Mathematical Biology

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The Fokker–Planck law of diffusion and pattern formation in heterogeneous environments

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Abstract We analyze the influence of spatially inhomogeneous diffusion on several common ecological problems. Diffusion is modeled with Fick's law and the Fokker–Planck law of diffusion. We discuss the differences between the two formalisms and when to use either the one or the other. In doing so, we start with a pure diffusion equation, then turn to a reaction–diffusion system with one logistically growing component which invades the spatial domain. We also look at systems of two reacting components, namely a trimolecular oscillating chemical model system and an excitable predator–prey model. Contrary to Fickian diffusion, spatial inhomogeneities promote spatial and spatiotemporal pattern formation in case of Fokker–Planck diffusion.

1 Introduction

Diffusion equations are often used to model the random movement of particles in space. They have also been applied to population dispersal and have provided fundamental insights into spatial ecology (Skellam 1951; Kierstead and Slobodkin 1953; Keller and Segel 1971; Skellam 1973; Andow et al. 1990; Holmes et al. 1994; Okubo and Levin

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2001; Malchow et al. 2008; Cantrell et al. 2010). Although spatial inhomogeneities are ubiquitous in nature, the strength of diffusion is often assumed to be homogeneous in space. In this case, Fick's (1855) and Fokker–Planck's laws (Fokker 1914; Planck 1917) of diffusion are identical. However, if there are spatial heterogeneities, these two laws yield very different results.

Usually, those papers that consider spatially varying diffusivities use piecewise constant coefficients of diffusion (Shigesada et al. 1987; Lutscher et al. 2006), or they use the classical Fick's law of diffusion (Benson et al. 1998; Maini et al. 1992; Kinezaki et al. 2006; Jin et al. 2014; Bengfort et al. 2014). The latter reads

$$
\begin{aligned}
\frac{\partial}{\partial t} u(x, t) &= \frac{\partial}{\partial x} \left(D(x) \frac{\partial}{\partial x} u(x, t) \right) \\
&= \frac{\partial D(x)}{\partial x} \frac{\partial u(x, t)}{\partial x} + D(x) \frac{\partial^2 u(x, t)}{\partial x^2},
\end{aligned}
\tag{1}
$$

where $u(x, t)$ is the local concentration of particles or, in ecology, individuals at position x and time t, and $D(x)$ is a spatially varying coefficient of diffusion. Throughout this paper, all equations are dimensionless. In a dimensionless diffusion equation, the coefficient of diffusion scales with the typical time- and length-scale chosen for the dimensionless variables. In appendix "Dimensionless diffusion equation" we transform a diffusion equation into a dimensionless form. This example additionally includes a reaction term.

An alternative way to model diffusion in heterogeneous media is the Fokker–Planck law of diffusion (Smoluchowski 1916; Chapman 1928; Kolmogorov 1931; Patlak 1953; Okubo and Levin 2001):

$$
\frac{\partial}{\partial t} u(x, t) = \frac{\partial^2}{\partial x^2} (D(x) u(x, t)).
\tag{2}
$$

Both laws of diffusion are special cases of the more general Fokker–Planck equation, which is a continuum equation for particles moving randomly in space and is explained in the next section. Fick's law and the Fokker–Planck law of diffusion differ in their assumptions about the underlying random movement. Fick's law assumes that the speed of each step of movement depends on the conditions at the end point of that step, whereas the Fokker–Planck law assumes that movement speed depends on the conditions at the starting point of each step. Again, this is discussed in detail in the following section.

Differentiating the diffusion term in Eq. (2) once, we obtain

$$
\frac{\partial}{\partial t} u(x, t) = \frac{\partial}{\partial x} \left(\underbrace{D(x) \frac{\partial u(x, t)}{\partial x}}_{\text{Fick's law}} + \underbrace{u(x, t) \frac{\partial D(x)}{\partial x}}_{\text{additional term}} \right).
\tag{3}
$$

Compared to Eq. (1), Eq. (3) includes an additional term proportional to $\frac{\partial D}{\partial x}$. Further differentiation yields

$$\frac{\partial}{\partial t} u(x,t) = \underbrace{D(x)\frac{\partial^2 u(x,t)}{\partial x^2} + \frac{\partial D(x)}{\partial x}\frac{\partial u(x,t)}{\partial x}}_{\text{Fick's law}}$$

$$+ \frac{\partial D(x)}{\partial x}\frac{\partial u(x,t)}{\partial x} + \underbrace{u(x,t)\frac{\partial^2 D(x)}{\partial x^2}}_{\text{growth adaptation term}} . \tag{4}$$

Equation (4) includes a term proportional to $\frac{\partial^2 D}{\partial x^2}$, i.e. to the curvature of the diffusivity. If the curvature is positive, there is extra net growth of the population. If the curvature is negative, there is additional net decay of the population. Hence, the growth adaptation term leads to growth in diffusion minima and to decay in diffusion maxima. In other words, the growth adaptation term generates a net shift of particles from diffusion maxima to diffusion minima. This implies an increased propensity of pattern formation and destabilization of uniform distributions of reaction components or populations.

The growth adaptation term vanishes if the second derivative of the diffusivity is zero. Hence, for diffusion coefficients that are linear in space, the only difference between the Fokker–Planck and Fickian law of diffusion is the second $\frac{\partial D(x)}{\partial x}\frac{\partial u(x,t)}{\partial x}$ term. If the diffusion coefficients are constant, Fokker–Planck's and Fick's law are equal.

Because diffusion models are a continuum description of a random motion process of many particles, they are often used to approximate the influence of a turbulent environment (Okubo 1971; Thomson 1984; Roberts and Webster 2002; Tabak and Tal 2004). However, because un-mixing by turbulence is unphysical (Holloway 1994), some authors (Hunter et al. 1993; Visser 1997) apply a "correction term" to the Fokker–Planck formulation, which compensates the additional term $\frac{\partial}{\partial x}(u(x,t)\frac{\partial D(x)}{\partial x})$ in Eq. (3) in order to avoid this effect. They refer to the work of Thomson (1987) who postulated the so called *well–mixed condition* which does not allow structuring of passive tracers due to diffusion. Those tracers are non-reacting particles which passively drift through the flow of the surrounding medium. Thomson formulated this criterion for models describing turbulent diffusion in water or air, where "initially well-mixed particles of tracers will remain so" (Thomson 1987, p. 534).

Contrary to this, van Milligen et al. (2005) showed that the Fokker–Planck law of diffusion is more in accordance with experimental data. In their experiment, they used water with an inhomogeneous concentration of gelatine to create a system with spatially inhomogeneous diffusion. As time went by, homogeneously distributed food color diffused towards areas of lower diffusion and created a concentration gradient. This is in contrast to Thomson's well–mixed condition and shows good agreement with the Fokker–Planck law of diffusion. Other physical experiments with moving particles, in plasmaphysics (Lançon et al. 2001; Whiteford et al. 2004), or cell movement in the brain (Belmonte-Beitia et al. 2013) show similar results. Hillen et al. (2013) showed that a Fokker–Planck diffusion model can even generate a Dirac-type mass concentration phenomenon in the large time limit.

The differences between these papers underline that the theory of diffusion and dispersion is not well understood yet and that the choice of the diffusion model is not trivial.

