

REPORT

Allee effect makes possible patchy invasion in a predator–prey system

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Abstract

The dynamics of interacting ecological populations results from the interplay between various deterministic and stochastic factors and this is particularly the case for the phenomenon of biological invasion. Whereas the spread of invasive species via propagation of a population front was shown to appear as a result of deterministic processes, the spread via formation, interaction and movement of separate patches has been recently attributed to the influence of environmental stochasticity. An appropriate understanding of the comparative importance of deterministic and stochastic mechanisms is still lacking, however. In this paper, we show that the patchy invasion appears to be possible also in a fully deterministic predator–prey model as a result of the Allee effect.

Keywords

Allee effect, biological invasion, predator–prey system.

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INTRODUCTION

Biological invasion is an issue of increasing importance in contemporary ecology and attracts considerable attention both from theoretical and field ecologists (Elton 1958; Drake *et al.* 1989; Hengselveld 1989; Shigesada & Kawasaki 1996). Among many issues related to species invasions, the patterns of spread are of particular interest. Deterministic models, usually formulated in terms of partial differential equations (e.g. Holmes *et al.* 1994), predict, as a typical pattern, the existence of a smooth population front propagating from the place where the invasive species was originally introduced. This is often observed in nature; moreover, sometimes even very simple deterministic models can indeed be in a good quantitative agreement with field data (Skellam 1951; Lubina & Levin 1988; Andow *et al.* 1990; Petrovskii & Shigesada 2001). However, it has also been a point of criticism because, in reality, invasion of species is not always described by travelling population fronts. There is a number of cases reported where the spreading of invasive species takes place via formation and irregular movement of separated patches rather than smooth fronts (Shigesada & Kawasaki 1996; Lewis & Pacala 2000; references therein). This disagreement has stimulated some authors to develop new models (e.g. see Shigesada *et al.* 1995), particularly, models allowing for environmental stochasticity (Lewis & Pacala 2000; Lewis 2000).

It seems, however, that the relative contribution from deterministic and stochastic mechanisms still remains obscure. Although it was shown by Lewis (2000) and Lewis & Pacala (2000) that stochasticity can lead to patchy invasion, it has also been shown recently by Malchow *et al.* (2001) that, in some cases, there exists a critical level of environmental noise. The systems with subcritical stochasticity are more driven by deterministic processes, i.e. exhibiting formation of spatio-temporal patterns typical for deterministic models. Another point is that sometimes it is difficult to distinguish between the impact of deterministic and stochastic factors. For instance, in bacterial ecology, computer simulations of complex spatio-temporal patterns of *Bacillus subtilis* based on stochastic models (Kawasaki *et al.* 1997) and deterministic models (Mimura *et al.* 2000) lead, within a certain parameter range, to very similar results.

Moreover, the existence and uniqueness of the travelling front solution was rigorously proved only for a few special cases, particularly, for a predator–prey system with logistic growth rate for the prey population, i.e. for the case when its per capita growth rate decreases monotonically (Dunbar 1984). Meanwhile, many species are subject to the Allee effect (Allee 1938) when the per capita growth rate is non-monotonic and can even become negative for small values of the population density (Berryman 1981; Lewis & Kareiva 1993). The Allee effect was shown to bring essential changes to the population dynamics (Amarasekare 1998; Dennis 1989; Gyllenberg *et al.* 1999). In this paper, we show by

means of numerical simulations that patchy invasion appears possible in a fully deterministic predator–prey model in the presence of the Allee effect.

MAIN EQUATIONS

We consider the following model of 2-D spatio-temporal population dynamics:

$$\frac{\partial H(X, Y, T)}{\partial T} = D_1 \left(\frac{\partial^2 H}{\partial X^2} + \frac{\partial^2 H}{\partial Y^2} \right) + F(H) - f(H, P), \tag{1}$$

$$\frac{\partial P(X, Y, T)}{\partial T} = D_2 \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right) + \kappa f(H, P) - MP \tag{2}$$

(cf. Segel & Jackson 1972; Nisbet & Gurney 1982; Murray 1989; Holmes *et al.* 1994; Shigesada & Kawasaki 1996; Sherratt 2001). Here H and P are the densities of prey and predator, respectively, at moment T and position (X, Y) . The function $F(H)$ describes prey multiplication, $f(H, P)$ describes predation, and the term MP stands for predator mortality. D_1 and D_2 are diffusivities and κ is the food utilization coefficient.

We assume that the predator response is of Holling type II which is usually parameterized as follows:

$$f(H, P) = A \frac{HP}{H + B} \tag{3}$$

where A is the predation rate and B is the half-saturation density.

