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Behavioural strategies in cyclic models: the effects of directional movement tactics

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ABSTRACT

We investigate behavioural strategies in stochastic simulations of systems with cyclic nonhierarchical dominance, as a generalisation of the rock-paper-scissors game. We introduce directional movement tactics to one out of the species, whose individuals move according to an innate or a conditioned response to a stimulus; individuals of the other species move randomly. The directional movement tactics allow the individuals to conquer or maintain territory, either attacking or anticipating or Safeguarding themselves. We study the effects of the behavioural strategies for individuals with different levels of perception of the neighbourhood. Besides, we investigate the case where not all individuals are conditioned to perform the behavioural strategy or where individuals that do not use the tactic for every move. We found that self-preservation behaviour is more profitable in terms of population growth, where the best result is achieved for individuals with large perception radius that always move according to the movement tactic. Our findings show that the attack tactics is more gainful for short perception radius and if the individuals alternate the tactic with random movement. For anticipation, the best result is achieved for individuals with long-range perception using the tactics rarely. Finally, we calculated the coexistence probability and found that, in addition to providing a greater spatial density for the species, the Safeguarding tactic is the least jeopardising to biodiversity. Our results may be useful for experimental and theoretical biologists to understand systems of species whose individuals behave strategically, and how coexistence is maintained in an uneven scenario.

Introduction

To understand biodiversity in nature, we need to know how interactions among individuals determine the formation and stability of ecosystems¹⁻³. To study a three-species system, where species cyclically dominate each other, many authors have used the rock-paper-scissors game⁴⁻⁷. In this model, the spatial interactions are classified as mobility, reproduction, and selection - scissors cut paper, paper wraps rock, rock crushes scissors⁸⁻¹². Extensions of this cyclic model have been addressed recently either adding more species¹³⁻¹⁷ or considering that interactions between species are not entirely symmetrical¹⁸⁻²¹. In this paper, we study cyclic nonhierarchical systems where individuals of one out of species use a movement tactic according to a specific behaviour, that is associated with a response or reaction to a given stimulus^{22,23}. We consider a class of the May-Leonard model with N species, $N \geq 5$. The selection rules are illustrated in Fig.1(a) for the case $N = 5$, where the arrows indicate a cyclic dominance among the species²⁴. Accordingly, individuals of species i gain natural resources by selecting individuals of species $i + 1$, with $i = 1, \dots, N$ and the cyclic identification $i = i + \kappa N$ where k is an integer. Unlike the standard model, where individuals of all species move randomly; here, the individuals of one out of the species move according to a specific tactic to conquer or maintain territory^{25,26}.

In our model, we assume three kinds of behaviour to describe systems where individuals respond to a stimulus either instinctively (innate behaviour) or based on the experience (conditioned behaviour)²⁷. Firstly, for the innate foraging behaviour - in which food resources are exploited - we define the Attack tactic: a directional movement that allows the individuals to go straight to areas mostly occupied by the individuals that they select²⁸⁻³¹. This means that individuals of species i move towards the direction with more individuals of species $i + 1$. Secondly, assuming a conditioned behaviour as a variant of the innate foraging behaviour, we define the Anticipation tactic. As the name of the tactic suggests, individuals of species i anticipate to the arrival of individuals of species $i + 1$, going to patches where their incoming is likely. This means that individuals of species i move towards the direction with more individuals of species $i + 2$ ^{32,33}. Finally, for the innate defence behaviour - which is a response to a stimulus to prevent any damage - we define the Safeguard tactic: individuals move towards territories mostly occupied by individuals that give them protection against selection. This means that individuals of species i move towards the

Figure 1. Selection rules and movement tactics for the case $N = 5$. **(a)** Illustration of the selection rules among the species, which represents a generalisation of the rock-paper-scissors game. **(b)** Illustration of the directional movement tactics for individuals of species 1. The solid green line represents the Attack tactic, where individuals move towards the direction with more individuals of species 2. The dashed green line shows the Anticipation tactic, that is a movement towards the path with more individuals of species 3. The dashed-dotted green line illustrates how individuals move when they perform the Safeguard tactic, going towards the direction with more individuals of species 4. The concentric circumference arcs in the right panel illustrate that individuals of species 2, 3, 4, and 5 always move randomly.

direction with more individuals of species $i - 2$ ^{34–39}.