Bringuier (2011) pointed out that Fick's law might be a good model in cases where diffusion itself has a physical origin like turbulent motion of the medium, in which the tracers drift. The inhomogeneity of diffusion in those cases arises from geometric conditions like boundary conditions of the system, which lead to spatially inhomogeneous turbulence. We will refer to this kind of diffusion as *physical diffusion*.

In contrast to that, Bringuier (2011) remarked that the Fokker–Planck law of diffusion is valid in cases where the inhomogeneity arises from a gradient in temperature and/or density of the medium. For example, molecular diffusion on a temperature gradient will lead to accumulation of molecules at cooler places. The Fokker–Planck law of diffusion is also a good description for population dynamics where individuals move differently based on local information. For instance, individuals move more slowly if the local environment has beneficial conditions, whereas they move faster in case of bad conditions (Turchin 1998; Cantrell et al. 2006). Keller and Segel (1971) and Lapidus and Levandowsky (1981) use the term *motility* for the diffusion coefficient in this context. We use the term *ecological diffusion* (Garlick et al. 2011) to make clear that this kind of diffusion has another origin than physical diffusion.

Because Fick's law is the most commonly used model of diffusion, here we apply the Fokker–Planck law of diffusion to some typical biological reaction-diffusion systems in inhomogeneous environmental conditions. We will point out a number of differences between the two formalisms and try to make clear under which conditions the one or the other is a more appropriate model.

Finally, we propose a model that combines the two formulations of diffusion. This is based on the assumption that diffusion has different origins, as is often the case when species change their movement behavior and adapt to varying environmental conditions.

2 The Fokker–Planck equation

We consider a one–dimensional stochastic trajectory of a particle (Visser 2008). The spatial position $x(t)$ at time t of this particle follows

$$x(t + \Delta t) - x(t) = \Lambda \Delta t + \xi \Delta \nu. \tag{5}$$

Here Δt is a small time step and $\Delta \nu$ is a Wiener process with mean $\langle \Delta \nu \rangle = 0$ and variance $\langle (\Delta \nu)^2 \rangle = \Delta t$. Λ is a drift and ξ the intensity of the stochastic process.

A general continuum equation for particles following a general random walk process like (5) is the Fokker–Planck equation (Okubo and Levin 2001, chapter 5):

$$\frac{\partial}{\partial t} u(x, t) = \frac{\partial}{\partial x} \left(-\Lambda(x) u(x, t) + \frac{\partial}{\partial x} (D(x) u(x, t)) \right)$$
$$= -\frac{\partial}{\partial x} (\Lambda(x) u(x, t)) + \frac{\partial^2}{\partial x^2} (D(x) u(x, t)), \tag{6}$$

which is also known as the Kolmogorov forward equation (Kolmogorov 1931) or Smoluchowski equation (Smoluchowski 1916). The diffusion coefficient $D(x)$ can be related to the intensity of the stochastic process:

$$D = \frac{\xi^2}{2n},$$
(7)

where n is the number of spatial dimensions (in this paper $n = 1$).

There are different options to specify the drift term $\Lambda(x)$. In general it can be any function, but the choice $\Lambda = \alpha \frac{\partial D}{\partial x}$ is especially interesting. $\alpha = 1$ leads to Fick's law (1). If we set $\alpha = 0$, the Fokker–Planck equation reduces to Eq. (2) which is called the Fokker–Planck law of diffusion (Bringuier 2011) and was first derived by Chapman (1928). Patlak (1953) developed Eq. (2) as a continuum equation for a correlated random walk and the special case that the probability for a particle moving with a certain velocity into a certain direction is the same for any direction.

The physical meaning of α can be understood by looking at the underlying stochastic process (Sattin 2008; Visser 2008; Potapov et al. 2014). If, on the one hand, the velocity of a randomly moving particle depends on the conditions at the starting point of each movement step, $\xi = \xi(x(t))$, we set $\alpha = 0$ and obtain the Fokker–Planck law of diffusion. If, on the other hand, the velocity of this particle depends on the conditions at the end point of each movement step, $\xi = \xi(x(t + \Delta t))$, we set $\alpha = 1$. In this sense the biological meaning of α is related to the amount of information an individual random walker has about its neighborhood. This can be the ability to perceive or remember its environment. Potapov et al. (2014) also analyzed the case $\alpha = -1$, which is not a subject of this paper. For turbulent diffusion, the choice of α is determined by Thomson's well mixed condition, which is fulfilled in case of $\alpha = 1$. However, in case of ecological diffusion, this condition does not need to hold, because living organisms have internal energy reserves that can be utilized to decrease entropy (Visser 2008). The choice of α then depends on the ability of the individual to sense its environment, and to "choose" its movement behavior based on this information.

If the individual adapts its movement behavior (e.g. speed) only to the local information of its current location, then α would be zero. Individuals which can sense the environment over a longer distance (optical or chemical sensors), or which can remember the conditions of places visited earlier (Fronhofer et al. 2013), have more information available and may behave differently. In this case, an appropriate choice is $0 < \alpha \le 1$. Colombo and Anteneodo (2015) used a similar ansatz to describe the coupling between favorable and unfavorable habitats in an ecological landscape.

3 Pattern formation without any reactions

To understand the effect of ecological diffusion on a system of partial differential equations, we first investigate the diffusion of passive tracers. Because there is no reaction of the tracers, we can readily see how the different descriptions of diffusion affect the system. This has been demonstrated by other authors before (Turchin 1998; Okubo and Levin 2001; Visser and Thygesen 2003; Garlick et al. 2011). Because it is essential to understand the effect on reaction-diffusion systems later on, a simple example is given which describes the mechanism of unmixing by the Fokker–Planck law of diffusion.
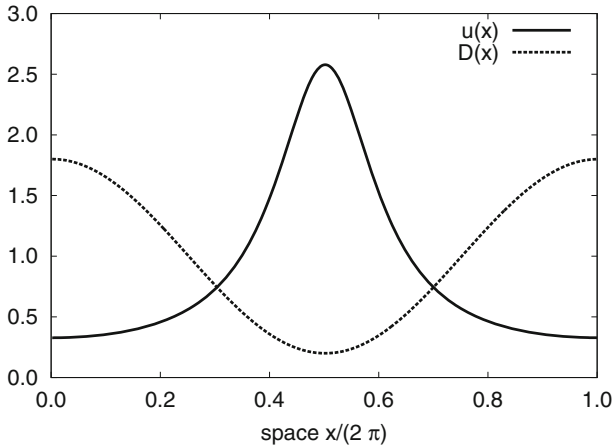
Fig. 1 Fokker–Planck law of diffusion ($\alpha = 0$): stationary pattern of passive tracers (*solid line*) for large t with a spatially inhomogeneous diffusion coefficient $D(x)$ (*dashed line*). Initial condition: $u(x, 0) = 1 \forall x$. The choice of the non-trivial initial condition does not change the result. Periodic boundary conditions

We look at a one–dimensional periodic domain with a spatially varying diffusion coefficient

$$D(x) = A + B \cos\left(\frac{2\pi}{\lambda}x\right) \quad \text{with } A > |B|, \tag{8}$$

where A is the spatial mean of $D(x)$, B its amplitude, and λ the wavelength of the periodic variability.

The steady state solution for the distribution of tracers $u(x) > 0$ is given by

$$u(x) = u_0 D(x)^{-(1-\alpha)}, \tag{9}$$

where u_0 is a constant. For a detailed derivation see appendix "Stationary solution of the Fokker–Planck equation".

