

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/232621609>

Stability and Instability incurred by Aggregation in Host-Parasitoid Systems

ARTICLE · JANUARY 2010

DOI: 10.1109/ICCMS.2010.162

READS

18

3 AUTHORS, INCLUDING:



Wenlong Li

Lanzhou University

59 PUBLICATIONS 929 CITATIONS

SEE PROFILE



The effect of colored noise on spatiotemporal dynamics of biological invasion in a diffusive predator–prey system

Wenting Wang^a, Wenlong Li^{b,*}, Zizhen Li^{a,c}, Hui Zhang^a

^a School of Mathematics and Statistics, Lanzhou University, Lanzhou, 730000, China

^b School of Pastoral Agriculture Science and Technology, Lanzhou, 730000, China

^c Key Laboratory of Arid and Grassland Agroecology of Ministry of Education, Lanzhou, 730000, China

ARTICLE INFO

Article history:

Received 8 November 2010

Received in revised form

21 December 2010

Accepted 25 December 2010

Biological invasion

Colored noise

Predator–prey

Spatiotemporal dynamics

ABSTRACT

Spatiotemporal dynamics of a predator–prey system is considered under the assumption that the predator is sensitive to colored noise. Mathematically, the model consists of two coupled diffusion–reactions. By means of extensive numerical simulations, the complex invasion pattern formations of the system are identified. The results show that a geographical invasion emerges without regional persistence when the intensity of colored noise is small. Remarkably, as the noise intensity increases, the species spreads via a patchy invasion only when the system is affected by red noise. Meanwhile, the relationship between local stability and global invasion is also considered. The predator, which becomes extinct in the system without diffusion, could invade locally when the system is affected by white noise. However, the local invasion is not followed by geographical spread.

© 2011 Elsevier Ireland Ltd. All rights reserved.

1. Introduction

Invasion by alien species has increasingly been recognized as one of the important problems in contemporary ecology and attracts considerable attention both from theoretical and field ecologists (Hengeveld, 1989; Hastings, 1996; Shigesada and Kawasaki, 1997; Frantzen and van den Bosch, 2000; Keitt et al., 2001; Petrovskii et al., 2005b). Among many issues related to biological invasion, the patterns and mechanisms of species spatial dispersal are of significant interest. Although the patterns of spread observed in nature are rather complicated, one can distinguish roughly between the two following scenarios (Hengeveld, 1989; Shigesada and Kawasaki, 1997; Lewis and Pacala, 2000; Morozov et al., 2008): (1) propagation of continuous travelling population fronts of high species density and (2) spread via formation and movement of patches of high density separated by areas with density close to zero. In the following, we will call the second scenario a patchy invasion. Identification of factors enhancing or hampering species spreading via propagation of a continuous population front or patchy invasion are problems of significant practical and theoretical importance. Especially in the case of patchy invasion the spatiotemporal dynamics should be more complicated and its origin has not been fully understood.

The origin of patchy invasion is often seen either in the case of environmental heterogeneity (Murray, 1989) or environmental stochasticity (Lewis, 2000; Lewis and Pacala, 2000). Indeed, the whole dynamics of ecological communities appears as a result of the interplay between numerous deterministic and stochastic factors. Holling (1973) emphasized the influence of noise in ecological dynamics and resilience. The noise may arise from stochastic disturbance of the external environment. Under the disturbance of noise, the species dynamics are always stochastic or seemingly stochastic. Petrovskii et al. (2005a) found that the patchy invasion can take place in a system of virally infected phytoplankton and zooplankton as a result of strong environmental noise. Sun et al. (2009) also argued that the noise can make patchy invasion possible in a predator–prey system with Allee effect. Recently, the potential importance of another characteristic of environmental noise has been recognized: the variance spectral, or the noise color (Kaitala et al., 1997; Xu and Li, 2003). White noise (or noise with a white variance spectrum) contains no temporal autocorrelation and is essentially a series of independent random numbers. For example, if a series of daily temperatures were white, tomorrow's temperature would be independent of today's temperature. Red noise, however, contains positive temporal autocorrelation: tomorrow's temperature is likely to be similar to today's. Recent theoretical investigations have suggested that population dynamics are sensitive to the noise color (Foley, 1994; Caswell and Cohen, 1995). Although several studies have referred to the effect of noise on the dispersal pattern formations (Lewis and Pacala, 2000; Malchow et al., 2002; Petrovskii et al., 2005b; Sun et al., 2009), there is

* Corresponding author.

E-mail addresses: wangwt05@lzu.cn (W. Wang), wlee@lzu.edu.cn (W. Li).

