conditions and initial values are the same because of the randomness inherent in the probability of treatments (electronic supplementary material, Fig. S2).

Discussion

According to Williams (1947), any insect in the wrong place is considered as pest. This definition is ambiguous because it is based on an individual’s point of view only. An insect may or may not be considered as pest insect using this definition. Here, we develop a quantitative characterization of pure pest insects. We calculate the long-term persistence of population while combining both dispersal and reproductive traits using the geometric mean fitness. Note that our approach has no correlation with real agricultural management because we assume in our model that agricultural management occurs at random for each habitat and for each timing. This assumption is unrealistic in the real world because each crop field has a schedule, which results in a high possibility that management will be carried out sequentially on untreated habitat. Moreover, pest management will occur depending not only on the schedule but also on the density of pests. We first consider the extreme condition where treatment is applied to all habitats except for one (Fig. 2, $n_s = 1$). Then we investigate the cases where there are less treated habitats (Figs. 2b, 3). These in silico investigations enable us to determine the parameter values that could drive and hinder the population of pest insects to persist. When there are few controlled habitats, we should allow more dispersal of pest insects to increase the probability of dispersing to a controlled habitat. That is, in some cases,

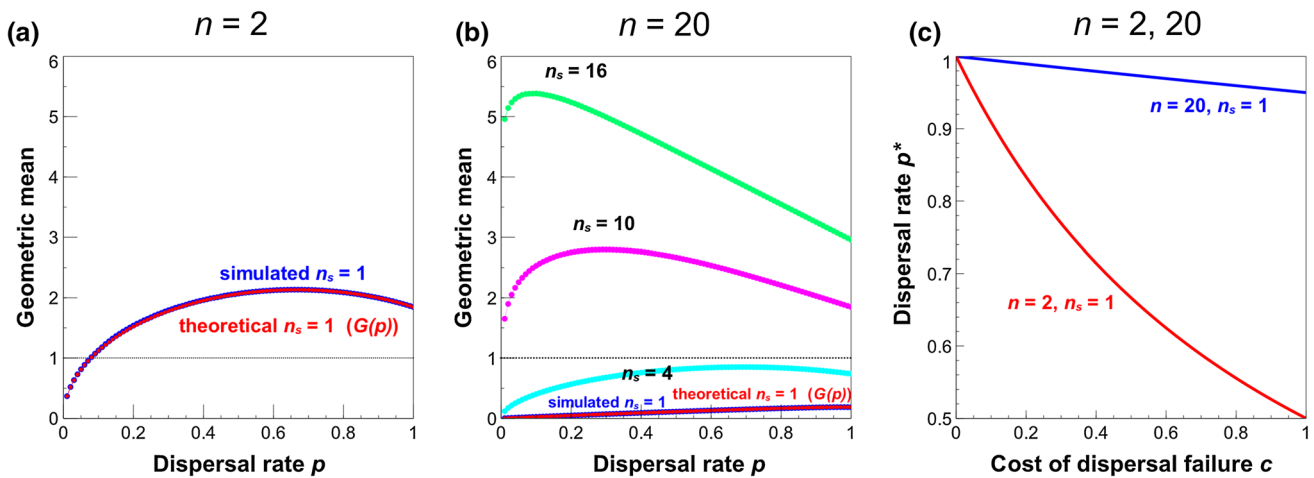


Fig. 2 Evaluation of the geometric mean fitness model. **a, b** By simulation for general case. Geometric mean growth rate (GM) with respect to dispersal rate p as influenced by number of habitats n and number of uncontrolled habitats n_s . In the simulations, we randomly select controlled patches ($n - n_s$) in each time step. We run 10,000 simulations and use the average geometric mean in the figure plots. Parameter values: $c = 0.5, r = 2, s_i(t) = 1$ and $N(0) > 0$. **a** $n = 2$, **b** $n = 20$. **c** By mathematical analysis for a special case. Dia-

gram shows the effect of the cost of dispersal failure c and number of habitat n ($= 2$ and 20) on optimal dispersal rate p^* (Eq. 4). We compute the population size in the next generation t using the equation $N_i(t + 1) = s_i(t)e^{r \left\{ (1 - p)N_i(t) + \frac{pdN(t)}{n} \right\}}$. We define r as the intrinsic growth rate, $s_i(t)$ is the survival rate of habitat i and $N(t)$ as the total population of pest insects at time t . Color figure online