In case of Fickian diffusion ($\alpha = 1$, Eq. 1), the homogeneous distribution is a steady state. This is because the term $D(x)\frac{\partial^2}{\partial x^2}u(x, t)$ in (1) will smooth any tracer distribution and $\frac{\partial}{\partial x}D(x)\frac{\partial}{\partial x}u(x, t)$ will vanish for $t \to \infty$.

Instead, if the Fokker–Planck equation with $\alpha = 0$ (Eq. 2) is used, the stationary state is proportional to the inverse of the coefficient of diffusion (see also Patlak 1953). This is illustrated in Fig. 1, where tracers move away from regions of high diffusivity and accumulate in regions of small diffusivity. The qualitative result for $t \to \infty$ is the same for any initial distribution $u(x, 0)$, and will also appear for any value $\alpha < 1$.

When we think of turbulent diffusion, these results also mean that the density of the medium (e.g. water) itself varies in space because of the inhomogeneous coefficient of diffusion. For an incompressible medium this is an unphysical feature. In this case other forces like pressure and gravity are stronger, so that an inhomogeneous water density is not generated by that mechanism. For living organisms like plankton other mechanisms are important and the well–mixed condition does not necessarily hold.

[Visser](2008) modeled the movement of zooplankton with Fokker-Planck diffusion ($\alpha = 0$) and [Garlick et al.](2011) used it to model the movement of deer.

4 Speed of spatial invasion

In the previous section we saw that the Fokker–Planck law of diffusion leads to a drift of particles to areas where the coefficient of diffusion has a local minimum. In this section we look at particles or organisms that change in number due to biological growth while they spread in space. In particular, we look at the speed of traveling waves of a logistically growing population, which is initially located in a small area in space. Due to diffusion, the population can spread in space ([Fisher 1937](); [Kolmogorov et al. 1937]()). The speed of this invasion depends on the strength, variability, *and* kind of diffusion.

Logistic growth in dimensional form is described here by the equation $dU/d\tau = \rho\,(1 - U/K)\,U$, where U is the dimensional species density, ρ is the intrinsic per-capita growth rate, and K is the carrying capacity. Using dimensionless quantities $u = U/K$, $\tau = tT_0$ and $r = \rho T_0$, where T_0 is a typical time unit of the system, we can add the scaled reaction term

$$f(u) = (r - u)u \tag{10}$$

to the right-hand side of Eqs. (1) and (6). In case of spatially periodic intrinsic per-capita growth rate, the emerging traveling wave will have a periodic shape as illustrated in Fig. 2. [Shigesada et al.](1987) called this a "traveling periodic wave".

[Shigesada et al.](1987) calculated a lower boundary for the speed of such a traveling wave. To this end, they assumed that the intrinsic per-capita growth rate $r(x)$ was
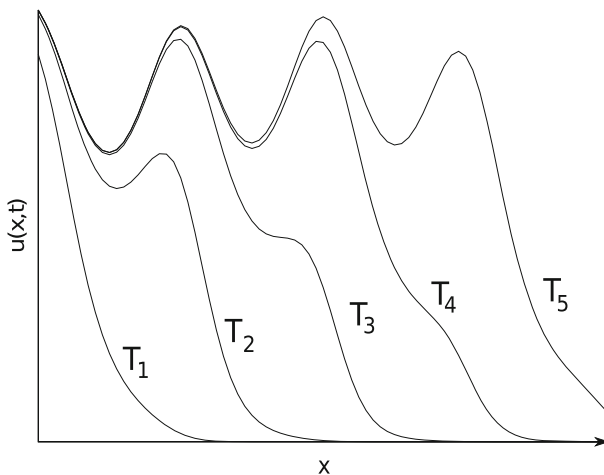
Fig. 2 Traveling periodic wave at different times $T_1 < T_2 < T_3 < T_4 < T_5$. Logistically growing population with spatially (sinusoidally) intrinsic per-capita growth rate and Fickian diffusion

spatially periodic but piecewise constant in space. Moreover, they assumed Fickian diffusion with a diffusivity $D(x)$ that varied also periodically and piecewise constant in space. In order to avoid the mathematical singularities in $\frac{\partial D}{\partial x}$ where $D(x)$ changes its value, they introduced the condition that the density $u(x)$ and the flux $D(x) \cdot \frac{\partial u}{\partial x}$ are continuous functions at the boundaries between patches of different $D(x)$. As the lower boundary c_{min} for the speed c of a traveling wave, they obtained

$$c \geq c_{min} = 2\sqrt{\langle r(x) \rangle_A \langle D(x) \rangle_H}, \tag{11}$$

where $\langle \cdot \rangle_H$ is the spatially harmonic and $\langle \cdot \rangle_A$ the arithmetic mean. Note that, if the wavelength λ of the spatially periodic variation of the diffusion coefficient (8) is extremely small, the lower bound c_{min} in Eq. (11) will be the actual wave speed, i.e., $\lim_{\lambda \to 0} c = c_{min}$.

Kinezaki et al. (2006) considered spatially periodic $D(x)$ and $r(x)$ that varied smoothly (sinusoidally) in space. They also assumed Fick's law of diffusion. We can write their model in the following form:

$$\frac{\partial u}{\partial t} = (\hat{r}(x) - u)u + \left[\frac{\partial}{\partial x} D(x) \frac{\partial}{\partial x} u + D(x) \frac{\partial^2}{\partial x^2} u \right], \tag{12}$$

where $D(x)$ is given by Eq. (8) and $r(x)$ by

$$\hat{r}(x) = r - (1 - \tilde{\alpha}) \frac{\partial^2 D(x)}{\partial x^2} \tag{13}$$

such that it varies spatially in anti-phase with $D(x)$. Parameter $\tilde{\alpha}$ changes the amplitude of the variability in $\hat{r}(x)$.

For the sake of comparison, we now consider a model that also uses a sinusoidal $D(x)$ but a constant per-capita growth rate r and the full Fokker–Planck equation as diffusion term:

$$\frac{\partial}{\partial t} u(x, t) = (r - u)u + \left[\frac{\partial^2}{\partial x^2} (D(x)u) - \frac{\partial}{\partial x} \left(\alpha u \frac{\partial D(x)}{\partial x} \right) \right].$$

Splitting the Fokker–Planck equation into separate terms, we can write this as a reaction term with spatially varying intrinsic per-capita growth rate $\hat{r}(x)$ and Fick's law of diffusion, plus an additional term called "FP_{add}":

$$\frac{\partial}{\partial t} u(x, t) = (\hat{r}(x) - u)u + \left[(2 - \alpha) \frac{\partial D(x)}{\partial x} \frac{\partial u}{\partial x} + D(x) \frac{\partial^2 u}{\partial x^2} \right]$$

$$= (\hat{r}(x) - u)u$$

$$+ \left[\underbrace{\frac{\partial D(x)}{\partial x} \frac{\partial u}{\partial x} + D(x) \frac{\partial^2 u}{\partial x^2}}_{\hat{=}\text{Fick's law}} + \underbrace{(1 - \alpha) \frac{\partial D(x)}{\partial x} \frac{\partial u}{\partial x}}_{\text{Term } 'FP_{add}'} \right], \tag{14}$$

where

$$\hat{r}(x) = r - (1 - \alpha)\frac{\partial^2 D(x)}{\partial x^2} = r - (1 - \alpha)\frac{4\pi^2}{\lambda^2}B\cos\left(\frac{2\pi}{\lambda}x\right) \tag{15}$$

is the effective intrinsic per-capita growth rate and varies again in anti-phase with $D(x)$. Parameter α comes from the Fokker–Planck equation; it has the same influence on the amplitude of $\tilde{r}(x)$ as $\tilde{\alpha}$ in Eq. (14), but in contrast to the Kinezaki model α obviously also affects the diffusion.

