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Directed migration shapes cooperation in spatial ecological  
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public goods games  
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23  
**Abstract**  
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From the microscopic to the macroscopic level, biological life exhibits directed migration  
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in response to environmental conditions. Chemotaxis enables microbes to sense and  
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move towards nutrient-rich regions or to avoid toxic ones. Socio-economic factors drive  
human populations from rural to urban areas. However, migration affects the quantity  
and quality of desirable resources. The effect of collective movement is especially  
significant when in response to the generation of public goods. Microbial communities  
can, for instance, alter their environment through the secretion of extracellular  
substances. Some substances provide antibiotic-resistance, others provide access to  
nutrients or promote motility. However, in all cases the maintenance of such public  
goods requires costly cooperation and is consequently susceptible to exploitation. The  
threat of exploitation becomes even more acute with motile individuals as defectors can  
avoid the consequences of their cheating.  
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Here, we propose a model to investigate the effects of targeted migration based on  
the production of ecological public goods and analyze the interplay between social  
conflicts and migration. In particular, individuals can locate attractive regions by  
moving towards higher cooperator densities or avoid unattractive regions by moving  
away from defectors. Both migration patterns not only shape an individual's immediate  
environment but also affects the population as a whole. For example, defectors hunting  
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cooperators in search of the public good have a homogenizing effect on population  
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densities. They limit the production of the public good and hence inhibit the growth of  
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the population. In contrast, aggregating cooperators promote the spontaneous formation  
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of heterogeneous density distributions. The positive feedback between cooperator  
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aggregation and public goods production, however, poses analytical and numerical  
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challenges due to its tendency to develop discontinuous distributions. Thus, different  
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modes of directed migration bear the potential to enhance or inhibit the emergence of  
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complex and sometimes dynamic spatial arrangements. Interestingly, whenever patterns  
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emerge in the form of heterogeneous density distributions, cooperation is promoted, on  
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average, population densities rise, and the risk of extinction is reduced.  
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## Author summary

The production and maintenance of shared environmental resources such as access to  
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nutrients in microbial communities or potable water in human societies require the  
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cooperation of groups of individuals. However, cooperation is costly and prone to  
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exploitation. If too many individuals follow selfish interests and spoil their environment,  
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the group and possibly the entire population suffers. Nevertheless, many forms of  
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biological life – from humans to microbes – migrate in response to resource availability.  
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Here, we analyze the interplay of the social conflict in public goods production and  
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targeted migration. In particular, we find that aggregation of cooperators can enhance  
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or trigger the spontaneous formation of heterogeneous spatial distributions, which  
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promote cooperation and result in higher population densities. Conversely, attempts to  
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avoid defectors increases the risk of extinction because it tends to homogenize  
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population distributions and lower population densities.  
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## Introduction

Directed migration is a phenomenon commonly observed in nature. Microbial  
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populations such as *Escherichia coli* actively seek areas with higher concentrations of  
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substances, such as amino-acids, through chemotaxis [1] and avoid toxic regions [2].  
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Birds sense seasonal changes and migrate to more hospitable climes [3]. Socio-economic  
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56 factors attract people from rural communities to cities [4]. In all cases, individuals  
57 migrate to improve their access to resources.

58 Environmental factors influence the abundance of resources, but some resources such  
59 as public goods are produced and maintained by the population itself and require  
60 cooperation. Prominent examples are drinking water, clean air or the climate on a  
61 global scale [5] as well as the production of extracellular substances to access food [6] or  
62 to grant resistance to antibiotics [7,8] on a microscopic scale. However, cooperation is  
63 costly and threatened by non-cooperating defectors [9]. Defectors are free-riders  
64 exploiting public goods without contributing themselves and hence the public resources  
65 dwindle whenever defection becomes common.

66 Ecological public goods introduce ecological dynamics into evolutionary games  
67 through variable population densities based on the production of the public good [10].  
68 Thus, defectors cause decreases in population densities, which results in smaller  
69 interaction group sizes. In sufficiently small groups cooperation may become dominant  
70 and the population can recover. This feedback between population densities and  
71 interaction group sizes enables cooperators and defectors to coexist. In particular, this  
72 includes the most interesting case where public goods production is crucial for the  
73 survival of the population [11]. This represent our baseline scario here.

74 In a spatial context, undirected movement introduces rich dynamics including the  
75 spontaneous emergence of heterogeneous density distributions resulting in pattern  
76 formation and chaotic spatio-temporal dynamics [12]. The pattern formation is driven  
77 by Turing instabilities [13], which have also been reported for purely ecological models  
78 such as predator-prey or chemotaxis models [14, 15]. Whenever patterns form,  
79 populations thrive through an increase in cooperation, raised population density, and  
80 reduced risk of extinction. However, spatio-temporal chaos and pattern formation also  
81 causes spatial heterogeneity in the abundance and availability of the public good, which  
82 naturally leaves some locations more attractive than others.

83 Through directed migration, cooperators and defectors can improve access to the  
84 public good by actively seeking cooperation or reduce exploitation by avoiding defection.  
85 Here, we extend the spatial ecological public goods game [12] by incorporating targeted  
86 migration in the “selection-diffusion” system, and analyze how directed migration  
87 shapes cooperation, and pattern formation, in particular. Based on the stability

analysis of the dynamical equations and supported by numerical integration, we derive  
88 detailed criteria for pattern formation for the different modes of migration.  
89

Directed migration can trigger, enhance or inhibit the spontaneous emergence of  
90 steady, quasi-steady or dynamic heterogeneous density distributions. Somewhat  
91 surprisingly, cooperators fleeing from defectors homogenize the density distribution, and  
92 endanger the population whenever cooperators spread themselves too thin. In contrast,  
93 if defectors avoid each other, cooperators can accumulate and patterns emerge. This  
94 allows cooperation to thrive under conditions, in which neither a well-mixed population  
95 nor a diffusing migration would survive. As expected, aggregating cooperators also  
96 facilitate pattern formation through positive feedback between cooperator densities and  
97 cooperator migration: cooperator aggregation gives rise to steeper gradients of the  
98 public good and thus creates even stronger incentives to migrate in towards those  
99 locations. However, the positive feedback comes with analytical and numerical  
100 challenges due to the potential to give rise to discontinuous distributions. Through the  
101 promotion or inhibition of spatial heterogeneity, directed migration is a critical  
102 determinant for cooperation, the survival of the population, and conducive to promoting  
103 and maintaining diversity of ecosystems.  
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## Ecological public goods 105

In traditional public goods games  $N$  individuals gather in a group and each individual  
106 chooses to cooperate and invest into a common pool at a cost  $c$ , or to defect and shirk  
107 the investment. The common pool is multiplied by a factor  $r > 1$  and equally divided  
108 among all individuals within the group. This results in a payoff of  $P_D = n_C \cdot rc/N$  for  
109 defectors and  $P_C = P_D - (1 - r/N)c$  for cooperators when facing  $n_C$  cooperators among  
110 the  $N - 1$  other group members. For  $r < N$  every participant is tempted to withhold  
111 their investment because  $P_C < P_D$  and hence to forego the benefits of the public good  
112 to the detriment of all. Had everyone cooperated the payoff would be  $(r - 1)c > 0$ . This  
113 conflict of interest between the group and the individual constitutes the social dilemma  
114 at the heart of public goods interactions [16–18]. Only for  $r > N$  these interests align.  
115

In well-mixed populations with normalized densities (frequencies) of cooperators,  $u$ ,  
116 and defectors,  $v = 1 - u$ , both strategies encounter, on average,  $n_C = u(N - 1)$   
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cooperators among their interaction partners in randomly assembled interaction groups. 118

In evolutionary game theory payoffs represent fitness and hence determine the rate of 119  
change of the population composition as captured by the replicator dynamics 120

$\partial_t u = u(1 - u)(P_C - P_D)$ , where  $\partial_t$  denotes the time derivative [19]. Consequently, 121  
cooperation dwindle,  $\partial_t u < 0$ , whenever cooperators obtain lower payoffs in the public 122  
goods game than defectors, i.e. if  $P_C - P_D = -c(1 - r/N) < 0$ . Indeed, for  $r < N$  123  
defection dominates and  $\partial_t u < 0$  always holds. Conversely, for  $r > N$  cooperation 124  
spreads in the population,  $\partial_t u > 0$ . 125

