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# Taxis-driven pattern formation in a predator-prey model with group defense

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## Abstract

We consider a reaction-diffusion(-taxis) predator-prey system with group defense in the prey. Taxis-driven instability can occur if the group defense influences the taxis rate (Wang et al., 2017). We elaborate that this mechanism is indeed possible but biologically unlikely to be responsible for pattern formation in such a system. Conversely, we show that patterns in excitable media such as **spatiotemporal** Sierpinski gasket patterns occur in the reaction-diffusion model as well as in the reaction-diffusion-taxis model. If group defense leads to a dome-shaped functional response, these patterns can have a rescue effect on the predator population in an invasion scenario. Preytaxis with prey repulsion at high prey densities can intensify this mechanism leading to taxis-induced persistence. In particular, taxis can increase parameter regimes of successful invasions and decrease minimum introduction areas necessary for a successful invasion. Last, we consider the mean period of the irregular oscillations. As a result of the underlying mechanism of the patterns, this period is two orders of magnitude smaller than the period in the nonspatial system. Counter-intuitively, faster-moving predators lead to lower oscillation periods and eventually to extinction of the predator population. The study does not only provide valuable insights on theoretical spatially explicit predator-prey models with group defense but also comparisons of ecological data with model simulations.

*Keywords:* predator invasion, group defense, reaction-diffusion, prey-taxis,

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1 **1. Introduction**

2 Systems of differential equations leading to oscillations are prevalent in  
 3 a whole variety of ecological models and mathematical biology in general  
 4 (Murray, 2002a). Relaxation oscillators are a particular type of oscilla-  
 5 tor that exhibit two different time scales. Many activator-inhibitor models  
 6 are of this type if the activator time-scale is much shorter (Meron, 2015).  
 7 Characteristic for such relaxation oscillators is the so-called excitement cy-  
 8 cle: resting  $\xrightarrow[\text{(slow)}]{\text{excitation}}$  excited  $\xrightarrow[\text{(fast)}]{\text{relaxation}}$  resting (Ermentrout and Rinzel, 1981).

9 With changes in parameters, this limit cycle can vanish via a homoclinic  
 10 bifurcation. The resulting system is then called excitable (Ermentrout and  
 11 Rinzel, 1981). Excitable means that perturbations above a threshold (super-  
 12 threshold perturbations) lead to an excitation cycle, i.e., a relatively long  
 13 excursion of the trajectory in the phase space. In contrast, a sub-threshold  
 14 perturbation leads to direct convergence to the linearly stable equilibrium  
 15 without such excitation behavior. Here, the excitation threshold is the sta-  
 16 ble manifold of the newly emerging saddle-node (Ermentrout and Rinzel,  
 17 1981; Kazantsev et al., 2003; Sevcikova and Marek, 1991).

18 Relaxation systems and systems with excitable kinetics are important for  
 19 biological systems because they can lead to the formation of spatiotempo-  
 20 ral patterns if the local kinetics are coupled with diffusive spread (Mendez  
 21 et al., 2010). The spatially explicit dynamical system is then referred to as  
 22 an excitable medium. It is well known that if the spatial domain is large  
 23 enough, many patterns can emerge from a limit cycle in a nonspatial system  
 24 also in systems without excitability (Conway et al., 1978). Examples for  
 25 this are chaos in the wake of invasion (Sherratt et al., 1995), spiral waves  
 26 (Keener and Tyson, 1986; Zaikin and Zhabotinsky, 1970), turbulence (Bär  
 27 and Eiswirth, 1993), and target patterns (Stich and Mikhailov, 2006; Tyson  
 28 and Fife, 1980). Experiments can reproduce such patterns (Irurzun et al.,  
 29 2004; Lee et al., 1994; Marino and Balle, 2005). The triangle-shaped so-called  
 30 Sierpinski gasket patterns give a particularly intriguing example (Hayase and  
 31 Ohta, 2000; Kazantsev et al., 2003). **Note that in this manuscript as  
 32 well as in the literature cited, Sierpinski gasket patterns refer to  
 33 a spatiotemporal phenomenon whereas the classical Sierpinski tri-  
 34 angle is a purely spatial pattern.** Even more intriguingly, these patterns

35 have indeed been observed in nature, for instance, on shell pigments (Lind-  
36 say, 1982; Meinhardt, 2009). They occur as a result of a combination of  
37 self-replicating pulses and different behavior occurring when pulses collide  
38 (Hayase, 1997). Self-replication denotes that a pulse splits into two pulses  
39 (Nishiura and Ueyama, 1999). If this pulse is traveling and the splitting pulse  
40 travels in the opposite direction, this phenomenon is denoted as backfiring  
41 (Mimura and Nagayama, 1997). Colliding pulses **are** only preserved under  
42 symmetric conditions (Hayase and Ohta, 2000). Such conditions are not  
43 possible with three existing pulses. In this case, annihilation occurs. Hence,  
44 every three pulse generations, the process repeats, and a pattern similar to  
45 Sierpinski gaskets emerges (Hayase and Ohta, 2000).

46 From an ecological perspective, it is essential to note that due to these  
47 patterns, the excitable nature of systems allows for persistent coexistence in  
48 spatially explicit systems that would otherwise not be possible. For instance,  
49 it can determine whether a biological invasion may be successful with poten-  
50 tially significant impacts on the whole ecosystem. Hence, it is essential to  
51 investigate such models in detail to understand diverse phenomena.

52 The dynamics in a classical pure reaction-diffusion system are well stud-  
53 ied. With a classical pure reaction-diffusion system, we refer to a system in  
54 which the matrix of diffusion coefficients is diagonal, and the diagonal entries  
55 are constants. Ecologically this means that only the gradient of a species de-  
56 termines the dispersal of the same species. This assumption is strong in  
57 ecological contexts, and relaxing this assumption can significantly alter the  
58 outcome of spatiotemporal models. Recently, Zemskov et al. (2017) showed  
59 that cross-diffusion in a Bonhoeffer-van der Pol model could lead to solitary  
60 pulses or wave trains. Solitary pulses correspond to single traveling pulses  
61 representing a homoclinic solution, whereas the term wave train describes a  
62 sequence of such pulses (Zemskov et al., 2017). Roussel and Wang (2004)  
63 have analyzed a Gray-Scott model with variable diffusion coefficients showing  
64 **that** the resulting inhomogeneity in diffusivities can suppress self-replicating  
65 behavior. Furthermore, including advection in a model with Dirichlet bound-  
66 ary conditions can lead to the existence of wave trains (Vidal-Henriquez et al.,  
67 2017). In ecological contexts, already Shigesada et al. (1979) examined that  
68 movement responses to environmental potentials allow for spatial coexistence  
69 of competing populations due to spatial segregation. More recently, Potts  
70 and Petrovskii (2017) reported that incorporating taxis can also determine  
71 invasion success in a competitive system. A more common example of an  
72 ecological justification for the occurrence of a non-diagonal diffusion matrix

73 is given by prey taxis, i.e., the dependence of predator movement on the  
74 prey density gradient. Brindley et al. (2005) summarized impacts of pursuit-  
75 evasion dynamics, i.e., prey avoiding predators and predators attracted by  
76 prey, on biological invasions. Bate and Hilker (2019) investigated the impact  
77 of prey taxis on the speed of traveling waves. Furthermore, Lee et al. (2009)  
78 examined the impact of taxis on pattern formation. In particular, prey at-  
79 traction tends to suppress Turing pattern formation. However, Wang et al.  
80 (2017) stated that prey repulsion can destabilize the spatial homogeneity of  
81 the system. A similar result was already obtained by Journé (1977) for a  
82 Lotka-Volterra system with cross-diffusion if the prey moves towards higher  
83 predator densities. Wang et al. (2017) justified prey repulsion by group de-  
84 fense in the prey. However, the theoretical justification lacks investigation  
85 of whether such a situation occurs in a reasonable range of parameters in  
86 an ecological system. Furthermore, in general, the impact of non-diagonal  
87 matrices of diffusion coefficients in ecological systems (cross-diffusion) is not  
88 well studied yet compared to the classic reaction-diffusion case.

