Coexistence of competitors mediated by nonlinear noise[*]

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Abstract. Stochastic reaction-diffusion equations are a popular modelling approach for studying interacting populations in a heterogeneous environment under the influence of environmental fluctuations. Although the theoretical basis of alternative models such as Fokker-Planck diffusion is not less convincing, movement of populations is most commonly modelled using the diffusion law due to Fick. An interesting feature of Fokker-Planck diffusion is the fact that for spatially varying diffusion coefficients the stationary solution is not a homogeneous distribution—in contrast to Fick's law of diffusion. Instead, concentration accumulates in regions of low diffusivity and tends to lower levels for areas of high diffusivity. Thus, we may interpret the stationary distribution of the Fokker-Planck diffusion as a reflection of different levels of habitat quality. Moreover, the most common model for environmental fluctuations, linear multiplicative noise, is based on the assumption that individuals respond independently to stochastic environmental fluctuations. For large population densities the assumption of independence is debatable and the model further implies that noise intensities can increase to arbitrarily high levels. Therefore, instead of the commonly used linear multiplicative noise model, we implement environmental variability by an alternative nonlinear noise term which never exceeds a certain maximum noise intensity. With Fokker-Planck diffusion and the nonlinear noise model replacing the classical approaches we investigate a simple invasive system based on the Lotka-Volterra competition model. We observe that the heterogeneous stationary distribution generated by Fokker-Planck diffusion generally facilitates the formation of segregated habitats of resident and invader. However, this segregation can be broken by nonlinear noise leading to coexistence of resident and invader across the whole spatial domain, an effect that would not be possible in the non-spatial version of the competition model for the parameters considered here.

1 Introduction

It is needless to give a broad review of the classical publications on spatial and spatiotemporal pattern formation in non-equilibrium nonlinear systems. However, on occasion of Ulrike's significant birthday, one should remember her seminal contributions to the theory of pattern formation in electrochemical systems from the eighties of last century [5,6,7], of course without forgetting all her impressive later work

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until today. In that mentioned early period of her academic career, one of us (H.M.) had the chance to learn from and to work with Ulrike in Werner Ebeling's research group at the Sektion Physik of Humboldt-Universität zu Berlin [17]. Later on, a theoretical bridging of electrochemical and ecological diffusive systems was found [16,18]. Ulrike became interested in ecological and environmental dynamics as well, and from time to time we manage to meet and to chat and sometimes even to work, cf. [1]. Also in the academic career of I.S., Ulrike Feudel has played an important role—Ulrike kindly served as an external examiner for his PhD defence. He has fond memories of being quizzed on the Lotka-Volterra competition model which also plays a central role in the study presented here.

Several important problems in ecology are associated with corresponding phenomena in pattern formation. For example, the study of biological invasions, the spread of a non-native species (the invader) in a habitat where a native species (the resident) is possibly considerably reduced or even driven to extinction, is closely related to the analysis of wave solutions in reaction-diffusion systems. The emergence of patterns in apparently relatively homogeneous habitats such as, for example, the patchiness of plankton or complex vegetation patterns is linked to the Turing instability [29] and its many variants involving a combination of diffusive and advective flows. Several detailed introductions to spatio-temporal patterns in ecology are available, for example, the classic by Okubo [22,23] or the more recent monograph by Malchow, Petrovskii and Venturino [20]. Mathematical models for interactions and movements of populations $\mathbf{X}(\mathbf{r}, t) = \{X_i(\mathbf{r}, t); \ i = 1, 2, \ldots, N\}$ in a heterogeneous and variable environment are often based on stochastic reaction-diffusion equations:

$$\frac{\partial X_i(\mathbf{r}, t)}{\partial t} = \underbrace{f_i(\mathbf{X}(\mathbf{r}, t))}_{\text{reaction}} + \underbrace{\nabla \cdot (-\boldsymbol{\mu}(\mathbf{x}, t)X_i(\mathbf{r}, t) + \nabla[D(\mathbf{r}, t)X_i(\mathbf{r}, t)])}_{\text{diffusion}} + \underbrace{g_i(\mathbf{X}(\mathbf{r}, t))\xi(\mathbf{r}, t)}_{\text{stochastic}} . \tag{1}$$

Here, the reaction terms $f_i(\mathbf{X}(\mathbf{r}, t))$ describe the interactions between individuals of a population with individuals of the same or a different population. This enables us to represent processes as diverse as transmission of infectious diseases, predator-prey interactions or competition for resources.

The diffusion term is derived from an underlying stochastic model of the movement of individuals. Consider the stochastic differential equation (SDE) for the position $\mathbf{X}_t \in \mathbb{R}^d$ of a particle that moves stochastically in d-dimensional space:

$$d\mathbf{X}_t = \boldsymbol{\mu}(\mathbf{X}_t, t)dt + \boldsymbol{\Sigma}(\mathbf{X}_t, t)d\mathbf{W}_t \tag{2}$$

