Spatial dynamics of a population with stage-dependent diffusion

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ABSTRACT

We explore the spatial dynamics of a population whose individuals go through life stages with very different dispersal capacities. We model it through a system of partial differential equations of the reaction–diffusion kind, with nonlinear diffusion terms that may depend on population density and on the stage. This model includes a few key biological ingredients: growth and saturation, life stage structure, small population effects, and diffusion dependent on the stage. In particular, we consider that adults exhibit two distinct classes: one highly mobile and the other less mobile but with higher fecundity rate, and the development of juveniles into one or the other depends on population density. We parametrize the model with estimated parameters of an insect species, the brown planthopper. We focus on a situation akin to an invasion of the species in a new habitat and find that the front of invasion is led by the most mobile adult class. We also show that the trade-off between dispersal and fecundity leads to invasion speed attaining its maximum at an intermediate value of the diffusion coefficient of the most mobile class.

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1. Introduction

The study of population dynamics with methods coming from dynamical system theory has proven very enriching and is at the core of many important results which have applications to ecology [1], epidemiology [2], and biomedical sciences [3,4]. Conversely, problems arising in these areas have suggested the exploration of new systems, which would not have otherwise attracted attention [5–7]. In this work we set out to consider the spatio-temporal dynamics of a population displaying life-stage dependent dispersal, with one stage dominating the spatial extent of the population, whereas the local dynamics comes from interactions between three classes. This will take us to a system of three partial differential equations of the reaction–diffusion kind, with diffusion also exhibiting nonlinear behavior. This problem is rooted in the widespread biological phenomenon of dispersal of insects that feature a first life-stage that is almost non-mobile, and an adult stage which may possibly be highly mobile. We will now describe more specifically one such system, which presents an adult stage that can be further divided in two sub-cases. In this situation, this species is said to be polyphenic.

Individuals of a polyphenic species may develop into two or more alternative phenotypes (the observable traits in individuals) in response to environmental cues, such as temperature, humidity or population density of individuals of the same species [8]. In this work we study the case of insects that can develop short or long wings (which allow larger flight ranges) in response to high population densities. In crowded areas, competition between individuals of the same species reduces the

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available resources, so long range dispersal is necessary to escape competition by colonizing new areas [9], and thus individuals tend to develop longer wings when they are born in high density areas.

In order to parametrize the model, we use data from one of the best documented species, the brown planthopper (*Nilaparvata lugens*), responsible for extensive damage to rice crops in Asia and Australia [10]. It may develop into two possible adult classes: brachypterous, which have truncated wings and thus are the least mobile class (LM-class), and macropterous, with fully formed wings, which is the most mobile class (MM-class). Since LM-class individuals avoid crowded areas, we postulate the dispersal behavior to be density dependent as well.

We study below the spatial dynamics of the sort of front propagation for the density of a wing-polyphenic species as above, over an unbounded spatial extension in the one-dimensional case. In order to do so, we need to consider a population with at least three classes: the nymph stage and the adult stage, which is subdivided into two possible classes (brachypterous and macropterous). We must also include a trade-off effect, as larger wingspan results in lower fecundity. Furthermore, we also consider an Allee effect, [11], that reflects the fact that at low density of adults fecundity is lower due to several possible effects, the most important being mate-finding difficulties, [12].

We are mainly interested in a situation akin to an invasion of the species in a new habitat. A natural question concerns the speed of the invasion front. Due to the above mentioned trade-off the dependence of the invasion speed depends non trivially on the diffusion coefficient of the MM-class stage. We will show that the invasion speed attains a maximum for an intermediate value of the diffusion constant of the most mobile class.

In Section 2, we introduce and discuss a mathematical model that can be used for analyzing effects of this short-wing or long-wing polyphenism. We divide the analysis into a local part, that is, the non-spatial dynamics and a spatial part, which takes into account the effects of diffusion. Section 3 presents numerical results for both local and spatial dynamics, focusing mainly on the structure of the invasion front and the invasion speed. Due to the mentioned trade-off, the invasion speed is shown not to depend monotonically on the MM-class diffusivity. We close the paper with a discussion of the results and a summary of our findings.