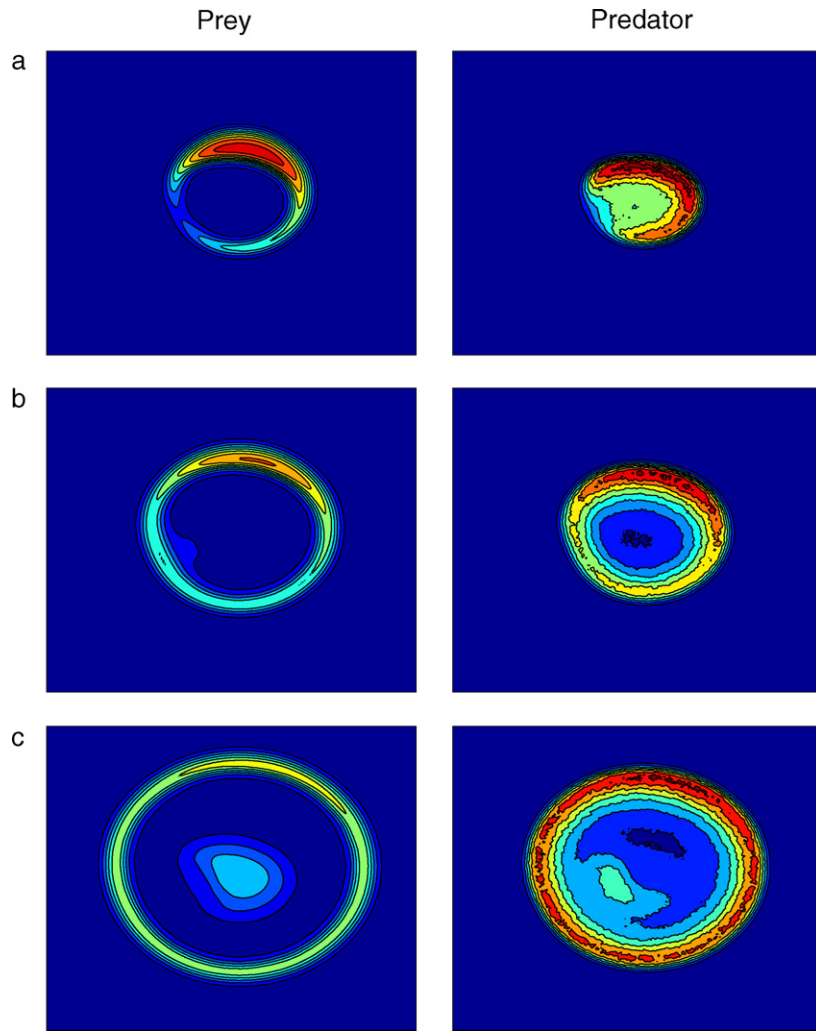


Fig. 1. Snapshots of the invasion regimes of the prey and predator at different moments for the system ((8)–(9)) affected by white noise. Parameter values: $\gamma = 0.3$, $\delta = 0.1$, $\alpha = 0.5$, $\beta = 0.2$, $c = 0$ and initial conditions ((12)–(13)) with $\delta_{11} = 30$, $\delta_{12} = 28$, $\delta_{21} = 15$, $\delta_{22} = 22$, $x_1 = 108$, $y_1 = 105$, $x_2 = 100$, $y_2 = 99$, $u_0 = 1$ and $v_0 = 0.4$. (a) $t = 150$, (b) $t = 300$, (c) $t = 500$.

no research on the spatiotemporal dynamics of species invasion responding to the noise of different colors.

Motivated by that, in this study, we focus on the influence of colored noise on the spatiotemporal pattern formation of a predator–prey system in a uniform environment. By means of extensive computer simulations, we make a thorough study of this system in connection to biological invasion and give a detailed classification of possible patterns of species spread. We show that the system spatiotemporal patterns are remarkably rich and complicated when disturbed by the noise of different colors. In particular, for a moderate noise intensity, there is a parameter range where the spread of invasive species occurs via patchy invasion. We also show that, as a result of the local interaction and colored noise, successful establishment of an exotic species does not necessarily lead to its geographical spread and also does not guarantee species regional persistence.

2. The model and method

We consider a two-dimensional model of predator–prey interaction in a homogeneous environment. According to a widely accepted approach (Murray, 1989; Malchow, 1993; Holmes et al., 1994; Shigesada and Kawasaki, 1997; Sherratt, 2001), the func-

tioning of a predator–prey community can be described by a reaction-diffusion system of the form:

$$\frac{\partial N(X, Y, T)}{\partial T} = D \left(\frac{\partial^2 N}{\partial X^2} + \frac{\partial^2 N}{\partial Y^2} \right) + F(N) - f(N, P), \quad (1)$$

$$\frac{\partial P(X, Y, T)}{\partial T} = D \left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2} \right) + \kappa f(N, P) - EP. \quad (2)$$

where, $N(X, Y, T)$ and $P(X, Y, T)$ are the abundance of prey and predator, respectively, at moment T and position (X, Y) . D is the diffusion coefficient. We assume that the diffusivities are equal for both species, which is the usual case in natural plankton communities where the mixing is mainly caused by marine turbulence. The function $F(N)$ describes the intrinsic growth of the prey, and $f(N, P)$ describes trophic interaction between the species, i.e., predation. The parameter E is the mortality rate of the predator, and κ is the coefficient of food utilization.

We assume that the local growth of the prey is logistic and the predator response is of Holling type II, which are usually parameterized as follows:

$$F(N) = rN \left(1 - \frac{N}{K} \right), \quad (3)$$

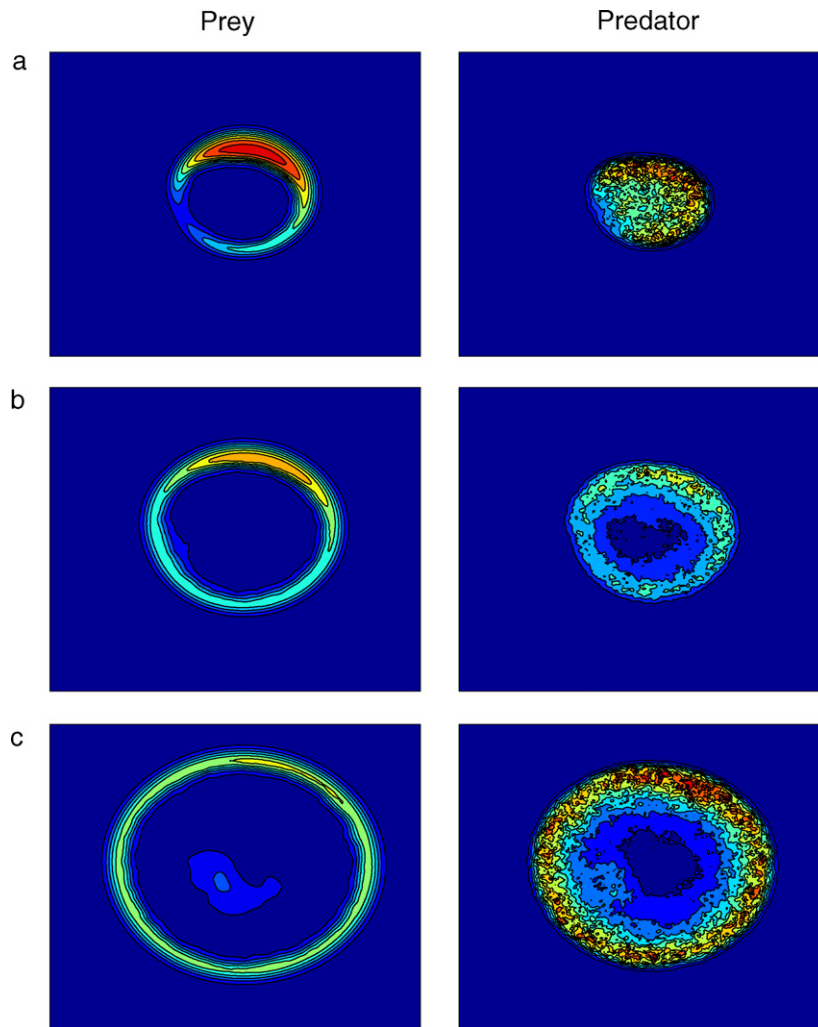


Fig. 2. Snapshots of the invasion regimes of the prey and predator at different moments for the system ((8)–(9)) affected by red noise. Parameter values: $\gamma=0.3$, $\delta=0.1$, $\alpha=0.5$, $\beta=0.2$, $c=0.8$ and the same initial conditions as in Fig. 1. (a) $t=150$, (b) $t=300$, (c) $t=500$.