The drift coefficients $\boldsymbol{\mu} : \mathbb{R}^d \times \mathbb{R}^+ \to \mathbb{R}^d$ account for deterministic movement of the particle, $d\mathbf{W}_t$ is a d-dimensional Wiener process and the matrix-valued intensity coefficients are $\boldsymbol{\Sigma} : \mathbb{R}^d \times \mathbb{R}^+ \to \mathbb{R}^{d \times d}$. An alternative description to the SDE (2) which enables us to calculate the stochastic location $\mathbf{X}_t$ of a particle is the probability density $p(\mathbf{x}, t)$ for finding the particle at position $\mathbf{x}$ at time t. This analogous representation of the system is especially suitable for considering a large population of particles because in this case, the probability density $p(\mathbf{x}, t)$ can be interpreted as the fraction of particles that are expected to be found at a location $\mathbf{x}$ at time t. The probability density $p(\mathbf{x}, t)$ can be shown to satisfy a deterministic partial differential equation (PDE), the Kolmogorov forward or Fokker-Planck equation [15], [23, chapter 5]

$$\frac{\partial}{\partial t}p(\mathbf{x}, t) = \nabla \cdot (-\boldsymbol{\mu}(\mathbf{x}, t)p(\mathbf{x}, t) + \nabla[D(\mathbf{x}, t)p(\mathbf{x}, t)]) \tag{3}$$

where ∇ is the gradient, $(\nabla \cdot)$ denotes the divergence operator and $D(\mathbf{x}, t)$ is related to the intensities $\boldsymbol{\Sigma}(\mathbf{x}, t)$ by the standard scalar product $\langle \cdot, \cdot \rangle$:

$$D_{i,j}(\mathbf{x}, t) = \langle \boldsymbol{\Sigma}_{i,\cdot}, \boldsymbol{\Sigma}_{j,\cdot} \rangle. \tag{4}$$

Now, choosing

$$\boldsymbol{\mu}(\mathbf{x}, t) := \alpha \nabla D(\mathbf{x}, t), \quad \alpha \in \mathbb{R}, \tag{5}$$

we obtain several alternative laws for the dynamics of the probability distribution $p(\mathbf{x}, t)$ i.e. the collective movement of the population. First, it is important to note that in this model different choices of the

parameter α only have an effect for spatially varying diffusion coefficients $D(\mathbf{x}, t)$, for $D(\mathbf{x}, t) := \text{const.}$ all laws derived for different α coincide. Second, the biological significance of the diffusion coefficients changes depending on the choice of α. For $\alpha = 1$ an easy calculation shows that (3) reduces to the well-known diffusion law due to Fick [8]

$$\frac{\partial}{\partial t} p(\mathbf{x}, t) = \nabla \cdot [D(\mathbf{x}, t) \nabla p(\mathbf{x}, t)] \tag{6}$$

which is the diffusion term most commonly used in modelling applications. Here, the flux $D(\mathbf{x}, t) \nabla p(\mathbf{x}, t)$ is proportional to the gradient of $p(\mathbf{x}, t)$ i.e. to local concentrations differences. Thus, for $\alpha = 1$, the diffusion coefficient $D(\mathbf{x}, t)$ simply is the rate at which concentration gradients are equilibrated. In the terminology of Okubo [23, chapter 5] who provides a mechanistic interpretation of several models presented in the classical publications by Skellam [27,28], Fick's law was therefore named "neutral" because the diffusion coefficients play no active role in determining local concentrations. In contrast, a law known as Fokker-Planck diffusion [10,24], obtained for $\alpha = 0$

$$\frac{\partial}{\partial t} p(\mathbf{x}, t) = \Delta[D(\mathbf{x}, t) p(\mathbf{x}, t)]. \tag{7}$$

varying diffusion coefficients $D(\mathbf{x}, t)$ increase the flux even for locally homogeneous $p(\mathbf{x}, t)$. Thus, for the Fokker-Planck law the diffusion coefficients $D(\mathbf{x}, t)$ can be interpreted as the tendency to leave a particular spatial location. Thus, this law of diffusion was named "repulsive". The "attractive" law obtained for $\alpha = 2$ (which we will not consider in this paper) was recently investigated by Potapov et al. [25]. In summary, as explained in more detail in [2], the drift term (5) is not only a phenomenological description but can be interpreted as the ability of an individual to respond to environmental conditions by "choosing" its direction of movement accordingly [11].

Third, from the different significances of the diffusion coefficients for different α it is not surprising that the stationary solution of (3) depends on the choice of this parameter. For "neutral" diffusion according to Fick's law (6) it is clear that the homogeneous distribution $p(\mathbf{x}, t) = 1$ is a stationary solution. But it is obvious that the stationary distribution cannot be homogeneous for the Fokker-Planck law (7) for spatially varying diffusion coefficients $D(\mathbf{x}, t)$. The reason can be understood by regarding (2). By choosing $\alpha = 0$,the movement of individual particles is purely stochastic but nevertheless for spatially inhomogeneous coefficients, the movement is biased towards directions of larger intensities $\boldsymbol{\Sigma}(\mathbf{x}, t)$. Similarly, we see that in the situation of Fick's law ($\alpha = 1$), the drift term $-\nabla D(\mathbf{x}, t)$ opposes the gradient of $D(\mathbf{x}, t)$ and in this way seems to exactly balance the bias of the movement towards larger diffusivities.

For many physicochemical systems, Fick's law is the model of choice due to the fact that the particles move in a purely passive way which is consistent with a flux opposed to the concentration gradient. But for biological populations whose individuals are able to actively influence their direction of movement, there is no reason to restrict ourselves to models based on Fick's law. Instead, it seems more appropriate to start from a general model for stochastic movement such as (3). However, regardless of possible interpretations of the stochastic movement of individuals underlying a particular diffusion term, the most important qualitative feature of the alternative models to Fick's law presented here is the fact that the stationary distributions of the populations are in most situations inhomogeneous. Indeed, Bengfort et al. [2] showed that Fokker-Planck diffusion leads to pattern formation for situations where this would not be expected for Fickian diffusion.