Assuming Allee dynamics for the prey population, its growth rate can be parameterized as follows (Lewis & Kareiva 1993):

$$F(H) = \left(\frac{4\omega}{(K - H_0)^2} \right) H(H - H_0)(K - H) \tag{4}$$

where K is the prey carrying capacity, ω is the maximum per capita growth rate and H_0 is the “threshold” ($H_0 < K$), so that for $H < H_0$ the growth rate becomes negative. H_0 can be considered as a measure of the intensity of the Allee effect: the less the value of H_0 is, the less prominent is the Allee effect. For $H_0 = -1$, eqn 4 is equivalent to the logistic population growth rate, see (Lewis & Kareiva 1993).

Equations 1, 2 with 3 and 4 contain a large number of parameters, that makes their numerical investigation cumbersome. However, by choosing appropriate scales for the variables (Nisbet & Gurney 1982; Murray 1989; Shigesada & Kawasaki 1996; for a more general discussion see Barenblatt 1996), the number of parameters can be lessened. Considering dimensionless variables $u = H/K$, $v = P/(\kappa K)$,

$t = aT$, $x = X(a/D_1)^{1/2}$, $y = Y(a/D_1)^{1/2}$ where $a = A\kappa K/B$, from eqns 1–2, we obtain:

$$\frac{\partial u(x, y, t)}{\partial t} = \left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + \gamma u(u - \beta)(1 - u) - \frac{uv}{1 + \alpha u}, \tag{5}$$

$$\frac{\partial v(x, y, t)}{\partial t} = \epsilon \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + \frac{uv}{1 + \alpha u} - \delta v. \tag{6}$$

Equations 5–6 contain five dimensionless parameters (against nine in the original equations), i.e. $\alpha = K/B$, $\beta = H_0/K$, $\gamma = 4\omega BK/(A\kappa(K - H_0)^2)$, $\delta = M/a$ and $\epsilon = D_2/D_1$. Thus, the behaviour of dimensionless solutions u and v appears to depend on five dimensionless combinations of the original parameters rather than on each of them separately.

Before proceeding to numerical simulations for the space-explicit model 5–6, it is worth giving a brief account of the properties of the “well-mixed”, spatially homogeneous system, i.e. eqns 5–6 without diffusion terms, and to stress the distinctions from the predator–prey model with the logistic growth.

For the system 5–6 without diffusion terms, there are four stationary states: $(0,0)$ $(\beta,0)$ $(1,0)$ and the coexistence state (u_*, v_*) where

$$u_* = \frac{\delta}{1 - \alpha\delta}, \quad v_* = \gamma(u_* - \beta)(1 - u_*)(1 + \alpha u_*). \tag{7}$$

Using the standard linear stability analysis (e.g. Murray 1989), it can be readily seen that $(0,0)$ is always a stable node. The steady states $(\beta,0)$ and $(1,0)$ are either nodes or saddle-points, depending on the relation between the parameters. The coexistence state (u_*, v_*) lies in the biologically meaningful domain $u > 0$, $v > 0$ under condition $\beta < u_* < 1$ (for these parameter values $(\beta,0)$ and $(1,0)$ are saddle-points) and it can be either a stable or unstable focus or a node. As the parameters vary in such a way that the value of u_* gradually decreases from 1 (when the coexistence state appears in the upper semiplane) toward β (when it leaves the upper semiplane), it first changes its type from a stable node to a stable focus and then loses its stability for $u_* = u_H$ (for the sake of brevity, we do not write down the expression for u_H here). The loss of stability is followed by the birth of a stable limit cycle as a result of the Hopf bifurcation. Numerical simulations show that, for further decrease in u_* , the limit cycle first grows in size and then disappears for $u_* = \bar{u}_*$ where $\beta < \bar{u}_* < u_H < 1$.

To compare, the predator–prey system with logistic growth of prey and Holling type II response of predator possesses only three steady states, one of which corresponds to coexistence of the species, e.g. see Petrovskii & Malchow (2000, 2001) for details. For the parameter values for which the coexistence state lays in the domain $u > 0$, $v > 0$, it can

also be either a focus or a node, and the loss of its stability is followed by formation of a stable limit cycle. However, in this case an important difference is that the limit cycle exists for all parameter values from the range where the coexistence state is unstable, and the spatio-temporal complexity of a predator-prey system is usually associated with its local oscillatory kinetics (Pascual 1993; Sherratt *et al.* 1995; Petrovskii & Malchow 1999).

Thus, the structure of the phase plane of the system 5–6 is obviously more complicated than the one corresponding to the system with logistic growth. One can expect that the spatio-temporal behaviour of the predator-prey system will also appear more complex as a result of the Allee effect. From the mathematical point of view, a remarkable distinction of the predator-prey system with the Allee dynamics for prey is that there is a parameter range where the coexistence state is unstable but no stable limit cycle exists, the only attractor being the “no-species” state (0,0).