$$f(N, P) = A \frac{NP}{N + H}. \quad (4)$$

where r is the maximal growth rate of the prey, K is the carrying capacity for the prey population, H is the half-saturation density, and A is the maximum predation rate.

For convenience, we introduce dimensionless variables

$$u = N/K, v = P/(\kappa K), t = aT, x = X(a/D)^{1/2}, y = Y(a/D)^{1/2}, \quad (5)$$

where $a = \kappa AK/H$, and new dimensionless parameters $\gamma = rH/kAK$, $\alpha = K/H$, $\delta = E/a$. Then, Eqs. (1) and (2) can be rewritten as:

$$\frac{\partial u(x, y, t)}{\partial t} = \left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + \gamma u(1 - u) - \frac{uv}{1 + \alpha u}, \quad (6)$$

$$\frac{\partial v(x, y, t)}{\partial t} = \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + \frac{uv}{1 + \alpha u} - \delta v. \quad (7)$$

In a predator–prey system, environmental noise may affect the populations in different ways. It may directly influence a population dynamics if the population is sensitive to it, or it may indirectly affect an insensitive population via a sensitive population. In the present study, we assume for simplicity that only the predator is sensitive to the noise. Combining with the noise term, we have the predator–prey system described by two partial differential equations of reaction-diffusion type as follows:

tions of reaction-diffusion type as follows:

$$\frac{\partial u(x, y, t)}{\partial t} = \left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + \gamma u(1 - u) - \frac{uv}{1 + \alpha u}, \quad (8)$$

$$\frac{\partial v(x, y, t)}{\partial t} = \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) + \frac{uv}{1 + \alpha u} + \psi(x, y, t)v - \delta v. \quad (9)$$

where $\psi(x, y, t)$ is a colored environmental noise. The noises enter the model in exactly the same manner as in the model studied by Ripa and Lundberg (1996) and Petchey et al. (1997). Here only a difference equation is given since Eqs. (8) and (9) will be solved numerically by a finite-difference method. The colored environment noise is described by

$$\psi_{t+1}(x, y) = c\psi_t(x, y) + \beta\epsilon_{t+1}(x, y). \quad (10)$$

where the parameter c controls the degree of the auto-correlation. If $c=0$, then there is no auto-correlation and the noise is white. For $0 < c < 1$, the noise is positively auto-correlated and the noise spectrum is reddened, while $-1 < c < 0$ implies negatively correlated noise, i.e. blue noise. $\epsilon_{t+1}(x, y)$ is a random normal deviate with zero mean and unit variance, and β determines the magnitude of the environmental fluctuations.

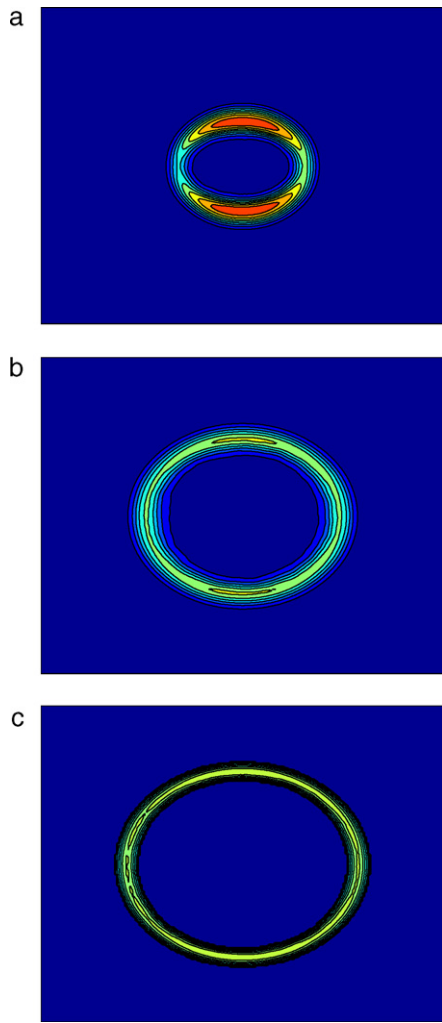


Fig. 3. Snapshots of invasion regime of the prey at different moments for the model ((8)–(9)) affected by white noise. Parameter values: $\gamma=0.3$, $\delta=0.1$, $\alpha=0.5$, $\beta=0.5$, $c=0$ and the same initial conditions as in Fig. 1. (a) $t=100$, (b) $t=300$, (c) $t=400$.

In order to provide guidelines on the spatiotemporal dynamics of the system given by Eqs. (8)–(9), it is important to consider the properties of the “well-mixed”, spatially homogeneous system, i.e., Eqs. (6)–(7) without diffusion terms. We first find that the system possesses three stationary states: $(0, 0)$ (total extinction), $(1, 0)$ (extinction of the predator), and the nontrivial state (u^*, v^*) (coexistence of prey and predator), where

$$u^* = \frac{\delta}{1 - \alpha\delta}, v^* = \gamma(1 - u^*)(1 + \alpha u^*). \quad (11)$$

By linear stability analysis, it can be readily seen that, for all nonnegative values of γ , α , and δ , the state $(0, 0)$ is a saddle point. The stationary point $(1, 0)$ is a saddle point if $(1 + \alpha)\delta < 1$, and a stable node if $\alpha\delta > 1$. The coexistence state (u^*, v^*) exists if $(1 + \alpha)\delta < 1$ and becomes unstable if $(1 + \alpha)\delta < 1 - \alpha$. In the latter case, the steady state is surrounded by a stable limit cycle and the kinetics of the system are oscillatory. These results provide helpful information for choosing parameter values for numerical simulations of the model (8)–(9) (Sherratt et al., 1995; Petrovskii, 1999).