Whereas Bengfort et al. [2] considered a wide range of deterministic models, most recently we have also investigated the combined influence of Fokker-Planck diffusion and stochastic environmental fluctuations. In the follow-up paper Bengfort et al. [3] we considered linear multiplicative Gaussian "white" noise (uncorrelated in space and in time) which is the most common model for fluctuations in environmental conditions such as temperature, nutrient availability etc. over time and/or in space. The general noise term $g_i(\mathbf{X})$ in (1) could, in principle, be used to account for several different sources apart from environmental noise. For example, by choosing a non-negative process $\xi(\mathbf{r}, t)$ and $g_i(\mathbf{X}) = \text{const.}$ the influence of *random immigration* might be implemented. From an individual-based model, the branching process, it can be derived that with $g_i(\mathbf{X}) \sim \sqrt{X_i}$ a model for *demographic stochasticity* is obtained. In

this article we will only consider *environmental stochasticity*. As mentioned above, the classical model for environmental noise is $g_i(\mathbf{X}) \sim X_i$. One crucial assumption of the branching process with random environment (BPRE), an individual-based model from which this scaling can be derived, is that environmental fluctuations affect each individual independently. Due to independence, an increase or decrease of each individual's likelihood to reproduce results in a proportional increase or decrease in the population's growth rate. In contrast, we have recently proposed an alternative model where the noise intensity saturates for large population densities [26]:

$$g_i(\mathbf{X}) = \frac{\omega_i X_i}{\gamma_i + X_i} \,. \tag{8}$$

In this model, which we proposed in slightly more general form in [26], the noise level g_i monotonically tends to a maximal noise intensity ω_i. The half-saturation constant $K := \gamma_i$ is the population density X_i at which half of the maximal noise intensity is reached. It is important to emphasise here that although this model thus makes a transition from linear multiplicative noise at low population densities to additive noise at large population densities this should not be interpreted as a transition from environmental stochasticity to random immigration. Rather, as mentioned above we exclusively consider environmental stochasticity for which we propose an alternative model where the noise intensity saturates for large densities instead of increasing linearly.

Like the linear multiplicative noise term, also the model (8) can be justified by underlying processes at the level of individuals. Let us consider the effect of fluctuations in nutrient abundance under intraspecific competition as a concrete example. For a small population density it is reasonable to assume that increased nutrient abundance elevates the reproductive success of each individual by a similar amount. In contrast, for a high population density, due to competition only the reproductive success of the strongest individuals may increase which leads to saturating growth at the population level. Similarly, if nutrients are scarce, stronger competitors might be less severely affected so that again at the population level the influence of decreased nutrient abundance is less than proportional to the population density. Regardless of the mechanistic interpretation given above, the most important qualitative difference of (8) to the multiplicative model is the fact that in the new model (8) the noise intensity is bounded.

The purpose of this study is to examine in more detail the combined effect of Fokker-Planck diffusion (7) and nonlinear noise (8). This is motivated by our most recent work where we found that by varying the standard approaches for modelling movement of populations [2] or environmental fluctuations [26], respectively, a wide range of interesting effects could be observed, even in well-known classical models such as the Lotka-Volterra competition model. On the one hand, Bengfort et al. revisited a wide range of classical deterministic reaction-diffusion models under the assumption that the movement of particles or members of a population was described by Fokker-Planck rather than Fickian diffusion. The greater propensity of the Fokker-Planck law for pattern formation was demonstrated for several examples [2]. Bengfort et al. [3] extended this study of deterministic systems with Fokker-Planck diffusion by adding environmental fluctuations modelled by the classical linear multiplicative white noise model. On the other hand, Siekmann and Malchow [26] investigated alternatives to the multiplicative noise model. They introduced the non-linear noise term (8) which, to the best of our knowledge, has not previously appeared in the literature and also studied correlated (coloured) rather than white noise. Siekmann and Malchow considered only Fickian diffusion with spatially homogeneous diffusion coefficients, so in this study we study Fokker-Planck diffusion with non-linear environmental noise (8). Like in Bengfort et al. [3] we model a biological invasion using the classical Lotka-Volterra model which enables us to compare our results obtained with non-linear noise (8) with the classical linear noise model.

2 The stochastic competition-diffusion model

The dynamics of a resident species X_1 and an invader X_2 is described by

$$\frac{\partial X_1}{\partial t} = (1 - X_1)X_1 - c_{12}X_1X_2 + d_1\Delta(X_1 D^*(x,y)) + g_1(X_1)\xi(\mathbf{r},t)\,, \tag{9}$$

$$\frac{\partial X_2}{\partial t} = (1 - X_2)X_2 - c_{21}X_1X_2 + d_2\Delta X_2 + g_2(X_2)\xi(\mathbf{r},t)\,. \tag{10}$$

The spatial dependency of the resident's diffusivity is chosen as

$$D^*(x,y) = D_0 + \begin{cases} a\left(\sin(20 \cdot r(x/L_x, y/L_y))\right)^k\,, & \text{if } 20 \cdot r(x/L_x, y/L_y) < 3\pi\,, \\ a\left(\sin(3\pi)\right)^k\,, & \text{else}\,. \end{cases} \tag{11}$$

with

$$r(x,y) = \sqrt{x^2 + y^2}$$

and L_x and L_y are the side lengths of the spatial domain. The side lengths chosen for this article are provided in (13). The parameter k is an even number witch controls the steepness of D^*. Throughout this paper we will use the parameters

$$D_0 = 1\,,\ a = 19\,,\ k = 8\,.$$

This functional form of the diffusivity $D^*(x,y)$, see Figure 1 for a plot, is meant to represent the resident's varying levels of preference for different areas of the spatial domain. The coefficient $D^*(x,y)$ can be regarded as being inversely proportional to the resident's preference for a particular location (x,y). Namely, the lower $D^*(x,y)$, the lower the tendency to leave (x,y) which can be interpreted as a high level of preference. How these preferences for different parts of the habitat affect the stationary distribution of the resident is fundamentally different for Fickian diffusion and Fokker-Planck diffusion. For Fickian diffusion the spatially heterogeneous diffusion coefficient $D^*(x,y)$ only affects the transient dynamics of the resident because the stationary distribution is always homogeneous, regardless of the particular functional form of $D^*(x,y)$. In contrast, for Fokker-Planck diffusion, the stationary solution is approximately inversely proportional to $D^*(x,y)$ which provides us with a simple model for a fragmented habitat that mimics the resident's levels of preference. In the absence of the invader X_2, the resident X_1 tends to the distribution shown in the right panel of Figure 1—note that for the initial condition we have always set the resident's population to zero within a square with a side length of 50 length units in order to mimic the onset of a biological invasion.

