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Invasive competition with Fokker-Planck diffusion and noise

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Abstract

Species competition in a fluctuating environment is often modelled with stochastic reaction-diffusion equations. In most cases the movement of individuals is described as Fickian diffusion. However, in heterogeneous environments this is not the first choice. Recently, it has been shown that Fokker-Planck diffusion describes the movement of species in a more realistic way. Fickian diffusion always leads to spatially uniform stationary distributions whereas the Fokker-Planck diffusion generates nonuniform solutions according to the heterogeneity of the environment and the corresponding spatial variation of diffusion. Species accumulate in regions of low diffusivity and tend to lower their densities in areas of high diffusivity. In the present paper, the impact of Fokker-Planck diffusion is studied with particular consideration of changing spatio-temporal population patterns during the competitive invasion of a spatially heterogeneous, populated habitat. The standard Lotka-Volterra competition model is applied to describe the resident-invader interaction. The resident is assumed to be adapted to the heterogeneous living conditions, i.e., its motion is modelled as space-dependent Fokker-Planck diffusion. The invader's diffusion is taken as neutral Fickian. Furthermore, it is shown that multiplicative environmental noise can either foster or hinder the invasion.

Keywords: Competition, invasion, Fokker-Planck diffusion, environmental noise

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1. Introduction

Biological invasions are a growing threat to biodiversity around the world. The spread of alien species can lead not only to the extinction of indigenous species, but also cause considerable economic damage in eco- and agro-ecosystems. These are, contrary to water-air-soil contamination, unfortunately mostly irreparable, since the invasive species constantly reproduce and often have no natural enemies. Well-known examples are the invasion of rabbits (Perrings et al., 2000) and cane toads (Urban et al., 2008) in Australia or the invasion of a Pacific oyster in the Dutch and German Wadden Sea (Diederich et al., 2005). Many of these invasions are caused by anthropogenic effects such as globalized traffic and trade or climate change. On the other hand it might be of interest to reintroduce a species into an ecosystem where it has been eradicated before.

Modelling the invasion process can help to identify mechanisms which foster or hinder successful invasions. Most ecological models on this subject describe species densities on a population level. Individual movement is often described as diffusive process. In a heterogeneous environment the mathematical formalism which describes this process in a realistic way depends strongly on the respective species abilities.

In a recent publication (Bengfort et al., 2016), different formulations for diffusivities have been assumed purely space-dependent. Spatial patterns may already occur without any interactions. For this setting, the spatially stationary solution has been derived. Furthermore, the speed of diffusive waves of a single logistically growing population has been analytically estimated, and conditions for the formation of spatio-temporal and Turing patterns in an excitable prey-predator system have been given.

Another recent publication (Siekmann and Malchow, 2016) has dealt with the control of invasion of a populated habitat by selective infection of the invader. Forthermore, the area is subject to uncorrelated and/or correlated environmental noise the resident is adapted to but the invading population not.

The present work shall link the two latter approaches. The Lotka-Volterra textbook model of the competition of two populations is combined with space-dependent Fokker-Planck diffusion of the residents, Fickian diffusion of the invaders and environmental noise. Two competing species, X_1 and X_2, are modelled with equal mutual competition rates but different movement abilities. It is assumed that the resident species is adapted to the environmental conditions in its habitat. Favourable regions are characterized by a lower diffusion coefficient whereas it is rather high in unfavourable patches. Hence, the resident species move fast in unfavourable regions and tend to remain in the favoured. On the other hand, the invader's diffusivity is spatially uniform, i.e., it moves independent of the environmental conditions. It will be shown that the spatial heterogeneity modelled by Fokker-Planck diffusion but also the external noise can foster or hinder the invasion.