Invasion of an alien species usually starts with a local introduction of exotic species; thus, relevant initial conditions for system (8)–(9) should be described by functions of compact support when the density of one or both species at the initial moment of time is non-zero only inside a certain domain. For that reason, we consider

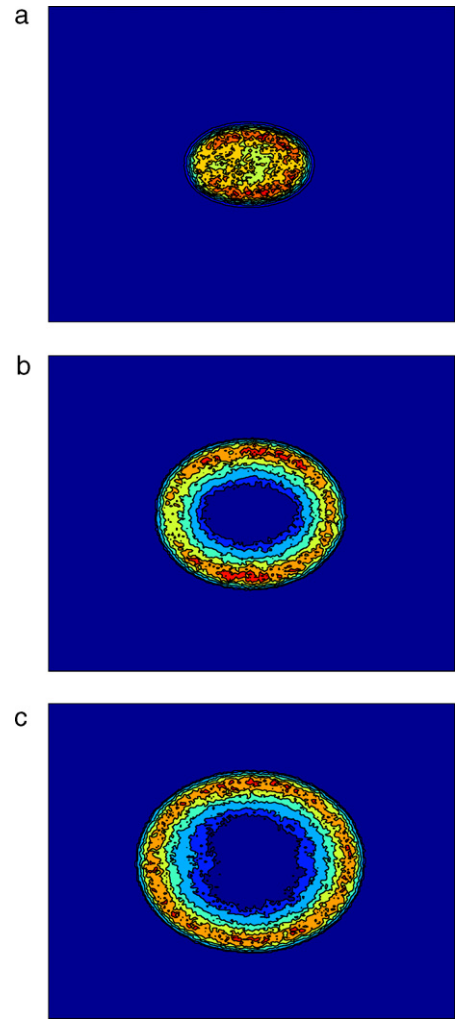


Fig. 4. Snapshots of invasion regime of the predator at different moments for the model ((8)–(9)) affected by white noise. Parameter values and initial conditions are the same as in Fig. 3. (a) $t=100$, (b) $t=300$, (c) $t=400$.

the initial conditions of the following form:

$$u(x, y, 0) = u_0 \text{ if } \left(\frac{x - x_1}{\sigma_{11}} \right)^2 + \left(\frac{y - y_1}{\sigma_{12}} \right)^2 \leq 1, \text{ otherwise } u(x, y, 0) = 0, \quad (12)$$

$$v(x, y, 0) = v_0 \text{ if } \left(\frac{x - x_2}{\sigma_{21}} \right)^2 + \left(\frac{y - y_2}{\sigma_{22}} \right)^2 \leq 1, \text{ otherwise } v(x, y, 0) = 0. \quad (13)$$

where u_0 , v_0 and σ_{ij} , x_i , y_j , $i = 1, 2$, $j = 1, 2$ are parameters with the obvious meanings.

3. Numerical results

In this section, the impact of colored noise on the spatiotemporal dynamics of the diffusive predator–prey system was studied by means of numerical simulations. The system (8)–(9) was solved numerically by finite differences. All simulations were run in a square numerical domain 200×200 and the explicit scheme was used. Sensitivity of the results with respect to the values of the grid steps was also checked and steps were chosen reasonably small to avoid any essential numerical artifact. The zero-flux boundary conditions were used at the boundary of the domain.

We chose the color and amplitude of noise as the controlling parameters to investigate the effect of colored noise on the regimes of biological invasion in the system (8)–(9). As blue noise