RESULTS OF COMPUTER SIMULATIONS

In order to study biological invasion in the model 5–6, the initial distribution of species was taken as follows:

$$u(x, y, 0) = U_0 \text{ if } x_{11} < x < x_{12} \text{ and } y_{11} < y < y_{12}, \text{ otherwise } u(x, y, 0) = 0, \tag{8}$$

$$v(x, y, 0) = V_0 \text{ if } x_{21} < x < x_{22} \text{ and } y_{21} < y < y_{22}, \text{ otherwise } v(x, y, 0) = 0 \tag{9}$$

where U_0, V_0 and $x_{ij}, y_{ij}, i = 1, 2, j = 1, 2$ are parameters. Equations 5–6 with the initial conditions 8–9 were solved numerically by finite-differences. In most cases we used the simple explicit scheme; however, in order to avoid any essential numerical artifact, some of the results were also reproduced using more advanced alternate directions scheme. Also the sensitivity of the results with respect to variations of the time-step and the space-step was checked, and the value of the steps were chosen reasonably small.

The choice of an appropriate parameter range constitutes a problem. The matter is that dimensionless eqns 5–6 still contain five parameters and that makes a regular search in the parameter space very time consuming. The main goal of this paper, however, is to understand a possible impact of the Allee effect on the pattern of spread of invasive populations. Thus, to run computer experiments we used parameter values from that parameter range where the system 5–6 exhibits its specific features associated with the impact of the Allee effect (see the end of the previous Section).

Figure 1 shows the spreading of the populations from the place of their introduction for the parameter set **S1**: $\epsilon = 1, \alpha = 0.1, \beta = 0.2, \gamma = 3.9, \delta = 0.5$. Only the distribution of

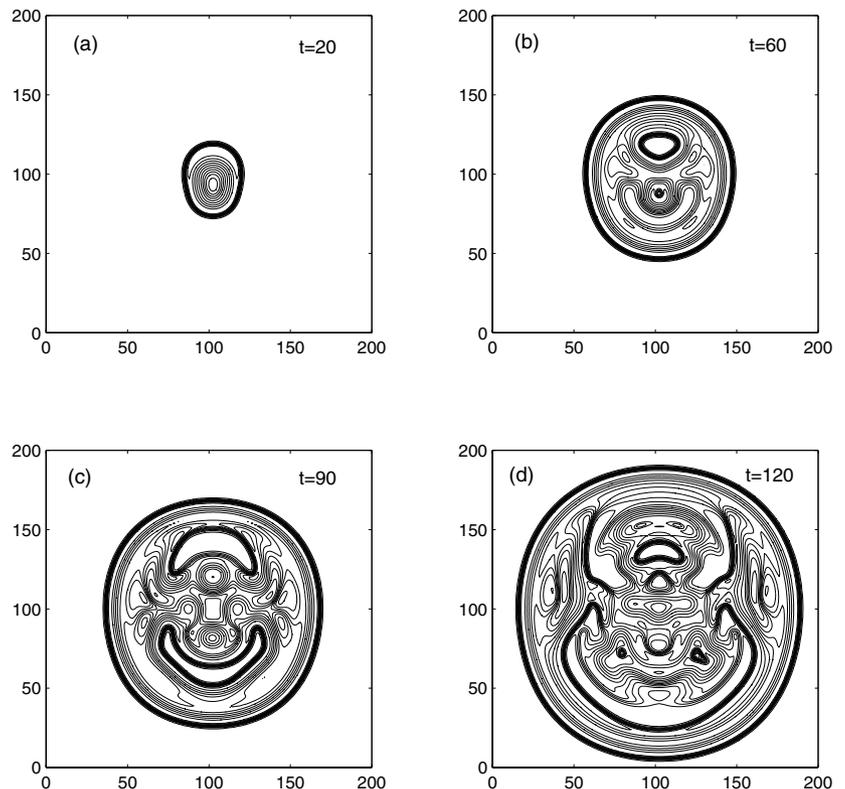


Figure 1 Isoclines of the prey density at different moments calculated for parameters $\epsilon = 1, \alpha = 0.1, \beta = 0.2, \gamma = 3.9, \delta = 0.5$ and initial conditions (8–9) with $U_0 = 1.2, V_0 = 0.2, x_{11} = 85, x_{12} = 105, x_{21} = 85, x_{22} = 95, y_{11} = 100, y_{12} = 105, y_{21} = 95, y_{22} = 115$. Thick lines arise from clustering different isoclines and thus correspond to sharp gradients in the species density. Outside the circular front the population density is zero.