It has been suggested that some individuals cannot perform the behavioural strategies^{40–42}. This happens because they have not yet learned or, somehow, they cannot put the tactic into practice. Therefore, to make the model more realistic, we describe the ability of the individual to execute the tactic by defining a conditioning factor. We can also interpret the conditioning factor as the frequency that individuals use the directional movement tactic, instead of moving randomly. We aim to discover what conditioning factor results in a higher spatial density of species i . In general, the best direction to move is found by distinguishing each individual in the neighbourhood^{41,43,44}. As this ability can vary for different species, we run simulations for a range of perception radius^{45,46}. Finally, we investigate how behavioural strategies affect the coexistence for a wide range of mobility probabilities⁴⁷.

Figure 2. Snapshots of 500^2 simulations of the generalisation of the rock-paper-scissors game illustrated in Fig. 1. Each dot shows either an individual (according to the colour scheme in Fig. 1) or an empty site (white dot). All simulations started from the same random initial conditions, and we captured the snapshots after 5000 generations. The snapshots show the spatial patterns for the standard model **(a)**, Attack **(b)**, Anticipation **(c)**, and Safeguard **(d)** tactics, respectively. See also the videos for the whole simulation for the Standard case (<https://youtu.be/Hd1XSpbB3Ac>), Attack (<https://youtu.be/5MTclpRL638>), Anticipation (<https://youtu.be/mSJFpQpYvqU>), and Safeguard (<https://youtu.be/PWLR9v3I5bA>). The results were obtained for the same perception radius, $R = 3$.

Results

We simulate the case with $N=5$ illustrated for the cases where individuals of species 1 move randomly (standard model), or use directional movement tactics (see Methods). Figure 2 shows the spatial patterns obtained from a 500^2 simulation running for a timespan of 5000 generations. Figure 2(a), 2(b), 2(c), and 2(d) show the spatial patterns captured at $t = 5000$ for the standard model, Attack, Anticipation, and Safeguard directional movement tactics, respectively. See also the videos for the entire simulation for the standard case (<https://youtu.be/Hd1XSpbB3Ac>), Attack (<https://youtu.be/5MTclpRL638>), Anticipation

Figure 3. Temporal changes of the species densities ρ_i during the simulations presented in Fig. 2. The colours indicate the species following the scheme in Fig. 1, while the grey line shows the density of empty spaces. (a) Standard case, <https://youtu.be/Hd1XSpbB3Ac>. (b) Attack tactic, <https://youtu.be/5MTclpRL638>. (c) Anticipation tactic, <https://youtu.be/mSJFpQpYvqU>. (d) Safeguard tactic, <https://youtu.be/PWLR9v3I5bA>.

(<https://youtu.be/mSJFpQpYvqU>), and Safeguard (<https://youtu.be/PWLR9v3I5bA>). We consider the same selection, mobility, and reproduction probabilities for all species, $s = m = r = 1/3$; the perception radius was set to $R = 3$. The colours follow the scheme in Fig. 1, where green, red, orange, dark blue, and cyan dots, represent individuals of species 1, 2, 3, 4, and 5, respectively. White dots indicate empty spaces. To quantify the dynamics of the territorial dominance of the species, we computed the spatial densities ρ_i as a function of time. Figure 3(a) depicts the results for the standard model whereas Figs. 3(b), 3(c), and 3(d) show how ρ_i changes when individuals of species 1 use Attack, Anticipation, and Safeguard tactics respectively. Additionally, in Fig. 4, the effects of the behaviour on the selection risks of each species were computed by ζ_i , that shows the probability of one individual of species i disappearing within a unit time interval. Figure 4(a) depicts the case where species 1 move randomly, while Figs. 4(b), 4(c), and 4(d) show the selection risks if individuals of species 1 move according to the Attack, Anticipation, and Safeguard tactics respectively. In Figs. 3 and 4, the colours identify the species according to Fig. 1, whereas in Fig. 3 the grey line shows the density of empty spaces.