89 Here, we will consider an excitable predator-prey system with group de-  
90 fense in the prey. Following Wang et al. (2017), we will first discuss taxis-  
91 driven Turing instability, and with that, we will show that this is indeed  
92 possible for certain parameter combinations for our model. However, we will  
93 conclude that these parameter combinations do not make sense for a group  
94 defense predator-prey system. In Section 3.2, we will confirm that excitation  
95 patterns can emerge in this system. We will discuss in more detail how the  
96 spatial system influences the local period of oscillations. This is important  
97 as the period is a characteristic feature of oscillating systems and thus plays  
98 a role in comparison with experiments. Then, we show an example of how  
99 taxis can increase the parameter regime and the range of initial conditions  
100 allowing for such patterns. Finally, we will discuss the results.

## 101 2. Model and methods

We consider a spatially explicit predator-prey model

$$\frac{\partial U}{\partial T} = F_U(U, V) + D_U \Delta U, \quad U(0, \vec{X}) = U_0(\vec{X}) \quad (1a)$$

$$\frac{\partial V}{\partial T} = F_V(U, V) + \nabla \cdot \sum_{i=1}^2 \mathbf{J}_i, \quad V(0, \vec{X}) = V_0(\vec{X}). \quad (1b)$$

102 Here,  $\vec{X}$  is the position vector and  $\Delta = \sum_{j=1}^n \frac{\partial^2 U}{\partial x_j^2}$  is the Laplace operator  
103 representing a randomly moving prey population.  $\nabla \mathbf{J}_i$  is the divergence of  
104 the flux. Throughout this study, we will distinguish two different cases. In  
105 the first case, we assume that  $i = 1$  and  $\mathbf{J}_1 = -D_V \nabla V$ , i.e., diffusive flux with  
106 a constant diffusion coefficient  $D_V$  modeling movement of the predator pop-  
107 ulation as well. In the second case, we consider  $i = 2$  with  $\mathbf{J}_2 = \tilde{\chi}_0 \tilde{\chi}(U) V \nabla U$   
108 additionally to the diffusive flux  $\mathbf{J}_1$ . This represents preytaxis with taxis rate  
109  $\tilde{\chi}_0 \tilde{\chi}(U)$ . Here, the predator movement is (partially) determined by the prey  
110 density gradient.

We assume a one-dimensional domain  $[0, L]$ , i.e.,  $j = 1$  throughout most of the study. Later on, we also use a square two-dimensional domain  $j = 2$  for one simulation to visualize the patterns. To prevent boundary effects, we assume periodic boundary conditions

$$U(0) = U(L), \quad U'(0) = U'(L), \quad (2a)$$

$$V(0) = V(L), \quad V'(0) = V'(L). \quad (2b)$$

As we consider a predator-prey model with group defense in the prey, we use the kinetic equations developed in Köhnke et al. (2020)

$$F_U(U, V) = U(r - cU) - V \frac{\beta \gamma U}{\gamma + \beta U + \gamma(U/C)^\nu} \quad (3a)$$

$$F_V(U, V) = eV \frac{\beta \gamma U}{\gamma + \beta U + \gamma(U/C)^\nu} - mV \quad (3b)$$

111 with  $\nu \geq 1$  and  $C < rc^{-1}$ . In a nutshell, the functional response has been  
112 derived by dividing the predator into handling and searching subpopulations  
113 of which only the searching subpopulation catches prey. These subpopula-  
114 tions are assumed to be in a quasi-steady state. The catch rate  $g(U)$ , in this  
115 case, is prey dependent and takes the form

$$g(U) = \frac{U}{1 + \left(\frac{U}{C}\right)^\nu}. \quad (4)$$

116 The prey grows logistically with growth rate  $r$  and intraspecific competition  
117 coefficient  $c$ . The predator dies linearly, with the mortality  $m$ . The rather  
118 complicated functional response represents group defense in the prey. In

119 particular,  $\beta$  is the search rate of the predator, and  $\gamma$  is the handling rate,  
 120 i.e., the handling time is  $H = \gamma^{-1}$ . The parameters  $C$  and  $\nu$  control the  
 121 collective defense.  $\nu$  controls the shape of the functional response. If  $\nu = 1$ ,  
 122 the functional response is saturating, whereas it is non-monotonic (or dome-  
 123 shaped) if  $\nu > 1$ . Higher values of  $\nu$  control how expressed the shape is. We  
 124 will refer to it as the strength of the collective defense.  $C$  can be referred  
 125 to as a critical defense value. It mainly affects the half-saturation density  
 126 in the prey in case of saturation and the critical prey density at which the  
 127 functional response has a maximum in case of a dome-shape. For a detailed  
 128 explanation regarding the functional response and also the analysis of the  
 129 nonspatial version of this model, we refer to Köhnke et al. (2020).

For convenience, the model can be nondimensionalized (see Appendix Ap-  
 pendix A for a description of all parameters and variables including their  
 dimensions). Scaling the state variables  $u = Ucr^{-1}$ ,  $v = V\beta r^{-1}$ ,  $x =$   
 $X(D_U r^{-1})^{-\frac{1}{2}}$ , and  $t = rT$ , and introducing new parameters  $\kappa = Cc(r)^{-1}$ ,  
 $\alpha = \beta r(\gamma c)^{-1}$ ,  $\mu = mr^{-1}$   $d = D_V D_U^{-1}$ ,  $\chi_0 = r\tilde{\chi}_0(cD_U)^{-1}$  and  $\epsilon = e\beta c^{-1}$   
 yields

$$\frac{\partial u}{\partial t} = u \left( 1 - u - \frac{v}{1 + \alpha u + (u\kappa^{-1})^\nu} \right) + \Delta u, u(0, x) = u_0(x), \quad (5a)$$

$$\frac{\partial v}{\partial t} = v \left( \frac{\epsilon u}{1 + \alpha u + (u\kappa^{-1})^\nu} - \mu \right) + d\Delta v - \nabla \cdot (\chi_0 \chi(u) v \nabla u), v(0, x) = v_0(x). \quad (5b)$$

130 Throughout this study, only the defense parameters  $\kappa$  and  $\nu$  as well as the  
 131 ratio of diffusion coefficients  $d$  and the taxis rate  $\chi_0 \chi(u)$  have been varied.  
 132 Table 1 lists the remaining parameters. They are based on a microtine rodent  
 mustelid model from Hanski and Korpimäki (1995).

Table 1: The rescaled dimensionless parameters are shown with their value used throughout this study.

Parameter	Value
$\alpha$	14.81
$\epsilon$	5.06
$\mu$	$2.47 \cdot 10^{-1}$



134 For the numerical treatment, we used a Strang splitting scheme as de-  
 135 scribed in Bate and Hilker (2019) with a forward-time central-space scheme  
 136 for the diffusion term, a fourth-order Runge-Kutta scheme for the reaction  
 137 term, and an upwind method as described in Saito (2007) for the taxis term.

As initial conditions, we assume an invasion scenario. In particular, the predator invades a prey population. For the one-dimensional domain, the initial conditions are

$$v_0(x) = (\tanh(x - 50) - \tanh(x - 150)) \frac{\tilde{v}(\kappa)}{2} \quad (6a)$$

$$u_0(x) = 1 - (\tanh(x - 50) - \tanh(x - 150)) \frac{1 - \tilde{u}(\kappa)}{2}. \quad (6b)$$

138 This is a continuous approximation of an invasion scenario in which the  
 139 predator is introduced in the subinterval of the domain  $x \in [50, 150]$  with  
 140 density  $\tilde{v}(\kappa)$ , whereas the prey is at its carrying capacity in the rest of the  
 141 domain. The values  $\tilde{u}(\kappa) > 0$  and  $\tilde{v}(\kappa) > 0$  are chosen such that they lie  
 142 above the stable manifold of the nontrivial saddle point, see Figure 6 and  
 143 corresponding text for further details.