Even though r was assumed constant in space, the spatial variation in the diffusion coefficient effectively leads to a variation in the intrinsic per-capita growth rate of the population if $\alpha < 1$. Hence, we can also observe traveling periodic waves.

Without the additional term 'FP_{add}', Eq. (14) would be equal to the system in Eq. (12) analyzed by Kinezaki et al. (2006). As the effective intrinsic per-capita growth rate $\hat{r}$ and the coefficient of diffusion oscillate in anti-phase, we might presume that the results of Kinezaki et al. (2006) also hold for model (14) based on the Fokker–Planck equation, but we will show in the following that this is not the case.

To this end, we compare the speeds c of the traveling periodic waves. We approximated these wave speeds by using a spatial domain with 20 oscillations in $D(x)$. As initial condition $u(x, 0)$ we used a Gaussian distribution with small variance in the center of the domain. We then determined the time Δt it took until the concentration at two locations of distance $\Delta x = 5\lambda/(2\pi)$ to each other reached a certain value. The wave speed is then defined as $c = \Delta x/\Delta t$.

Figure 3a shows the speed c of a traveling wave of an initially localized population using the Kinezaki model (12). In case of constant diffusion ($B = 0$), the speed c does not vary with $\tilde{\alpha}$. In this case $\hat{r}(x)$ is a constant as well. If $\tilde{\alpha} = 0$, the amplitude of $\tilde{r}(x)$ is maximal. There is a maximum of the wave speed at $B \approx 0.75$. For increasing $\tilde{\alpha}$, the amplitude of $\hat{r}(x)$ decreases and so the wave speed decreases as well. This result has been observed by Kinezaki et al. (2006).

Figure 3b shows the wave speeds when using the Fokker–Planck equation with constant r as in Eq. (14). For $\alpha < 1$ and $B > 0$, the population also forms traveling periodic waves because of the variations in the effective per-capita growth rate. Nevertheless, the wave speed c is nearly unchanged with varying α, even for large B. This must be due to the additional term 'FP_{add}' in Eq. (14), as this term is the only difference to the Kinezaki model. In the numerical simulations considered here, the additional term apparently slows down the traveling periodic wave for small values of α. The additional term 'FP_{add}' can be interpreted as an advection term with advective speed $(1 - \alpha)\partial D(x)/\partial x$. As the gradient of $D(x)$ averages zero over a period, this suggests that it is the variability in the heterogeneous diffusivity that seems to slow down the traveling wave for small α and thus makes the difference to the Fickian diffusion used by Kinezaki et al. (2006). in this case slows down the front speed for small values of α.

Therefore, the presumption that the additional term 'FP_{add}' has a neglectable influence on the invasion speed is wrong. The Fokker–Planck law of diffusion can create traveling periodic waves without a significant change in the front speed as the amplitude in the growth rate varies.
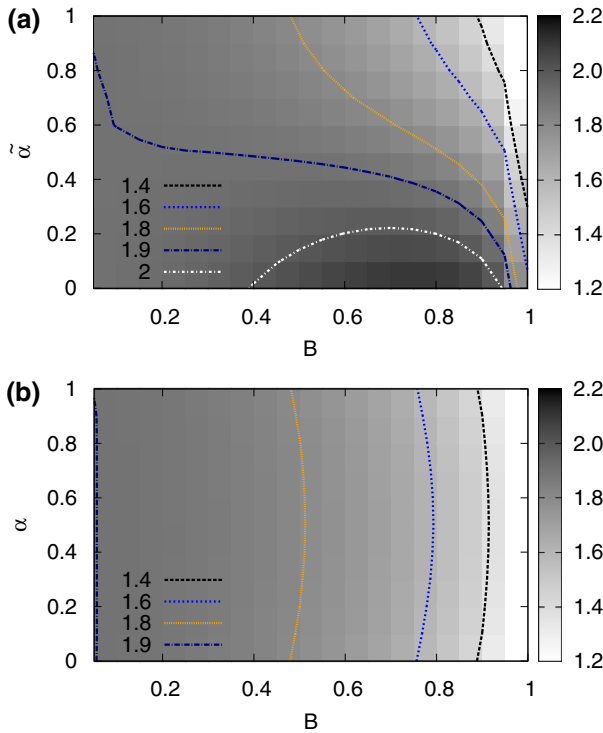
Fig. 3 **a** Speed c of traveling periodic waves with Fick's law of diffusion and spatially varying intrinsic per-capita growth rate (Eq. (12)). **b** Speed c of traveling periodic waves with the Fokker–Planck equation and constant intrinsic per-capita growth rate (Eq. 14). In both cases $D(x)$ is given by Eq. (8) and $r = 1$. The front speed approaches zero if the amplitude of $D(x)$, B, equals the mean value of $D(x)$, $A = 1$, because then $D(x)$ becomes zero at $x = \lambda/2 \cdot (2m + 1)$ with $m \in \mathbf{N}$. The parameters α and $\tilde{\alpha}$ change the amplitude of the effective intrinsic per-capita growth rates. Note that α is also found in the additional term 'FP_{add}' which comes from the Fokker–Planck equation. The lines are isolines for different values of c

5 Turing instability driven by inhomogeneous diffusion

Now we look at a more complex system with two interacting components. The two of them have different abilities to move in space. A system with two interacting components is said to exhibit a diffusion-driven instability (Turing 1952) if a uniform steady state is stable to spatially homogeneous perturbations but unstable to spatially inhomogeneous perturbations. In those cases, a stable spatially inhomogeneous solution of the model equations may exist. The two components, u and v, in those models must have significantly different coefficients of diffusion D_u and D_v, they must be of activator–inhibitor type, and the spatially inhomogeneous perturbation must be supercritical.

Like Maini et al. (1992), we analyse the Schnakenberg model (1979), which is one of the simplest activator-inhibitor models. Maini et al. (1992) showed that using Fick's law of diffusion, i.e., $\alpha = 1$, spatially inhomogeneous diffusion can produce isolated spatial patterns. The non–dimensional model equations, as used in Maini et al. (1992), read:
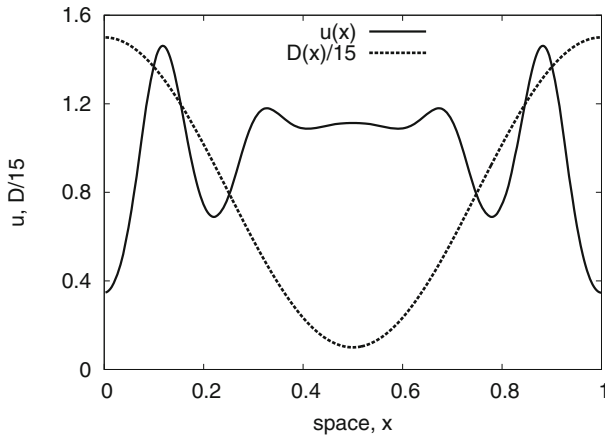
Fig. 4 Turing pattern from initially homogeneously distributed state variables u and v. In areas where $D(x) = D_v(x)/D_u = (8 + 7 \cdot \cos(2\pi x))$ is too small, i.e. around $x = 0.5$, no pattern-formation occurs. $a = 0.1, b = 0.9, \gamma = 2000$; initial conditions are the values of the local stationary solution $v(x, 0) = 0.9, u(x, 0) = 1$. The values for a, b and γ are also used in Maini et al. (1992). $D(x)$ varies in a similar range of values