2. Methods

Interactions and movements of populations in a heterogeneous and variable environment are often modelled with stochastic reaction-diffusion equations. Diffusive fluxes in ecology can differ due to specifics of the population's relationships and environmental heterogeneity. They might be neutral cf. eq. (1), attractive (2) or repulsive (3), i.e., for N populations

$$\vec{j}_{in} = -D_i(\vec{r}, \mathbf{X})\, \vec{\nabla} X_i(\vec{r}, t)\,, \tag{1}$$

$$\vec{j}_{ia} = -D_i^2(\vec{r}, \mathbf{X})\, \vec{\nabla} \left[\frac{X_i(\vec{r}, t)}{D_i(\vec{r}, \mathbf{X})} \right] = +X_i(\vec{r}, t) \vec{\nabla} D_i(\vec{r}, \mathbf{X}) - D_i(\vec{r}, \mathbf{X})\, \vec{\nabla} X_i(\vec{r}, t)\,, \tag{2}$$

$$\vec{j}_{ir} = -\vec{\nabla} \left[D_i(\vec{r}, \mathbf{X}) X_i(\vec{r}, t) \right] = -X_i(\vec{r}, t) \vec{\nabla} D_i(\vec{r}, \mathbf{X}) - D_i(\vec{r}, \mathbf{X})\, \vec{\nabla} X_i(\vec{r}, t)\,; \tag{3}$$

$$i = 1, 2, \ldots, N.$$

The usual notation is used: $\mathbf{X}(\vec{r}, t) = \{X_i(\vec{r}, t);\ i = 1, 2, \ldots, N\}$ is the vector of population densities at position $\vec{r} = \{x, y\}$ and time t and $D_i(\vec{r}, \mathbf{X})$ their possibly space- and density-dependent diffusion coefficient. The formulations (1–3) have been elaborated by Skellam (1951; 1973, and nicely summarized by Okubo (1980), see also Aronson (1985) and Murray (1989). In order to complete the list of ecodiffusive fluxes in heterogeneous media, one could add the flux in environmental potentials $U(\vec{r})$

$$\vec{j}_{ip} = \vec{j}_{ik} + \gamma_i X_i(\vec{r}, t) \vec{\nabla}\, U(\vec{r});\ i = 1, 2, \ldots, N; \tag{4}$$

where γ_i is called the coefficient of affinity of X_i to the environment and index k can be n, a and r respectively, i.e., one of the fluxes (1–3) can be applied. The minima of $U(\vec{r})$ correspond to preferable and, therefore, attracting habitats. The latter concept has been derived from the ideas of habitat value and environmental density (Morisita, 1971; Shigesada and Teramoto, 1978).

The neutral diffusion is also called Fickian (Fick, 1855) whereas the repulsive type is named after Fokker and Planck (1914; 1917). For a certain density dependence of diffusion, the latter has been used for modelling the spatial segregation of populations (Shigesada et al., 1979; Mimura and Kawasaki, 1980) as well as the formation of Turing patterns (Malchow, 1988).

2.1. The stochastic competition-diffusion model

The dynamics of resident X_1 and invader X_2 is described by

$$\frac{\partial X_1}{\partial t} = (1 - X_1)X_1 - c_{12}X_1X_2 + d_1\nabla^2(X_1 D^*(x,y)) + g_1(X_1)\xi(\vec{r},t)\,, \tag{5}$$

$$\frac{\partial X_2}{\partial t} = (1 - X_2)X_2 - c_{21}X_1X_2 + d_2\nabla^2 X_2 + g_2(X_2)\xi(\vec{r},t)\,. \tag{6}$$

c_{12} and c_{21} are parameters to describe the strength of interspecific competition between X_1 and X_2. d_1 and d_2 are constant parameters to describe the strength of diffusion. Both species are assumed to grow logistically. The space dependence of the resident's diffusivity is chosen as

$$D^*(x,y) = D_0 + \begin{cases} a\left(\sin(\sqrt{x^2+y^2})\right)^m & \text{if } \sqrt{x^2+y^2} < 3\pi\,, \\ a\left(\sin(3\pi)\right)^m & \text{else}\,. \end{cases} \tag{7}$$

This spatially varying diffusivity is meant to represent a simple fragmented landscape with a varying habitat quality for species X_1. The parameter m is an even number which controls the steepness of D^*. Zero-flux boundary conditions are assumed. In order to avoid effects from spatial heterogeneities at the boundaries, D^* is set constant for $\sqrt{x^2+y^2} < 3\pi$, whereas $x = 0$, $y = 0$ defines the center of the landscape.