Initially, individuals of all species are distributed aleatorily on the grid. Because of the random initial condition, selection interactions are more frequent in the initial stage of the simulation, during the spatial pattern formation. According to Fig. 2(a), in the standard case, there is a symmetric formation of spirals whose adjacent arms are mostly occupied by species that do not select each other (see also video <https://youtu.be/Hd1XSpbB3Ac>). The spatial dominance is cyclic as well as the selection risks, as depicted in Fig. 3(a) and Fig. 4(a). This symmetry is broken because of the unevenness introduced when individuals of species 1 use a directional movement tactic. Firstly, if the individuals of species 1 use the Attack tactic, they have more chances of selecting because they move towards the direction with more individuals of species 2 - even though the selection probability s is the same for all species. The higher selection rate for species 1 is responsible for the alternating territorial dominance verified in the spatial pattern formation shown in the video <https://youtu.be/5MTclpRL638> (see Ref.¹⁹). When the number of individuals of species 2 decreases, the population of species 3 rises, reducing the population of species 4 and allowing the population growth of species 5. Therefore, more individuals of species 5 implies in higher selection risk of species 1, as it is showed in Fig. 4(b). As a result, although the species 1 select more, it does not dominate when choosing the Attack tactic. Instead, species 3 is more abundant, as it is depicted in Fig. 3(b). Secondly, if the individuals of species 1 use the Anticipation tactic (they go towards the direction with more individuals of species 3), species 2 is preserved, and its population grows. There is a consequent reduction of the number of individuals of species 3, allowing the population of species 4 to grow, which limits the number of individuals of species 5. Even though this scenario appears to be favourable to species 1, we verified that the fewer individuals of species 5 do not imply a less selection risk for species 1, as it is shown in Fig. 4(c). The selection risk of species 1 is high because its population growth is restricted since individuals of species 1 go apart from individuals of species 2,

Figure 4. Dynamics of the selection risks of the species densities ζ_i for the simulations presented in Fig. 2. The colours indicate the species following the scheme in Fig. 1. (a) Standard case, <https://youtu.be/Hd1XSpB3Ac>. (b) Attack tactic, <https://youtu.be/5MTclpRL638>. (c) Anticipation tactic, <https://youtu.be/mSJFpQpYvqU>. (d) Safeguard tactic, <https://youtu.be/PWLR9v3I5bA>.

which make it difficult to conquer territory (see also video <https://youtu.be/mSJFpQpYvqU>). Thirdly, if the Safeguard tactic is used, the population growth of species 1 is expected due to the protection provided by individuals of species 4 against eventual attacks of individuals of species 5. Mostly, when the individuals of species 5 approach individuals of species 1, they find guards, which destroy them. This effect is reinforced with the population growth of species 2, which controls the population size of species 3, leading to a higher abundance of individuals of species 4 - the more individuals of species 4, the more available refuges for species 1. The result is a relevant decreasing in the selection risk of the species 1, as it is depicted in Fig. 4(d). As a consequence, the density of species 1 is the highest, according to Fig. 3, that shows that species 1 dominate during the entire simulation, with species 4 being the second most abundant one. See also video <https://youtu.be/PWLR9v3I5bA>.

Autocorrelation Function

To quantify the effects of the directional movement tactics on the spatial patterns, we calculated the spatial autocorrelation function $C_i(r)$ for all species, with $i = 1, \dots, 5$ (See Methods). Figures 5(a), 5(b), and 5(c) show the spatial autocorrelation function for the cases where individuals of species 1 use the Attack, Anticipation, and Safeguard tactics, respectively. We

Figure 5. Autocorrelation functions C_i for each movement tactic. The colours follow the scheme in Fig. 1. (a), (b), and (c) depict the cases where individuals of species 1 use Attack, Anticipation, and Safeguard tactics, respectively. The results were obtained using $R = 3$. The dashed black line represents the autocorrelation function for the standard case (std), that is the same for all species. The horizontal purple dashed line indicates the threshold assumed to calculate the characteristic length.