We ensure that resident and invader do not differ in competitive strength by letting the competition parameters coincide

$$c_{12} = c_{21} = 1.2$$

Because both c_{12} and c_{21} exceed unity, the system is in the bistable parameter range i.e. in the absence of diffusion or noise the competitor with the larger initial density will drive its opponent to extinction. For spatially extended systems, Malchow et al. showed that survival depends on the ratio of the diffusion coefficients of invader and resident—in general, the competitor with the larger diffusion coefficient prevails [19]. Because the spatially varying diffusion coefficient $d_1 \cdot D^*(x,y)$ of the resident is larger than the constant diffusion coefficient d_2 of the invader in some areas and smaller in others, it is expected from Malchow et al. [19] that the spatial domain becomes segregated. Whereas in some regions invasion is successful due to relatively low diffusivity of the resident, other areas act as barriers for invasion where the resident's diffusivity is relatively high. The initial condition is indicated in Figures 1 and 2, the invader is set to zero and the resident is initialised with the spatially heterogeneous stationary distribution in the whole spatial domain except for a patch in the upper left. Here, the resident is set to zero whereas the invader is set to its carrying capacity 1. An exception is one simulation (see Figures 8 and 9) where we
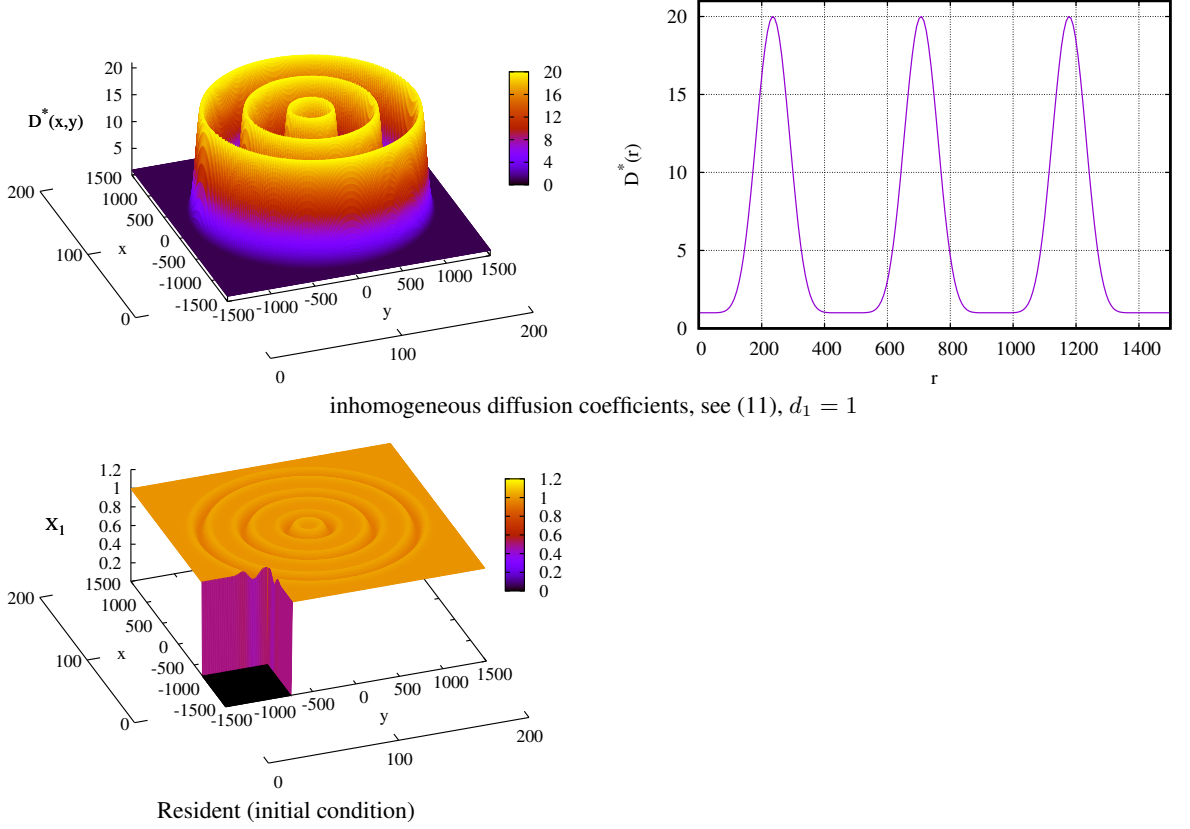
inhomogeneous diffusion coefficients, see (11), $d_1 = 1$

Resident (initial condition)

Fig. 1. Profile of Fokker-Planck diffusion and initial setting for residents

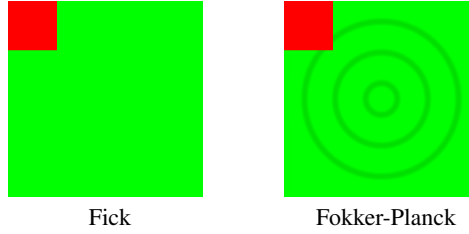Fick   Fokker-Planck

Fig. 2. 2D projection of initial settings for population densities (green = resident, red = invader), cf. Figure 1.

compare the spatially varying diffusion coefficients $D^*(x, y)$ with homogeneous diffusion coefficients—there the resident is initialised with a spatially homogeneous distribution.