the prey density is shown because the density of predator exhibits qualitatively similar features. Clearly, in this case the species invasion takes place via a scenario that is rather typical for the systems without the Allee effect (Sherratt *et al.* 1995, 1997; Petrovskii & Malchow 2000; Sherratt 2001): the populations spread into the empty space via propagation of a population front which is followed by formation of irregular spatio-temporal patterns (for a discussion of similar issues see also (Yachi *et al.* 1989; Petrovskii *et al.* 2001)). Note that, since the diffusivities here are the same for prey and predator, the patterns cannot arise because of Turing instability (Segel & Jackson 1972; Levin & Segel 1976) and should be ascribed to another mechanism (Medvinsky *et al.* 2001; Petrovskii & Malchow 2001). Although this invasion regime seems to be of high ecological relevance, it is not of primary interest for the

purposes of our present study because it only gives a generalization of the pattern of spread already well-known for other systems. The Allee effect does not bring any significant modification to the spatio-temporal dynamics in this case.

However, the situation may become essentially different for other parameter values. Figure 2 shows the spreading of the populations from the place of their introduction for the parameter set **S2**: $\varepsilon = 1$, $\alpha = 0.1$, $\beta = 0.2$, $\gamma = 3.9$, $\delta = 0.37$. Although at the beginning of the invasion some kind of population front is formed, see Fig. 2(a), at later stages the front breaks into pieces (Figs 2b–2d). Further spreading of the populations takes place via the irregular dynamics of separate patches. In the course of time, the patches move (due to evasion–pursuit mechanism, e.g. see Murray 1989; p. 315), merge, disappear and produce new

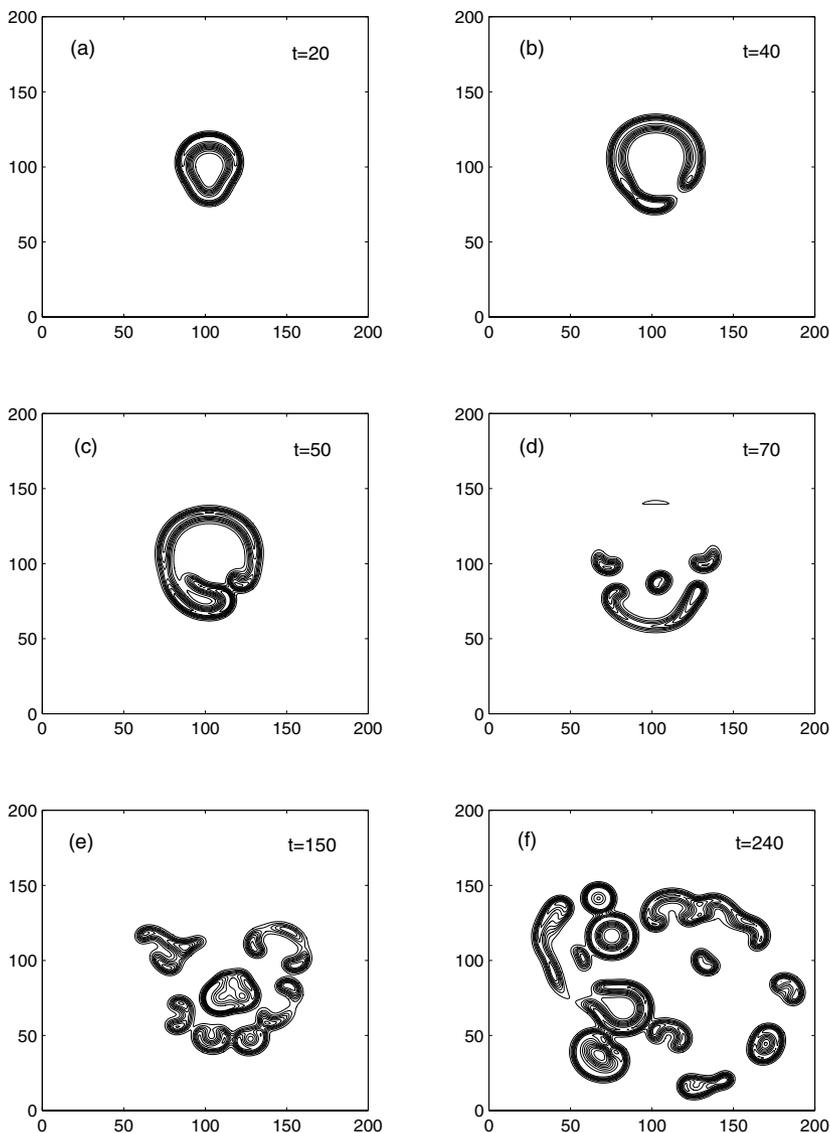


Figure 2 Isoclines of the prey density at different moments obtained for the parameters $\varepsilon = 1$, $\alpha = 0.1$, $\beta = 0.2$, $\gamma = 3.9$, $\delta = 0.37$ and the same initial conditions as in Fig. 1. Thick lines correspond to sharp gradients in the species density and thus show the boundary of the patches. Inside the patches the prey density is on the order of carrying capacity, outside the patches it is approximately zero. The spatial distribution of predator exhibits qualitatively similar features and therefore is not shown.

patches, and gradually the populations invade the whole domain, cf. Figs 2(d)–2(f).