The replicator equation does not take ecological quantities such as variable 126  
population densities into account. In ecological systems, the presence of the public good 127  
promotes population growth through improved access to food resources [6] or increased 128  
resistance to environmental threats such as antibiotics [7]. The interplay between 129  
ecological and evolutionary dynamics in such ecological public goods interactions is 130  
captured by 131

$$\partial_t u = u [w(b + f_C) - d] \quad (1a)$$

$$\partial_t v = v \underbrace{[w(b + f_D) - d]}_{\text{ecological dynamics}}, \quad (1b)$$

where  $w = 1 - u - v$  reflects reproductive opportunities that diminish for increasing 132  
population densities [11]. Selection is based on ecological public goods interactions 133  
affecting the birth rates of cooperators and defectors through their average payoffs  $f_C$  134  
and  $f_D$ , respectively, while the death rate is constant,  $d$ . More specifically, the effective 135  
birthrates,  $w(b + f_i)$ , are determined by 136

$$f_D = r \frac{u}{u + v} \left( 1 - \frac{1 - w^N}{(u + v)N} \right) c, \quad (2a)$$

$$f_C = f_D - \left( 1 + (r - 1)w^{N-1} - r \frac{1 - w^N}{(u + v)N} \right) c \quad (2b)$$

plus the baseline birthrate,  $b$ , because in the limit  $v \rightarrow 1$  the payoff  $f_C$  can become 137  
negative, which is biologically not meaningful [11]. The ecological dynamics results in 138  
variable interaction group sizes with an effective, expected group size of  $S = (u + v)N$ . 139  
Thus, as long as  $S > r$ , defection dominates, the public resource is overexploited and 140

the population density declines. Consequently, interactions occur in smaller groups and  
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returns are split among fewer individuals. For sufficiently small groups,  $S < r$ ,  
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cooperation becomes favourable again, the population density recovers,  $S$  increases and  
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the cycle continues.  
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Even in the absence of spatial dimensions, rich dynamics are observed especially  
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under environmental stress,  $d > b$ , where the survival of the population hinges on the  
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availability of the public good [10]. Varying population densities enable the coexistence  
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of cooperators and defectors. More specifically, an interior equilibrium  $Q$  undergoes a  
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Hopf-bifurcation [20] when increasing the rate of return of the public good,  $r$ , giving rise  
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to stable and unstable limit cycles [11]. For  $r < r_{\text{Hopf}}$ ,  $Q$  is unstable, and well-mixed  
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populations are doomed. However, for  $r > r_{\text{Hopf}}$ , the equilibrium  $Q$  allows cooperators  
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and defectors to coexist but the basin of attraction of the equilibrium  $Q$  remains limited.  
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More specifically, if cooperators are too rare for the public goods production to offset  
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the death rate  $d$ , or if defectors abound, the population may still go extinct.  
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Here we focus on the case where the death rate exceeds the baseline birthrate,  $d > b$ ,  
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such that only the production of the public good can prevent extinction. This scenario  
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can be interpreted as a microbial population in a biocide where the multiplication factor  
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 $r$  reflects the effectivity of the public good to oppose the detrimental effect of the toxic  
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environment. The following extensions explore the effects of different modes of motility  
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on the public goods production and survival of the population.  
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## Materials and methods

### Spatial ecological public goods

The spatial dynamics of ecological public good interactions with undirected (diffusive)  
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migration can be formulated as a selection-diffusion process  
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$$\partial_t u = u [w(b + f_C) - d] + D_C \nabla^2 u \quad (3a)$$

$$\partial_t v = \underbrace{v [w(b + f_D) - d]}_{\text{ecological dynamics}} + \underbrace{D_D \nabla^2 v}_{\text{undirected migration}}, \quad (3b)$$

where the diffusion constants  $D_C$  and  $D_D$  reflect the migration of cooperators and defectors, respectively [12]. In spatial settings, undirected migration promotes coexistence of cooperators and defectors even if the coexistence equilibrium  $Q$  is unstable. In particular, if defectors run faster than cooperators,  $D_D > D_C$ , the dynamics exhibit Turing instabilities, where cooperators serve as activators and defectors as inhibitors. This enables the population to survive through spontaneous pattern formation. Close to the Hopf-bifurcation with  $r < r_{\text{Hopf}}$  ( $Q$  unstable), the influence of temporal oscillations gives rise to chaotic spatio-temporal dynamics [21], which facilitate population survival even for equal diffusion rates,  $D_D = D_C$ . Conversely, for slower diffusion of defectors,  $D_D < D_C$ , activation through cooperation is no longer tenable, spatial effects disappear and either results in homogeneous coexistence for  $r > r_{\text{Hopf}}$  ( $Q$  stable) or extinction for  $r < r_{\text{Hopf}}$ . This implies that attempts of cooperators at outrunning defectors are futile.

Here, we extend the spatial ecological public goods model, Eq. (3), by introducing *directed* migration, which enables cooperators and defectors to bias their movement towards more attractive regions.

$$\partial_t u = u [w(b + f_C) - d] + D_C \nabla^2 u - A_C \nabla \cdot (uw \nabla u) + R_C \nabla \cdot (uw \nabla v) \quad (4a)$$

$$\partial_t v = v \underbrace{[w(b + f_D) - d]}_{\text{ecological dynamics}} + \underbrace{D_D \nabla^2 v}_{\text{undirected migration}} - \underbrace{A_D \nabla \cdot (vw \nabla u)}_{\text{attraction toward cooperation}} + \underbrace{R_D \nabla \cdot (vw \nabla v)}_{\text{repulsion from defectors}}, \quad (4b)$$

with  $A_C, A_D, R_C, R_D \geq 0$  and where terms of the form  $-K \nabla \cdot (\phi w \nabla \psi)$  reflect that individuals of type  $\phi$  are attracted to the gradient of type  $\psi$  proportional to reproductive opportunities,  $w$ , at a non-negative rate  $K$  (for a detailed microscopic derivation see S1 Appendix). The density of cooperators directly translates into the rate of production of public goods and hence serves as a proxy for its availability and the quality of the environment. For example, the term  $-A_D \nabla \cdot (vw \nabla u)$  reflects *hunting defectors* in search of public goods that are attracted to higher densities of cooperators at a rate  $A_D$ . Note that the negative sign indicates movement toward higher densities. Similarly,  $-A_C \nabla \cdot (uw \nabla u)$  represents *aggregating cooperators* that are attracted to their kind. In contrast, the density of defectors serves as a proxy to avoid exploitation and reduce competition. Instead of directly sensing the density of defectors their excretions

**Fig 1. Pattern formation under directed migration.** Snapshots of the density distribution of cooperators (green) and defectors (red) across the periodic  $L \times L$  domain after  $t = 0, 50, 100, 200, 1000, 2000$  generations. The color brightness indicates the density with coexistence (yellow) and vacant space (black). (A) Spreading defectors spontaneously form and settle in quasi-steady patterns ( $R_D = 8$ ). (B) Chaotic spatio-temporal dynamics unfold for hunting defectors ( $A_D = 4$ ). (C) Aggregating cooperators induce positive feedback: as more cooperators leave scarcely populated areas in favor of highly cooperative locations, the divide between neighbouring areas grows and discontinuities can develop at the interfaces. ( $A_C = 1$ )  
Parameters: public goods interaction:  $b = 1, r = 2.325, d = 1.2, N = 8, c = 1$ ; diffusion:  $D_C = D_D = 0.1$ ; directed movement:  $A_C = A_D = R_C = R_D = 0$ , unless otherwise indicated; discretization in space and time:  $L = 75, dx = 0.375, dt = 0.01$ ; noisy Gaussian initial condition:  $u(x, y) = v(x, y) = 1/5 \cdot \exp[-((x - L/2)^2 + (y - L/2)^2)/16^2]$ .