### 144 3. Results

#### 145 3.1. Taxis-driven instability

We start by considering Turing instabilities. In particular, we consider small heterogeneous perturbations  $\delta_u(x, t)$  and  $\delta_v(x, t)$  around the stationary coexistence state

$$u(x, t) = u_s + \delta_u(x, t), \quad v(x, t) = v_s + \delta_v(x, t), \quad (7a)$$

$$\delta_u(x, t) = a_1 e^{\sigma t} \cos qx, \quad \delta_v(x, t) = a_2 e^{\sigma t} \cos qx, \quad (7b)$$

146 see for instance Edelstein-Keshet (2005); Malchow et al. (2007). It is well  
 147 known that independent of the form of the functional response developed  
 148 above, diffusive instability leading to Turing patterns can never be possible as  
 149  $Tr(J) < 0$  and  $a_{11}D_2 + a_{22}D_1 > 0$  is not possible if  $a_{22} = 0$  (Edelstein-Keshet,  
 150 2005; Fasani and Rinaldi, 2011). Note that pure prey-taxis does also not  
 151 have a destabilizing effect on a locally stable steady state (Lee et al., 2009).  
 152 However, Wang et al. (2017) have shown that it may indeed be destabilizing

153 if the taxis-rate  $\chi = \chi(u)$  is not constant. In this case, neglecting nonlinear  
 154 perturbation terms, we get

$$\begin{pmatrix} \delta_u(x, t)_t \\ \delta_v(x, t)_t \end{pmatrix} = \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix} \begin{pmatrix} \delta_u(x, t) \\ \delta_v(x, t) \end{pmatrix} + \begin{pmatrix} 1 & 0 \\ -\chi_0\chi(u_s) & d \end{pmatrix} \begin{pmatrix} \delta_u(x, t)_{xx} \\ \delta_v(x, t)_{xx} \end{pmatrix} \quad (8)$$

155 for the temporal evolution of the perturbations. Here  $m_{ij}$  represents the  
 156 entries of the Jacobian of the nonspatial version of Equation (5) evaluated  
 157 at the stationary solution  $(u_s, v_s)$ . Note that we assume, that  $\chi(u)$  depends  
 158 linearly on  $u$  and that we can thus neglect  $\chi(\delta_u(x, t))\delta_v(x, t)_{xx}$ . Inserting  
 159 the perturbations, and neglecting the trivial case of  $a_1 = a_2 = 0$  we get the  
 160 characteristic equation

$$\sigma^2 - \psi_1\sigma + \psi_2 = 0 \quad (9)$$

with

$$\psi_1 = (m_{11} + m_{22} - (1 + d)k), \quad (10a)$$

$$\psi_2 = H(q^2) = dk^2 - k(m_{22} + dm_{11} + m_{12}v_s\chi_0\chi(u_s)) + m_{11}m_{22} - m_{12}m_{21}, \quad (10b)$$

161 where  $k = q^2$ . Equation (10a) is always negative in the spatial case if it  
 162 is negative in the nonspatial case. Furthermore, as already stated in Wang  
 163 et al. (2017), if  $\chi_0\chi(u) > 0 \forall u$ , taxis-driven instability is not possible as  
 164  $m_{12} < 0$ . However, taxis-driven instability can be possible if  $\chi(u_s) < 0$ . A  
 165 justification for  $\chi(u_s) < 0$  is group defense (Wang et al., 2017). In particular,  
 166 the predator avoids areas in which the prey populations are at defending  
 167 densities. Regarding the taxis rate, this means  $\chi(u) > 0 \forall u < u_c$  and  
 168  $\chi(u) < 0 \forall u > u_c$ . A simple representation may be a linearly decreasing  
 169 taxis rate

$$\chi(u) = 1 - \frac{u}{u_c}. \quad (11)$$

170 The **right** panel of Figure 1 shows a particular example of the emergence  
 171 of spatiotemporal patterns due to preytaxis for such a given prey-dependent  
 172 taxis rate. The **left** panel shows different combinations of  $\kappa$  and  $\chi_0$ . It  
 173 visualizes that low values of  $u_c$  and high values of  $\chi_0$  are necessary for taxis-  
 174 driven instability. The colored region in Figure 2 shows the maximum value  
 175 of  $u_c$  that can lead to taxis-driven instabilities — i.e., where negative values  
 176 of Equation (10b) are possible — for different combinations of  $\nu$  and  $\kappa$ .

177 However, in the following, we elaborate on why a taxis-driven instabil-  
 178 ity is possible but not biologically meaningful in a collective defense model,

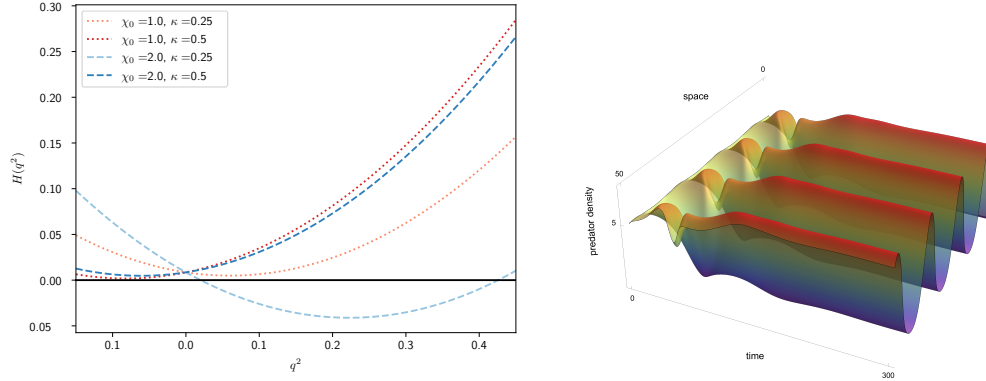


Figure 1: **Taxis-driven instability can occur if group defense leads to predator repulsion.** The **right** panel shows the emergence of taxis-driven instability for Equation (5) with parameters as stated in Table 1 and  $\chi_0 = 2$ . Note that only a part of the domain is shown for visualization. The taxis rate is assumed to be  $\chi(u) = 1 - uu_c^{-1}$  with  $u_c = \kappa = 0.25$ . The **left** panel shows  $H(q^2)$  as given by Equation (10b) for different values of  $u_c$  and  $\chi_0$ .

179 as presented in this study. Recall that taxis-driven instability destabilizes  
 180 a nonspatially stable stationary coexistence state. Such instability can only  
 181 occur if  $\chi(u_s) < 0$  (necessary). However, for an individual predator, repul-  
 182 sion from a high prey density does only make sense if  $g'(u) < 0 \forall u > u_c$ ,  
 183 i.e., if the catch rate is decreasing with higher prey densities. A necessary  
 184 condition for the stability of the stationary coexistence state, however, is  
 185  $g'(u_s) > 0$  corresponding to a positive determinant of the coexistence state  
 186 (Köhnke et al., 2020). Hence, taxis-driven instability requiring  $\chi(u_s) < 0$  is  
 187 ecologically only meaningful for parameter combinations in which it is likely  
 188 that  $\chi(u_s) \geq 0$ , which is a contradiction.