For simplicity, just uncorrelated white noise $\xi(\vec{r},t)$ is applied here, i.e.,

$$\langle \xi(\vec{r},t) \rangle = 0\,, \langle \xi(\vec{r}_1,t_1)\xi(\vec{r}_2,t_2) \rangle = \delta(\vec{r}_1 - \vec{r}_2)\delta(t_1 - t_2) \tag{8}$$

with linearly density dependent noise intensities

$$g_i(X_i) = \omega_i X_i\,; i = 1,2\,. \tag{9}$$

2.2. Numerical methods

We integrate the equations (5) and (6) numerically with a splitted scheme. Therefor we use a different method to solve the diffusion terms than we use for the reaction and noise terms on the right hand side of the equations. Both numericl methods are explaind in the following.

2.2.1. Crank-Nicolson scheme for two dimensions with Fokker-Planck diffusion

We split the Laplace operator into two parts. First, we calculate the diffusion in one spatial dimension (x), second we do the same for the other spatial dimension (y).

$$\frac{\partial X}{\partial t} = \vec{\nabla}^2(XD) = \frac{\partial^2(XD)}{\partial x^2} + \frac{\partial^2(XD)}{\partial y^2}, \tag{10}$$

where X is the population density and D its spatially varying diffusion coefficient which can be written as

$$D(x,y) = d_1 D^*(x,y) \tag{11}$$

with $d_1 = const$ and $D^*(x,y) \neq 0\ \forall\ x,y$. Now we formulate the Crank-Nicolson algorithm (Crank and Nicolson, 1947) for one spatial dimension as follows

$$\begin{aligned}\frac{X_k^{t+\Delta t} - X_k^t}{\Delta t} &= \frac{d_1}{2\Delta x^2}\left(X_{k+1}^{t+\Delta t}D_{k+1}^* - 2X_k^{t+\Delta t}D_k^* + X_{k-1}^{t+\Delta t}D_{k-1}^*\right.\\ &\qquad \left.+X_{k+1}^{t}D_{k+1}^* - 2X_k^{t}D_k^* + X_{k-1}^{t}D_{k-1}^*\right). \end{aligned}\tag{12}$$

Here $k \in (1,n)$ is the index of the spatial position of X, whereas t is the time which varies with a discrete time step Δt. With $\alpha = d_1\dfrac{\Delta t}{\Delta x^2}$ we can write this as a system of linear equations

$$\mathbf{A}\left(\vec{X}^{t+\Delta t}\vec{D}^*\right) = \mathbf{B}\left(\vec{X}^{t}\vec{D}^*\right) \tag{13}$$

where $\vec{X}$ and $\vec{D}^*$ are vectors of length n including the values of X_k and D_k^* at each spatial position in one dimension $k \in (1,n)$. $\mathbf{A}$ and $\mathbf{B}$ are the $(n \times n)$ tridiagonal matrices

$$\mathbf{A} = \begin{pmatrix} 2\left(\frac{1}{D_1^*}+\alpha\right) & -\alpha & 0 & \dots & 0 \\ -\alpha & \ddots & -\alpha & 0 & \vdots \\ 0 & -\alpha & \ddots & \ddots & 0 \\ \vdots & \dots & \ddots & \ddots & -\alpha \\ 0 & \dots & & -\alpha & 2\left(\frac{1}{D_n^*}+\alpha\right) \end{pmatrix},$$

$$\mathbf{B} = \begin{pmatrix} 2\left(\frac{1}{D_1^*}-\alpha\right) & \alpha & 0 & \dots & 0 \\ \alpha & \ddots & \alpha & 0 & \vdots \\ 0 & \alpha & \ddots & \ddots & 0 \\ \vdots & \dots & \ddots & \ddots & \alpha \\ 0 & \dots & & \alpha & 2\left(\frac{1}{D_n^*}-\alpha\right) \end{pmatrix}.$$

This implicit scheme has been proven to be unconditionally stable for two spatial dimensions in case of homogeneous diffusion. A strictly positive D^* does not change the von-Neumann stability criterion given by Crank and Nicolson (1947).