averaged the results using the spatial patterns at $t = 5000$ generations from a set of 100 different initial conditions. We assumed $R = 3$. The dashed black line shows the autocorrelation function for the standard model, that is the same for all species. We computed the characteristic length l_i , defined as $C(l) = 0.15$ in every case, as illustrated by the purple dashed lines. If individuals of all species move randomly, $l_i = 14$, with $i = 1, \dots, 5$. However, if individuals of species 1 moves according to the Attack tactic, the characteristic length of species 1, 3, and 4 enlarges ($l_1 = 17$, $l_3 = 0.16$, and $l_4 = 0.14$) while the characteristic length of species 2 and 5 decreases ($l_2 = 12$ and $l_5 = 0.13$). For the Anticipation tactic, the characteristic length enlarges for all species ($l_1 = 18$, $l_2 = 22$, $l_3 = 22$, $l_4 = 20$, and $l_5 = 18$). Finally, for the Safeguard tactic, with exception of the species 3 whose characteristic length decreases ($l_3 = 12$), all other species have an elongation in the characteristic length ($l_1 = 16$, $l_2 = 15$, $l_4 = 16$, and $l_5 = 17$).

The Influence of the Perception Radius

To understand the role of the perception radius on the behavioural strategies, we run a series of 500^2 simulations for $1 \leq R \leq 5$. Figures 6(a), 6(b), and 6(c) depict the mean species densities $\langle \rho_i \rangle$, with $i = 0, \dots, 5$, for the Attack, Anticipation, and Safeguard tactics used by individuals of species 1, respectively. Figures 6(d), 6(e), and 6(f) depict the selection risks $\langle \zeta_i \rangle$, with $i = 0, \dots, 5$, for the Attack, Anticipation, and Safeguard tactics, respectively. The results show the averaged values of species densities and selection risks during the second half of the simulation, from a set of 100 simulations with different initial conditions (the error bars are smaller than the symbol). First, we found that $\langle \rho_i \rangle = 0.195$ and $\langle \zeta_i \rangle = 0.028$ for all species ($i = 1, \dots, 5$), and $\langle \rho_0 \rangle = 0.025$, when individuals of species 1 do not use any behavioural strategies (the standard case).

Figure 6. Mean species densities $\langle \rho_i \rangle$ and mean selection risks $\langle \zeta_i \rangle$ for a range of perception radius R . The results were averaged from a set of 500^2 simulations with 100 different random initial conditions. $R = 0$ represents the standard case. (a), (b), and (c) show $\langle \rho_i \rangle$ for Attack, Anticipation, and Safeguard tactics, respectively. (d), (e), and (f) depict $\langle \zeta_i \rangle$ for Attack, Anticipation, and Safeguard tactics, respectively. (a), (b), and (c) show $\langle \rho_i \rangle$ for Attack, Anticipation, and Safeguard tactics, respectively.

In the case of Attack tactic, the directional mobility is advantageous for species 1 for $R < 3$. Figure 6(a) shows that $\langle \rho_2 \rangle < 0.195$ for any R . In comparison with the standard case, this indicates a harmful effect on the population of species 2, benefitting species 3. Indeed, the selection risk of species 2 is always higher than in the standard model, as it is depicted in Fig. 6(d). As the perception radius grows, the damage on the population of species 2 becomes more significant. But, a higher $\langle \zeta_2 \rangle$ does not imply a growth of the population of species 1. For the Anticipation tactic, for a large R , the chances of the direction with more individuals of species 3 attracting individuals of species 1 are greater, i.e., it is more likely that individuals of species 1 discard the path with more individuals of species 2. This is propitious to species 2 conquer territory. For $R > 2$, this territorial dominance is such significant that allows that individuals of species 1 find individuals of species 2 due to the Anticipation movement tactic. However, although the Anticipation tactic represents a profit in terms of spatial density for species 1 for $R > 2$, it is not advantageous when compared with the standard mobility: $\langle \rho_1 \rangle < 0.195$ for any perception radius. Furthermore, the Anticipation movement tactic by individuals of species 1 provokes a reduction of selection risks for all species.

This effect is reflected in a lower density of empty spaces, and becomes more relevant when R enlarges. Finally, according to Fig. 6(c), the Safeguard tactic is profitable for species 1 when compared with the standard model, irrespective of R . Moreover, the larger the perception radius is, the more efficient the behavioural strategy is - the reduction of the selection risk of species 1 becomes significant. However, for $R > 3$, the high density of the species 1 results in small unavoidable population growth of species 5, which controls the population growth of species 1.