from public goods consumption could reflect the poor quality of the environment. Thus, 192  
 $R_C \nabla \cdot (uw \nabla v)$  reflects *fleeing cooperators* that avoid higher densities of defectors at a 193  
rate  $R_C$ , whereas  $R_D \nabla \cdot (vw \nabla v)$  refers to *spreading defectors* that steer clear of their 194  
kind. 195

Rich dynamics unfold under directed migration as showcased in Fig. 1, ranging from 196  
the spontaneous formation of quasi-stable or stable patterns (Fig. 1A) and 197  
ever-changing, chaotic spatio-temporal dynamics (Fig. 1B) to cooperators aggregating 198  
under a self-reinforcing migration response (positive feedback, Fig. 1C). 199

## Results

An overview of the long-term effects of the four types of directed migration on spatial 201  
ecological public goods interactions is summarized in Fig. 2. Each type has distinct 202  
effects on pattern formation and population survival. For  $r < r_{\text{Hopf}}$ , aggregating 203  
cooperators,  $A_C$ , (see Fig. 2A) and spreading defectors,  $R_D$ , (see Fig. 2D) increase the 204  
chances of survival by promoting spontaneous formation of heterogeneous density 205  
distributions. For aggregating cooperators, this process is facilitated by a slower rate of 206  
expansion. In particular, aggregating cooperators directly oppose the effects of 207  
cooperator diffusion  $D_C$  and can even bring population expansion to a halt (see panel A 208  
in S2 Figure). In fact, sufficiently high  $A_C$  triggers a positive feedback between 209  
cooperator densities (or public goods production) and aggregation, which pose 210  
analytical and numerical challenges discussed below. In contrast, hunting defectors,  $A_D$ , 211  
increase competition in areas where cooperators aggregate (see Fig. 2C) and fleeing 212

**Fig 2. Spatial dynamics for the four types of directed migration.** Each of the four panels (A)-(D) shows snapshots of the spatial distributions after  $t = 2000$  generations as a function of the multiplication factor  $r$  when varying one of the four modes of migration. The bottom row shows the dynamics of purely diffusive migration in the proximity of  $r_{\text{Hopf}} \approx 2.365$  as a reference. (A) Aggregating cooperators oppose the effects of diffusion and hence slow down the population expansion. The positive feedback between cooperator densities and aggregation can cause discontinuous distributions and the breakdown of numerical methods. (B) Hunting defectors increase competition in areas where cooperators concentrate. This allows cooperators to escape into unpopulated terrain but also increases the risk of extinction. (C) Fleeing cooperators avoid defectors and hence readily explore vacant space but with the defectors at their tails also tend to spread themselves too thin and risk extinction. (D) Spreading defectors reduce exploitation on cooperator aggregates and consequently promote pattern formation as well as population survival. *Parameters* as in Fig. 1 unless otherwise indicated.

cooperators,  $R_C$ , explore space to avoid exploitation (see Fig. 2B). In both cases 213  
cooperator densities and hence the concentration of the public good are evened out. 214  
This suppresses pattern formation and renders the population more prone to extinction 215  
through global temporal fluctuations. For  $r > r_{\text{Hopf}}$ , coexistence of cooperators and 216  
defectors in well-mixed populations is stable and the spatial patterns tend to fade away. 217  
The only exception is the aggregation of cooperators, which may prevent expansion and 218  
hence colonization of empty territory. 219

## Emerging patterns

Public goods production and population survival are both crucially linked to the 220  
spontaneous emergence of spatial patterns. Here we derive necessary conditions for the 221  
onset of pattern formation. An analytical understanding of the pattern formation 222  
process is obtained by considering homogeneous population densities reflecting the 223  
coexistence equilibrium  $Q$  of the well-mixed population dynamics, Eq. (1). A small 224  
perturbation  $p(t, x, y) = \epsilon \exp(ik(x + y) - t)$  of mode  $k$ , where  $k = 0$  reflects the 225  
temporal mode and  $k > 0$  spatial modes, may get amplified by the dynamics and give 226  
rise to the emergence of heterogeneous density distributions, also called Turing 227  
patterns [13]. The linearized dynamics in the vicinity of  $Q = (u_{\text{eq}}, v_{\text{eq}}, w_{\text{eq}})$  is given by 228  
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$$\begin{pmatrix} \partial_t \hat{u} \\ \partial_t \hat{v} \end{pmatrix} = (J_I + k^2 J_S) \cdot \begin{pmatrix} \hat{u} \\ \hat{v} \end{pmatrix}, \quad (5)$$

where  $\hat{u} = u - u_{\text{eq}}$ ,  $\hat{v} = v - v_{\text{eq}}$  and  $J_I, J_S$  represent the Jacobians from public goods interactions and spatial migration (directed and undirected), respectively:

$$J_I = \begin{bmatrix} a_{CC} & a_{CD} \\ a_{DC} & a_{DD} \end{bmatrix} = \begin{bmatrix} -u_{\text{eq}}d/w_{\text{eq}} + u_{\text{eq}}w_{\text{eq}} \partial_u f_C & -u_{\text{eq}}d/w_{\text{eq}} + u_{\text{eq}}w_{\text{eq}} \partial_v f_C \\ -v_{\text{eq}}d/w_{\text{eq}} + v_{\text{eq}}w_{\text{eq}} \partial_u f_D & -v_{\text{eq}}d/w_{\text{eq}} + v_{\text{eq}}w_{\text{eq}} \partial_v f_D \end{bmatrix}, \quad (6a)$$

$$J_S = \begin{bmatrix} s_{CC} & s_{CD} \\ s_{DC} & s_{DD} \end{bmatrix} = 2 \cdot \begin{bmatrix} A_C u_{\text{eq}} w_{\text{eq}} - D_C & -R_C u_{\text{eq}} w_{\text{eq}} \\ A_D v_{\text{eq}} w_{\text{eq}} & -R_D v_{\text{eq}} w_{\text{eq}} - D_D \end{bmatrix}. \quad (6b)$$

The largest eigenvalue (real part) of  $J_I + k^2 J_S$  is a function of  $k$  and is called the dispersion relation  $\lambda(k)$  (see S2 Appendix). Modes with  $\lambda(k) > 0$  are unstable indicating the potential for spatial patterns to emerge. If the spatial Jacobian  $J_S$  admits eigenvalues with positive real parts then  $\lambda(k) > 0$  holds for all sufficiently large  $k$ , i.e. all spatial perturbations of sufficiently high frequency are unstable. This is not meaningful in natural systems. In order to ensure  $\lambda(k) < 0$  for  $k \rightarrow \infty$ , the condition  $\det(J_S) > 0$  or, more precisely,  $D_C > A_C u_{\text{eq}} w_{\text{eq}}$  is required, which means that at the homogeneous equilibrium, the effects of diffusion (undirected migration) need to outweigh effects of cooperator aggregation.

In spite of the above restrictions, intermediate modes can nevertheless become unstable through a combination of selection and migration. A necessary condition for pattern formation is

$$\underbrace{-a_{DD}(A_C u_{\text{eq}} w_{\text{eq}} - D_C) - a_{DC} R_C u_{\text{eq}} w_{\text{eq}}}_{\substack{>0 \\ \text{activation through} \\ \text{cooperator migration}}} > \underbrace{-a_{CD} A_D v_{\text{eq}} w_{\text{eq}} + a_{CC}(-R_D v_{\text{eq}} w_{\text{eq}} - D_D)}_{\substack{>0 \\ \text{inhibition through} \\ \text{defector migration}}}, \quad (7)$$

see S2 Appendix for details. Consequently, faster aggregating cooperators or spreading defectors (increased  $A_C, R_D$ ) or slower undirected cooperator migration (decreased  $D_C$ ) promote the development of heterogeneous patterns by actively or passively promoting cooperator aggregation. In contrast, faster directed migration of defectors towards cooperation or of cooperators away from defection (increased  $A_D, R_C$ ) as well as slower undirected defector migration (decreased  $D_D$ ) all increase exploitation of the public

**Fig 3. Pattern formation under competing forms of directed migration.**

(A), (C) Cooperator aggregation results in smooth patterns for small  $A_C$ , which are suppressed by increasing  $A_D$ ,  $R_C$ . However, for larger  $A_C$  the positive feedback between aggregation and densities of cooperators dominates. This eliminates defectors and gives rise to discontinuous distributions. Consequently, directed migration triggered by defector densities through  $A_D$  or  $R_C$  no longer matters. (B), (D) Spreading defectors,  $R_D$ , also promote pattern formation but maintain smooth patterns, while increases in  $A_D$ ,  $R_C$  again suppress them. *Parameters:* Multiplication factor  $r = 2.4$ ,  $D_D = 0.5 > D_C = 0.1$  to observe smooth patterns for  $A_C$ ; snapshots taken at  $t = 2000$ ; Gaussian initial configuration without noise. Other parameters as in Fig. 1.

good, reduce the efficacy of cooperator aggregation and hence suppress pattern formation. Fig. 3 depicts the competing effects of activating and inhibiting forms of directed migration. The most unstable mode determines the characteristic length scale of the emerging spatial patterns (see S2 Appendix).