An important point to be stressed here is that parameter set **S2** is not a singular one and the phenomenon of the spreading of invasive species via formation, interaction and movement of separated patches can be observed for various parameter values. In particular, it can be observed when the species diffusivities are not equal. Figure 3 shows the spreading of the species from the place of their initial distribution calculated for the parameter set **S3**: $\varepsilon = 1.2$, $\alpha = 0.1$, $\beta = 0.2$, $\gamma = 4.0$, $\delta = 0.38$. Obviously, in this case the invasion exhibits essentially the same features. No population front exists except for the early stages of invasion (see Figs 3a–3c) and the species invade the domain via the dynamics of separate patches, cf. Figs 3(d)–3(f).

Although some contorted sections of the front may be observed also for the later stages, e.g. see Fig. 3(f), a continuous circular front never reappears. Qualitatively similar dynamics can be observed for $\varepsilon < 1$ also; for instance, the following parameter set **S4**, i.e. $\varepsilon = 0.9$, $\alpha = 0.1$, $\beta = 0.2$, $\gamma = 3.6$, $\delta = 0.37$, leads to the same pattern of spread as shown in Figs 2 and 3.

For all the three parameter sets, i.e. **S2**, **S3** and **S4**, the local kinetics is specific for the system with the Allee effect, i.e. the coexistence state is unstable but no stable limit cycle exists. We have to mention, however, that there is no one-to-one correspondence between this parameter range and the patchy regime of invasion. Moreover, in the case that only one parameter is varied the phenomenon appears to be rather sensitive to the parameter changes. A variation for