### 189 3.2. Patterns in excitable media

190 Apart from taxis-driven patterns, oscillatory patterns can arise due to  
 191 the Hopf instability (Bär, 2019). In this section, we aim to investigate the  
 192 potential impact of taxis on the occurrence of such patterns. Figure 2 shows  
 193 in which parameter region of  $\nu$  and  $\kappa$  representing the strength of group  
 194 defense and its critical values, such patterns can occur. In the colored re-  
 195 gion, taxis-induced patterns can emerge as described in Section 3.1. In the  
 196 nonspatial case, this region corresponds to stable stationary coexistence be-

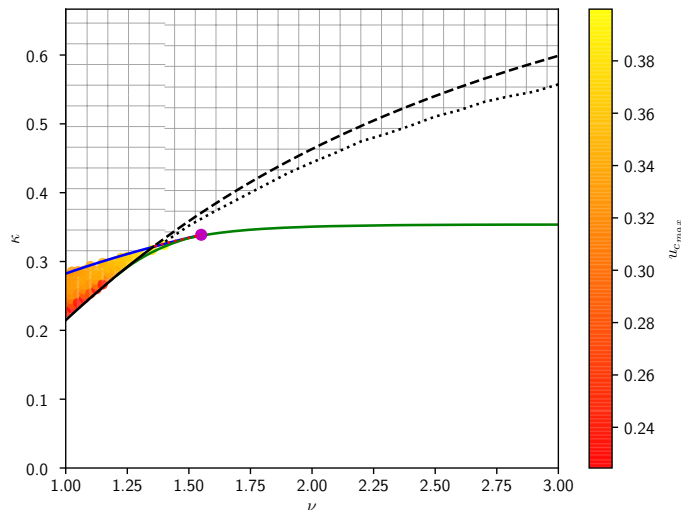


Figure 2: **Diffusion-induced oscillatory patterns can rescue the predator from extinction.** A two-dimensional bifurcation diagram of the critical defense value  $\kappa$  and the strength of the group defense  $\nu$  is shown. The green line, blue, and solid black lines depict saddle-node, Hopf, and transcritical bifurcations, respectively. The black dashed line corresponds to a transcritical bifurcation and a homoclinic bifurcation, which co-occur. Below this curve, the predator goes extinct in the nonspatial case. In the spatial system, the predator persists in parameter regions until the dotted line (the hatched region) for some initial conditions. The color represents the maximum critical value  $u_c$  in Equation (11) that allows for taxis-induced pattern formation. The magenta dot represents a Bogdanov-Takens bifurcation point. Parameters are  $d = 1$ ,  $\chi_0 = 0$  except for the case of taxis-induced instability (colored region). Here,  $d = 1$  and  $\chi_0 = 2$ . The remaining parameters are as stated in Table 1. We used XPPAUT (Ermentrout, 2002) for the computation of the nonspatial bifurcation curves and performed numerical simulations to calculate the colored regions and the dotted line.

197 tween predator and prey. Above this line and above the dashed black line, a  
 198 limit cycle exists. This limit cycle vanishes due to a homoclinic bifurcation  
 199 that co-occurs with a transcritical bifurcation. In the spatial system, the  
 200 limit cycle turns into spatiotemporal patterns that persist until the dotted  
 201 line in the whole hatched region. Hence, the diffusion (without taxis, i.e.,  
 202  $\chi_0 = 0$ ) rescues the predator from extinction in the parameter regime be-  
 203 tween the dotted and the dashed lines. Note that on the left-hand side of

204 the Bogdanov-Takens bifurcation point, bistability between the limit cycle  
205 and the prey-only state and between the stationary coexistence state and  
206 the prey-only state can emerge. However, this corresponds to a very limited  
207 region for this parameter set and is thus not further considered here. The in-  
208 terested reader is referred to Köhnke et al. (2020). Here, we want to focus on  
209 the emergence of the spatiotemporal patterns. In particular, Figure 2 shows  
210 that the emergence of patterns critically depends on the critical defense value  
211  $\kappa$ . In the following, we will recall mechanisms of diffusion induced patterns  
212 in relaxation and excitable systems.

213 We start considering the emerging patterns for the case of a stable limit  
214 cycle. Figure 3 shows the spatiotemporal dynamics of Equation (5) without  
215 preytaxis. The predator population starts at a high density in the middle of  
216 the domain, whereas the prey is abundant all over the domain. The predator  
217 invasion takes place in the form of various traveling pulses leading to an  
218 intriguing triangle invasion shape. Such a triangle shape is often referred  
219 to as a Sierpinski gasket pattern (Hayase and Ohta, 2000; Kazantsev et al.,  
220 2003). It occurs due to self-replicating pulses and exists in diverse excitable  
221 systems (Hayase and Ohta, 2000). In particular, it emerges as preservation  
222 occurs for completely symmetric pulse collisions only, whereas non-symmetric  
223 pulse collisions lead to annihilation (Hayase and Ohta, 2000). However, note  
224 that such a triangle pattern can also be explained only focussing on the  
225 excitability of the system.

226 The slow-fast dynamics of the relaxation system govern the system dy-  
227 namics. Here, the local dynamics between the carrying capacity and ap-  
228 proximately the maximum of the limit cycle with respect to the predator  
229 correspond to the exciting (slow) process. In contrast, the local dynamics  
230 between the maximum and the origin correspond to the relaxation (fast)  
231 process in the relaxation system. Figure 4 shows the phase plane, including  
232 a vector field, and the limit cycle (black dashed lines) in panel a) for the  
233 nonspatial model. The magenta regions denote regions in the phase plane in  
234 which the trajectory of a point in space stays for relatively long times. In  
235 particular, the spatial trajectory roughly follows the limit cycle with a ten-  
236 dency to lower predator values due to the diffusive losses. The values were  
237 obtained numerically via a simulation of the one-dimensional system. They  
238 correspond to a particular point in space.

239 In the spatially explicit system, the diffusion acts as a perturbation from  
240 neighboring regions in space. This diffusive force is large compared to the low  
241 magnitude of the local rate of change close to the carrying capacity. Heuris-

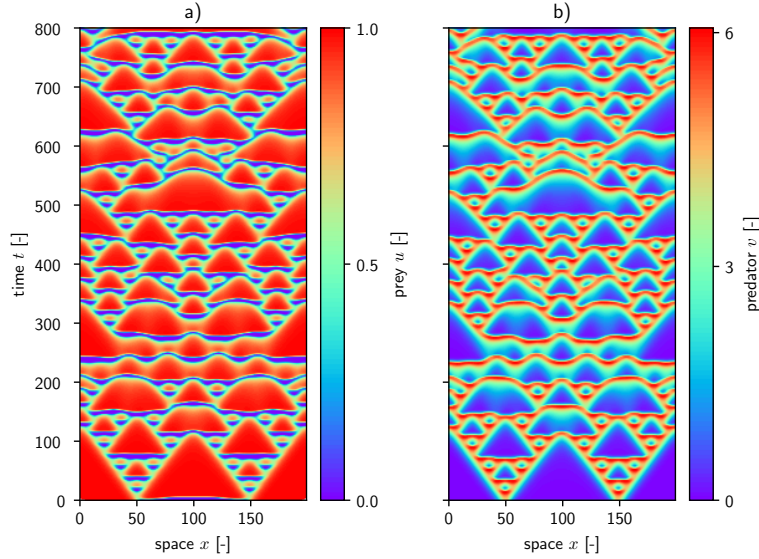


Figure 3: **Diffusion can lead to intriguing excitability patterns such as Sierpinski gasket patterns.** The spatiotemporal dynamics of Equation (5) with  $j = 1$  is shown. The defense parameters are  $\nu = 3$  and  $\kappa = 0.67$ . The diffusivities of the populations are equal, i.e.,  $d = 1$ , while we do not consider preytaxis, i.e.,  $\chi_0 = 0$ . The remaining parameters are as stated in Table 1.