Hunting defectors,  $A_D$ , and fleeing cooperators,  $R_C$ , exhibit similar homogenizing effects. In contrast, significant qualitative differences arise in the promotion of pattern formation due to aggregating cooperators,  $A_C$ , and spreading defectors,  $R_D$ , in the sense that aggregating cooperators have the potential to fully suppress defection. In this case neither increases in  $A_D$  nor in  $R_C$  are capable of counteracting the positive feedback induced by  $A_C$  to recover coexistence.

## Aggregating cooperators

The positive feedback between cooperator densities and cooperator migration is intrinsic to aggregating cooperators. Regions of higher cooperator densities attract cooperators, which further increases their densities and, more importantly, the gradient along the periphery. As a result the region exerts an even stronger attraction. In fact, for sufficiently large  $A_C$  the attraction prevents cooperators from exploring the available space thus the population remains localized. The potential of aggregating cooperators to give rise to discontinuous distributions through positive feedback lies at the core of the necessary condition that diffusion must outweigh aggregation at the homogeneous equilibrium:  $D_C > A_C u_{\text{eq}} w_{\text{eq}}$ . However, this condition is conservative and no longer sufficient for heterogeneous distributions. The gradient in cooperator densities,  $\nabla u$ , promotes further aggregation of cooperators despite being limited by reproductive opportunities,  $w$ , see Eq. (4). As a consequence the gradient further increases and

**Fig 4. Effects of directed migration on population densities and frequency of cooperation as compared to unstructured populations.** In the absence of directed migration (undirected migration only) homogeneous coexistence results with densities  $Q = (u_{\text{eq}}, v_{\text{eq}})$ . The two panels depict the ratio of the average spatial population density to the population density in unstructured populations,  $r_p = (\bar{u} + \bar{v}) : (u_{\text{eq}} + v_{\text{eq}})$  (black solid line), and the ratio of the average cooperator frequency to their frequency in unstructured populations,  $r_c = \bar{u}/(\bar{u} + \bar{v}) : u_{\text{eq}}/(u_{\text{eq}} + v_{\text{eq}})$  (green solid line) for (A) cooperator aggregation,  $A_C$ , and (B) spreading defectors,  $R_D$ . (A) increasing  $A_C$  gives rise to four dynamical regimes: (i) homogeneity maintained, (ii) formation of smooth patterns, (iii) discontinuities emerge, and (iv) population expansion prevented. (B) increasing  $R_D$  only results in two regimes: (i) homogeneity (ii) formation of smooth patterns. In order to facilitate comparisons of regions (i) and (ii) across panels the large effects of discontinuities in (iii) and (iv) refer to the scale on the right of panel (A). In either case, heterogeneous distributions increase (average) population densities and cooperator frequencies. In (A), once discontinuities develop, populations consist exclusively of cooperators. The decrease in  $r_p$  for large  $A_C$  relates to the fact that populations are unable to expand and hence the ratio depends on the initial configuration. In contrast,  $r_c$  remains unaffected because defectors are absent and cooperators are at the maximum frequency. *Parameters* as in Fig. 3.

discontinuities in the density distribution can develop. Interestingly, this effect turns out to be strong enough to completely suppress defection (c.f. Fig. 3). However, increasing gradients require finer discretization to numerically integrate the selection-migration dynamics, Eq. (4), and hence the emerging distributions depend on the discretization. The manifestation of discontinuous distributions becomes increasingly likely for larger values of  $A_C$  (see S3 Figure) but can also be triggered by pattern formation or large gradients in initial distributions. Increased and differing diffusion rates,  $D_D > D_C$ , or spreading defectors,  $R_D$ , lower the threshold for pattern formation and are additionally required to reliably observe smooth patterns through aggregating cooperators,  $A_C$ .

## Social dynamics

Directed migration not only promotes or inhibits spontaneous pattern formation but also affects the frequency of cooperators as well as the population density and hence the survival of the population. Whenever patterns develop, cooperation is promoted and population densities consequently rise, see Fig. 4.

This effect extends to multiplication factors below  $r_{\text{Hopf}}$ , which cannot sustain unstructured populations. In this domain, undirected migration is capable of inducing spatial heterogeneity for  $D_D > D_C$  and thereby promotes the survival of the population.

Aggregating cooperators,  $A_C$ , and spreading defectors,  $R_D$ , further promote pattern formation and population survival even under conditions such as  $D_C \geq D_D$ , where undirected migration alone is unable to support the population, c.f. Eq. (7) and Fig. 2A, D. Moreover, the positive feedback of aggregating cooperators coupled with limited reproductive opportunities, offers the intriguing prospect that defectors can potentially get crowded out and driven to extinction, see Fig. 2A and Fig. 4A.

## Discussion

Cooperation is doomed in traditional public goods games – as paraphrased by Hardin’s “Tragedy of the Commons” [9]. In contrast, in ecological public goods interactions cooperators and defectors can coexist through the feedback between variable population densities and interaction group sizes [10] even if the reproductive performance and survival of the population hinges on the availability of public goods.

The introduction of continuous spatial dimensions allows population densities and social composition to vary across the domain. For undirected migration the ratio between the rates of cooperator and defector migration is crucial [12]. For  $D_C > D_D$ , the population either settles in a homogeneous state with densities corresponding to the well-mixed coexistence equilibrium  $Q$ , if it is stable ( $r > r_{\text{Hopf}}$ ), or goes extinct if  $Q$  is unstable ( $r < r_{\text{Hopf}}$ ). In either case, attempts of cooperators at avoiding exploitation by outrunning defectors are futile. For  $D_C = D_D$ , chaotic spatio-temporal dynamics enable the population to survive for  $r$  slightly below  $r_{\text{Hopf}}$  [21]. However, for  $D_C < D_D$  cooperation is promoted through Turing instabilities that result in quasi-stable or dynamical patterns that increase cooperator frequency, overall population density, and enhance population survival.