$$
\frac{\partial u}{\partial t} = \gamma \left(a - u + u^2 v \right) + \frac{\partial^2 u}{\partial x^2},
$$
$$
\frac{\partial v}{\partial t} = \gamma \left(b - u^2 v \right) + \frac{\partial}{\partial x} \left(D(x) \frac{\partial v}{\partial x} \right),
\tag{16}
$$

where v and u are non-dimensional values for some chemical concentrations, with v being the activator and u the inhibitor. $D(x) = \frac{D_v(x)}{D_u}$ is the ratio of the two coefficients of diffusion, which can vary in space if D_v varies in space. Maini et al. (1992) assumed that D_u is constant and that $D_v(x)$ is controlled by the inhomogeneous concentration of some regulatory chemical. γ is a scale factor proportional to the length of the domain, a and b are positive constants.

We change system (16) by using the Fokker–Planck law of diffusion ($\alpha = 0$) and obtain

$$
\frac{\partial u}{\partial t} = \gamma \left(a - u + u^2 v \right) + \frac{\partial^2 u}{\partial x^2},
$$
$$
\frac{\partial v}{\partial t} = \gamma \left(b - u^2 v \right) + \frac{\partial^2}{\partial x^2} \left(D(x) v(x, t) \right).
\tag{17}
$$

If we use formulation (16), it is well known that we need a spatially inhomogeneous perturbation in our initial conditions to create Turing patterns. These disturbances must be located in areas where the ratio $D(x)$ of the two coefficients of diffusion is large enough.

If, on the other hand, formulation (17) is used, Turing patterns appear for homogeneous non-zero initial conditions, i.e. in the absence of any perturbation. This is shown in Fig. 4. The spatially inhomogeneous perturbation which drives the Turing pattern

has its internal origin in the diffusion itself and does not need any external forcing or inhomogeneous initial conditions. Like in the simulations by Maini et al. (1992), the patterns are localized at areas with large $D(x)$.
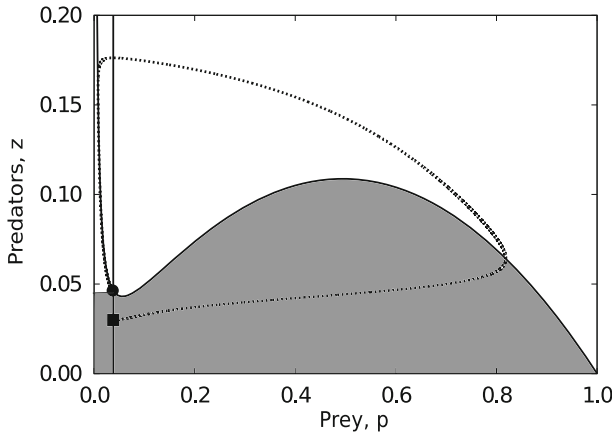
Maini et al. (1992) suggest the possibility that the mechanism of Turing patterns is involved in the developmental process of spatial patterns in an early embryo. They conclude that the dependence on the initial conditions in their model with Fickian diffusion is a "drawback as most development processes are robust." (p. 211) We have shown that using the Fokker–Planck law of diffusion yields the desired robustness of the pattern formation, because the pattern formation is initialized by the inhomogeneous diffusion and does not need random fluctuations or an initially inhomogeneous distribution of u or v.

6 Interaction of turbulence and ecological diffusion: example of spatially and temporally periodic blooms in an excitable plankton model

So far we have assumed that particles or organisms move according to either Fickian or Fokker–Planck diffusion. In reality, however, some species may use a combination of physical and ecological diffusion. For instance, consider the random movement of zooplankton cells. On the one hand, they are exposed to their hydrodynamic environment, which is characterized by random flows in the water, which may be described by Fick's law of diffusion with a spatially inhomogeneous diffusion coefficient $D_{turb}(x)$. On the other hand, zooplankton are able to swim actively. Here, we assume that they do so in search of prey, and that their active random motion can be described by ecological diffusion. More specifically, we assume that in a calm environment with little turbulence zooplankton frequently change their position to find prey. However, if zooplankton is located in a turbulent region, they encounter prey due to the turbulence and there is no need for active swimming. Hence, ecological diffusion depends on the turbulence of the environment. The spatial inhomogeneity of the diffusion describing the active random movement, $D_{eco}(x)$, thus varies in anti–phase with the inhomogeneity of $D_{turb}(x)$. In contrast to D_{turb}, the ecological diffusion D_{eco} does not have to satisfy the well-mixed condition because there is no physical reason for the predators to remain in a uniform distribution while they move. In Sect. 3 we showed that depending on the swimming behavior and the knowledge of the individuals about their environment, this can lead to spatial aggregation of the predators. In this section we show that this can have a major effect on the spatiotemporal dynamic of a predator–prey system.

Let us consider a system of a prey species p (algae) which is consumed by a predator species z (zooplankton). We describe the movement of the predators by a combination of Fick's and Fokker–Planck's laws of diffusion to describe physical and ecological diffusion, respectively:

$$\frac{\partial p}{\partial t} = f(p, z) + \frac{\partial}{\partial x}\left(D_{turb}(x)\frac{\partial}{\partial x}p\right),$$

$$\frac{\partial z}{\partial t} = g(p, z) + \frac{\partial}{\partial x}\left(D_{turb}(x)\frac{\partial}{\partial x}z\right) + \frac{\partial^2}{\partial x^2}\left(D_{eco}(x)z\right). \tag{18}$$

Fig. 5 Nullclines (*solid lines*) of the Truscott–Brindley model (19). If a trajectory starts in the gray area, both population densities markedly increase before they return to the nontrivial stationary state. A sample trajectory (*dotted line*) starts at the *black rectangle* within the *gray area* and ends at the stationary state marked with a *dot*. Parameter values: $\beta = 0.43$, $\nu = 0.053$, $\gamma = 0.05$ and $\omega = 0.34$

All quantities are dimensionless. σ_{turb} and σ_{eco} are scaling factors for the different kinds of diffusion. They describe the speed of diffusion in comparison to the biological dynamics. The distinction between ecological and physical diffusion is similar to the model by Jin et al. (2014). In contrast to their model, we do not assume constant ecological diffusion. The functions $f(p, z)$ and $g(p, z)$ represent the vital dynamics of the two species, for which we consider a predator–prey model used by Truscott and Brindley (1994) to describe the interaction of oceanic phyto- and zooplankton:

$$\frac{\mathrm{d}p}{\mathrm{d}t} = \beta p \left(1 - p\right) - \frac{p^2}{\nu^2 + p^2} z = f(p, z),$$

$$\frac{\mathrm{d}z}{\mathrm{d}t} = \gamma \left(\frac{p^2}{\nu^2 + p^2} - \omega \right) z = g(p, z). \tag{19}$$

The prey grow logistically while they are grazed by the predators with a Holling-type III functional response. Here, β is the maximal per-capita growth rate of the prey plankton–species p, ν is the half saturation density of prey for the predator species z, γ a factor describing the different time scales of the two dynamics, and ω is the per-capita mortality rate of the predators.