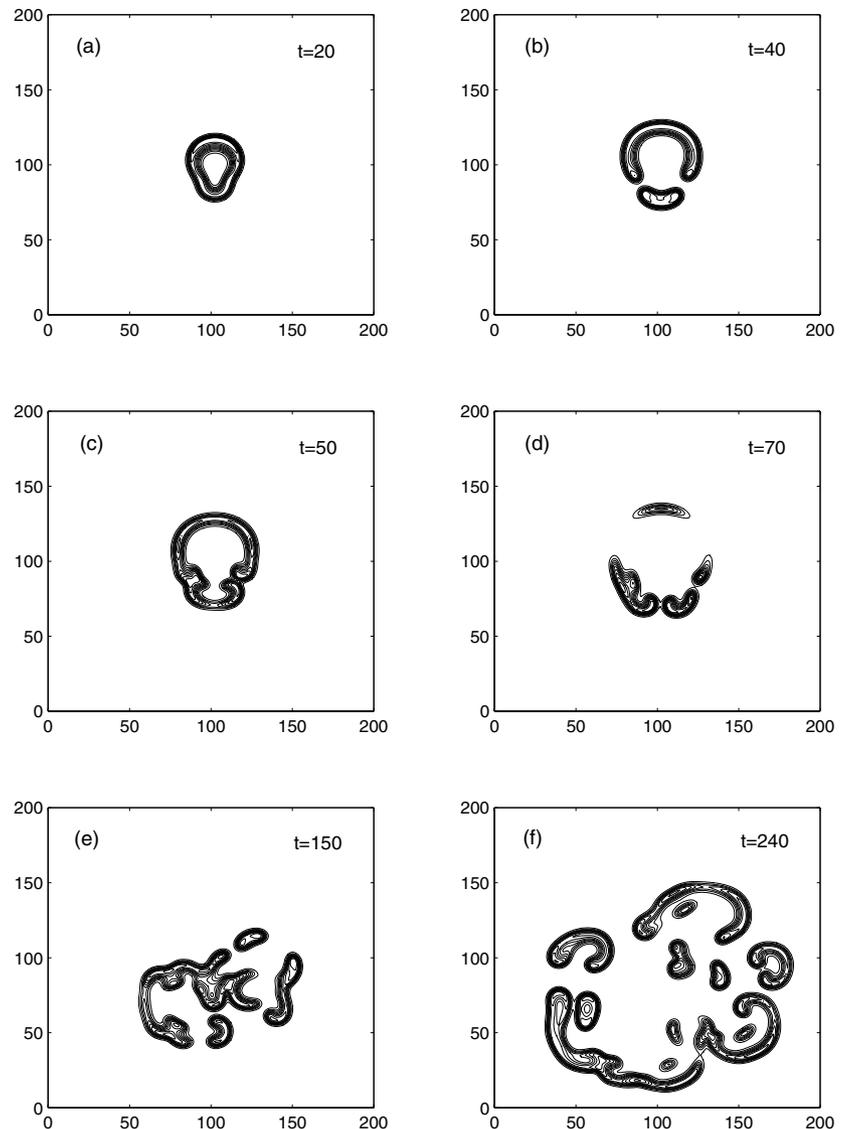


Figure 3 Isoclines of the prey density obtained at different moments for parameters $\varepsilon = 1.2$, $\alpha = 0.1$, $\beta = 0.2$, $\gamma = 4.0$, $\delta = 0.38$ and the same initial conditions as in Fig. 1. Thick lines show the boundaries of separate patches.

more than a few per cent already destroys the patchy invasion even though the properties of the phase plane of the system remain unchanged. The alternative pattern of spread which typically appears is the one shown in Fig. 1, i.e. propagation of a population front with the formation of irregular spatio-temporal patterns in its wake. However, much larger parameter variations still may leave the patchy regime of invasion unchanged in case the variations are consistent: in case one of the parameters is changed to make the predator “stronger”, another one (or a few) parameter(s) must be changed correspondingly either to make the predator “weaker” again or to make the prey “stronger” as well. For instance, an increase in the predator diffusivity must be compensated with an increase in the predator mortality and/or an increase in the prey growth rate, cf. sets **S2** and **S3**.

An important remark is that, as we observed in computer experiments, the patchy invasion can also occur for $\alpha = 0$, i.e. when the term describing predation becomes bilinear, as in the classical Lotka–Volterra model. For instance, for the parameter set **S5**, i.e. $\varepsilon = 1$, $\alpha = 0$, $\beta = 0.2$, $\gamma = 4.0$, $\delta = 0.39$, the spread of the species from the place of their introduction follows the same scenario as shown in Figs 2 and 3 (for the sake of brevity, we do not provide separate figures). This is a direct consequence of the Allee effect. Indeed, for the predator–prey system with logistic growth and predation described by the bilinear term, the coexistence state is always stable and the formation of smooth population fronts is a must (Dunbar 1984; Murray 1989).

To obtain insight into the problem from a somewhat different standpoint, we also repeated our simulations for smaller values of β (correspondingly, larger values of γ , see the definition of γ below eqns 5–6) leaving other parameters unchanged. For all the parameter sets where the patchy invasion was observed, i.e. **S2** to **S5**, a decrease in β for more than a few per cent changes the pattern of spread to the propagation of smooth continuous population fronts (in spite of the corresponding increase in γ which can be expected to compensate for the decrease in β , see above). Since smaller β means a less prominent Allee effect (see the comments below eqn 4), it gives another indication that it is the Allee effect that makes possible the patchy invasion in the model 5–6.

It is important to note that the deterministic mechanism of patchy invasion reported in this paper arises as a result of the interplay between the Allee effect and the predator–prey interactions. To demonstrate that, we repeated all the simulations with $V_0 = 0$ (see eqns 8–9). In the absence of predator, the invasion of prey always takes place via propagation of a smooth continuous population front; this is in full agreement with the results of previous authors (Lewis & Kareiva 1993).

For those parameter sets where the patchy invasion was observed, we also checked the robustness of the phenomenon to the variation of the sizes of the domains originally inhabited by prey and predator. We obtained that, as long as the sizes were of the same order (that corresponds to a “conjoint” invasion by prey and predator), the invasion remains patchy and follows the scenario shown in Figs 2 and 3. However, the pattern of spread changes in case the predator invades the area already invaded by the prey. The invasion of the predator into the space inhabited by the prey always takes place via propagation of a smooth continuous front (e.g. in the manner shown in Fig. 1) even when the domain originally inhabited by the predator has a shape more complicated than a rectangle, and no patchy invasion has been observed in this case.

CONCLUDING REMARKS

We showed that a fully deterministic predator–prey model (5–6) with the Allee dynamics for prey can predict a patchy invasion for the parameter range where the model has specific features caused by the Allee effect, i.e. the coexistence state is unstable but no stable limit cycle exists. Since the pattern of spread of invasive species via the dynamics and interaction of separate patches is rather typical in nature (Lewis & Pacala 2000), our results seem to have evident ecological meaning. We want to mention, however, that it would be unwise to reduce such a complex phenomenon as patchy invasion to manifestation of only one process or mechanism. There can hardly be any doubt that biological invasions in nature occur due to the contribution from and the interplay between different factors, e.g. specifics of the landscape structure (Andow *et al.* 1990), behavioural structure of the invasive population(s) (Shigesada *et al.* 1995), and environmental stochasticity (Lewis & Pacala 2000; Lewis 2000). However, the mechanism of patchy invasion which we considered in this paper is new, and thus our results make a certain progress in understanding the processes underlying the spreading of invasive species.