The Role of the Conditioning Factor

We studied how the proportion of conditioned individuals of species 1 influences the results. We calculated the average density of species 1, $\langle \rho_1 \rangle$ for the entire range of conditioning factor, $0 \leq \alpha \leq 1$. The results were obtained by averaging 100 different initial conditions of 500^2 simulations, running until 5000 generations (we discarded the first halves of the simulations). Figure 7 depicts the variation of $\langle \rho_1 \rangle$ in terms of α for $R = 3$, with $\alpha = 0$ representing the standard case. The results show that Anticipation tactic is disadvantageous for species 1: the spatial densities $\langle \rho_1 \rangle$ is lower than the standard case, irrespective of α . In contrast, Safeguard tactic is always gainful - the more frequently the Safeguard tactic is used, the greater the fraction of the grid is occupied by individuals of the species 1. Concerning to the Attack tactic, the results show that for $0 < \alpha < 1$, there is a growth of $\langle \rho_1 \rangle$, that is maximum for $\alpha = 0.4$.

Figure 7. Average density of species 1, $\langle \rho_1 \rangle$, in terms of the conditioning factor α . The green, pink, and yellow lines show the results for the case of individuals of species 1 moving according to Attack, Anticipation, and Safeguard directional tactics, respectively. $\alpha = 0$ represents the standard case. The results were obtained using $R = 3$.

Coexistence Probability

To observe the effects of the directional movement tactics on the biodiversity, we calculated the coexistence probability for each case. To this purpose, we performed simulations using 100^2 lattices, running until 10000 generations. We averaged the coexistence probabilities for a set of 100 initial conditions. The grey line in Figure 8 shows the coexistence probability for the standard model. The green, pink, and yellow lines show the results for individuals of species 1 using Attack, Anticipation and Safeguard directional tactics, respectively. Solid lines and dashed lines show the results for $R = 2$ and $R = 4$, respectively. Generally speaking, the chances of individuals of all species remain at the end of the simulation decrease as m grows, independent of the specific behavioural strategy. Furthermore, whether individuals of species 1 move directionally, the coexistence is less probable to maintain. The results indicate that for small R , Anticipation is the tactic that threatens the most coexistence, while for large R is Attack tactic that most puts biodiversity in risk. In both cases, Safeguard tactics is the directional movement that less endangers the coexistence.

Discussion

We investigated the stochastic model of N species, with odd $N \geq 5$. In this model, selection rules are a generalisation of the nonhierarchical cyclic rock-paper-scissors game. Based on the individual's behaviour, we explored a variety of directional movement tactics for one out of the species. Although the directional mobility of only one species, the cyclicity of the game changes the population growth for all species. The results depend on how far the individual can perceive the neighbourhood and the fraction of individuals that can perform the behavioural strategy.

For a generic number of species N , the spatial patterns are formed by spirals with N arms. The adjacent arms are mostly occupied by individuals of species that do not select each other. For example, for a system with $N = 5$ species, the spiral arms are occupied by individuals of species in the following order: $\{i + 1; i - 2; i; i + 2; i - 1\}$. For an arbitrary N , there are $(N - 3)/2$ arms between the spatial concentrations of individuals of species i and $i + 1$, with $i=0, \dots, 5..$ This means that for the Attack

Figure 8. Coexistence probability as a function of the mobility probability m . The solid grey line shows the coexistence probability for the standard model. The green, pink, and yellow lines show the results for the case of individuals of species 1 moving according to Attack, Anticipation, and Safeguard directional tactics, respectively. Solid lines and dashed lines show the results for $R = 2$ and $R = 4$, respectively.

tactic to be efficient, the perception radius R must be larger as the number of species increases. In contrast, regardless of the number of species, the efficiency of Anticipation and Safeguard tactics is not ruined for large N . The reason is that the spiral arms occupied mostly by individuals of the species i are always adjacent to the arms populated by individuals of the species $i + 2$ (immediate internal arm) and of the arms mainly formed by individuals of the species $i - 2$ (immediate external arm). However, a long-range perception improves the individuals' accuracy to identify the better region to move. In the specific case of Anticipation tactic, individuals of species i find where the individuals $i + 2$ concentrate, moving towards the opposite direction to the spiral wave propagation. This reduces the selection risks of all species, and, consequently, the density of empty spaces. On the other hand, if the Safeguard tactic is applied, groups of individuals of the $i - 2$ species are perceived, which makes individuals of species i to move towards the direction the spiral wave propagate.