Through undirected migration heterogenous density distributions of cooperators and defectors spontaneously arise. Consequently the abundance of public goods varies across space and renders some regions more attractive than others. This provides a natural incentive for directed migration – either to avoid poor areas or to seek out better ones. For example, chemotactic bacteria aggregate in patches in response to excreted attractants [22] or try to escape oxidative stress [2]. Instead of explicitly modelling the concentration of public goods and its waste products to assess the quality of the

environment, we use the density of cooperators and defectors as proxies for the 320 availability of public goods and the degree of exploitation, respectively. Thus, seeking 321 cooperation and avoiding defection allows individuals to increase their access to public 322 goods and improve their reproductive potential. Interestingly, even though the two 323 migration patterns appear very similar, they may actually trigger movements in 324 opposite directions. For example, cooperators that seek their kind aggregate at the 325 centre of cooperative areas. The resulting increase in public goods also benefits defectors 326 in that same location and may attract more defectors, which increases competition and 327 exploitation. In contrast, cooperators that avoid defectors tend to migrate towards the 328 periphery of cooperative areas and thereby effectively counteract cooperator aggregation. 329 Analogous arguments apply to defectors seeking cooperators or avoiding their kind, 330 respectively, but with opposite effects. More specifically, spreading defectors indirectly 331 support cooperator aggregation by creating (temporary) refuges with low exploitation. 332

As a consequence, directed migration can both enhance as well as inhibit pattern 333 formation. More specifically, aggregating cooperators or spreading defectors both 334 promote or even trigger pattern formation. In particular, this extends into unfavourable 335 parameter regions that otherwise result in extinction, such as when cooperators outpace 336 defector,  $D_C \geq D_D$ , or small multiplication factors  $r$ , see Fig. 2A,D. Conversely, fleeing 337 cooperators and hunting defectors suppress pattern formation by levelling out 338 population densities. For  $r < r_{\text{Hopf}}$  this increases the risk of extinction. The 339 complementary effects of the different modes of directed migration are captured in 340 Eq. (7), which provides an analytical threshold for the onset of pattern formation. 341 Regardless of whether spatial heterogeneities arise through directed or undirected 342 migration, they invariably increase both the average frequency of cooperators as well as 343 the average density of populations as compared to unstructured populations, see Fig. 4, 344 and thus improves the odds of population survival. 345

Traditionally the effects of spatial structure in evolutionary games have been 346 investigated based on lattices or more general network structures [23, 24]. Such discrete 347 spatial arrangements are capable of supporting cooperation because they enable 348 cooperators to form clusters and thereby reduce exploitation by defectors. This effect is 349 further enhanced by success-driven migration [25]. In contrast, in our setup space is 350 continuous and the state of the population represented by density distributions of 351

cooperators and defectors. This difference is crucial and renders cooperation even more 352 challenging because, in general, the density of defectors may become arbitrarily small 353 but never and nowhere zero within finite times. As a consequence cooperators are 354 always subject to exploitation by defectors. In fact, in the absence of ecological 355 dynamics and constant population densities cooperators invariably disappear (if  $r < N$ ) 356 or, conversely, take over (if  $r > N$ ), just as in well-mixed populations. 357

Notably, the only exception to this rule refers to the aggregation of cooperators 358 because this mode of directed migration can trigger a positive feedback between 359 densities and migration of cooperators: increases in density due to cooperator 360 aggregation result in steeper gradients, which heightens the attraction and hence further 361 increases their density. As a result, cooperator densities may not only remain localized 362 but also eliminate defectors. However, this positive feedback results in analytical and 363 numerical challenges because it gives rise to discontinuous distributions. Yet, those 364 challenges are common among models incorporating aggregation. For example, the 365 Keller-Segel chemotaxis model predicts infinite population densities after finite 366 times [26–29]. Even though a mathematical artifact, those singularities are associated 367 with the inherent feedback between chemotaxis and the secretion of chemical 368 attractants [15]. 369

Nevertheless, the most striking feature of directed migration is the potential of 370 aggregating cooperators to crowd out and eliminate defectors altogether, see Fig. 2A, 371 Fig. 3A,C, Fig. 4A. Unfortunately this intriguing phenomenon is linked to the positive 372 feedback that gives rise to discontinuous distributions and hence eludes further analysis 373 based on the present framework, Eq. (4). Somewhat surprisingly, the reduced 374 aggregation rate due to a lack of reproductive opportunities, represented by the term 375  $w\nabla u$ , turns out to be insufficient to maintain smooth numerical solutions. 376

Motility plays an important role in biofilms. Microbes excrete extracellular 377 substances to generate and maintain this protective film. Free-riders benefit from the 378 protection without contributing, which gives rise to the public goods dilemma. 379 Experiments indicate that not only the inherent social conflict plays a vital role in the 380 effective secretion of biofilms [30] but also the microbes motility [31–33]. Biofilms are no 381 longer generated when deactivating the movement apparatus through deliberate 382 mutations [34]. When specifically targeting the ability to chemotact, biofilm production 383

significantly varies across microbes and experimental setups [31]. This sensitivity of  
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public goods production in response to different types of migration is reflected in our  
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model.  
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The complex interplay between ecological public goods and motility shapes  
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population densities and distributions as well as their social composition. Not only does  
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migration affect the production of the public good but some public goods also alter the  
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motility of their producers. For example biofilms increase viscosity and reduce the  
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motility of microbes or even segregate populations [35]. Conversely, *Paenibacillus*  
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collectively lubricate hard surfaces to enhance population expansion [36]. Either  
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scenario creates intriguing opportunities for novel feedback mechanisms where migration  
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not only shapes the production and availability of the public good but where the public  
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good represents the very infrastructure needed to stay put or migrate more efficiently.  
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## Supplementary Information

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### S1 Appendix. Derivation of directed migration terms.

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### S2 Appendix. Pattern formation: Dispersion relation and derivation of necessary criteria.

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**S1 Figure. Dispersion relation for directed migration.** (A) aggregating cooperators,  $A_C$ , and (D) spreading defectors,  $R_D$ , have both the potential to cause spatial instabilities through increased migration. In the process, the dominant mode  $k_*$  increases with increased aggregating cooperators,  $A_C$ , and decreases with spreading defectors,  $R_D$ . In contrast, (C) hunting defectors  $A_D$  and (D) fleeing cooperators  $R_C$  stabilize the system. *Parameters:*  $2.4 = r > r_{\text{Hopf}}$  (such that  $\lambda(0) < 0$ ), as well as  $D_C > A_C u_{\text{eq}} w_{\text{eq}}$  (to ensure  $\lambda(k) < 0$  for  $k \rightarrow \infty$ ). (A), (D)  $D_D = 0.5$ , (B),(C)  $D_D = 0.7$ . Other parameters as in Fig. 1.

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**S2 Figure. Spatial and temporal dynamics for different types of directed migration.** Each panel illustrates the dynamics for a single type of directed migration as a function of the multiplication factor  $r$  in the proximity of  $r_{\text{Hopf}}$ . The small rectangles depict the cross section of the density distribution through the middle of the square  $L \times L$  domain as a function of time from top to bottom. The color brightness indicates the density of cooperation (green) and defection (red) with coexistence (yellow) and vacant space (black). (A) Aggregating cooperators oppose the effects of diffusion and hence slow down the population expansion. The positive feedback between cooperator densities and aggregation can cause discontinuous distributions and the breakdown of numerical methods. (B) Hunting defectors increase competition in areas where cooperators concentrate. This allows cooperators to escape into unpopulated terrain but also increases the risk of extinction. (C) Fleeing cooperators avoid defectors and hence readily explore vacant space but with the defectors at their tails also tend to spread themselves too thin and risk extinction. (D) Spreading defectors again promote pattern formation and thereby support the survival of the population.

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*Parameters:* same as in Fig. 1 but with Gaussian initial condition without noise and

$t = 250$ .

**S3 Figure. Pattern formation and discontinuities for aggregating** 425

**cooperators**  $A_C$ .. Analytical findings distinguish three domains based on  $A_C$  and the 426 multiplication factor  $r$ : (i) aggregation is sufficiently strong to destabilize the 427 homogeneous equilibrium (grey shaded region,  $A_C u_{\text{eq}} w_{\text{eq}} > D_C$ ); (ii) unstable modes 428 give rise to pattern formation (red shaded region, see Eq. (S4) in S2 Appendix); (iii) 429 stable homogeneous coexistence (unshaded region). However, initial conditions 430 significantly impact the emerging dynamics. Heterogeneous initial distributions trigger 431 migration and aggregation of cooperators. Discontinuities emerge within 250 432 generations from a Gaussian initial distribution when the selection-diffusion system is 433 numerically integrated (above dashed horizontal line). Below the dashed horizontal-line, 434 patterns emerge (in red shaded region) or homogeneous coexistence is regained (in 435 unshaded region) as predicted. For small  $r$  heterogeneous distributions are unable to 436 develop and the population goes extinct (left of dashed vertical line). *Parameters:* same 437 as in S2 Fig, except  $D_D = 0.5$  to promote smooth patterns. 438