242 tically speaking, the diffusive force of patches with initially high predator  
 243 densities pushes the adjacent patches without predator to higher densities.  
 244 Concurrently, the predator density of the patches with initially high predator  
 245 densities shrinks due to the local dynamics and the diffusive losses. As this  
 246 process repeats itself, it leads to propagating pulses in both directions, and a  
 247 triangle shape emerges. If such pulses meet, the neighboring area is already  
 248 excited, and hence, the pulse cannot propagate any further (Meinhardt and  
 249 Klingler, 1987). The larger triangles emerge if neighboring areas in the ex-  
 250 cited state become larger due to several pulses meeting at the same time. In  
 251 this case, the excitation wave can only propagate outwards. This excitation  
 252 wave represents the initial wave (Meinhardt and Klingler, 1987). Note that  
 253 the local dynamics must be slow enough to observe a rather distinct triangle  
 254 pattern.

255 In our case, the Sierpinski gasket pattern is distorted due to two different  
 256 reasons. First, the initially large predator patch leads to two initial pulses

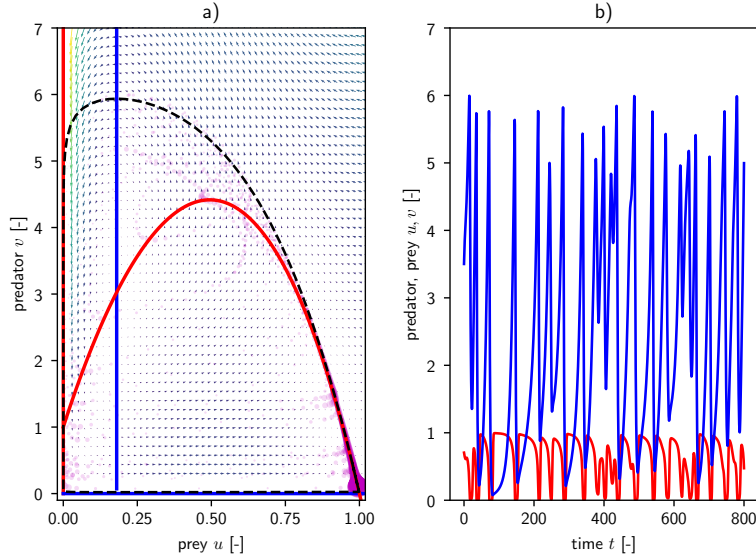


Figure 4: **Phase plane analysis, including spatial trajectories indicates that the slow-fast dynamics of the system drive the emerging patterns.** In both panels, red lines correspond to the prey, whereas blue lines correspond to the predator (nullclines in panel a) and solutions at one spatial point in b)). Panel a) shows a phase portrait with a vector field for the nonspatial model. The dashed line shows the limit cycle. Magenta regions correspond to regions in which the spatial system at one particular point in space stays for relatively long times. Panel b) shows the time series corresponding to the magenta regions. The magenta regions and the time series were calculated for a particular point in space. The parameters are as stated in Figure 3.

257 at the border of the initially occupied patches. When the invasion waves  
 258 resulting from these separate pulses meet, the clear Sierpinski gasket pattern  
 259 gets destroyed. Second, the large triangles with very low predator densities  
 260 get blurry probably as a result of the local dynamics which are not negligibly  
 261 small on this time scale anymore. As a result of these perturbations, locally,  
 262 these oscillations appear irregular, as shown in panel b) of Figure 4.

263 Figure 5 shows an example of these spatiotemporal patterns for a param-  
 264 eter combination that leads to extinction of the predator in the nonspatial  
 265 model in two dimensions. In this case, the relaxation system has become  
 266 excitable as the stable limit cycle has been destroyed via a homoclinic bi-  
 267 furcation. The predator spreads via pulsating circles visible at  $t = 250$  and  
 268  $t = 500$ . This propagation directly translates to a spatiotemporal pattern

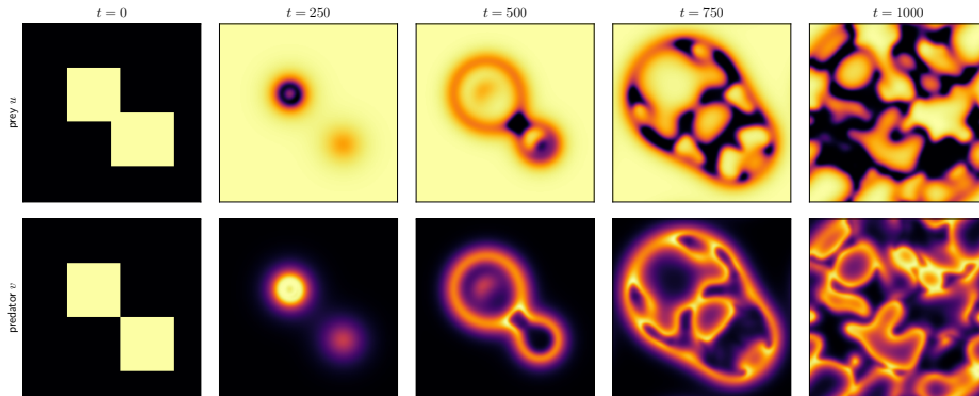


Figure 5: **Nonsymmetrical initial conditions can lead to irregular spatiotemporal patterns.** The spatial configuration for prey (upper row) and predator (lower row) is shown. Lighter colors correspond to higher densities. Parameters are such that the carrying capacity is the only stable stationary solution in the nonspatial model. In particular,  $d = 1$ ,  $\kappa = 0.57$ ,  $\chi_0 = 0$ , and  $\nu = 3$ . The remaining parameters are as stated in Table 1.

269 similar to the one in Figure 3, although it is less regular due to the different  
 270 initial conditions. Conversely to the classical excitation pulse (Müller, 2019),  
 271 the propagation of the excitation happens not only in one direction, but the  
 272 area behind the excited state becomes excitable quickly again. This so-called  
 273 wave splitting occurs if the diffusion is sufficiently strong to excite the wake  
 274 of the wave (Petrov et al., 1994). Experiments have reproduced such a phe-  
 275 nomenon (Manz and Steinbock, 2006). In the present system, it is primarily  
 276 due to the fast dynamics behind the upper cluster in Figure 4. In the final  
 277 configuration, it is apparent that the prey is abundant at high densities over  
 278 parts of the domain, whereas the predator is mainly abundant at distinct  
 279 lines. Furthermore, some parts exist in which neither prey nor predator is  
 280 abundant. This is consistent with the magenta regions in Figure 4. The sys-  
 281 tem stays in the neighborhood of the two (semi-)trivial equilibria due to the  
 282 slow local dynamics, but also at coexistence regions close to the maximum  
 283 of the nontrivial prey nullcline.

284 It is known that traveling pulses in excitable systems exhibit a strong  
 285 dependence on initial conditions (Murray, 2002b). In particular, the stable  
 286 manifold of the saddle gives the excitation threshold (Ermentrout and Rinzel,  
 287 1981; Kazantsev et al., 2003; Sevcikova and Marek, 1991). The right panel of  
 288 Figure 6 shows the dependence of pattern formation on the initial conditions



289 in the present system. This dependence is particularly relevant in an invasion  
 290 scenario. The initial conditions need to start above the stable manifold.