In order to implement zero-flux boundary conditions we have to add the term $-\alpha$ to the matrix components $\mathbf{A}_{11}$ and $\mathbf{A}_{nn}$, and the term α to the matrix components $\mathbf{B}_{11}$ and $\mathbf{B}_{nn}$. To calculate the distribution of X^t at time step $t + \Delta t$, we have to multiply the vector $\vec{X}^t$ with the spatially varying coefficient of diffusion $\vec{D}^*$ and solve the equation $\mathbf{A}\vec{Y} = \mathbf{B}\vec{X}$, where $\vec{X}$ is a input-vector (in our case $\vec{X}^t \cdot \vec{D}^*$) and $\vec{Y}$ is a output-vector. After that the components of the output-vector $\vec{Y}$ has to be divided with the corresponding components of the vector $\vec{D}^*$, which is temporally constant in order to get the distribution $X^{t+\Delta t}$. Once this scheme has been performed for each row in one spatial direction it has to be repeated for the other spatial dimension in every time step.

2.2.2. Derivative-free Milstein method for interactions and noise

For numerical integration of the interaction and noise terms, the derivative-free Milstein method is used (Milstein, 1995; Kloeden and Platen, 1999). The Milstein scheme reads for white noise (8,9) with time step Δt and in Stratonovich interpretation

$$X_i^{t+\Delta t} = X_i^t + f_i(X_i^t)\Delta t + \omega_i X_i^t \Delta W_i + \frac{\omega_i}{2}\left[f_i(X_i^t)\sqrt{\Delta t} + \omega_i X_i^t\right](\Delta W_i)^2 \,, \tag{14}$$

with

$$\Delta W_i = W_i^{t+\Delta t} - W_i^t \sim \sqrt{\Delta t}\,\mathcal{N}(0,1)\,,$$

where W_i^t is a Wiener process and $\mathcal{N}(0,1)$ stands for the normal distribution with zero mean and unity variance. The required uniformly distributed random numbers are generated with the Mersenne Twister (Matsumoto and Nishimura, 1998), the normally distributed random numbers with the common Box-Muller algorithm (Box and Muller, 1958). More details about this scheme can be found in Siekmann and Malchow (2016).

3. Numerical simulations and results

The model as well as the algorithms described in this paper were implemented in `FORTRAN`. The above mentioned numerical schemes are performed successively for each time step. The dimensionless spatial model describes a rectangular domain with a length of $L_x =$

$L_y = 3000$ with 200×200 grid points and zero-flux boundary conditions. The temporal and spatial step sizes h_t, h_x and h_y were

$$h_t = 0.02, h_x = h_y = 15. \tag{15}$$

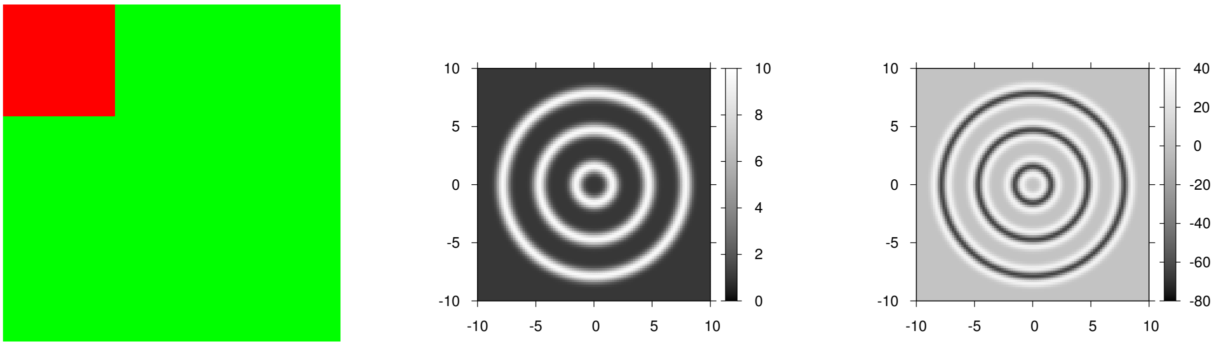
The following parameters have been applied:

$$D_0 = 1\,,\ m = 8\,,\ c_{12} = c_{21} = 1.2\,.$$

The parameter values are chosen arbitrarily without a limitation of generality. We set $D_0 = 1$ because this is the minimal value for D^*. In this case the diffusivity of both species can directly be spotted from d_1 and d_2. The effect of Fokker-Planck diffusion depends on the heterogeneity of the coefficient of diffusion. We set $m = 8$ in order to generate large values in the first and second derivative of D^*. Because both species are described with equal competition parameters (c_{12} and c_{21}), the difference in the coefficient of diffusion determines whether or not an invasion of species X_2 is successful in case of homogeneous D, i.e., $a = 0$, cf. eq. (7). Both c_{12} and c_{21} exceed unity, so that the system is in a bistable parameter range. In case of a non-spatial model without diffusion or noise the species with a larger initial density will become dominant and drive its opponent to extinction.

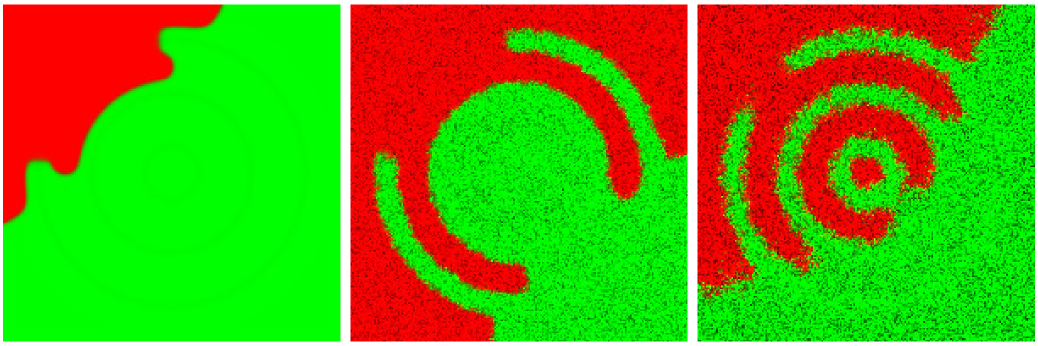
Due to its spatial variation, the diffusivity $d_1 \cdot D^*$ of the native species X_1 can be greater or less than the constant invader's diffusion coefficient d_2. An invasion will be successful only in those areas where $d_2 > d_1 \cdot D^*$ (Fig. 2). Areas with a high diffusivity of the native species act as barrier for the invasion. This fits well earlier published results on diffusion-controlled competitive invasions (Malchow et al., 2011). In this scenario multiplicative density-dependent noise (8,9) accelerates the speed of invasion (Fig. 2b). However, strong noise can push the invader through the barriers of large resident diffusivity and induce the invasion of further regions with low resident diffusivity.

Because of the Fokker-Planck diffusion in eq. (5), the spatial distribution of the resident species, X_1, develops proportional to $\nabla^2 D^*(x, y)$, as described in Bengfort et al. (2016). If this effect is strong enough, the reduced resident concentration in areas with high resident diffusivity enables an invasion of species X_2, even if the diffusivity of X_1 is larger than the diffusivity of X_2 everywhere in the domain (Fig. 3). In this scenario, multiplicative density-dependent noise has a decelerating effect on the speed of invasion (Fig. 3b).



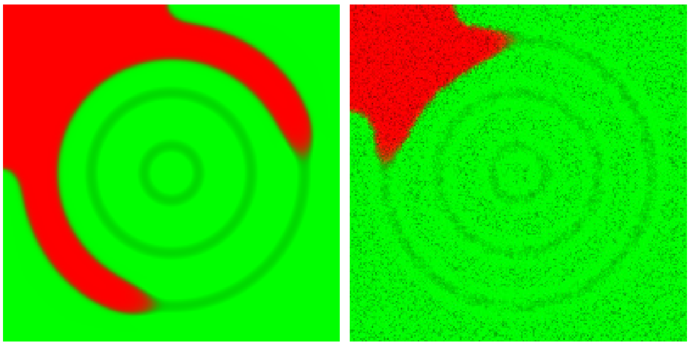
(a) Initial distribution (b) $D^*(x, y)$ for $a = 9$ (c) $\nabla^2 D^*(x, y)$ for $a = 9$