2. Mathematical model

In general, the life cycle of insects consists of several stages, beginning with egg, then nymphal or larval stages, and finally the adult stage. For the case at hand, we can lump together all the immature stages into a single class, which we call the nymph class (N), since they do not have distinct spatial behavior. The two adult forms, however, present very different dispersal capacities, so we include two adult forms in the model: brachypterous (B) – the least mobile class (LM-class), and macropterous (M) – the most mobile class (MM-class).

We first develop a model for the local dynamics containing all biological aspects that are not related to the spatial dynamics, which will be introduced later in a suitable way.

2.1. Local dynamics

We start with the population dynamics in a single location, disregarding spatial dynamics for the moment, in order to understand how the population invasion unfolds from the introduction of a few MM-class individuals. We use a common approach to model stage structure populations [3], with adult stages giving birth to nymphs, that may develop into either class of adults, and a limitation to the total population due to resource depletion.

First, we take into account the strong trade-off between dispersal capacity and production of offspring (fecundity rate): MM-class individuals invest a lot of energy into developing wings, while LM-class ones can use that energy for egg production, thus exhibiting a much larger fecundity [10].

Second, the environmental cue leading to the development of individuals into either LM- or MM-class is the population density at early stages of development. The general pattern is that at low densities most individuals develop into LM-class adults, while MM-class adults develop under higher densities.

Third, we introduce a reduction in the fecundity due to effects of small population density (called Allee effects) [11,13], that may be caused by several factors, among which the difficulty of finding mates at small densities is thought to be the most important [12].

The local dynamics of this system will be given by the following set of equations:

$$\frac{dN}{dt} = f(B, M)(B + vM) - aN, \tag{1a}$$

$$\frac{dB}{dt} = (1 - S(N)) \frac{aN}{1 + \frac{N}{K}} - bB, \tag{1b}$$

$$\frac{dM}{dt} = S(N) \frac{aN}{1 + \frac{N}{K}} - mM, \tag{1c}$$

where f is the effective fecundity rate, $S(N)$ is the proportion of developing nymphs that turn into MM-class adults (and thus $1 - S(N)$ develop into LM-class), and the other parameters are as described in Table 1. The resource limitation is given by the survival of nymphs into adults: while aN nymphs leave their class, only a fraction $\frac{1}{1+N/K}$ of those reach an adult stage.

We model the proportion of developing nymphs that turn into MM-class adults, $S(N)$, as a logistic function,

$$S(N) = S_{min} + (S_{max} - S_{min}) \frac{e^{(N-\sigma)/\gamma}}{1 + e^{(N-\sigma)/\gamma}}, \qquad (2)$$

which is illustrated in Fig. 1. As discussed above, development of nymphs is dominated by LM-class adults at low N and by MM-class for high N.

The trade-off in fecundity between LM-and MM-classes is modeled by a decreased recruitment rate for MM-class adults, given by the factor v, smaller than one, in the first of the above equations.

The small population effects are modeled through the fecundity f that is small when adult densities are small and quickly grows to a maximum fecundity f_0 when densities increase. The particular formulation used here is also not essential to the model, but has been applied to other systems (see review in [13]). Its form, sketched in Fig. 2, is given by:

$$f(B, M) = f_0 \left[1 - e^{\frac{-(B+M)}{C}} \right]. \qquad (3)$$

where the constant C is a density scale that regulates for which densities the effect is important.

2.2. Spatial spread

The full model is built in the traditional way by introducing diffusion terms into the local dynamic equations (1) [14]. We consider a one-dimensional unbounded domain, although the extension to higher dimensions would be trivial. This yields the following set of equations:

$$\frac{\partial N}{\partial t} = f(B, M)(B + vM) - aN + D_N \frac{\partial^2 N}{\partial x^2}, \qquad (4a)$$

$$\frac{\partial B}{\partial t} = (1 - S(N)) \frac{aN}{1 + \frac{N}{K}} - bB + D_B \frac{\partial^2 B}{\partial x^2}, \qquad (4b)$$

$$\frac{\partial M}{\partial t} = S(N) \frac{aN}{1 + \frac{N}{K}} - mM + \frac{\partial^2}{\partial x^2} [D_M(1 + \alpha N)M], \qquad (4c)$$

where D_N, D_B and D_M are diffusion coefficients, and the population densities N, B and M now depend on space (x) in addition of time (t).