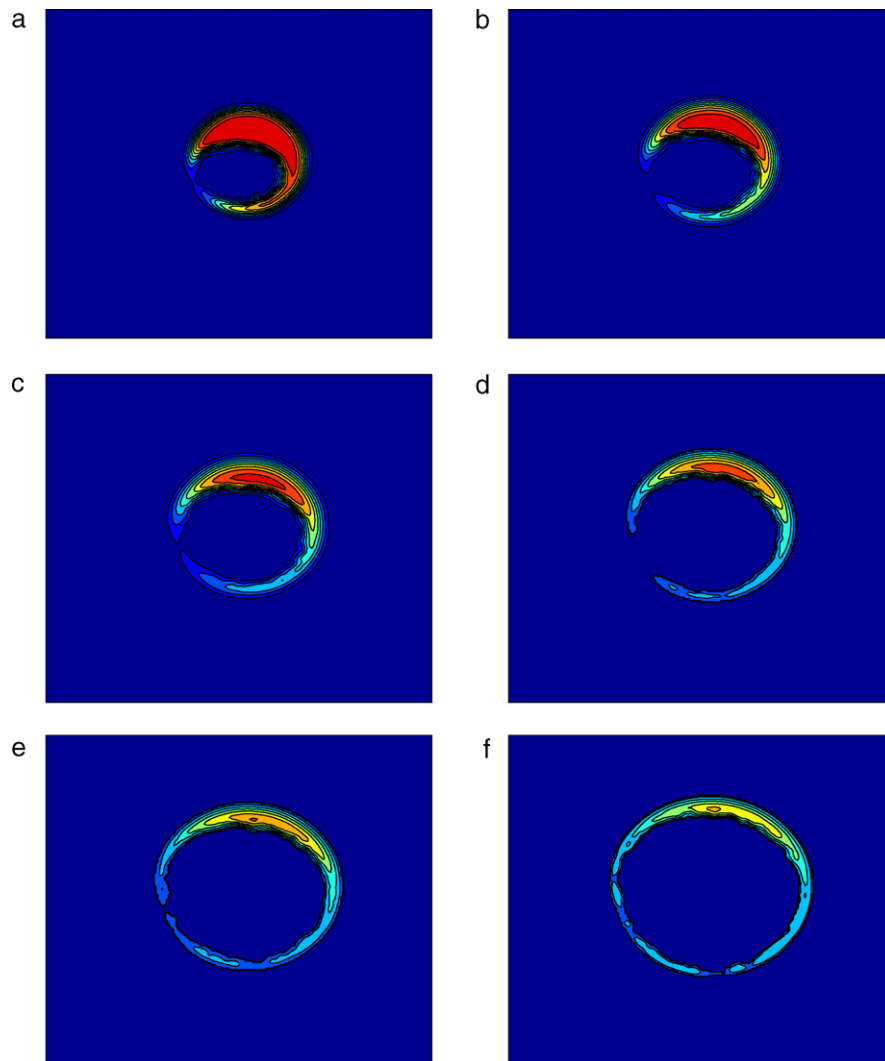


Fig. 5. Snapshots of invasion regime of the prey at different moments for the model ((8)–(9)) affected by red noise. Parameter values: $\gamma = 0.3$, $\delta = 0.1$, $\alpha = 0.5$, $\beta = 0.5$, $c = 0.8$ and the same initial conditions as in Fig. 1. (a) $t = 50$, (b) $t = 100$, (c) $t = 150$, (d) $t = 200$, (e) $t = 250$, (f) $t = 300$.

is rare in the natural world (Petchey et al., 1997), we do not include $-1 < c < 0$ here. Referring to the dynamics of a real ecological community, the smaller the population density is, the higher is the probability of species extinction due to stochastic environmental fluctuations (Goel and Richter-Dyn, 1974; Lande, 1993). Thus, the species can be treated as extinction when its population density becomes sufficiently small (Gilpin, 1972; May, 1972, 1974). This approach to virtually incorporate environmental noise into a fully deterministic model is known as the “practical stability concept” (Brauer and Soudack, 1978; Legovic, 1987).

Results of simulations show that there arise some qualitatively different patterns of invasion when the diffusive predator–prey system is affected by colored noise. Typically, for the small intensity of noise ($\beta = 0.2$), the predator spreads via propagation of population fronts with spatiotemporal oscillations in the wake and the prey spreads by travelling population rings when the system is affected by white noise ($c = 0$) (Fig. 1). However, the predator spread takes place via “abnormal” travelling fronts with spatially highly heterogeneous species distribution behind when the system is disturbed by red noise ($c = 0.8$) (Fig. 2).

A further increase in intensity of noise ($\beta = 0.5$) makes the prey expand through travelling population rings from the place where the species is initially introduced (Fig. 3). This pattern formation caused by white noise is similar to above situations. As time increases, the predator will also travel through rings which is heterogeneous (Fig. 4). In this case, the species are absent both in front of the front and behind the front. This type of system dynamics is somewhat paradoxical from an ecological point of view because successful species spread (propagation of population front of invasive species) nonetheless leads to invasion failure (no species behind the front) (Morozov et al., 2006).

Remarkably, the invasion patterns become essentially different when the system is affected by red noise ($c = 0.8$). Although the spread pattern of the prey is similar to travelling population rings at the beginning of the invasion (Fig. 5a), the front gradually breaks into pieces at later stages (Fig. 5b–f). This result indicates that the spread of the prey population takes place via the irregular dynamics of separate patches when the system is disturbed by red noise. Fig. 6 shows the invasion regimes of the predator population, which have a complex structure. The predator population spreads over space via irregular motion of sep-

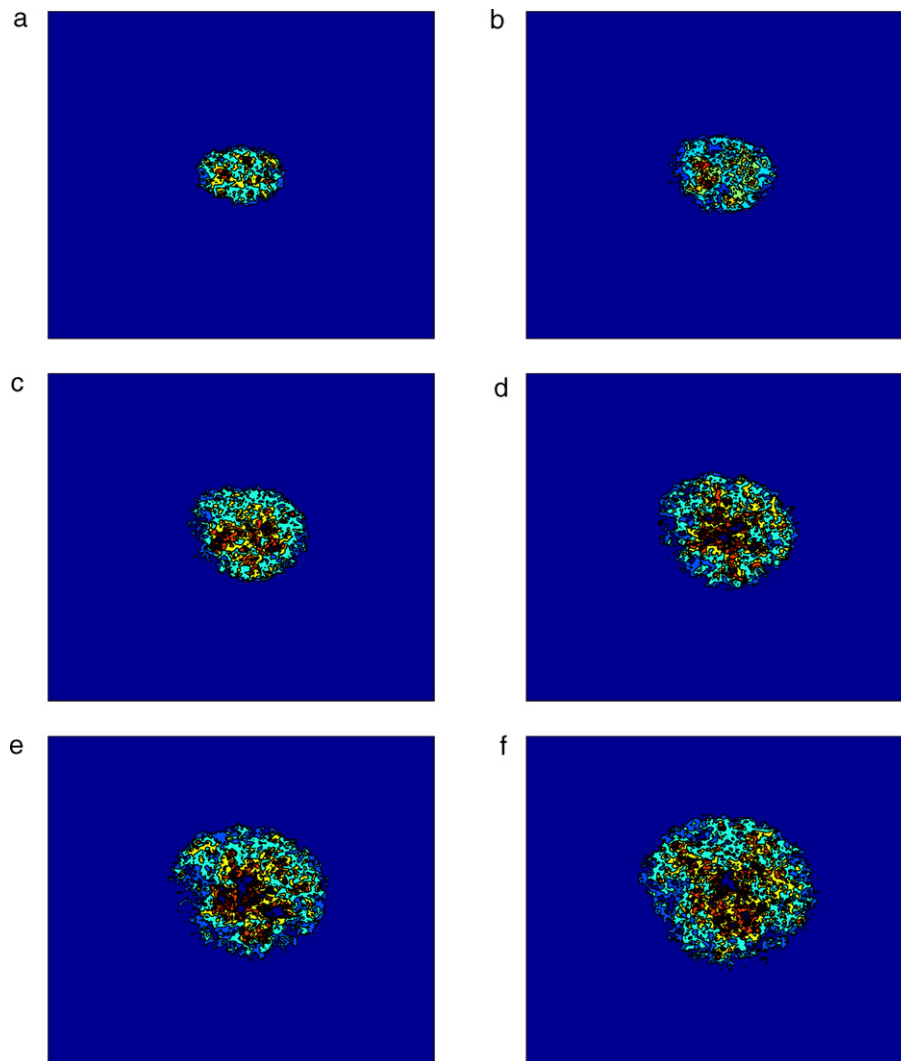


Fig. 6. Snapshots of invasion regime of the predator at different moments for the model ((8)–(9)) affected by red noise. Parameter values and initial conditions are the same as in Fig. 5. (a) $t = 50$, (b) $t = 100$, (c) $t = 150$, (d) $t = 200$, (e) $t = 250$, (f) $t = 300$.

arate patches and no continuous front arises; this is the patchy invasion.