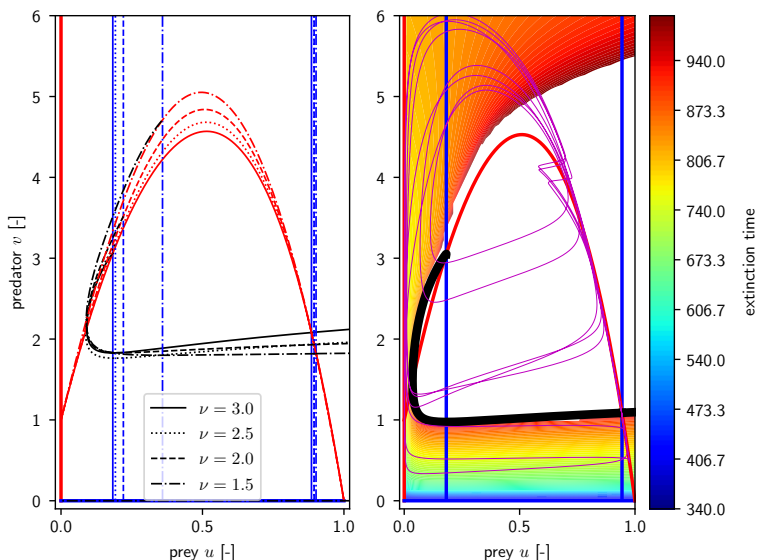


Figure 6: **The dependence of the rescue effect on the stable manifold leads to a strong dependence on initial conditions for invasion scenarios.** The left panel shows phase portraits for different values of  $\nu$ . In particular, it is shown how the nontrivial nullclines and the stable manifold of the saddle (right coexistence solution) change with respect to  $\nu$ . The extinction time, i.e., the time until the carrying capacity is reached, is color-coded. In the white area, the predator does not go extinct in the spatiotemporal model. The magenta line shows a trajectory at one particular point in space. Colors are as in Figure 4. The parameters are as in Figure 5.

290

291 Starting above the stable manifold allows the system to converge to the  
 292 capacity via the unstable manifold of the saddle which has a form similar to  
 293 the limit cycle. Hence, the system passes through high predator densities,  
 294 and the mechanism takes place as described before. Thus, in an invasion  
 295 scenario, the predator needs to be introduced at sufficiently high densities to  
 296 ensure its survival.

297 However, this is necessary but not sufficient because if the initial predator  
 298 population densities are too high, the predator goes extinct. Starting at very  
 299 high predator densities, the local dynamics becomes too fast (cf. vector field  
 300 in Figure 4), and the system would converge to the prey **carrying** capacity

301 (and thus below the excitation threshold) too quickly.

302 Keeping in mind that the stable manifold is a separatrix, we look at the  
303 phase space configuration for the lowest value of  $\kappa$  for which patterns emerge  
304 for a given  $\nu$  (cf. dotted line in Figure 2). The left panel of Figure 6 visualizes  
305 the results. This value seems to be predominantly driven by the right preda-  
306 tor nullcline, as this is the same (accounting for numerical uncertainties) for  
307 all values of  $\nu$ . If the right nullcline is shifted further to the left with lower  
308 values of  $C$ , numerical simulations indicate that the threshold is too high for  
309 excitability via the diffusive force. In other words, the diffusion cannot push  
310 the spatial areas that are close to the carrying capacity in the phase portrait  
311 over the stable manifold of the saddle-node. Note that this does not depend  
312 on the magnitude of the diffusion coefficient but on the predator density in  
313 the wake of the invasion wave and the spatial extent of the wake. If the  
314 spatial extent and/or the density is too small/low, the predator goes extinct  
315 before it can excite the neighboring areas. Numerical simulations with other  
316 parameter combinations, in particular different diffusion coefficients, suggest  
317 that this is indeed the underlying mechanism.

318 It is known, that the spatiotemporal dynamics in excitable systems can  
319 lead to spatially triangular, but temporally irregular patterns (Kazantsev  
320 et al., 2003). Although it is also known that the local oscillation period is  
321 shorter in a perturbed excitable system, the exact impact is not well inves-  
322 tigated (Crucifix, 2012). **In the nonspatial system, the period of the  
323 limit cycle diverges approaching the homoclinic bifurcation (see  
324 red line in Figure 7).** In the spatial system the mean period also increases  
325 with decreasing  $\kappa$ , cf. blue dots in the left panel of Figure 7. We calculated  
326 the mean period as the mean of periods over all spatial grid cells. In turn,  
327 we calculated the mean of each spatial grid cell as the mean periods over  
328 a time interval  $t \in [1000, 10000]$  to neglect transient behavior. The spatial  
329 period is two orders of magnitude smaller than in the nonspatial case. For  
330 comparisons of model simulations with ecological time series, the period is an  
331 important indicator. As ecological systems are naturally spatially explicit,  
332 it is essential to know that diffusion in relaxation systems can reduce the  
333 period significantly. The reason is that the diffusion shortens the excitation  
334 time, which is mainly contributing the most to the length of the period. Fur-  
335 thermore, interestingly, the period has a local maximum at the homoclinic  
336 bifurcation ( $\kappa \gtrsim 0.6$ ) as the dynamics shortly before the homoclinic orbit  
337 becomes very slow. However, this effect is not very prominent.

338 As the mechanism given suggests that the period is short, particularly

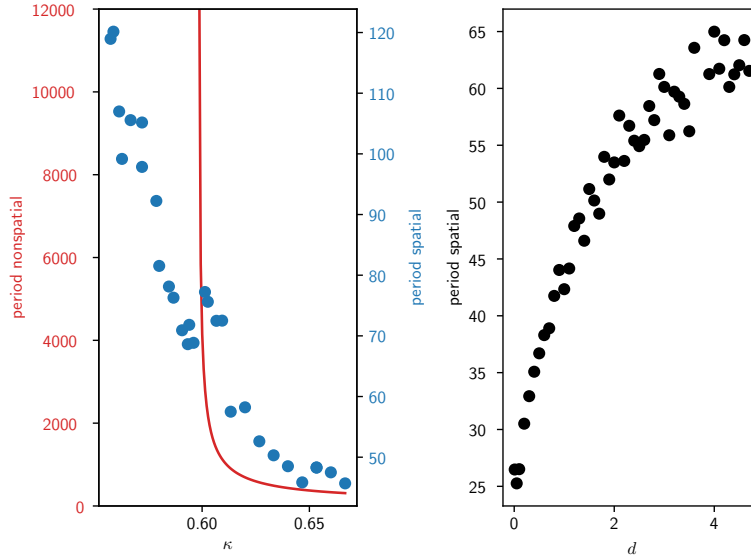


Figure 7: **Diffusion shortens the oscillation period by two orders of magnitude.** The period of the oscillations is shown for the nonspatial model (red) and the spatial model (blue). In the nonspatial model, the period diverges when it approaches the homoclinic bifurcation. Conversely, the period increases beyond this bifurcation point in the spatial model. The right panel shows that this is rather independent of the value of  $d$  as the order of magnitude is the same. However, the ratio of diffusivities also influences the period (see text for further details). Parameters are as in Figure 5 for the spatial model and as in Figure 4 in the nonspatial model. For the right panel,  $\kappa = 0.59$  is assumed.

339 due to the movement of the predator populations, we also show the impact  
 340 of different ratios of predator/prey diffusivities. In the right panel of Fig-  
 341 ure 7, it is shown that the period increases with higher values of  $d$ . This  
 342 is counter-intuitive at first glance as one could assume that higher predator  
 343 dispersal enhances the rescuing effect and decreases the period. However,  
 344 as already mentioned, the rescue effect depends strongly on the extent of  
 345 the predator patches. With higher diffusivity, approximately the same popu-  
 346 lation spreads over a larger area. Hence, for an individual cell, the rescue  
 347 effect is smaller, and the period becomes longer. As the patch sizes with high  
 348 predator densities do not change with respect to  $d$ , this effect is saturating.  
 349 If  $d$  becomes larger, the rescue effect becomes even impossible.

350 Ecologically, this is counter-intuitive as higher movement abilities are

351 usually assumed to correspond to higher invasion abilities. Hence, we showed  
 352 that for relaxation systems, this could indeed be the other way round.

### 353 3.3. Preytaxis in excitable media

354 Recall that the lowest  $\kappa$  allowing for spatiotemporal patterns is deter-  
 355 mined by the stable manifold of the saddle-node. With this, we can now  
 356 investigate the impact of taxis. In particular, we consider two different cases  
 apart from the diffusion-only case, which are sketched in Figure 8.