We numerically solve (9), (10) using an alternating direction implicit (ADI) scheme for efficiently implementing the Crank-Nicholson method [4] as described previously [3]. The stochastic terms for which we use the Stratonovich interpretations are numerically integrated with the derivative-free Milstein method [13,21] as explained in [26]. For most simulations the temporal and spatial step sizes h_t, h_x and h_y were

$$h_t = 0.02, h_x = h_y = 15 \tag{12}$$

except for Figures 8 and 9 where a smaller temporal step width of $h_t = 0.002$ was required. We chose a grid with 200×200 grid points so that we obtain system lengths $L_x = L_y = 3,000$ and assumed that

the origin is in the centre of the spatial domain so that the spatial range extends from $(x_0, y_)) = -1,500$ to $(x_{\max}, y_{\max}) = 1,500$. In summary, the spatial parameters were

$$x_0 = y_0 = -1,500, x_{\max} = y_{\max} = 1,500, L_x = L_y = 3,000, N_x = N_y = 200 \qquad (13)$$

for all simulations.

3 Numerical simulations and results

We assess the influence of the non-linear noise model (8) on the success of the invasion by considering two different scenarios. In Section 3.1 both resident and invader are parametrised so that (8) resembles linear noise for population densities between zero and around 1 (see Figure 3). In Section 3.2 we lower the half-saturation constant γ_2 so that (8) is clearly non-linear already at low population densities of the invader while leaving the parameters of the resident unchanged (see Figure 3). This enables us to distinguish effects that are due to the nonlinearity of (8) from results that mainly depend on the interplay of noise intensities with other parameters. The model (8) can be seen as a generalisation of the linear model—whereas the results of Section 3.1 could be obtained with linear noise this is not true for those from Section 3.2 for reasons to be explained in the Discussion. Parameters for the simulations presented are summarised in Table 3.

Fig.	d_1	d_2	a	ω_1	ω_2	γ_1	γ_2
4	5	25	19	1.0	2.0	10.0	10.0
5	25	5	19	1.0	2.0	10.0	10.0
6	25	12.5	19	1.0	2.0	10.0	10.0
7	25	12.5	19	1.0	4.0	10.0	10.0
8	25	12.5	19	1.0	4.0	10.0	1.0
9	25	12.5	0	1.0	4.0	10.0	1.0

Table 1. Parameter values for the simulations presented in Figures 4-9.

3.1 Spatial segregation for approximately linear noise

For parameter sets where (8) resembles linear multiplicative noise with low intensities we observe front waves. Depending on the velocity of the wave, the invader either succeeds in expanding the initial patch or it is displaced by the resident. Because it is well-known that the wave speed increases with increasing diffusion coefficients we investigate the success of invasion depending on various choices of the scaling parameters d_1 and d_2 of the resident's and invader's diffusivities. The influence of the ratio of d_1 and d_2 is demonstrated in Figures 4-6. For Figures 4 and 5, the only difference between both parameter sets is that d_1 and d_2 are swapped. Consistent with Malchow et al. [19] if d_1 is low compared to d_2, the invasion is successful (Figure 4) whereas it fails for d_1 much larger than d_2 (Figure 5), although the invader initially seems to be able to enter the realm of the resident ($t = 100$). Interestingly, Figure 4 shows that even in the case of successful invasion, the invader is not able to invade the whole spatial domain. Due to the spatially inhomogeneous stationary distribution of the resident (see Figure 1) its competitive strength varies across the spatial domain, it is higher for areas where the resident population is high. Thus, the "rings" where the resident population is low are easier to invade whereas the areas next to these "rings" where the resident population is relatively high act as barriers that may halt the invasion. Thus, we observe the segregation of the spatial domain in one habitat inhabited by the invader and one habitat occupied by the resident. For Figure 6, the diffusivity d_2 has been increased in comparison with Figure 5. In contrast to the former situation, the invader not only manages to enter a ring where the resident population is relatively low
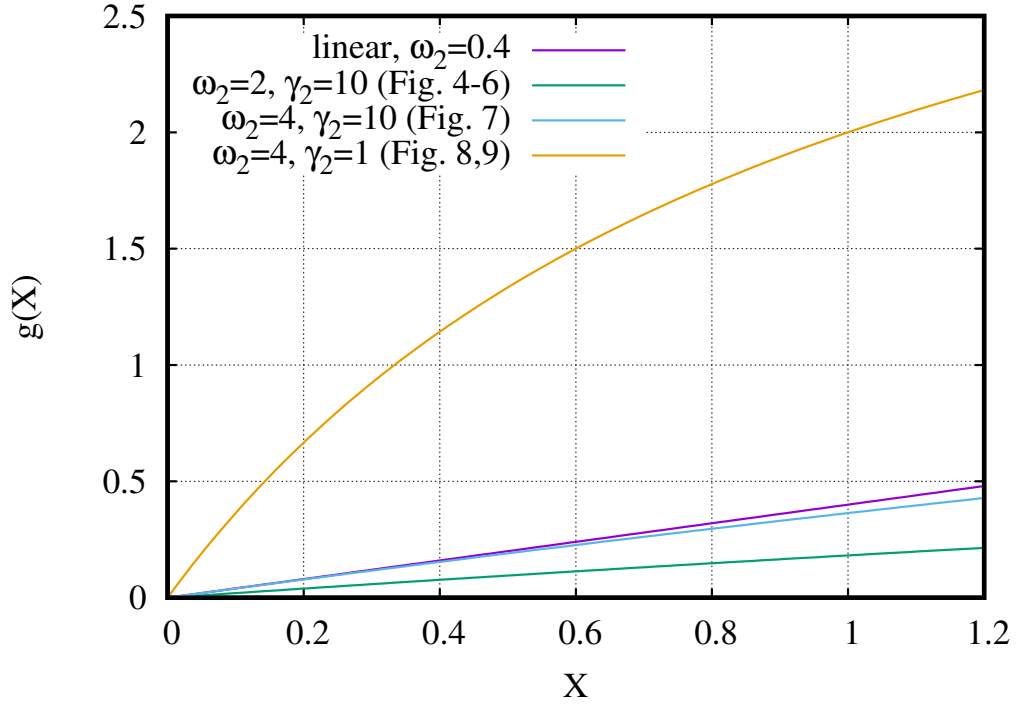
Fig. 3. The shape of the invader's noise term (8) for population densities ranging from zero to slightly above the carrying capacity 1. For $\gamma_2 = 10$, the function $g_2(\mathbf{X})$ (8) deviates only slightly from the linear model whereas the non-linearity is obvious for $\gamma_2 = 1$. For the resident, $\gamma_2 = 10$ was chosen for all simulations.
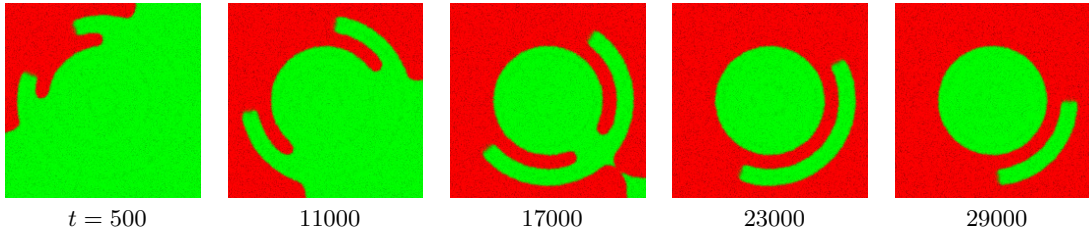