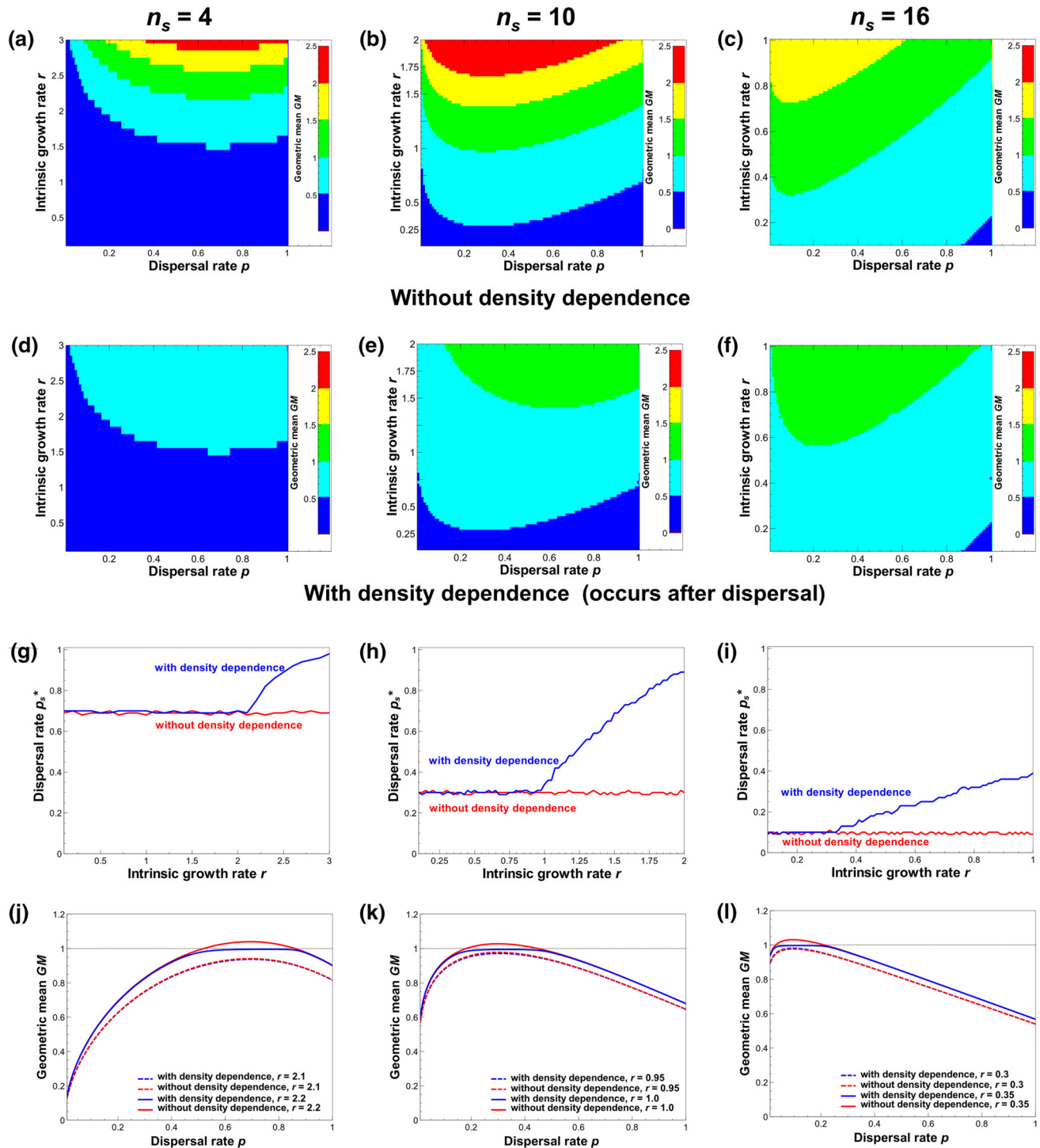


Fig. 3 Population geometric mean GM with/without density dependence. **a–c** Geometric mean GM without density dependence. **d–f** Geometric mean GM with density dependence. **g–i** Optimal dispersal rate p^* as influenced by the intrinsic growth rate r . **j–l** Minimum growth rate value needed to achieve a positive geometric mean GM and its corresponding dispersal rate p . In the simulations, we randomly select treated habitats ($n - n_s$) in each

time step. Note that n is the number of habitats and n_s is the number of untreated habitats. We run 10,000 simulations and use the average geometric mean in the figure plots. Parameter values: $c = 0.5$, $n = 20$, $s_i(t) = 1$ and $0 < N(0) \leq K_i$ where c is the cost of dispersal failure, $s_i(t)$ is the survival rate of habitat i , K_i is the carrying capacity of habitat i , $N(t)$ is the total population at time t . **a, d, g** $n_s = 4$, **b, e, h** $n_s = 10$, **c, f, i** $n_s = 16$. Color figure online

we can minimize the population growth rate of pest insects by allowing them to disperse to other habitats including those treated locations.