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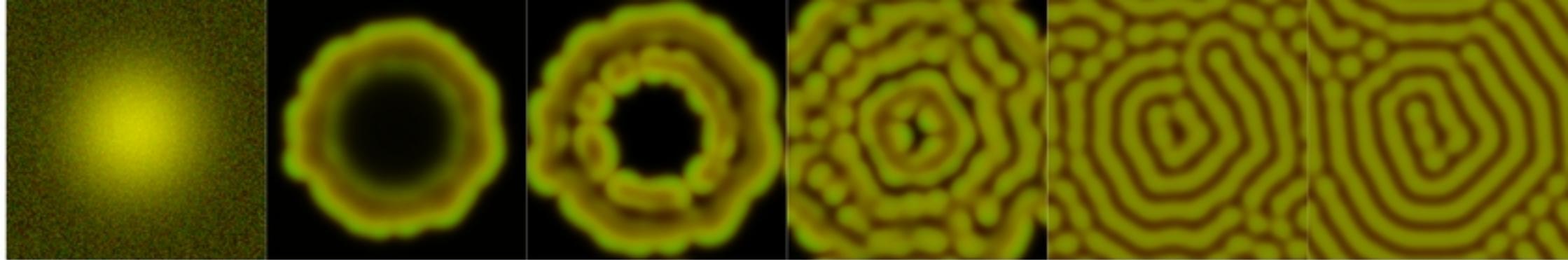
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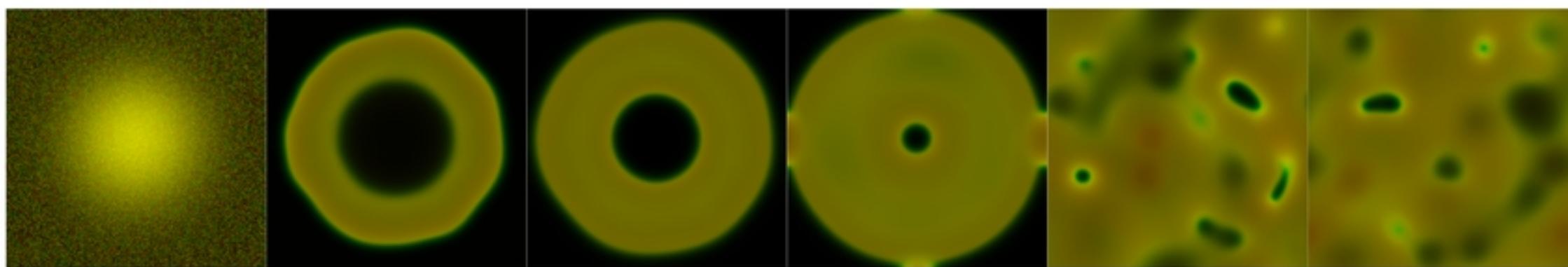
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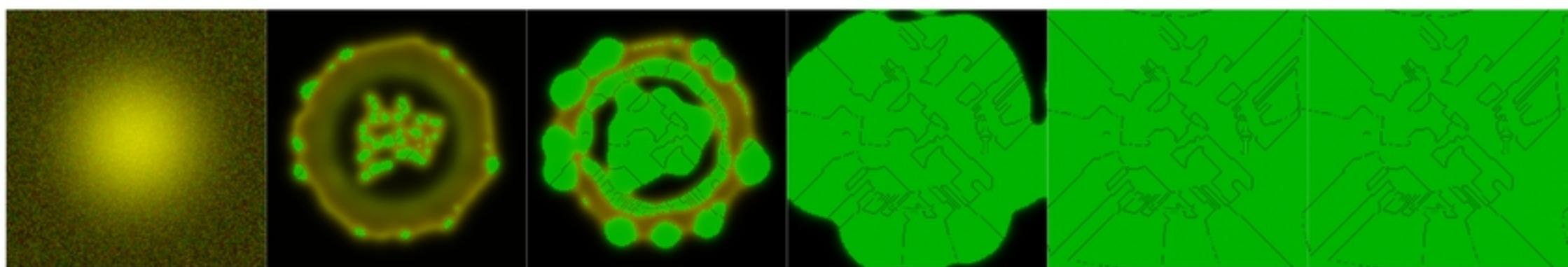
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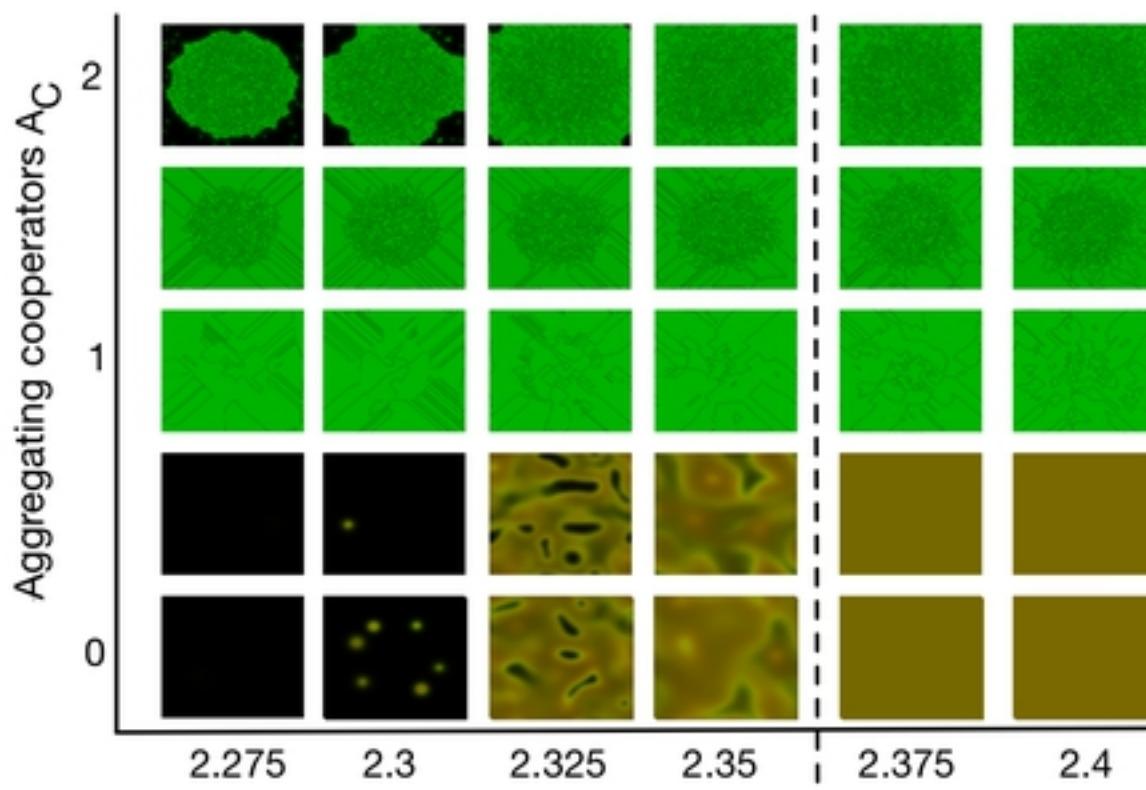
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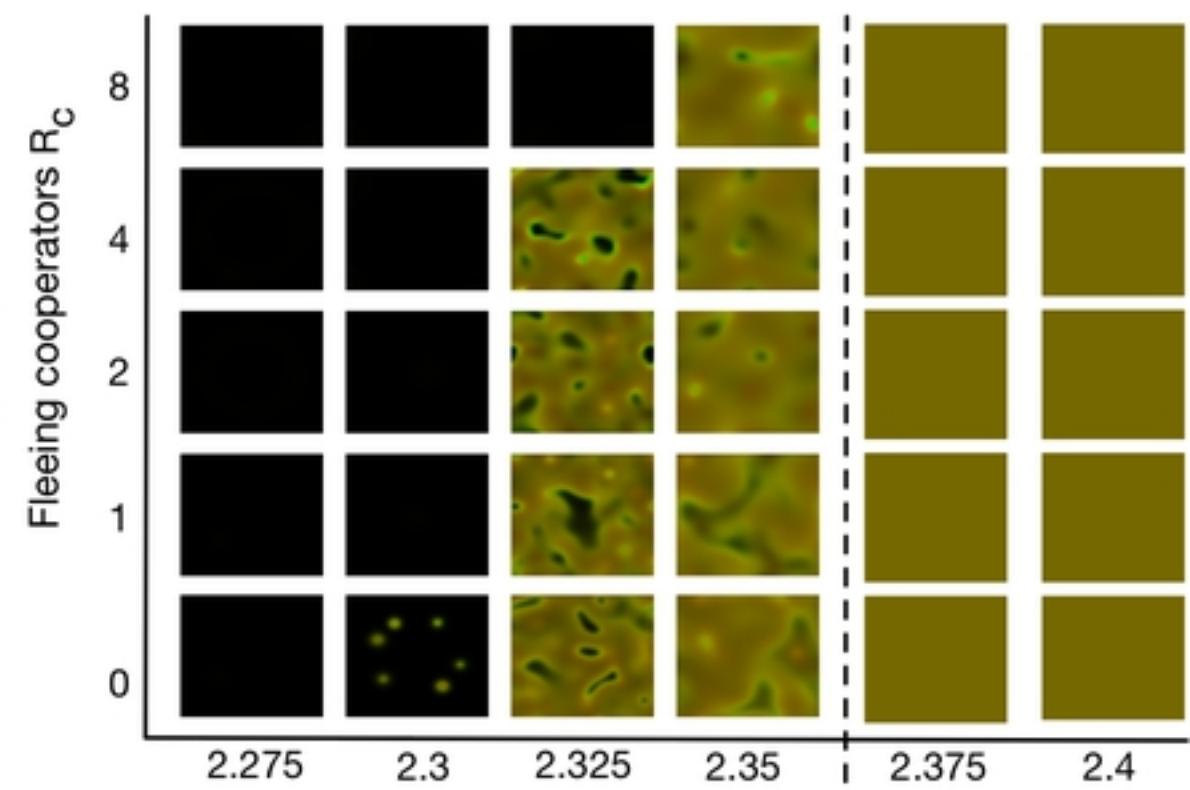
Generations  $t$