$t = 500$ 11000   17000   23000   29000

Fig. 4. Successful invasion for a low diffusivity of the resident compared with the invader.

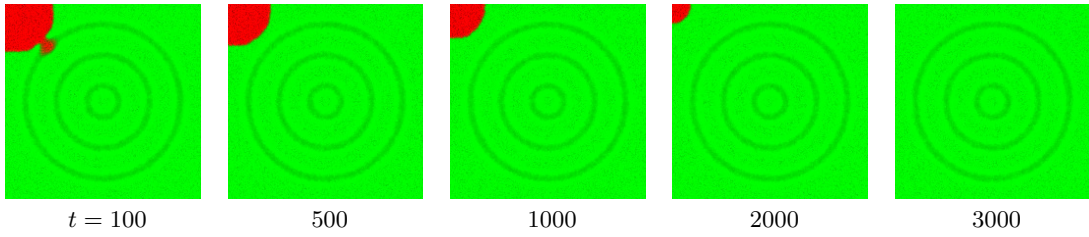$t = 100$ 500   1000   2000   3000

Fig. 5. Invasion fails if the invader's diffusivity is low compared with the resident.

(see Figure 1) but very slowly succeeds in establishing itself by displacing the resident. However, the invader is displaced from its initial patch. Therefore, like in Figure 4 we end up with spatially segregated habitats because ultimately, the invader remains "sandwiched" between barriers created by regions where the resident population is high.
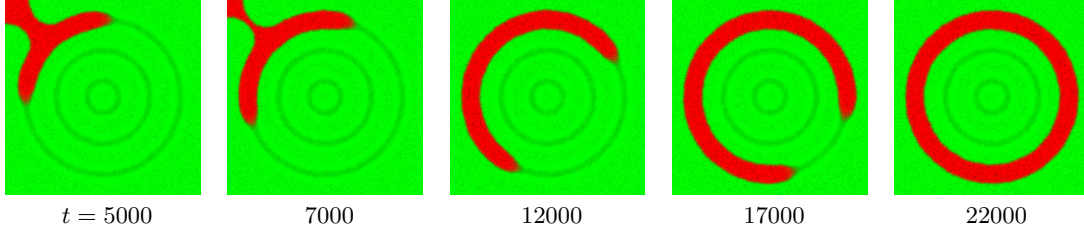

| $t = 5000$ | 7000 | 12000 | 17000 | 22000 |

Fig. 6. For an intermediate level of invader's diffusivity the invader manages to occupy a less preferred area of the resident's original habitat.

Increasing the noise intensity of the invader increases its ability to cross invasion barriers caused by large values of the diffusion coefficient $D^*(x, y)$ of the resident. Consistently, in Figure 7 we observe a similar situation as in our initial simulation (Figure 4) with low diffusivity of the resident in comparison with the invader. In contrast to the previous simulation (Figure 6) the invader also manages to expand its initial patch rather than only establishing itself in an area where the resident population is relatively low.
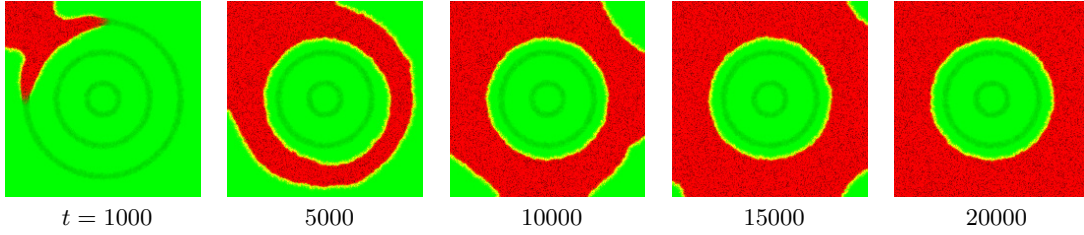

| $t = 1000$ | 5000 | 10000 | 15000 | 20000 |

Fig. 7. Increasing the invader's noise intensity ω_2 has a similar effect as increasing diffusivity, in comparison with Figure 6 the invader establishes itself in a larger spatial domain.