The diffusion term in the equation for M above has the unusual feature of a nonlinear term, parametrized by α, dependent on $N(x, t)$, the density of nymphs, which comes from the observed behavior of crowd avoidance by species in the field. This makes the diffusion space-dependent, and it is not obvious how to proceed, since the Fickian equation is not equivalent to the Fokker–Planck formulation of the problem. It has been argued [15,16] that the use of the Fokker–Planck equation as above is more appropriate for population dynamics, as it can be derived from the underlying stochastic process, thus giving a mechanistic interpretation to the term, in contrast with the phenomenological Fickian law.

Table 1
Summary of parameters used. The values presented are suitable for the brown planthopper species [10], although we do not aim here to a precise model parametrization.

| Parameter	Description	Value
f_0	Maximum fecundity rate	10 day^{-1}
v	Relative MM-class fecundity	0.6
m	MM-class death rate *per capita*	0.05 day^{-1}
b	LM-class death rate *per capita*	0.05 day^{-1}
a	Maturation rate of nymphs	0.03 day^{-1}
K	Population density affecting nymph survival	5 nymphs/m
C	Minimum propagule size	0.05
S_{min}	Minimum proportion of MM-class generated	0
S_{max}	Maximum proportion of MM-class generated	1
σ	Nymphal density scale for MM/LM-class switch	100
γ	Density range of MM/LM-class switching	40
D_N	Nymph diffusion coefficient	0.1 m^2/day
D_M	MM-class diffusion coefficient	300 m^2/day
D_B	LM-class diffusion coefficient	1 m^2/day
α	Crowd-induced drift	0.01
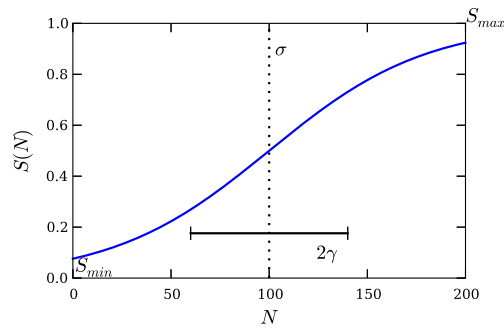
Fig. 1. Nymph development $S(N)$ goes mostly into LM-class adults ($S(N) \approx S_{min}$) at low densities and increase for nymph densities over σ, turning mostly into MM-class under high densities ($S(N) \approx S_{max}$).
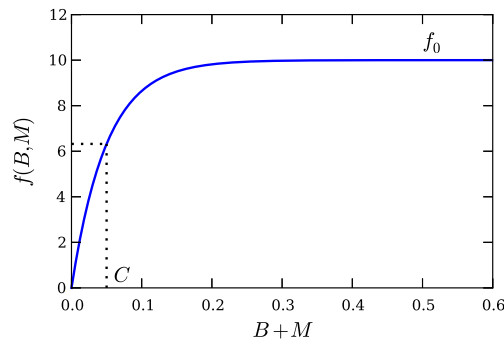

Fig. 2. Fecundity function $f(B,M)$ is small when total adult population $B + M$ is small, but increases quickly to its maximum f_0 when the adult population approaches C.

3. Results

3.1. Local dynamics

With the model in place, we ask what dynamics it entails for a population of insects invading a new habitat. The resulting dynamics, showed in Fig. 3, usually begins with a small amount of MM-class adults, which give birth to nymphs that, initially, develop into LM-class adults. After a phase of rapid population growth, higher densities of nymphs lead to the development of MM-class individuals, and then an equilibrium population density. When that initial population is small, though, it is not viable due to small population effects (Allee effect), and goes to extinction (inset in Fig. 3). We do not explore the full dynamics that results of Eq. (1), for general values of the parameters. Rather, we stay as close as possible to realistic values that are likely to be consistent with field observations.
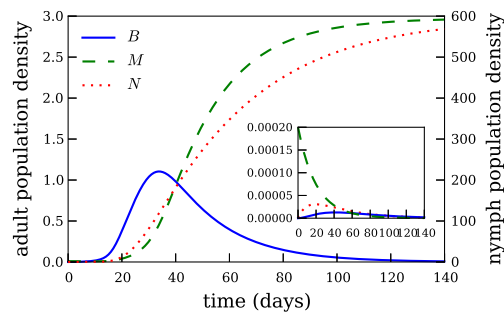