Considering this phenomenon in a wider perspective, it ought to be mentioned that the deterministic spatio-temporal dynamics of interacting agents via the movement and interaction of separate patches has been observed earlier in a few chemical and physical systems (Pearson 1993; Krischer & Mikhailov 1994; Ermentrout *et al.* 1997). However, those results were obtained for the systems with the properties essentially different from the predator–prey model and the ecological implications of the phenomenon have never been considered.

One of the curious points of the reported mechanism of patchy invasion is that, for those parameter values where the patchy invasion was observed in the model (5–6), the only

attractor in the phase plane of the corresponding well-mixed system is the “no species” state (0,0). Thus, while in the spatially homogeneous case the species would inevitably go extinct, in the model with explicit space the populations not only persist due to formation of spatio-temporal pattern but can even invade the whole domain.

We want to mention that the fact that the patchy invasion in the model (5–6) can take place when the species interaction is described by the bilinear term (i.e. for $\alpha = 0$) opens the possibility for another application. The model (5–6) with $\alpha = 0$ is mathematically close to the SI model of the epidemic spread, e.g. see (Murray 1989; chapter 20), and thus our results can also be interpreted as a patchy spread of a certain infectious disease.

In this paper, we were more concerned with reporting the new mechanism of patchy invasion rather than with investigating it in every detail. Thus, a number of problems are open. First of all, we want to stress that the Allee effect gives only a necessary condition for the patchy invasion in the model (5–6), not a sufficient one. What causes additional restrictions on the parameter values remains obscure and will become a subject of future research. Also, to understand the phenomenon better, the nature of the instability leading to the breakdown of the circular front (cf. Figures 2a.b and 3a.b) should be revealed. Our results seem to indicate that it is not a usual front instability with respect to small perturbations (see Mimura *et al.* 2000; references therein), otherwise it could be observed as well in the case of the invasion of predator into the area inhabited by prey.

From the standpoint of prospective ecological applications, it seems interesting to reveal the correlation between the cases of patchy invasion in nature and the existence of Allee effect in the populations of invasive species. Another question is whether the irregular spatial patterns arising in the course of patchy invasion in the predator–prey system with the Allee effect has chaotic features. The positive answer would imply, as an immediate consequence, that one cannot make a long-time prediction about the position of separated patches. Some recent results point out that this type of spatio-temporal dynamics is chaotic (Pascual 1993; Sherratt *et al.* 1995, 1997; Petrovskii & Malchow 1999, 2001; Medvinsky *et al.* 2001). Although the patchy invasion itself is rather robust with respect to the choice of initial conditions (unless the domain originally inhabited by prey becomes much larger than that inhabited by predator, cf. the end of Section on results of computer simulations), our computer simulations indicate that the position of individual patches is rather sensitive to the details of the initial distribution. This issue, however, should be given a more careful consideration and will become a subject of a separate study.

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REFERENCES

- Allee, W.C. (1938). *The Social Life of Animals*. Norton, New York.
- Amarasekare, P. (1998). Interactions between local dynamics and dispersal: insights from single species models. *Theor. Pop. Biol.*, 53, 44–59.
- Andow, D.A., Kareiva, P.M., Levin, S.A. & Okubo, A. (1990). Spread of invading organisms. *Landscape Ecol.*, 4, 177–188.
- Barenblatt, G.I. (1996). *Scaling, Self-Similarity, and Intermediate Asymptotics*. Cambridge University Press, Cambridge.
- Berryman, A.A. (1981). *Population Systems: A General Introduction*. Plenum Press, New York.
- Dennis, B. (1989). Allee effects: population growth, critical density, and the chance of extinction. *Nat. Res. Model.*, 3, 481–538.
- Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M. & Williamson, M., eds. (1989). *Biological Invasions: A Global Perspective*. John Wiley, New York.
- Dunbar, S.R. (1984). Travelling wave solutions of diffusive Lotka–Volterra equations: a heteroclinic connection in \mathbf{R}^4 . *Trans. Am. Math. Soc.*, 268, 557–594.
- Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Ermentrout, B., Chen, X. & Chen, Z. (1997). Transition fronts and localized structures in bistable reaction–diffusion equations. *Physica D*, 108, 147–167.
- Gyllenberg, M., Hemminki, J. & Tammaru, T. (1999). Allee effects can both conserve and create spatial heterogeneity in population densities. *Theor. Pop. Biol.*, 56, 231–242.
- Hengselveld, R. (1989). *Dynamics of Biological Invasions*. Chapman & Hall, London.
- Holmes, E.E., Lewis, M.A., Banks, J.E. & Veit, R.R. (1994). Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology*, 75, 17–29.
- Kawasaki, K., Mochizuki, A., Matsushita, M., Umeda, T. & Shigesada, N. (1997). Modeling spatio-temporal patterns generated by *Bacillus subtilis*. *J. Theor. Biol.*, 188, 177–185.
- Krischer, K. & Mikhailov, A. (1994). Bifurcation to traveling spots in reaction–diffusion systems. *Phys. Rev. Lett.*, 73, 3165–3168.
- Levin, S.A. & Segel, L.A. (1976). Hypothesis for origin of planktonic patchiness. *Nature*, 259, 659.
- Lewis, M.A. (2000). Spread rate for a nonlinear stochastic invasion. *J. Math. Biol.*, 41, 430–454.
- Lewis, M.A. & Kareiva, P. (1993). Allee dynamics and the spread of invading organisms. *Theor. Pop. Biol.*, 43, 141–158.
- Lewis, M.A. & Pacala, S. (2000). Modeling and analysis of stochastic invasion processes. *J. Math. Biol.*, 41, 387–429.
- Lubina, J. & Levin, S. (1988). The spread of a reinvading organism: range expansion of the California sea otter. *Am. Nat.*, 131, 526–543.