In summary, for Fokker-Planck diffusion and a noise term (8) in the weakly non-linear parameter regime, we observe that the strength of a competitor can be elevated by increasing the diffusivity or the noise intensity. Due to the spatially inhomogeneous diffusion coefficients $D^*(x, y)$ of the resident we observe segregation of the spatial domain in distinct habitats of invader and resident whose boundaries can be related to the stationary distribution of the resident (Figure 1).

3.2 Coexistence of resident and invader in mixed habitats for nonlinear noise

Whereas in the previous section we presented results meant to relate the nonlinear noise model (8) to the classical linear model we now demonstrate that invader and resident can coexist in the whole spatial domain, a result that cannot be observed for corresponding parameters of the linear model. From the previous section we expect that increasing the invader's noise intensity ω_2 would increase its competitive strength so that it can invade the whole spatial domain and displace the resident. This is indeed true (results not shown) but here we show that we can even achieve coexistence of both population. By time lowering the half-saturation constant γ_2 (which gives (8) a more "nonlinear" shape (Figure 3)) we can compensate

for the increase of the noise intensity ω_2 and avoid displacing the resident. In order to demonstrate that the emergence of a mixed habitat of resident and invader across the whole spatial domain depends little on the underlying model of spatio-temporal dispersal but is mostly mediated by the noise term we present results for both Fokker-Planck diffusion with spatially varying diffusion coefficients D^*x, y as well as spatially homogeneous diffusion coefficients for which the diffusion laws derived from (2) coincide.

Figure 8 shows that for spatially varying diffusion coefficients both populations quickly mix. The initial invader patch develops into a mixed front consisting of both resident and invader that replaces the area formerly occupied only by the resident. Although eventually the whole spatial domain is occupied by a mixed population of invaders and residents the resident population remains heterogeneous with a qualitatively similar distribution as in the initial condition (Figure 1).

The behaviour is analogous for spatially homogeneous diffusion coefficients (Figure 9) but in contrast to the results previously shown (Figure 8) now also the resident population is distributed homogeneously as expected.
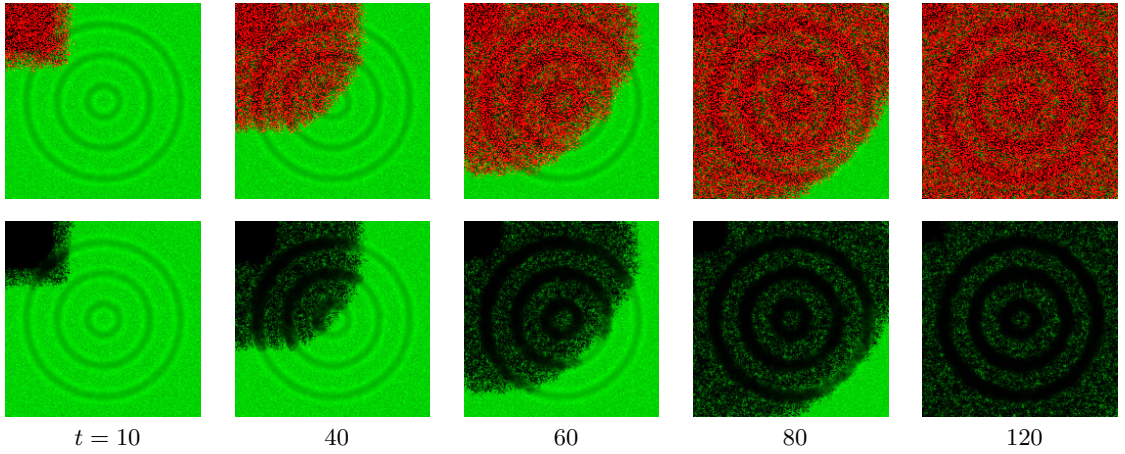

Fig. 8. Coexistence of resident and invader mediated by noise. In the first row both populations are plotted whereas in the second plot we only show the resident population in order to make its spatially heterogeneous distribution more obvious.
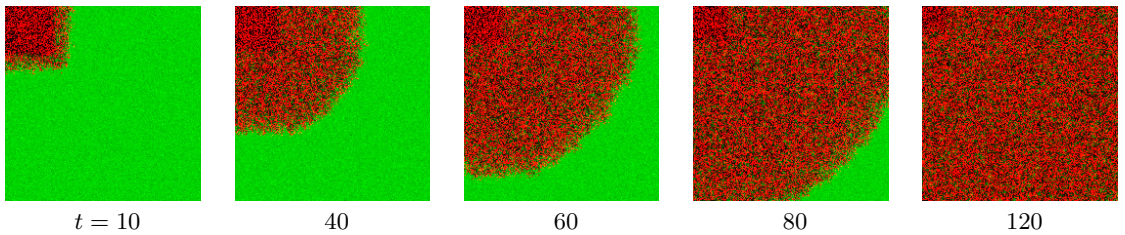

Fig. 9. Coexistence mediated by the nonlinear noise term (8) is also observed for spatially homogeneous diffusion coefficients. The results look very similar to Figure 8 except (as expected) for the spatial heterogeneities observed in the previous simulation.