Fig. 3. In an invasion scenario, LM-class density (B) grows quickly at first, and is replaced later by MM-class adults (M), and finally the system reaches an equilibrium. Parameters from Table 1, with initial conditions $M = 0.01$, $N = B = 0$. **Inset:** Small initial density ($M = 2 \times 10^{-4}$, $N = B = 0$) leads to extinction.

3.2. Spatial dynamics

We solved the PDE model given by Eq. (4) over an infinite spatial domain using vanishing conditions at infinity, and a compact initial condition composed only of MM-class adults. We show in Fig. 4 snapshots of the solution at different times. Initially, populations of nymphs and LM-class individuals are zero, and there is a small and localized population of MM-class adults, mimicking the arrival of MM-class migrants in an area otherwise uninhabited by this species.

The general picture which can be drawn from the numerical results is that of an expanding population showing a front-like behavior, as is the case of many reaction–diffusion systems [17]. After the first phase of the invasion process, corresponding to the front region, the population settles to its equilibrium state, displaying the class structure of the equilibrium local dynamics. More interesting, however, is the behavior at the front, which reflects the different characteristics of each class. Fig. 4 shows how the invasion is led by the MM-class, and followed later by the other classes, with high densities of LM-class adults close to the front (but not at its edge), and dominance of MM-class adults in the areas where the equilibrium is reached, in the center of the domain.

Measuring densities is a highly non-trivial task as we cannot have full access to the entire population. In order to put ourselves in touch with measurable quantities, we will focus on the speed of the invasion front and its dependence on the diffusivity of the MM-class population. This speed depends strongly on MM-class diffusivity, whose individuals are the first settlers. One could expect that the higher the diffusivity, the higher the speed, but a high diffusivity that comes from insects with longer wings has a higher cost in terms of reproductive capacity. A lower reproductive capacity, in turn, tends to decrease the invasion speed. For instance, in the single species dynamics with logistic growth and diffusion, given by the Fisher–Kolmogorov equation, the velocity of the invasion front is given by $\sqrt{rD}$ [18], with r being the reproductive rate of the species. In summary, a trade-off between diffusivity and reproductive capacity will directly affect the invasion speed. The trade-off is represented mathematically by linking D_M and v in equations (4). We expect v to decrease when D_M increases. Let's assume, for sake of simplicity, that this dependence is linear:

$$v = a + bD_M \qquad (5)$$

and such that $v = 1$ if $D_M = D_B$ and $v = 0.6$ when $D_M = 300$, an amount consistent with the Table (1) resulting in $a = 1$ and $b = -0.4/300$.

Fig. 5 shows the speed of the invasion front in terms of D_M. Velocities for the front are obtained in the following way: we calculate the solution to Eq. (4) and intercept this solution with an arbitrarily small value. Next we follow the interception point and calculate its speed.