In all the above cases, the parameter values were chosen to make sure the species locally coexist, i.e. the coexistence state (u^*, v^*) was stable in the system (6)–(7) without diffusion terms. In order to exhaust all possible types of the system dynamics, we also explored the situation that the attractor is the “predator extinct” state $(1, 0)$. When the system is not affected by noise, the prey population spreads via propagation of continuous fronts with spatially homogeneous species distribution behind, while the evolution of the initial predator species distribution seems to be a state of quasistationary fronts (Fig. 7). When the system is disturbed by white noise, the predator remains localized inside a certain area for a long time and goes extinct eventually (Fig. 8). In other words, the predator populations cannot invade successfully due to the disturbance of white noise. However, the predator population may spread slowly through patchy invasion when the system is affected by red noise (Fig. 9). Here we only considered the dynamics of the predator population since the distribution of prey in the disturbed system is qualitative similar to that without disturbance.

4. Discussion

In this study, we have investigated the effect of colored noise on spatiotemporal dynamics of a predator–prey model. By obtaining the dispersion relation and making numerical simulations, we found the dispersal pattern formations of invasion species became much more complex under the influence of the noise color. Results here demonstrate that the invasion patterns could also be affected by the intensity of noise. Disturbed by weak noise, the predator–prey system for prey exhibits such a pattern of spread as a geographical invasion without regional persistence (Figs. 1 and 2). It is worth noting that the noise color does not have a relatively large impact on invasion patterns of the prey when its intensity is small. However, the spread patterns of the predator are different when the system is affected by the noise of different color. White noise could make the predator population spread via smooth travelling fronts, while red noise changes the invasion regime of the predator to “abnormal” travelling fronts with spatially highly heterogeneous species distribution behind (Figs. 1 and 2).

Furthermore, the increase of the noise intensity has a drastic impact on the dispersal pattern formation of the species. When

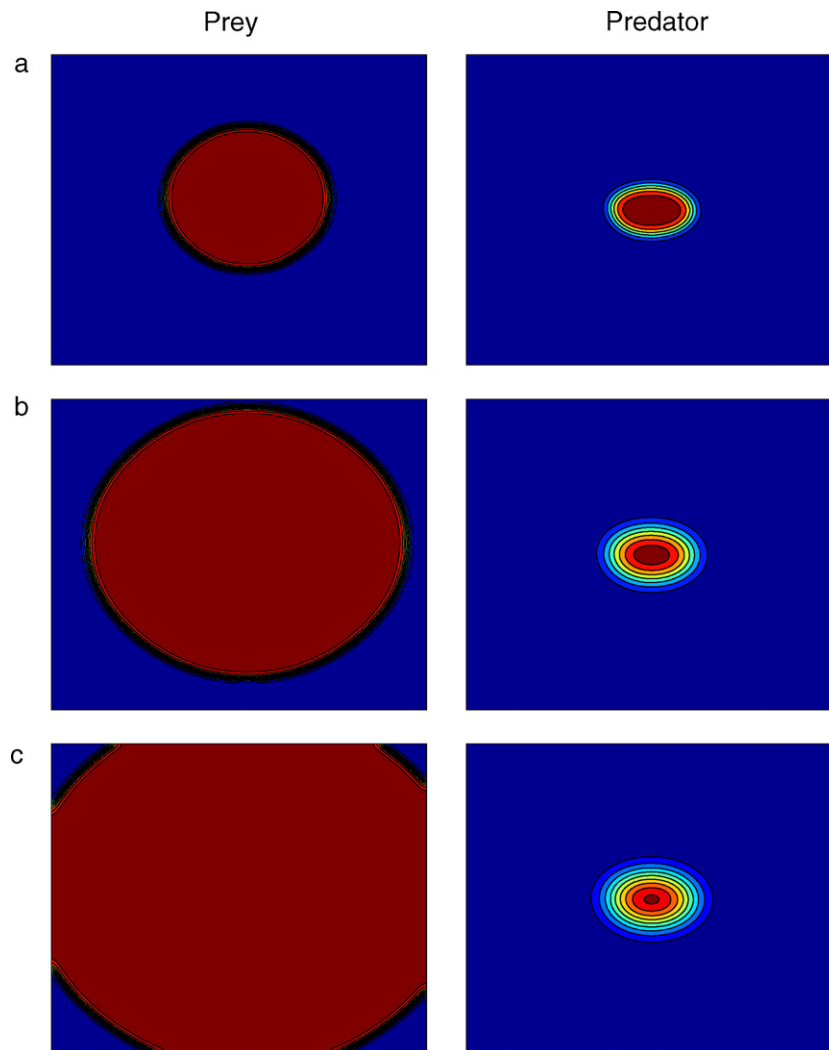


Fig. 7. Snapshots of invasion regimes of the prey and predator at different moments for the model ((8)–(9)) without the interference of noise. Parameter values: $\gamma = 1.3$, $\delta = 0.8$, $\alpha = 0.5$ and the same initial conditions as in Fig. 1. (a) $t = 50$, (b) $t = 150$, (c) $t = 300$.

the predator–prey model is affected by red noise, the prey spreads through travelling population rings from the place where the species is initially introduced and then the rings break into patches (Fig. 5), and the predator invades via a patchy spread (Fig. 6). It was shown by Lewis (2000) and Lewis and Pacala (2000) that stochasticity can lead to patchy invasion. It has also been shown recently by Malchow et al. (2002) that, in some cases, there exists a critical level of environmental noise. Our results have verified their perspectives, and given a further conclusion that red noise can incur patchy invasion in the predator–prey system.