Figure 1: Initial settings for densities (green = resident, red = invader) and resident's diffusivity



(a) $t = 3900\,;\, \omega_1 = \omega_2 = 0$ (b) $t = 3900\,;\, \omega_1 = \omega_2 = 0.4$ (c) $t = 600\,;\, \omega_1 = \omega_2 = 0.6$

Figure 2: $d_1 = 5$, $d_2 = 25$, $a = 9$: The density of the resident species is reduced in areas of large D^*. The invader successfully invades the space, where it has a larger coefficient of diffusion as the resident species. Density-dependent multiplicative noise accelerates the invasion in areas of small D^*. Areas with large D^* act as a barrier for the invasion. Strong noise can break through these barriers and induces invasion of X_2 in the inner circles with small D^*. Video sequences showing the dynamical process are included in the online version of this document. (Click on the image.)



(a) $\omega_1 = \omega_2 = 0$ (b) $\omega_1 = \omega_2 = 0.25$

Figure 3: $t = 4400$, $d_1 = 30$, $d_2 = 25$, $a = 19$; large $\nabla^2 D(\vec{r})$: Due to the reduced resident concentration in areas of large D^* invasion is possible even though the invader has a smaller coefficient of diffusion everywhere in the spatial domain. Noise reduces the invasion speed. Strong noise can invert the invasion. Video sequences showing the dynamical process are included in the online version of this document. (Click on the image.)

4. Discussion

This Fokker-Planck type modelling of the movement of organisms generates patterns in the spatial population distribution which correspond to the spatial variation of the diffusion coefficient. If this effect is small (small spatial derivatives in D^*), the competitor can invade the domain in areas where its (spatially constant) coefficient of diffusion is larger than that of the resident species. This is not surprising because both species are described with equal parameters for growth and competition so that diffusivity determines the success of invasion if the size of the initial patch of the invading species exceeds the related critical patch size. This is also the case if the resident would follow Fickian diffusion with a heterogeneous coefficient of diffusion. In a non-deterministic environment, where the populations are subject to stochastic fluctuations, the speed of invasion increases with increasing noise intensity. Strong noise can also induce invasions in areas which are perfectly protected against an invasion in the deterministic case. If the pattern forming effect of the Fokker-Planck diffusion is stronger, invasion is possible even though the coefficient of the invader is smaller than the one of the resident species everywhere in the domain. Contrary to the former example, noise has a negative effect on the success of invasion. This is caused by the fact, that the density dependent noise counteract the pattern forming properties of the Fokker-Planck diffusion. The resident species benefits from the homogenising effect of the noise because it has a larger coefficient of diffusion than the invader. A Fickian diffusion for the resident can not reproduce these patterns. In this case the resident would outcompete the invader because of its larger coefficient of diffusion.

5. Conclusions

It has been shown that a non-uniform diffusivity, i.e., Fokker-Planck diffusion, of a resident species in a spatially heterogeneous habitat can have different effects on the ability of a similar competing species to invade the habitat.

Spatiotemporal Gaussian noise was applied in order to model the variability of the environment. For future research it would be interesting to investigate the effect of spatially and/or temporally colored noise in combination with the Fokker-Planck diffusion which generates patterns in the resident species with a certain wavelength.

Here, it was assumed that only the resident species favours certain areas in the domain and consequently move with a spatially varying speed and is therefore described with Fokker-

Planck diffusion. One can also think of an inverse situation where the resident species is described with constant Fickian diffusion and the invader follows the Fokker-Planck description. From a theoretical point of view this scenario is not as interesting because the invader starts in a relatively small spatial domain where the heterogeneity in the coefficient of diffusion does not play a crucial role. A situation in which both species follow a Fokker-Planck description and favour the same or different spatial domains was not part of this study. This will be subject of future investigations.

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References

Aronson, D.G., 1985. The role of diffusion in mathematical population biology: Skellam revisited, in: Capasso, V., Grosso, E., Paveri-Fontana, S.L. (Eds.), Mathematics in Biology and Medicine. Springer, Berlin. volume 56 of *Lecture Notes in Biomathematics*, pp. 2–6.