We also studied the scenario where not all individuals are not conditioned to perform the directional movement tactics. The results also revealed how the spatial densities are affected whether the individuals alternate between moving directionally and walking randomly on the lattice. The most interesting case is if individuals use the Attack tactic: it is more beneficial when part of the individuals to be not aligned with behavioural strategies. For example, for $R = 3$, the better territorial dominance of species 1 occurs when 40% of individuals use the Attack tactic. This is the best scenario for the species 1 because its population will benefit from the most significant growth compared to the standard case. This may contribute for explaining the existence of species whose part of the individuals are not able to learn or perceive the neighbourhood (see^{41,42}, for example). On the other hand, for the Safeguard tactic, whether a fraction of individuals moves randomly, there is only a reduction of the effects of the behavioural strategy. We conclude that the best scenario for the Safeguard tactic is when the totality of the individuals always move directionally. Finally, for the Anticipation tactic, independent of the fraction of the conditioned individuals, there is a decline in the spatial density of species 1 when compared with the standard case. For the case of $R = 3$, the worst situation is when 70% of individuals are aligned with the tactics.

We stress that, in our model, a single species evolves into one of the movement tactics, while the others continue with random mobility. In this scenario, when an individual of the species i anticipates, it aims to arrive earlier in the areas where individuals of the species $i + 1$ will multiply. However, individuals of species $i + 1$ do not walk directly towards the place the individual of species i is waiting for them, but it depends on the stochasticity in the random movement. Suppose a different scenario, where, except for the species i , all other species uses Attack tactic. In this case, individuals of the species i are guaranteed that individuals of the species $i + 2$ will go wherever they are, intensifying the effects of the Anticipation tactics presented in this paper. Likewise, when individuals of species i use the Safeguard tactic, and every species else performs the Attack tactic, the result on population dynamics is highlighted. As individuals of species $i - 1$ chase individuals of species i , the shelter offered by individuals of the species $i - 2$ becomes more relevant. This leads to the conclusion that the effects of the Anticipation and Safeguard tactics are more significant when individuals of other species use the Attack tactics. However, this considerable effect can compromise the coexistence of species due to the cyclic nonhierarchical chain. Our outcomes show that if individuals of one out of the species move directionally, the coexistence probability decreases, independent of the tactic used. Furthermore, coexistence is more threatened for large perception radius.

To the best of our knowledge, this is the first time that simulations were performed assuming that all individuals within the perception range equally influence the directional movement tactic. Recently, some authors addressed a model for directional movement in which the individual's perception decreases exponentially with the distance⁴⁸. In that model, an individual chooses

the direction to move mostly influenced by the first immediate neighbours, independent of its perception radius. Another difference in that model is that directional mobility is the same for all species. This makes the effects of the individual's behaviour to be compensated by the cyclic dominance of the game. Here, we focused on how a directional movement tactic used by one out of the species changes all species densities and the coexistence probability.

The main result of our investigation indicates that the individual's behaviour plays a central role in population dynamics of spatial biological systems. Our statistical results are robust and reveal that the behaviour of self-preservation is more profitable in terms of population growth. The simulations showed that Safeguard is the directional movement tactic that brings more profit in terms of spatial density when compared with the standard model. More, the highest gain is achieved if: i) the perception radius of the individuals is maximum; ii) the totality of individuals always perform the Safeguard tactics. In opposite, the Attack tactic is more beneficial for the species if individuals have a short perception radius and intercalate between directional and random motion. Finally, the results suggest that Anticipation tactic is disadvantageous, independent of the perception radius and the fraction of the conditioned individuals. Our findings may be useful not only to understand population dynamics and biodiversity but also to describe complex systems in other areas of nonlinear science.