Finally, the relationship between local stability and global invasion was discussed. Our results indicate that when the predator is extinct in the system (6)–(7) without diffusion terms, the predator invades locally and the regional persistence is not followed by geographical spread when the system (8)–(9) is affected by white noise (Fig. 8). In contrast, the predator could spread slowly through patchy invasion when the system is affected by red noise (Fig. 9). Ripa and Lundberg (1996) showed that the probability of extinction in a single-species, single-patch model decreased as noise color was reddened. As they suggested, red noise could make the predator geographically invade when the species cannot survive without considering the spatial factor. However, Petrovskii et al. (2005b) have argued that white noise can enhance population

persistence and patchy invasion. The different results arise here perhaps because of the different interacting mechanism among species.

Sun et al. (2009) have found that white noise can make patchy invasion possible in a predator–prey system. However, the prey in the system is subject to the Allee effect. Petrovskii et al. (2002) have shown that patchy invasion appears to be possible also in a fully deterministic predator–prey model as a result of Allee effect. They also found that patchy invasion can take place in a system of virally infected phytoplankton and zooplankton as a result of strong environmental noise (Petrovskii et al., 2005a). Therefore, there is a question of which factors incur the patchy invasion in the system described in the work of Sun et al. (2009), white noise or the Allee effect? In this research, we were more concerned with the effect of the noise of different colors on the invasion patterns of the predator–prey system. Unlike the result of Sun et al., we found that only red noise can make the species spread via patchy invasion in a predator–prey system. From the standpoint of prospective ecological applications, it seems important to reveal the correlation between the regimes of biological invasion and the color of environment noise. This issue is a first attempt to address the spatiotemporal dynamics of biological invasion affected by the noise of different colors and will become a subject of a separate study.

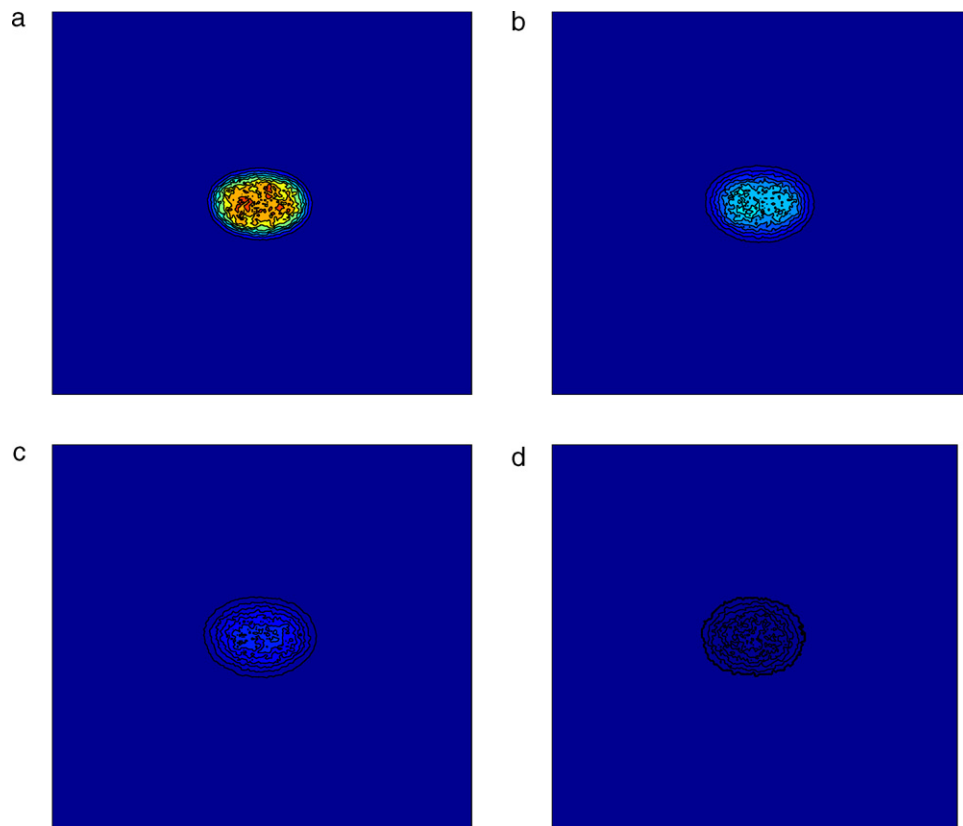


Fig. 8. Snapshots of invasion regime of the predator at different moments for the model ((8)–(9)) affected by white noise. Parameter values: $c=0$, $\beta=0.5$ and the other parameters and the initial conditions are the same as in Fig. 7. (a) $t=50$, (b) $t=150$, (c) $t=300$, (d) $t=450$.