Bengfort, M., Malchow, H., Hilker, F.M., 2016. The Fokker-Planck law of diffusion and pattern formation in heterogeneous media. Journal of Mathematical Biology 73, 683–704.

Box, G.E.P., Muller, M.E., 1958. A note on the generation of random normal deviates. Annals of Mathematical Statistics 29, 610–611.

Crank, J., Nicolson, P., 1947. A practical method for numerical evaluation of solutions of partial differential equations of the heat-conduction type. Mathematical Proceedings of the Cambridge Philosophical Society 43, 50–67.

Diederich, S., Nehls, G., van Beusekom, J.E.E., Reise, K., 2005. Introduced Pacific oysters *Crassostrea gigas* in the northern Wadden Sea: invasion accelerated by warm summers? Helgoland Marine Research 59, 97–106.

Fick, A., 1855. Ueber Diffusion. Annalen der Physik 170, 59–86 (in German).

Fokker, A.D., 1914. Die mittlere Energie rotierender elektrischer Dipole im Strahlungsfeld. Annalen der Physik 348, 810–820 (in German).

Kloeden, P.E., Platen, E., 1999. Numerical solution of stochastic differential equations. volume 23 of *Applications of Mathematics*. Springer, Berlin.

Malchow, H., 1988. Spatial patterning of interacting and dispersing populations. Memoirs of the Faculty of Science, Kyoto University (Series of Biology) 13, 83–100.

Malchow, H., James, A., Brown, R., 2011. Competitive and diffusive invasion in a noisy environment. Mathematical Medicine and Biology 28, 153–163.

Matsumoto, M., Nishimura, T., 1998. Mersenne Twister: a 623-dimensionally equidistributed uniform pseudorandom number generator. ACM Transactions on Modeling and Computer Simulation 8, 3–30.

Milstein, G.N., 1995. Numerical integration of stochastic differential equations. volume 313 of *Mathematics and Its Applications*. Kluwer Academic Publishers, Dordrecht.

Mimura, M., Kawasaki, K., 1980. Spatial segregation in competitive interaction-diffusion equations. Journal of Mathematical Biology 9, 49–64.

Morisita, M., 1971. Measuring of habitat value by the "environmental density" method, in: Patil, C.D., Pielou, E.C., Waters, W.E. (Eds.), Spatial patterns and statistical distributions. The Pennsylvania State University Press, University Park. volume 1 of *Statistical Ecology*, pp. 379–401.

Murray, J.D., 1989. Mathematical biology. volume 19 of *Biomathematics Texts*. Springer, Berlin.

Okubo, A., 1980. Diffusion and ecological problems: Mathematical models. volume 10 of *Biomathematics Texts*. Springer, Berlin.

Perrings, C., Dalmazzone, S., Williamson, M.H., 2000. The economics of biological invasions. Edward Elgar Publishing.

Planck, M., 1917. Über einen Satz der statistischen Dynamik und seine Erweiterung in der Quantentheorie. Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften XXIV, 324–341 (in German).

Shigesada, N., Kawasaki, K., Teramoto, E., 1979. Spatial segregation of interacting species. Journal of Theoretical Biology 79, 83–99.

Shigesada, N., Teramoto, E., 1978. A consideration on the theory of environmental density. Japanese Journal of Ecology 28, 1–8 (in Japanese).

Siekmann, I., Malchow, H., 2016. Fighting enemies and noise: Competition of residents and invaders in a stochastically fluctuating environment. Mathematical Modelling of Natural Phenomena 11, 120–140.

Skellam, J.G., 1951. Random dispersal in theoretical populations. Biometrika 38, 196–218.

Skellam, J.G., 1973. The formulation and interpretation of mathematical models of diffusionary processes in population biology, in: Bartlett, M.S., Hiorns, R. (Eds.), The mathematical theory of the dynamics of biological populations. Academic Press, New York, pp. 63–85.

Urban, M.C., Phillips, B.L., Skelly, D.K., Shine, R., 2008. A toad more traveled: The heterogeneous invasion dynamics of cane toads in Australia. The American Naturalist 171, E134–E148.