Fig1

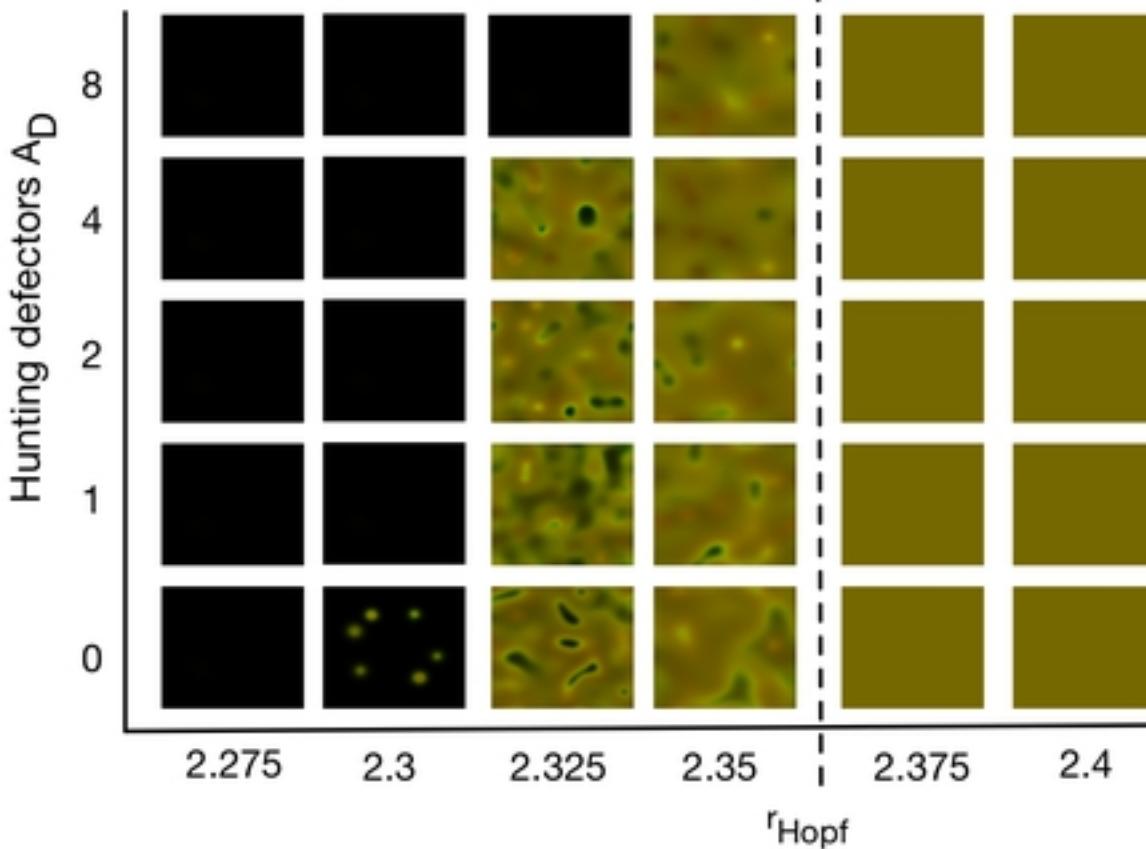
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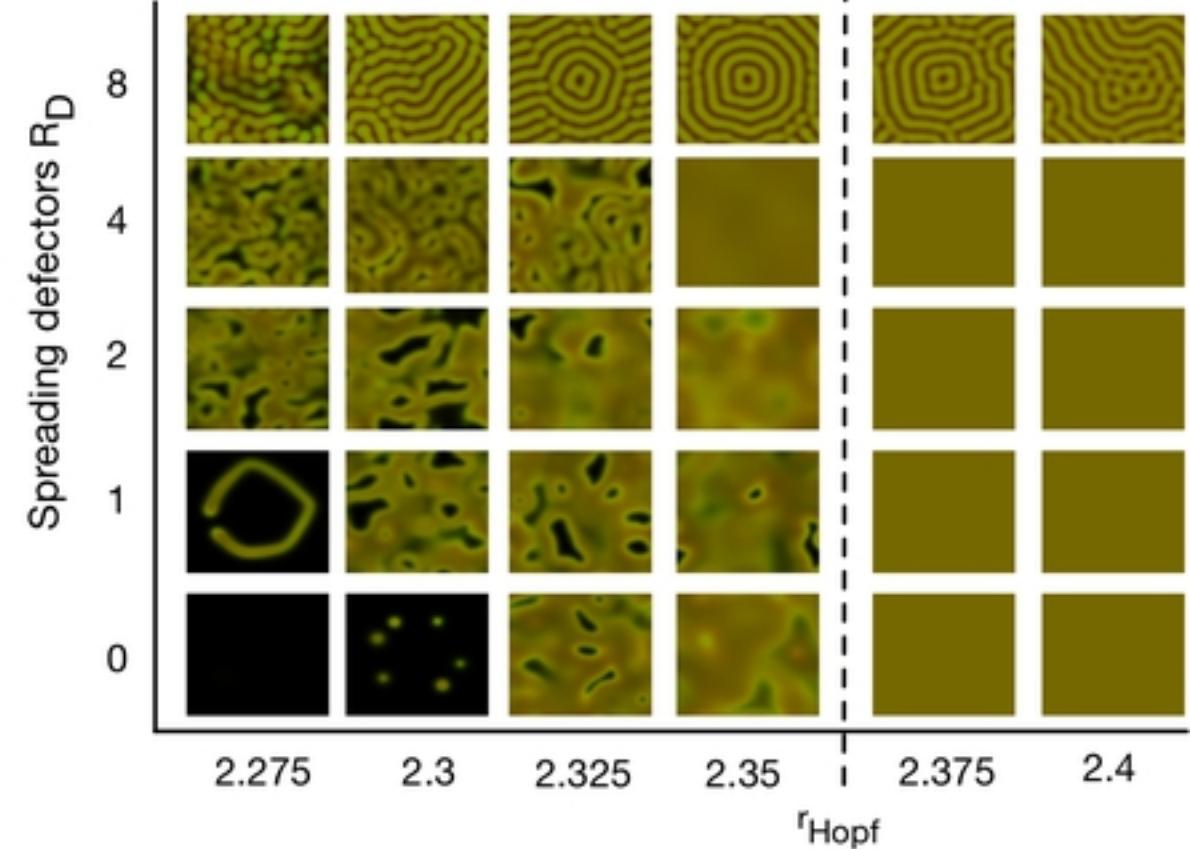