Methods

The simulations were performed in square lattices of $\mathcal{N}$ sites, with periodic boundary conditions. We assumed random initial conditions, where each grid site is empty or contains at most one individual of a species that is chosen aleatorily. The total number of individuals of species i is I_i , where $i = 1, \dots, 5$, and the total number of empty sites is I_0 . The simulations started with the same number of individuals of each species, $I_i = \mathcal{N}/5$. There is no empty space initially, $I_0 = 0$.

Our model is described by pairwise interactions: selection ($i \rightarrow j$), with $j = i + 1$; mobility ($i \rightarrow i$), where i may be either an individual of any species or an empty site; reproduction ($i \rightarrow ii$), with $i \neq j = 1, 2, 3, 4, 5$, where $\otimes$ means an empty space. We defined the selection, mobility, and reproduction probabilities as s , m and r , respectively, which are the same for all species. The interactions were implemented by assuming the Neumann neighbourhood, i.e., individuals may interact with one of their four immediate neighbours. The simulation algorithm follows three steps: i.) selecting a random occupied grid point to be the active position; ii.) drawing one of its four neighbour sites to be the passive position; iii.) randomly choosing an interaction to be executed by the individual at the active position. If the content of the active and passive positions (steps i and ii) allow the raffled interaction (step iii) to be performed, one timestep is counted. Otherwise, the three steps are redone. Once an individual of species 1 occupies the active position, and mobility interaction is sorted, the passive position in step ii is discarded: a new passive position is assumed according to the directional movement tactic. The time unit, generation, is defined as the necessary time to $\mathcal{N}$ timesteps to occur. The directional mobility is implemented by checking the content of all grid points within a disc of radius R , centred at the active position. The individual of species 1 switches position with the immediate neighbour in the direction with more individuals of the target species (species 2, 3 or 4, for Attack, Anticipation, or Safeguard tactics, respectively). In the event of a tie, a draw between the tied directions is made.

Spatial patterns were observed by capturing snapshots from a 500^2 lattice with a timespan of $t = 5000$ generations, running for $m = r = s = 1/3$. The spatial displacement of the species was studied by means of the spatial autocorrelation function, defined by

$$C(r') = \sum_{|\vec{r}'|=x+y} \frac{C(\vec{r}')}{\min(2N - (x+y+1), (x+y+1))}.$$

This function is computed from the Fourier transform of the spectral density as $C(r') = \mathcal{F}^{-1}\{S(\vec{k})\}/C(0)$, where the spectral density $S(\vec{k})$ is given by $S(\vec{k}) = \sum_{\vec{k}_x, \vec{k}_y} \phi(\vec{k})$, with $\phi(\vec{k}) = \mathcal{F}\{\phi(\vec{r}) - \langle \phi \rangle\}$. The function $\phi(\vec{r})$ represents the species in the position $\vec{r}$ in the lattice (we assumed 0, 1, 2, 3, 4, and 5, for empty sites, and individuals of species 1, 2, 3, 4, and 5, respectively). The results were averaged by analysing the spatial distribution of individuals from a set of 100 simulations, running in 500^2 lattices, at $t = 5000$ generations. The characteristic length l_i is defined as $C(l) = 0.15$.

The temporal dynamics of the system was studied by means of the species density ρ_i , defined as the fraction of the grid occupied by species i at time t , i.e., $\rho_i = I_i/\mathcal{N}$, with $i = 1, \dots, 5$. Furthermore, the selection risk ζ_i was found utilising the ratio between the number of selected individuals of species i , during a generation, and the initial amount of individuals in this interval - the results were averaged for each 50 generations. The conditioning factor, α , represents the proportion of individuals of species 1. This means that every time an individual of species 1 moves, there is a probability α of using the directional movement tactic, instead of moving randomly. The mean value of the species density and the selection risk i , $\langle \rho_i \rangle$ and $\langle \zeta_i \rangle$, were computed by averaging ρ_i and ζ_i , respectively. To average the results, we considered only the second half of each simulation. We run 100 simulations until $t = 5000$ generations in 500^2 lattices for $0 < \alpha < 1$ in intervals of $\delta \alpha = 0.1$, with $R = 3$. Finally, the coexistence was studied by performing 100 simulations in 100^2 lattices, running until 10000 generations, for $0.05 < m < 0.95$ in intervals of $\delta m = 0.05$, with $R = 2$ and $R = 4$. The coexistence probability is the percentage of the implementations in which individuals of all species are present at the end of the simulation.