For a pure pest using only crop plants, we find that the right combination of the intrinsic growth rate (r) and its optimal dispersal rate (p^*) are needed to achieve

$GM \geq 1$ (Fig. 3a–f and electronic supplementary material, Fig. S1). If the intrinsic growth rate is large ($r > r_{thres}$) then there is a range of dispersal rate ($p_{min} \leq p_s^* \leq p_{max}$) that can sustain the population of pest insects (Fig. 3j–l and electronic supplementary material, Fig. S1). On the other hand, if the intrinsic growth rate is below the minimum ($r < r_{thres}$), the population will become extinct. Therefore, a pure pest can be characterized quantitatively as follows: *A pure pest can escape extinction of local habitats by achieving optimal dispersal rate and sufficiently large reproduction when a part of farmland habitats are safe (no pest control/harvesting/planting varieties of pest-resistant crops), that is, $GM(r, p) \geq 1$ if $r \geq r_{thres}$ and $p = p_s^*$.*

Many wild insects cannot invade the farmlands because they cannot persist against the dependent mortality of pest control, harvesting or by planting varieties of crops that destroy the farmland habitats. To develop a necessary condition to become an agricultural pest, we calculate the persistence of population over time t with/without density dependence. For a temporal pest using both crop and wild plants, the positive growth rate GM is achieved by the combination of dispersal between farm and wild habitats (Yoshimura and Jansen 1996; Jansen and Yoshimura 1998). Note that the optimal geometric mean fitness increases with n_s , but dispersal rate p shifts to a lower value. Many pest insects (e.g., cabbage butterflies, *Pieris* spp.) causing serious damage on crops use wild host plants to escape the extinction of their offspring (Yoshimura and Jansen 1996; Jansen and Yoshimura 1998). In this case, temporal substitution of farmland habitats by wild host plants satisfies the condition for persistence instead of long-distance dispersal. In either case, geometric mean fitness becomes a fitness measure for risk-spreading adaptation, instead of the usual arithmetic mean fitness (Yoshimura and Clark 1991; Metz et al. 1992; Yoshimura and Jansen 1996). In some pest populations, density dependence may lower the population growth. In the case when density-dependence occurs before or after dispersal (Eqs. 1 and 5), the estimated values of the geometric mean fitness without including density dependence should be sufficiently larger than unity ($GM > 1$), so that GM with density dependence = 1 (Fig. 3).

The current approach models the population dynamics of pests in many habitats. Two studies show a quite different approach of pest population dynamics: dynamics of pest habitats (Levins 1969; Ives and Settle 1997). In their approach, the temporal dynamics of the number of pest patches (habitats denoted N) are only considered, irrespective of the pest population size of each habitats. In their model, these two patches are the same, even if one patch contains a single individual and another say, ten thousand. Because of this simplicity, their models are analytically solvable. Therefore, their approach should be very useful in evaluating the pest infection trends in a large geographical area. In contrast, our approach may be useful in evaluating the dispersal (behavioral) characteristics of pest insects. The exact

relationship between the two approaches is a remaining question in future.

Many species of insects inhabit farmlands but only few of them are considered agricultural pests. To escape catastrophic habitat crashes, caused by unavoidable and unpredictable pest control and harvesting, these pest insects presumably have an optimal dispersal rate, which reduces the risk of total extinction. Note that the optimal dispersal rate cannot be estimated by the arithmetic mean fitness because its maximum (highest productivity) is achieved at zero dispersal rate. The current approach provides the optimal dispersal rate of pest insects that cannot be estimated by the traditional methods. A key rate to be a pure pest is the combination of optimal dispersal rate and sufficiently large reproduction to keep a positive growth rate for a long period of time. Population of pest insects living in an environment where some habitats are occasionally destroyed may achieve its maximal growth rate when they spread the risk of local extinction (Yoshimura and Jansen 1996; Jansen and Yoshimura 1998; Maslov and Sneppen 2015b). Stem borers are usually serious pests in farmlands (Hoffmann and Frodsham 1993; Sun et al. 1993; Rahman et al. 2004; Bamaiyi and Joan 2011). These pests are considered to be pure pests, because they do not use wild substitute host plants. Adult stem borers can travel more than 100 km (Sun et al. 1993). A certain rate of dispersal and sufficiently high intrinsic growth rate are necessary to keep the persistence of their population for a long period of time. These are the conditions of the insects to survive in an agricultural field as a pure pest.

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Author contributions MKAG, VAAJ and JY conceived the study. MKAG, KA, HI, SM and JY built and analyzed the model. MKAG and GI built a program and ran the simulations. MKAG, JFR, VAAJ and JY developed and clarified the interpretation of the model and wrote the manuscript. MKAG is the lead author. All authors reviewed the manuscript and gave final approval for publication.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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