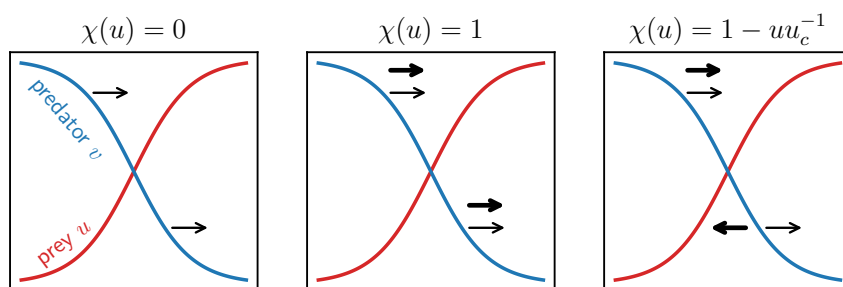


Figure 8: **The influence of taxis depends on the form of the taxis rate.** The sketch of the impact of three different forms of the taxis rate  $\chi(u)$  are shown. The left panel shows the case with only diffusive flux denoted by thin arrows. The middle panel shows a case with preytaxis and diffusion and the right panel shows a case with Equation (11) as taxis rate and diffusion.

357 The left panel shows a pure diffusion case with  $\chi_0 = 0$ . The thin ar-  
 358 rows denote the direction of the diffusive flux down the predator gradient.  
 359 Considering preytaxis, in a typical situation, this flux is even enhanced, see  
 360 the middle patch of Figure 8. The diffusive flux denoted by the thin arrows  
 361 stays as before, but the tactic flux indicated by the thick arrows enhances the  
 362 overall flux. A typical situation means that the sign of the gradient of the  
 363 predator density is opposite to the sign of the gradient of the prey density.  
 364 If pure diffusion does not allow for pattern formation, the additional tactic  
 365 flux does not change that. The reason is that the predator density in the  
 366 wake will spread over a larger area, making it impossible to push neighboring  
 367 spatial areas over the excitation threshold. The right panel refers to a tac-  
 368 tic flux representing predator movement response to group defense. At low  
 369 prey densities, the predator moves up the prey density gradient. However,  
 370 at high prey densities, the predator tries to avoid the prey and moves down  
 371 the prey gradient. Here, taxis-driven pattern formation can occur. Figure 9  
 372

373 shows such a situation in which, in **the** absence of taxis, the predator would  
 374 go extinct. The magenta regions denote regions in which the prey is below

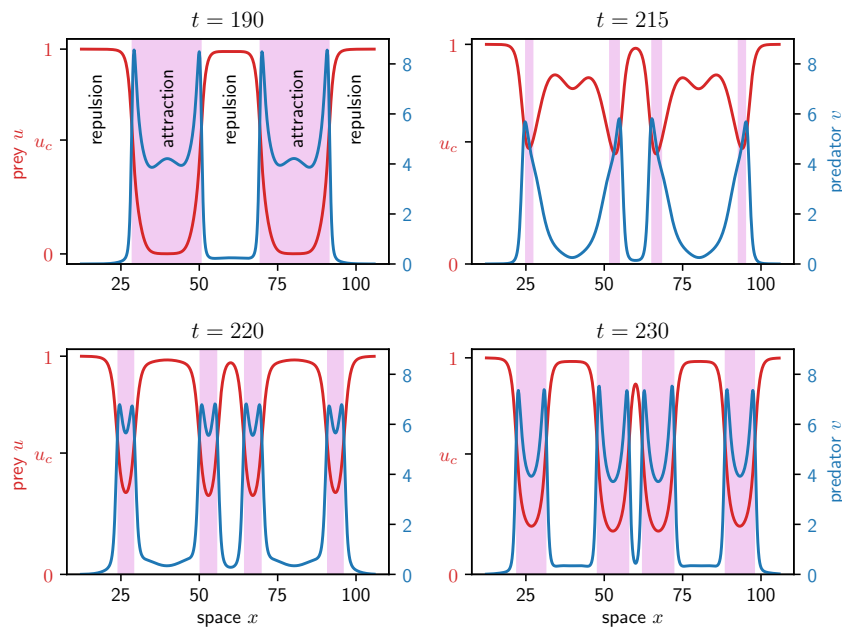


Figure 9: **Taxis can lead to a successful predator invasion.** Snapshots at different time steps for the same spatial region are shown. The taxis rate is given by Equation (11) with  $\chi_0 = 7$ ,  $u_c = \kappa$ , and  $d = 0.4$ . The remaining parameters are as in Figure 5.

374  
 375 the critical density and thus, the predator would move the prey gradient up-  
 376 wards. The prey repulsion happens mainly in regions in which the predator  
 377 is only at low densities. This increases the predator density at the peak of  
 378 the leading edge, cf. upper left panel. Due to that, the predator is still at  
 379 high densities when the prey converges to its carrying capacity in the neigh-  
 380 boring areas again, cf. upper right panel. From this state, the predator can  
 381 perturb the adjacent regions to excite the system again, cf. lower left panel.  
 382 From here, the excitation cycle can start again, cf. lower right panel. With-  
 383 out taxis, the predator would have spread faster to the regions of high prey  
 384 densities in the upper panels. Due to that, the predator densities would have  
 385 been too low to excite the adjacent regions again.

386 This taxis-driven pattern formation can have two different effects. First,  
 387 it can increase the values of  $\kappa$  allowing for pattern formation. However,

388 this depends on the magnitude of the taxis and the critical value  $u_c$ . In  
 389 particular, if the value is too high, the effect would be too low. Conversely,  
 390 if the value is too low, the predator would just tend to aggregate. Second, it  
 391 allows for smaller initial predator patches that lead to a successful invasion  
 visualized by Figure 10. In particular, with a high taxis rate, the minimum

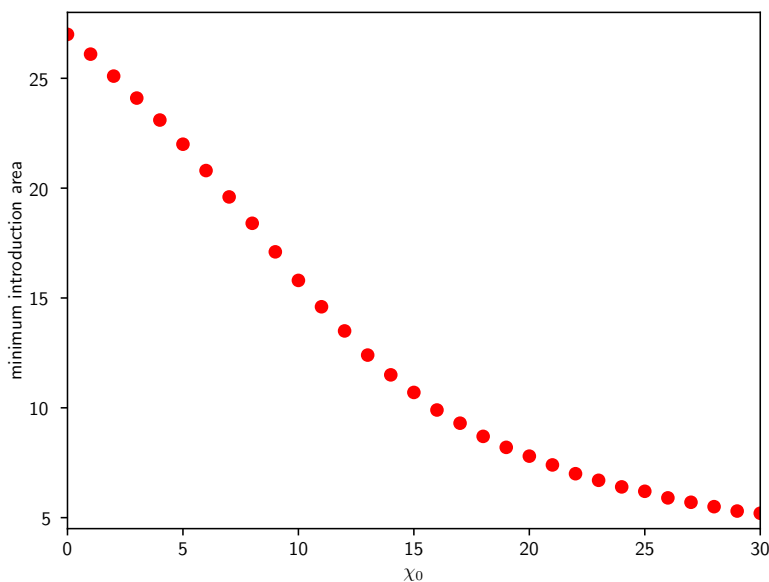


Figure 10: **Critical introduction areas necessary for successful spread can become smaller with higher taxis rates.** The initially occupied area necessary for a successful predator establishment is shown depending on the magnitude of the taxis. Taxis rate is given by Equation (11) with varying  $\chi_0$ ,  $u_c = \kappa$ , and  $d = 0.4$ . The remaining parameters are as in Figure 5.