The values of these parameters are taken from Truscott and Brindley (1994) ($\beta = 0.43$, $\nu = 0.053$, $\gamma = 0.05$ and $\omega = 0.34$) and are such to describe a plankton system. Using these values, the model (19) has a unique non-trivial stable stationary solution. However, if a supercritical perturbation applied to one of the stationary variables, the system becomes excited and the two populations grow to large values before they return to the stable stationary state (Fig. 5).

For the sake of simplicity, we assume that the ecological diffusion D_{eco} varies linearly with the turbulent diffusion D_{turb}. In case of a sinusoidal varying turbulent diffusion this means that the ecological diffusion varies in anti–phase with the turbulent diffusion (Fig. 6a). In our simulations we chose
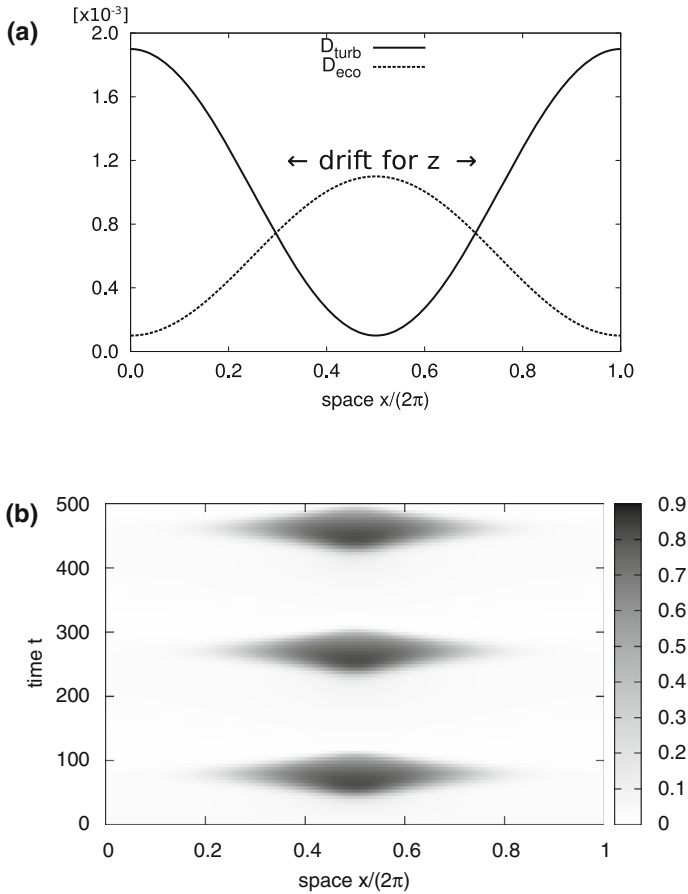
Fig. 6 a Turbulent and ecological diffusion vary in anti-phase. $D_{turb}(x) = 10^{-3}(1 + 0.9 \cos(2\pi x))$. $D_{eco} = 10^{-3}(0.6 - 0.5 \cos(2\pi x))$. This leads to an effective drift of predators z to areas of low values of D_{eco}. **b** Periodic blooms in an excitable predator–prey system with periodic boundary conditions. Prey concentration in space and time. Initial conditions are the stationary solutions of system (19)

$$D_{turb}(x) = 10^{-3} \cdot (1 + 0.9 \cos(2\pi x)) \text{ and} \tag{20}$$

$$D_{eco}(x) = 10^{-3} \cdot (0.6 - 0.5 \cos(2\pi x)). \tag{21}$$

The magnitude of the dimensionless diffusion coefficients scales with the spatial domain.

Without reaction terms, the Fokker–Planck law in the predators' equation leads to an accumulation of predators in regions with small D_{eco} (and, here, large D_{turb}) and a reduction of the concentration of predators in areas with large D_{eco}. Turbulent diffusion (D_{turb}) described by Fick's law of diffusion has a smoothing effect on any inhomogeneities in the species' concentrations. The prey distribution would be homogeneous without reaction terms, because we assume that phytoplankton is not able to swim actively and, therefore, follows only turbulent diffusion modeled by Fick's law.

In the full system with reaction and diffusion terms, initially homogeneously distributed predators will not remain so. Instead, their concentration will approach a stationary state $\sim \text{constant}/D_{eco}(x)$. Locally reduced density of predators can initialize plankton blooms as illustrated in Fig. 5. Once a bloom occurs locally, it "infects" its neighborhood and a traveling pulse of excitation propagates through the spatially extended system.

Even though the system is excitable everywhere in space, the pulse of excitation does not propagate to areas with small values of D_{eco}. The reason for this is the same mechanism which initializes the bloom in areas with large values of $D_{eco}(x)$. The density of predators is higher in areas with small values of $D_{eco}(x)$. This stabilizes the stationary state and the pulse can not excite the system here. The prey concentration undergoes only insignificant variations in these areas.

As shown in Fig. 6b, the maximum densities of prey in time and space are located in areas of minimal D_{turb} and maximal D_{eco}. To initialize a bloom, the spatial derivatives of the ecological diffusion have to be large enough. Otherwise the smoothing effect of D_{turb} destroys any inhomogeneity in the plankton distributions. The negative influence of turbulent diffusion on the variation in the density of actively swimming plankton has been observed for vertical mixing by Maar et al. (2003). High ecological diffusion does not automatically induce stronger inhomogeneities. This can be seen more clearly if we look at the diffusion terms in detail. To this end we rearrange the second equation of system (19) as follows.

$$
\begin{aligned}
\frac{\partial z}{\partial t} - g(p, z) &= \frac{\partial}{\partial x}\left(D_{turb}(x)\frac{\partial}{\partial x}z\right) + \frac{\partial^2}{\partial x^2}\left(D_{eco}(x)z\right) \\
&= \frac{\partial z}{\partial x}\left(\frac{\partial(D_{turb}(x) + 2D_{eco}(x))}{\partial x}\right) \\
&\quad + \frac{\partial^2 z}{\partial x^2}\left(D_{turb}(x) + D_{eco}(x)\right) + z\frac{\partial^2 D_{eco}(x)}{\partial x^2}.
\end{aligned}
$$

With $D(x) \equiv D_{turb}(x) + D_{eco}(x)$ we get

$$
\begin{aligned}
\frac{\partial z}{\partial t} - g(p, z) &= \frac{\partial z}{\partial x}\left(\frac{\partial(D(x) + D_{eco}(x))}{\partial x}\right) + D(x)\frac{\partial^2 z}{\partial x^2} + z\frac{\partial^2 D_{eco}(x)}{\partial x^2} \\
&= \underbrace{\frac{\partial z}{\partial x}\left(\frac{\partial D(x)}{\partial x}\right) + D(x)\frac{\partial^2 z}{\partial x^2}x}_{\text{Fickian diffusion (smoothing)}} + \underbrace{\frac{\partial z}{\partial x}\frac{\partial D_{eco}(x)}{\partial x} + z\frac{\partial^2 D_{eco}(x)}{\partial x^2}}_{\text{enables spatial inhomogeneity of } z}.
\end{aligned}
$$

So a higher mean value of $D_{turb}(x)$ or $D_{eco}(x)$ leads to a stronger smoothing effect. Aggregation of z can only arise from the terms proportional to the derivatives of D_{eco}. Especially the term proportional to $\frac{\partial^2}{\partial x^2}D_{eco}(x)$ has an effect on initially homogeneously distributed z. In order to generate a plankton bloom, this suggests that higher mean values of $D(x)$ require larger values of $\frac{\partial^2}{\partial x^2}D_{eco}(x)$, too (Fig. 7).