As show in Fig. 5, the speed is not monotonically increasing with D_M. Due to the trade-off, diffusivities greater than a certain value represent populations with a small reproductive rate. It results in the existence of a maximal invasion velocity. In the next section we discuss why this pattern is indeed expected.
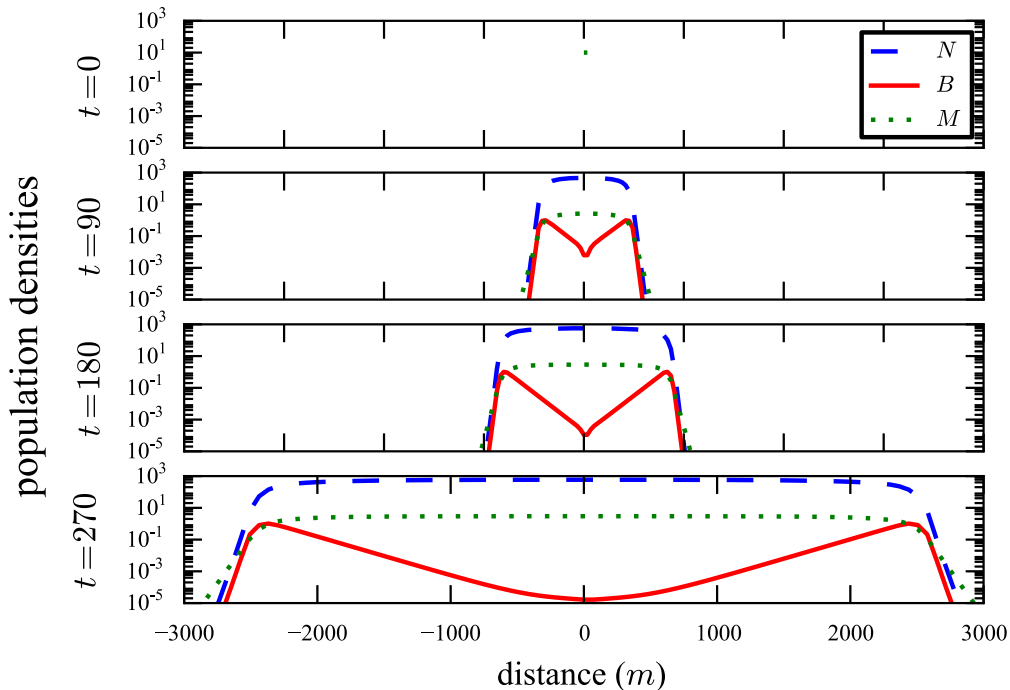

Fig. 4. Successive snapshots of the solutions, showing populations expanding and reaching an equilibrium. Parameters are given in Table 1 and the initial condition is $N(x) = B(x) = 0$ and $M(x) = 0.5$ for $-25 < x < 25$.
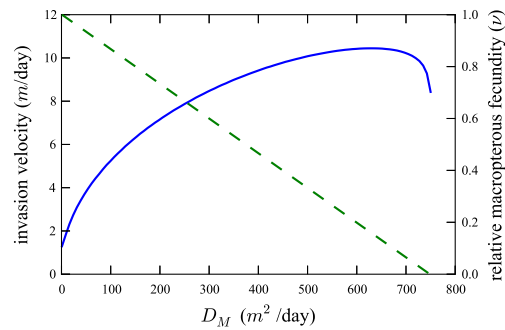
Fig. 5. Trade-off between MM-class diffusivity (D_M) and fecundity (v, dashed line) leads to a maximum value for invasion speed (solid line) at an intermediate value for D_M.

4. Summary and general comments

In this article we have addressed the spatial dynamics of a stage-structured population, incorporating several relevant biological facts. Most important is that the diffusion coefficient is stage dependent and is linked to a trade-off between growth rate and dispersal ability. Moreover, the model incorporates the morphological phenomenon that when the density of immature individuals is high, more most-mobile adult insects emerge leading to the colonization of new areas. Parameters for the model have been extracted from data referring to a particular insect species, the brown planthopper.

The model (4) provides a simulation tool that we have used to predict and visualize a full cycle for the insect population. Although we parameterized our model with data for a particular species, it is clear that the mechanisms described are of a more general nature. Trade-offs between diffusivity and reproductive rate are expected for many species, Allee effects are also quite general. So, even with a different parameterization, the patterns obtained here are also to be expected.

We considered a trade-off between MM-class diffusivity and reproduction rate, which leads to a non-trivial dependence of the invasion speed on the diffusivity, namely, that there is a value of the diffusion coefficient for which the speed is maximal. This fact is expected for evolutionary reasons. Since an individual to arrive before the other represents a clear competitive advantage, if there were no trade-off, the best evolutionary strategy would always favor the highest possible diffusivity, a fact that is not expected. Due to the reproductive cost, there is a value to D_M which represents the balance between costs and benefits of high diffusivity.

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