392 introduction area necessary for a successful invasion is more than five times  
 393 lower. The reason for this relation is also the 'effective use' of the predator  
 394 peaks, as described above. However, the impact seems to be saturating with  
 395 high taxis rates. This may be due to **the fact** that with high  $\chi_0$ , the prey  
 396 attraction coupled with the diffusive motion is already too high even though  
 397 they only occur at densities below  $u_c$ . Due to this, specific neighboring  
 398 areas cannot become excited, and the predator goes extinct quickly. On  
 399 the other hand, the saturating effect can also simply be reducible to the  
 400

401 fact that negative areas are not possible. Hence, the minimum introduction  
402 areas must converge to values greater than or equal to zero for high taxis  
403 rates. Independent of the exact mechanism, this is an important finding from  
404 an invasion perspective because particularly the initial phases introduction,  
405 reproduction, and survival are critical states in determining invasion success  
406 (Blackburn et al., 2011).

#### 407 4. Discussion and Conclusion

408 In this study, we extended the predator-prey model incorporating group  
409 defense proposed in Köhnke et al. (2020) by spatial spread. Wang et al.  
410 (2017) have shown that taxis-driven instability can occur in such a system  
411 if group defense is present. Although we find the same conditions for taxis-  
412 driven instability and provide numerical examples for it, we challenge the hy-  
413 pothesis that such patterns can occur in group defense predator-prey models.  
414 In particular, we have shown that for the model considered in this study, such  
415 a phenomenon can only occur if the predator movement is not ecologically  
416 optimal.

417 In contrast, we have shown that excitability patterns may indeed emerge  
418 if the homogeneous system has a limit cycle. As the amplitude of the limit  
419 cycle can be very high corresponding to temporary low population densi-  
420 ties, such spatial patterns can be interpreted as a rescue effect (Brown and  
421 Kodric-Brown, 1977) as they may increase the resilience of the system against  
422 environmental perturbations. However, note that spatially synchronized ex-  
423 ternal forcings, such as the weather, can synchronize the oscillations again if  
424 they are large enough (Liebhold et al., 2004). Furthermore, it is well known  
425 that coupled oscillators in experiments can synchronize their phase, a phe-  
426 nomenon known as phase locking (Marek and Stuchl, 1975; Murray, 2002a).

427 The spatiotemporal patterns also sustain beyond the homoclinic bifurca-  
428 tion that is destroying the limit cycle in the nonspatial system. This phe-  
429 nomenon is well known for relaxation oscillators that become excitable media  
430 after the vanishing of the limit cycle. We have proposed evidence showing  
431 that the underlying mechanism for the patterns is indeed given by the diffu-  
432 sive force coupled with the slow and fast dynamics in the nonspatial system  
433 (Müller, 2019). In this case, the limit cycle vanishes via a homoclinic bi-  
434 furcation. With bifurcation analysis, we have shown that this effect only  
435 occurs for  $\nu > 1$  corresponding to a dome-shaped functional response. This  
436 is a phenomenon that is not possible in the system with a simple saturating

437 functional response as it relies on the existence of two nontrivial stationary  
438 solutions. Hence, this can be interpreted as a defense-induced phenomenon.  
439 However, note that also a saturating functional response can represent group  
440 defense if a critical prey density does not exist, see Köhnke et al. (2020) for  
441 further details.

442 Furthermore, we refer to the spatiotemporal patterns as invasion pat-  
443 terns as they strongly depend on initial conditions that may correspond to  
444 an invasion scenario. This is also a known feature of such excitable systems  
445 (Murray, 2002b). In our case, the predator as the invader needs to be absent  
446 in some regions but present in the other regions at sufficiently high densities.  
447 In particular, we have shown the importance of the stable manifold of the  
448 saddle-node for the existence of such patterns. First, the initial conditions  
449 must lie over the stable manifold, and second, the stable manifold needs  
450 to be sufficiently low such that the diffusion can push the system beyond  
451 it. Furthermore, if the predator is above the excitation threshold all over  
452 the domain, the diffusive rescue effect cannot take place even if one applies  
453 small perturbations to the initial conditions. Already Ermentrout and Rinzel  
454 (1981) report the criticality of the stable manifold of the saddle as a pertur-  
455 bation threshold. However, the specific region allowing for spatial patterns  
456 also depends on the vector field of the local system. In particular, we have  
457 shown that initial conditions that are too high lead to the extinction of the  
458 predator.

459 Moreover, we considered the mean period of the rather irregular spa-  
460 tial oscillations at each point in space. Counter-intuitively, higher predator  
461 motility increases the mean period and can eventually suppress the rescue ef-  
462 fect. Generally, the period is two orders of magnitude lower than the regular  
463 oscillations in the nonspatial system. This is due to the diffusive pertur-  
464 bations decreasing the time the system spends in the destabilizing region  
465 of the phase plane close to the prey carrying capacity. Note that including  
466 environmental noise in models with relaxation dynamics has the same effect  
467 based on the same mechanism (Crucifix, 2012). As most natural systems  
468 may indeed include space, movement, and environmental perturbations, this  
469 makes a comparison of ecological time series with model simulations challeng-  
470 ing. This is because ecological time series are often measured at a particular  
471 point in space, and the period is a crucial feature of such a time series. Thus,  
472 if the considered system shows slow-fast dynamics, a spatial component is  
473 necessary for a reliable comparison.

474 Numerical simulations indicate that the minimum critical defense value



475 allowing for such spatiotemporal patterns is driven by the configuration of  
476 the nullclines and the stable manifold of the saddle that is destroying the  
477 limit cycle. Keeping this mechanism in mind, we investigated the effect of  
478 preytaxis. In particular, we have shown that preytaxis representing avoid-  
479 ance of large prey groups can extend the parameter regime corresponding to  
480 a rescue effect even further. In terms of a biological invasion of the predator,  
481 the initial (introduced) predator patch size leading to a successful establish-  
482 ment of the predator can be significantly smaller than without preytaxis.

483 Note that for the simulations performed in this study, the excitability  
484 patterns remained non-stationary in space and time for all the simulation  
485 time. However, Petrov et al. (1994) reported that steady wave interaction  
486 could lead to wave locking and accompanying stationary patterns in the  
487 long run. Even with extensive simulations, we did not find such a scenario.  
488 However, this would depend on a combination of simulation time and the  
489 size of the domain and may still exist for some combinations.

490 Finally, we want to emphasize that the main aim of this study was to  
491 identify possible impacts of taxis on the occurrence of spatiotemporal pat-  
492 terns in a group defense predator-prey model. Although we question that  
493 Turing patterns are driven by taxis in a group defense setting, excitability  
494 patterns can at least partly occur due to taxis. Hence, like various other stud-  
495 ies in the field of population dynamics (e.g., Bate and Hilker, 2019; Potts and  
496 Petrovskii, 2017; Shigesada et al., 1979), this suggests that the impact of not  
497 only self-diffusive movement should get broader attention in future research.

## 498 **Appendix A. Dimensions**

499 Table A.2 summarizes the meaning of the parameters and state variables  
500 including their dimensions.

Table A.2: The dimensions of the parameters and state variables as used in Equation (1) as well as their biological meaning are shown with T, N, and L representing dimensions of time, population size, and length respectively. Here, we assume one spatial dimension.

	<b>Meaning</b>	<b>Dimension</b>
$U$	prey	N
$V$	predator	N
$T$	time	T
$X$	space	L
$r$	prey growth rate	$T^{-1}$
$c$	prey competition coefficient	$(TN)^{-1}$
$\beta$	search rate of the predator	$(TN)^{-1}$
$\gamma$	handling rate	$T^{-1}$
$C$	critical defense value	N
$\nu$	strength of collective defense	-
$e$	conversion efficiency	-
$m$	predator mortality	$T^{-1}$
$D_U$	prey diffusion coefficient	$L^2T^{-1}$
$D_V$	predator diffusion coefficient	$L^2T^{-1}$
$\tilde{\chi}_0$	prey taxis coefficient	$L^2(NT)^{-1}$

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