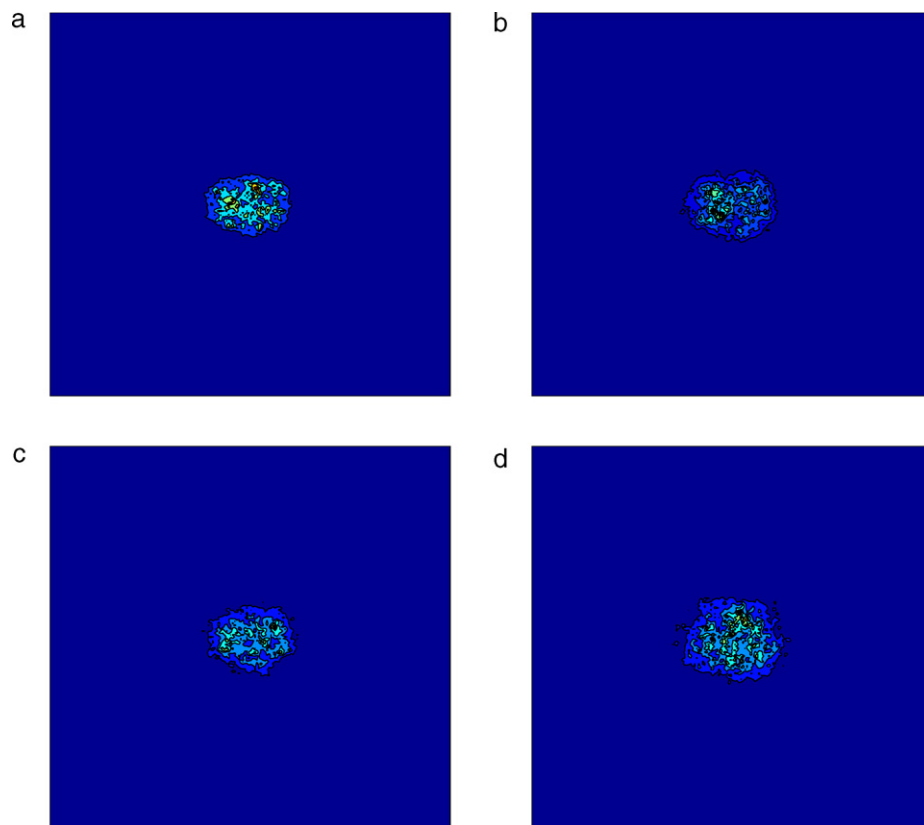


Fig. 9. Snapshots of invasion regime of the predator at different moments for the model ((8)–(9)) affected by red noise. Parameter values: $c=0.8$, $\beta=0.5$ and the other parameters and the initial conditions are the same as in Fig. 7. (a) $t=50$, (b) $t=150$, (c) $t=300$, (d) $t=450$.

Acknowledgement

We are grateful to M. Su and Z. Liu for editorial helps and the constructive comments received from the anonymous reviewer and the editor. This work was supported by the National Natural Science Foundation of China (30700100, 30970478, 30970491).

References

- Brauer, F., Soudack, A.C., 1978. Response of predator–prey nutrient enrichment and proportional harvesting. *Int. J. Control* 27, 65–86.
- Caswell, H., Cohen, J.E., 1995. Red, white and blue: environmental variance spectra and coexistence in metapopulations. *J. Theor. Biol.* 176, 301–316.
- Foley, P., 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conserv. Biol.* 8, 124–137.
- Frantzen, J., van den Bosch, F., 2000. Spread of organisms: can travelling and dispersive waves be distinguished? *Basic Appl. Ecol.* 1, 83–91.
- Gilpin, M.E., 1972. Enriched predator–prey systems: theoretical stability. *Science* 177, 902–904.
- Goel, N.S., Richter-Dyn, N., 1974. *Stochastic Models in Biology*. Academic Press, New York.
- Hastings, A., 1996. Models of spatial spread: a synthesis. *Biol. Conserv.* 78, 143–148.
- Hengeveld, R., 1989. *Dynamics of Biological Invasions*. Chapman and Hall, London.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4, 1–23.
- 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.
- Kaitala, V., Ylikarjula, J., Ranta, E., Lunderberg, P., 1997. Population dynamics and the colour of environmental noise. *Proc. R. Soc. Lond. B* 264, 943–948.
- Keitt, T.H., Lewis, M.A., Holt, R.D., 2001. Allee effects, invasion pinning, and species borders. *Am. Nat.* 157, 203–216.
- Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142, 911–922.
- Legovic, T., 1987. A recent increase in jellyfish populations: a predator–prey model and its implications. *Ecol. Modell.* 38, 243–256.
- Lewis, M.A., 2000. Spread rate for a nonlinear stochastic invasion. *J. Math. Biol.* 41, 430–454.
- Lewis, M.A., Pacala, S., 2000. Modeling and analysis of stochastic invasion processes. *J. Math. Biol.* 41, 387–429.
- Malchow, H., 1993. Spatio-temporal pattern formation in nonlinear nonequilibrium plankton dynamics. *Proc. R. Soc. Lond. B* 251, 103–109.
- Malchow, H., Petrovskii, S.V., Medvinsky, A.B., 2002. Numerical study of plankton–fish dynamics in a spatially structured and noisy environment. *Ecol. Modell.* 149, 247–255.
- May, R.M., 1972. Limit cycles in predator–prey communities. *Science* 177, 900–902.
- May, R.M., 1974. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- Morozov, A., Petrovskii, S.V., Li, B.L., 2006. Spatiotemporal complexity of patchy invasion in a predator–prey system with the Allee effect. *J. Theor. Biol.* 238, 18–35.
- Morozov, A., Ruan, S., Li, B.L., 2008. Patterns of patchy spread in multi-species reaction–diffusion models. *Ecol. Complex.* 5, 313–328.
- Murray, J.D., 1989. *Mathematical Biology*. Springer, Berlin.
- Petchey, O.L., Gonzalez, A., Wilson, H.B., 1997. Effects of population persistence: the interaction between environmental noise colour, intraspecific competition and space. *Proc. R. Soc. Lond. B* 264, 1841–1847.
- Petrovskii, S.V., 1999. Plankton front waves accelerated by marine turbulence. *J. Marine Systems* 21, 179–188.
- Petrovskii, S.V., Malchow, H., Hilker, F., Venturino, E., 2005a. Patterns of patchy spread in deterministic and stochastic models of biological invasion and biological control. *Biol. Invasions* 7, 771–793.
- Petrovskii, S.V., Morozov, A.Y., Venturino, E., 2002. Allee effect makes possible patchy invasion in a predator–prey system. *Ecol. Lett.* 5, 345–352.
- Petrovskii, S.V., Morozov, A.Y., Li, B.L., 2005b. Regimes of biological invasion in a predator–prey system with the Allee effect. *Bull. Math. Biol.* 67, 637–661.
- Ripa, J., Lundberg, P., 1996. Noise colour and the risk of population extinction. *Proc. R. Soc. Lond. B* 263, 1751–1753.
- Sherratt, J.A., 2001. Periodic travelling waves in cyclic predator–prey systems. *Ecol. Lett.* 4, 30–37.
- Sherratt, J.A., Lewis, M.A., Fowler, A.C., 1995. Ecological chaos in the wake of invasion. *Proc. Natl. Acad. Sci. USA* 92, 2524–2528.
- Shigesada, N., Kawasaki, K., 1997. *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford.
- Sun, G.Q., Jin, Z., Li, L., Liu, Q.X., 2009. The role of noise in a predator–prey model with Allee effect. *J. Biol. Phys.* 35, 185–196.
- Xu, C., Li, Z., 2003. Population dynamics and the color of environmental noise: a study on a three-species food chain system. *Ecol. Res.* 18, 145–154.