Although a direct effect of turbulent diffusion on biological processes can be observed only on relatively small scales (Powell et al. 1975), our results show that
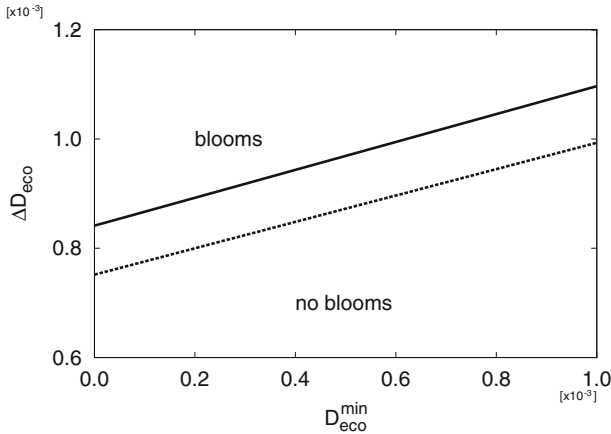
Fig. 7 Numerically analyzed values of D_{eco}^{min} (the minimal value of $D_{eco}(x)$) and ΔD_{eco} (the amplitude of $D_{eco}(x)$) where periodic blooms occur in a spatially diffusive system with $D_{eco}(x) = D_{eco}^{min} + \frac{\Delta D_{eco}}{2}(1 - \cos(2\pi x))$. D_{eco}^{min} is the minimal value of $D_{eco}(x)$ and ΔD_{eco} is the difference between its maximal and its minimal value. *Solid line* $D_{turb}(x) = 10^{-3}(1 + 0.9\cos(2\pi x))$; *dashed line* $D_{turb}(x) = 10^{-3}(0.5 + 0.4\cos(2\pi x))$; we tested whether or not the value of the prey concentration exceeded a threshold of 0.5 at least twice, to define if there are periodic blooms in the system. Initial conditions are the stationary solutions of system (19). For parameter values above the line, blooms occur

inhomogeneous physical mixing on small scales can have visible indirect effects on larger scales in form of plankton blooms.

The choice of the connection between D_{eco} and D_{turb} as in Eqs. (20) and (21) is arbitrary. We assume that predators do not have to actively swim under turbulent conditions and save energy by just passively drifting with the flow. Similar behavior of zooplankton in turbulent environments have been studied theoretically by Yamazaki et al. (2004) and Visser et al. (2009). In the experiments of Saiz and Alcaraz (1992), a turbulent environment increased the frequency and the velocity displayed in the jumping behavior of copepods. This is in contrast to our assumptions, but the effects are similar (see appendix "Plankton model with turbulent and ecological diffusion in phase").

7 Conclusion

Even though spatial heterogeneities are all around in nature, diffusion problems are almost exclusively modeled with spatially homogeneous or piecewise constant coefficients of diffusion. In those cases, there is no difference between the Fickian and the Fokker–Planck description. However, there is no reason to exclusively consider the rather specific type of piecewise constant or linear heterogeneities. In fact, spatial inhomogeneities that vary nonlinearly in space seem much more common. If spatially nonlinearly changing diffusion coefficients are essential, the accurate choice of the mathematical description of diffusion is not trivial.

It turns out that pattern formation in spatially inhomogeneous diffusive systems is considerably more prevalent if the diffusion is described by the Fokker–Planck law rather than by Fick's law. This is because of the strong influence of the second derivative of the coefficient of diffusion in the Fokker–Planck law, which results in a drift of individuals/particles into areas with small coefficients of diffusion.

Our main results are as follows:

– As already pointed out by other authors, the Fokker–Planck equation (6) with $\Lambda = \alpha \frac{\partial D}{\partial x}$ and $\alpha < 1$ enables pattern formation in inhomogeneous systems even in a diffusive system without any reactions.
– The Fokker–Planck diffusion influences the speed of a traveling wave of a spreading population. It also enables traveling periodic waves without a spatially varying intrinsic per-capita growth rate of the population.
– In two-component systems, in which the difference of the diffusion coefficients of the components varies inhomogeneously in space, Turing patterns can be formed even from homogeneous non-perturbed initial conditions of the components.
– In excitable systems, Fokker–Planck diffusion can locally destabilize the stationary state and initialize blooms.

Because Fokker–Planck diffusion is used to model ecological diffusion, these results can be important for many models which deal with biological components. Especially because of the pattern-forming tendencies, our results may be interesting with respect to the formation of oceanic plankton blooms. Systems where the origin of the inhomogeneity of diffusion arises only from hydrodynamics, Fick's law of diffusion is supposed to be a more accurate description (Bringuier 2011). However, if other mechanisms than turbulent diffusion create spatial inhomogeneous diffusion, aggregation of individuals in certain areas of space is possible. This has been investigated by Visser and Thygesen (2003) with different random walk models for motile zooplankton. In this case, the Fokker–Planck law of diffusion might play an important role in the formation of patterns and blooms in some biological systems. In a previous paper (Bengfort et al. 2014), we analyzed periodic blooms generated by a system in which the biological parameters such as the carrying capacity of prey and the half saturation density in the predators' functional response vary in space because of different environmental conditions. Contrary to that, the periodic blooms in the present paper do not emerge because of locally changing parameters in the vital dynamics but solely originate from the spatial heterogeneity of the Fokker–Planck diffusion.

In the paper we mentioned above we also analyzed the impact of the terms $\frac{\partial D}{\partial x} \frac{\partial C_i}{\partial x}$ in different excitable plankton models where C_i are the densities of different species, D is the coefficient of diffusion, and x the spatial variable. Fick's law of diffusion was used. It was shown that these terms have different effects in different models concerning the ability to generate propagating pulses of high plankton density similar to Sect. 6 in the present paper. Equation (2) shows that these terms are also part of the Fokker–Planck law of diffusion, but multiplied with a factor of 2. So this effect would be twice as strong as in Fick's law even for a linearly varying coefficient of diffusion.

Anderson et al. (2012) used the Fokker–Planck law of diffusion in a reaction–diffusion–advection model where the coefficient of diffusion and the velocity are functions of a species' density which changes in space and time. This leads to an

indirect dependence of the diffusion coefficient on space and time. Similarly to our results, this formulation supports spatial pattern formation. However, as outlined in Anderson et al. (2012), the stabilities in their model do not rely on activator–inhibitor interactions, which is why they are based on a different mechanism.

In addition to an increased propensity for species agglomeration, this paper has demonstrated that there is still a gap in our understanding of diffusion. In particular, we suggest there may be a scope for combined approaches where organisms adapt their movement behavior to environmental conditions.