4 Discussion

We have studied a biological invasion based on a spatio-temporal Lotka-Volterra competition model under the influence of stochastic environmental fluctuations. We found surprisingly rich dynamics after replacing the two standard models for movement of populations and environmental variability. Instead of Fickian diffusion, dispersal of the resident was modelled by the so-called Fokker-Planck law of diffusion. Moreover, we have replaced linear multiplicative noise by a model for which noise intensities saturate with increasing population densities. This accounts for the fact that for large population densities individuals are similarly affected by stochastic perturbations rather than responding independently. At the level of the population the effect of this assumption is that the noise intensity does not exceed a certain upper bound even for large population densities. Nevertheless, we can also parametrise the model (8) so that it resembles linear multiplicative noise for a certain range of population densities (Figure 3), thus, it can be regarded as a generalisation of linear multiplicative noise. In Section 3.1 we chose parameters for which the noise (8) is approximately linear in the relevant range of population densities which enables us to compare our new model with the standard model for environmental fluctuations. At the same time, the results from Section 3.1 help us to explain why the mixed front consisting of residents and invaders presented in Section 3.2 is an effect that is due to the non-linear noise (8) and not likely to be reproduced with linear multiplicative noise.

We deliberately chose equal parameters for both competitors which enables us to easily assess the competitive advantage of diffusivity i.e. the speed at which a population moves and the noise intensity i.e. the susceptibility of a population to environmental fluctuations. In the situation of symmetric competitors with competition coefficients $c_{12} = c_{21} = c$ it is well-known for the non-spatial deterministic version of the model (9), (10) that the population with the largest initial population displaces its competitor. Thus, it is plausible that the behaviour of the full stochastic spatio-temporal can be explained to a large extent by comparing at which speed front waves of each of the populations propagate into empty space. Because locally the competitor with the larger initial population wins we expect that the population with the ability to spread faster into a previously uninhabited domain will outcompete the other population. Of course, a rigorous investigation of this effect would require to quantitatively study front wave solutions of bistable systems under the influence of noise. A method for this has been developed by Khain et al. [12] but a more detailed study of the wave solutions is beyond the scope of this article.

In the light of these considerations the results from Section 3.1 shown in Figures 4-7 can be easily interpreted. In the absence of the competitor, resident and invader both reduce to the Fisher equation [9,14], albeit in the case of the resident with a spatially varying diffusion coefficient. For the Fisher equation it is known that both increasing the diffusivity or the noise intensity increase the front wave speed. Thus, we expect that the outcome of competition is determined by a combined effect of diffusivity and noise intensity which is indeed what Figures 4-7 show. It is an interesting additional feature of the results that the invader is in many situations unable to displace the resident completely from the whole spatial domain. Instead, the front wave of the invader stalls and a stationary solution resembling segregated habitats of resident and invader emerges. The inability of the invader to further propagate into the resident's domain is due to the heterogeneous stationary distribution of the resident which is typical for Fokker-Planck diffusion. In areas where the diffusion coefficients $D^*(x, y)$ are high, the density of the resident is low. Because the reaction terms of both competitors are identical, this low resident population provides an opportunity for the invader to take over these regions (see Figure 6). In contrast, just next to less densely inhabited rings the resident population reaches their maximum density (see Figure 1), so these parts of the spatial domain act as barriers for the invader. It follows that the result presented in Figure 6 strongly depends on the Fokker-Planck model, for Fickian diffusion the invader would go extinct. We remark that also for solutions resembling spatially segregated habitats, so-called "pinned competitive fronts", methods for more detailed analysis have been developed in the physics literature [30].

Because the stationary population density of the resident is low for high values of the spatially varying diffusion coefficients $D^*(x, y)$ and high for low values, we interpret the relative magnitude of $D^*(x, y)$ as the resident's propensity for avoiding particular parts of the spatial domain. The spatially heterogeneous stationary distribution of the resident can therefore be regarded as a habitat which is inhabited according to the resident's preference. Thus, Fokker-Planck diffusion naturally allows us to capture varying levels

of preference for different parts of the environment. This provides additional motivation for using Fokker-Planck diffusion as a standard model of dispersal alongside classical Fickian diffusion.

The emergence of a mixed front of resident and invader for increased noise intensity of the invader (Figures 8, 9) is an effect that is primarily due to the nonlinearity of the noise term. From the results presented in Figures 4-7 it is clear that for linear or approximately linear noise, the invader will eventually outcompete the resident when the noise level is increased beyond the intensity $\omega_2 = 4$ of Figure 7 (results not shown). By lowering γ_2 as in Figures 8, 9 we obtain high noise levels at low densities of the invader but due to saturation noise levels are much lower compared to linear noise at large population densities (see Figure 3). With very large noise levels for high population densities the invader would reach much higher maximum population numbers so that it could easily outcompete the resident. This effect is, however, balanced in the saturated noise model $g(\mathbf{X})$ for $\omega_2 = 4$ and $\gamma_2 = 1$ so that coexistence in a mixed habitat that eventually covers the whole spatial domain becomes possible. This result is particularly interesting because in the non-spatial model, coexistence would never be possible for the parameters considered here. At the same time, we demonstrated that this case depends little on the spatially varying diffusion coefficients $D^*(x, y)$ or the Fokker-Planck law of diffusion—for spatially homogeneous diffusion coefficients the solutions are qualitatively very similar except, of course, the spatial heterogeneity of the resident population (compare Figures 8 and 9).

In summary, we observe that with the nonlinear noise term (8) we obtain completely different predictions than with linear multiplicative noise, the standard model for environmental fluctuations. Because it is unclear if a strong underlying assumption of this model—that individuals respond to environmental fluctuations independently—is still fulfilled for large population densities, in our opinion this strongly indicates that it is important to extend the modelling approaches for environmental stochasticity beyond linear multiplicative noise.

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