- Malchow, H., Petrovskii, S.V. & Medvinsky, A.B. (2001). Numerical study of plankton–fish dynamics in a spatially structured and noisy environment. *Ecol. Modelling*, in press.
- Medvinsky, A.B., Petrovskii, S.V., Tikhonov, D.A., Tikhonova, I.A., Ivanitsky, G.R., Venturino, E. & Malchow, H. (2001). Biological factors underlying regularity and chaos in aquatic ecosystems: simple models of complex dynamics. *J. Biosci.*, 26, 77–108.
- Mimura, M., Sakaguchi, H. & Matsushita, M. (2000). Reaction–diffusion modelling of bacterial colony patterns. *Physica A*, 282, 283–303.
- Murray, J.D. (1989). *Mathematical Biology*. Springer-Verlag, Berlin.
- Nisbet, R.M. & Gurney, W.S.C. (1982). *Modelling Fluctuating Populations*. Wiley, Chichester.
- Pascual, M. (1993). Diffusion-induced chaos in a spatial predator–prey system. *Proc. R. Soc. B*, 251, 1–7.
- Pearson, J.E. (1993). Complex patterns in a simple system. *Science*, 261, 189–192.
- Petrovskii, S.V., Kawasaki, K., Takasu, F. & Shigesada, N. (2001). Diffusive waves, dynamical stabilization, and spatio-temporal chaos in a community of three competitive species. *Jap. J. Industr. Appl. Math.*, 18, 459–481.
- Petrovskii, S.V. & Malchow, H. (1999). A minimal model of pattern formation in a prey–predator system. *Math. Computer Modelling*, 29, 49–63.
- Petrovskii, S.V. & Malchow, H. (2000). Critical phenomena in plankton communities: KISS model revisited. *Nonlinear Analysis: Real World Applications*, 1, 37–51.
- Petrovskii, S.V. & Malchow, H. (2001). Wave of chaos: new mechanism of pattern formation in spatio-temporal population dynamics. *Theor. Pop. Biol.*, 59, 157–174.
- Petrovskii, S.V. & Shigesada, N. (2001). Some exact solutions of a generalized Fisher equation related to the problem of biological invasion. *Math. Biosci.*, 172, 73–94.
- Segel, L.A. & Jackson, J.L. (1972). Dissipative structure: an explanation and an ecological example. *J. Theor. Biol.*, 37, 545–559.
- Sherratt, J.A. (2001). Periodic travelling waves in cyclic predator–prey systems. *Ecol. Lett.*, 4, 30–37.
- Sherratt, J.A., Eagan, B.T. & Lewis, M.A. (1997). Oscillations and chaos behind predator–prey invasion: mathematical artifact or ecological reality? *Phil. Trans. R. Soc. B*, 352, 21–38.
- Sherratt, J.A., Lewis, M.A. & Fowler, A.C. (1995). Ecological chaos in the wake of invasion. *Proc. Nat. Acad. Sci. U.S.A.*, 92, 2524–2528.
- Shigesada, N. & Kawasaki, K. (1996). *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford.
- Shigesada, N., Kawasaki, K. & Takeda, Y. (1995). Modeling stratified diffusion in biological invasions. *Am. Nat.*, 146, 229–251.
- Skellam, J. (1951). Random dispersal in theoretical populations. *Biometrika*, 38, 196–218.
- Yachi, S., Kawasaki, K., Shigesada, N. & Teramoto, E. (1989). Spatial patterns of propagating waves of fox rabies. *Forma*, 4, 3–12.

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