Fig2

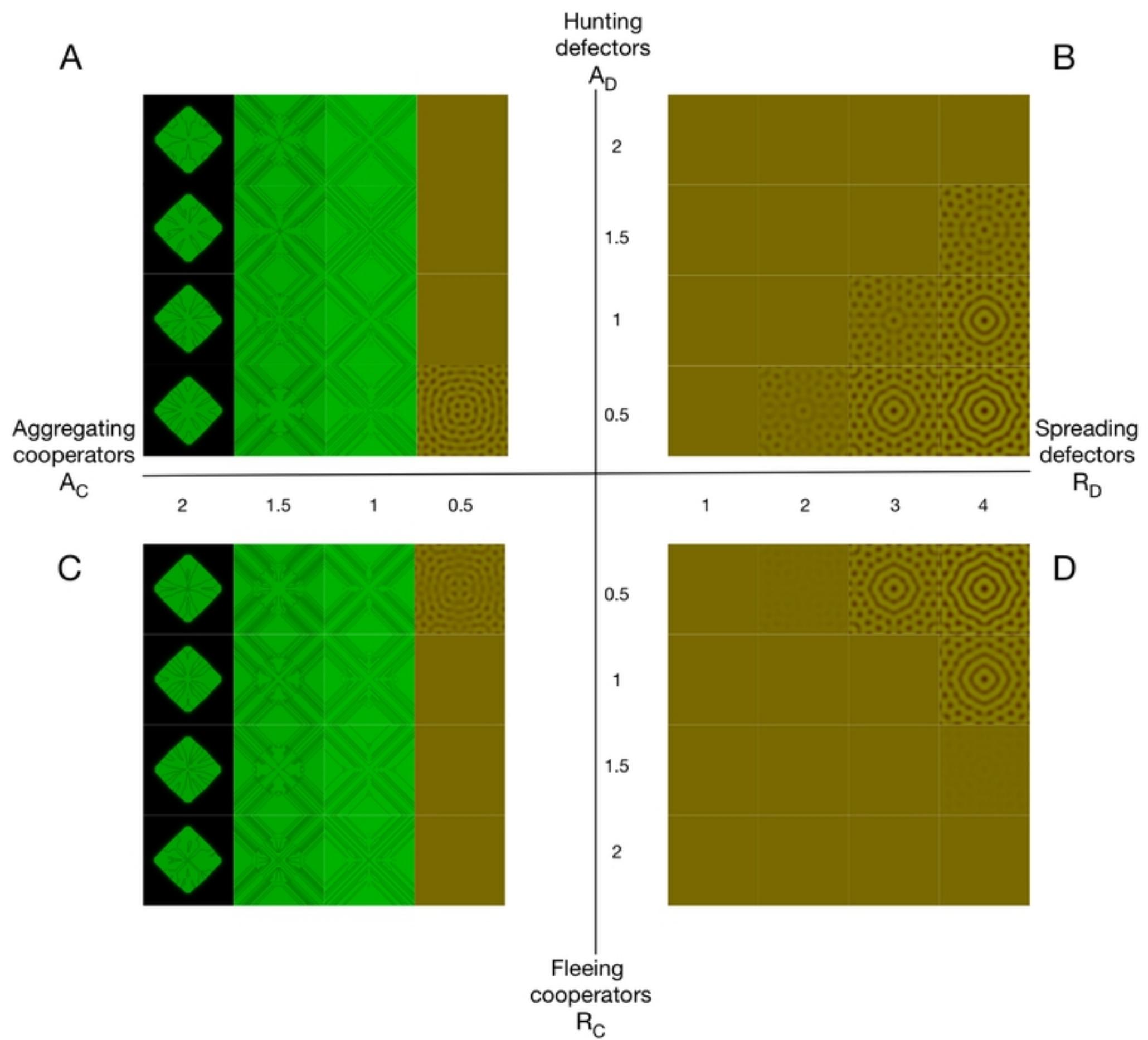


Fig3

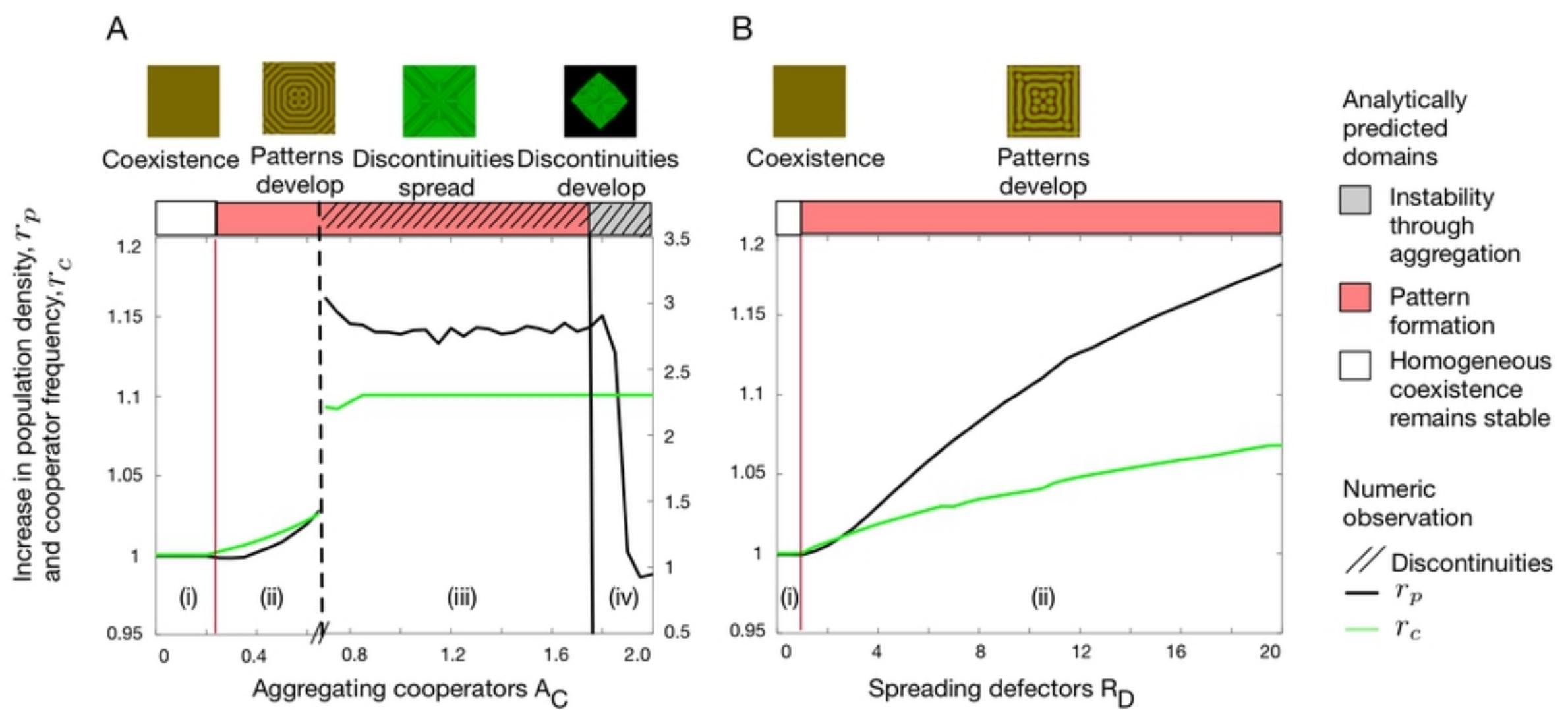


Fig4