Appendix

Dimensionless diffusion equation

We transform a reaction–diffusion–equation with the Fokker–Planck equation into a dimensionless form. The original equation reads

$$\frac{\partial U}{\partial \tau} = f(U) - \frac{\partial}{\partial X}\left(\alpha \frac{\partial \delta(X)}{\partial X} U\right) + \frac{\partial^2}{\partial X^2}(\delta(X)U), \tag{22}$$

where U has the dimension of a concentration, X is the spatial variable, τ has the dimension of time, and $\delta(X)$ is a diffusion coefficient with dimension space^2/time. We introduce dimensionless variables: $u = U/U_0$, $t = \tau/T_0$, and $x = X/X_0$. U_0, T_0, and X_0 are constants with the dimension of U, T, or X, respectively.
Using these variables gives

$$\frac{\partial u}{\partial t} = f(uU_0)\frac{T_0}{U_0} - \frac{T_0}{X_0^2}\frac{\partial}{\partial x}\left(\alpha \frac{\partial \delta(X)}{\partial x} u\right) + \frac{T_0}{X_0^2}\frac{\partial^2}{\partial x^2}(\delta(X)u). \tag{23}$$

Now we can define a dimensionless coefficient of diffusion $D(x) \equiv \delta(xX_0)\frac{T_0}{X_0^2}$. This coefficient scales with the timescale T_0 and the scaling factor of space X_0. The final, dimensionless version of the Fokker–Planck equation with a reaction term then reads

$$\frac{\partial u}{\partial t} = F(u) - \frac{\partial}{\partial x}\left(\alpha \frac{\partial D(x)}{\partial x} u\right) + \frac{\partial^2}{\partial x^2}(D(x)u), \tag{24}$$

where $F(u)$ is a dimensionless formulation of the reaction term $f(U)$.

Stationary solution of the Fokker–Planck equation

A stationary solution to the Fokker–Planck equation (6) with $\Lambda = \alpha\frac{\partial D}{\partial x}$ has to fulfil the following condition:

$$0 = -\frac{\partial}{\partial x}\left(\alpha \left(\frac{\partial D(x)}{\partial x}\right) u(x)\right) + \frac{\partial^2}{\partial x^2}(D(x)u(x))$$

$$c = (1-\alpha)\left(\frac{\partial D(x)}{\partial x}\right) u(x) + D(x)\frac{\partial u(x)}{\partial x},$$

where x is a constant. Using the ansatz $u(x) = k\exp(f(x)) > 0$ with an unknown function $f(x)$ we get

$$c = (1-\alpha)u(x)\frac{\partial D(x)}{\partial x} + D(x)u(x)\frac{df(x)}{dx}$$

$$\Rightarrow \frac{df(x)}{dx} = \frac{c}{D(x)} - (1-\alpha)\frac{1}{D(x)}\frac{\partial D(x)}{\partial x} \quad \text{if } D(x) \neq 0 \text{ and } u(x) \neq 0$$

$$\Rightarrow f(x) = c\int_0^x \frac{1}{D(x')}dx' - (1-\alpha)\left(\ln|D(x)| + c^*\right),$$

where c^* is another constant. Substituting $f(x)$ into the ansatz we made for $u(x)$ gives us the steady state solution for the Fokker–Planck equation:

$$u(x) = \exp\left(c\int_0^x \frac{1}{D(x')}dx'\right) u_0 D(x)^{-(1-\alpha)} \quad \text{with } u_0 = k \cdot \exp(-(1-\alpha)c^*).$$

We used periodic boundary conditions. In our case with $D(x) = A + B\cos(2\pi x)$, $D(x)$ is a periodic function with the same values at $x = 0$ and $x = L$, where L is the length of the spatial domain. The same must hold for $u(x)$. Therefore the constant c must be set to zero. The solution reads

$$u(x) = u_0 D(x)^{-(1-\alpha)},$$

where the constant u_0 depends on the initial conditions,

$$u_0 = \frac{\int_0^L u(x, t=0)dx}{\int_0^L D(x)^{-(1-\alpha)}dx}.$$

Plankton model with turbulent and ecological diffusion in phase

To study the effect of ecological diffusion, which varies in phase with the turbulent diffusion D_{turb}, we set $D_{eco}^{(2)}(x) = D_{turb}(x)$. In this case, the zooplankton is drifted to areas with small D_{turb}, and blooms occur with the same mechanism as in the previous simulations (Fig. 8). The drifting effect caused by the Fokker–Planck law of diffusion has to be stronger than in the former case (where D_{turb} and D_{eco} are in anti-phase) to create a bloom (Fig. 9). This is because the smoothing effect of D_{turb} prevails in areas where the predators are diminished by the drift.
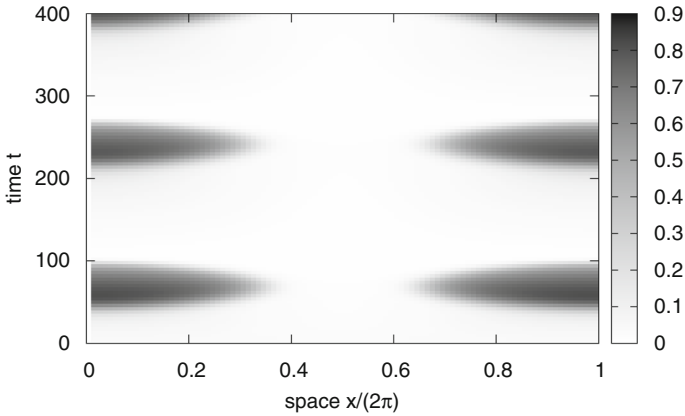
Fig. 8 Spatial and temporal periodic blooms in an excitable predator–prey system with periodic boundary conditions. Only prey concentrations are shown. Turbulent and ecological diffusion vary in phase. $D_{turb}(x) = D_{eco}^{(2)}(x) = (1 + 0.9\cos(2\pi x))10^{-3}$. The initial condition is a homogeneous distribution of the stationary solution of system (19)
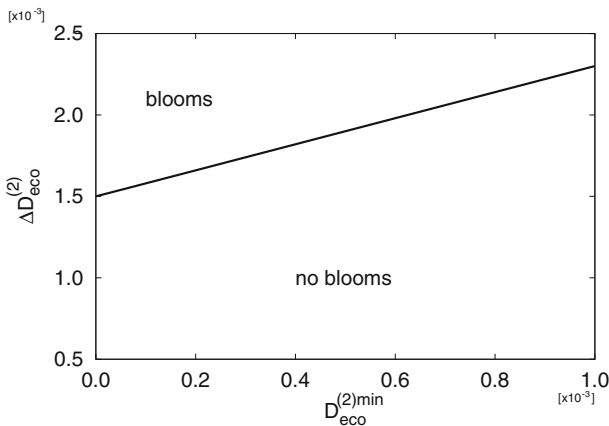
Fig. 9 Numerically analyzed values of $D_{eco}^{(2)min}$ and $\Delta D_{eco}^{(2)}$ where excitation occur in a spatially diffusive system with $D_{eco}^{(2)} = (D_{eco}^{(2)min} + \Delta \frac{D_{eco}^{(2)}}{2}(1 + \cos(2\pi x)))$. $D_{turb}(x) = 10^{-3} \cdot (1 + 0.9\cos(2\pi x))$. We tested whether the value of the prey concentration exceeded a threshold of 0.5 for at least two times or not, to define if there are periodic blooms in the system. Homogeneous initial conditions are the stationary solutions of system (19). Note that the values of $\Delta D_{eco}^{(2)}$ are much larger than in the case in which D_{eco} and D_{turb} vary in anti-phase (Fig. 7)

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