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Author contributions statement

J. M. conceived the research project. B.M. performed the numerical simulations. J. M. and B.M. analysed the results, wrote and revised the manuscript.

Figures

Figure 1

Selection rules and movement tactics for the case $N = 5$. (a) Illustration of the selection rules among the species, which represents a generalisation of the rock-paper-scissors game. (b) Illustration of the directional movement tactics for individuals of species 1. The solid green line represents the Attack tactic, where individuals move towards the direction with more individuals of species 2. The dashed green line shows the Anticipation tactic, that is a movement towards the path with more individuals of species 3. The dashed-dotted green line illustrates how individuals move when they perform the Safeguard tactic, going towards the direction with more individuals of species 4. The concentric circumference arcs in the right panel illustrate that individuals of species 2, 3, 4, and 5 always move randomly.

Figure 2

Snapshots of 5002 simulations of the generalisation of the rock-paper-scissors game illustrated in Fig. 1. Each dot shows either an individual (according to the colour scheme in Fig. 1) or an empty site (white dot). All simulations started from the same random initial conditions, and we captured the snapshots

after 5000 generations. The snapshots show the spatial patterns for the standard model (a), Attack (b), Anticipation (c), and Safeguard (d) tactics, respectively. See also the videos for the whole simulation for the Standard case (<https://youtu.be/Hd1XSpbB3Ac>), Attack (<https://youtu.be/5MTclpRL638>), Anticipation (<https://youtu.be/mSJFpQpYvqU>), and Safeguard (<https://youtu.be/PWLR9v3I5bA>). The results were obtained for the same perception radius, $R = 3$.

Figure 3

Temporal changes of the species densities ρ_i during the simulations presented in Fig. 2. The colours indicate the species following the scheme in Fig. 1, while the grey line shows the density of empty spaces. (a) Standard case, <https://youtu.be/Hd1XSpbB3Ac>. (b) Attack tactic, <https://youtu.be/5MTclpRL638>. (c) Anticipation tactic, <https://youtu.be/mSJFpQpYvqU>. (d) Safeguard tactic, <https://youtu.be/PWLR9v3I5bA>.

Figure 4

Dynamics of the selection risks of the species densities z_i for the simulations presented in Fig. 2. The colours indicate the species following the scheme in Fig. 1. (a) Standard case, <https://youtu.be/Hd1XSpbB3Ac>. (b) Attack tactic, <https://youtu.be/5MTclpRL638>. (c) Anticipation tactic, <https://youtu.be/mSJFpQpYvqU>. (d) Safeguard tactic, <https://youtu.be/PWLR9v3I5bA>.

Figure 5

Autocorrelation functions C_i for each movement tactic. The colours follow the scheme in Fig. 1. (a), (b), and (c) depict the cases where individuals of species 1 use Attack, Anticipation, and Safeguard tactics, respectively. The results were obtained using $R = 3$. The dashed black line represents the autocorrelation function for the standard case (std), that is the same for all species. The horizontal purple dashed line indicates the threshold assumed to calculate the characteristic length.

Figure 6

Mean species densities h_{ri} and mean selection risks h_{zi} for a range of perception radius R . The results were averaged from a set of 5002 simulations with 100 different random initial conditions. $R = 0$ represents the standard case. (a), (b), and (c) show h_{ri} for Attack, Anticipation, and Safeguard tactics, respectively. (d), (e), and (f) depict h_{zi} for Attack, Anticipation, and Safeguard tactics, respectively. (a), (b), and (c) show h_{ri} for Attack, Anticipation, and Safeguard tactics, respectively.

Figure 7

Average density of species 1, $hr1i$, in terms of the conditioning factor a . The green, pink, and yellow lines show the results for the case of individuals of species 1 moving according to Attack, Anticipation, and Safeguard directional tactics, respectively. $a = 0$ represents the standard case. The results were obtained using $R = 3$.

Figure 8

Coexistence probability as a function of the mobility probability m . The solid grey line shows the coexistence probability for the standard model. The green, pink, and yellow lines show the results for the case of individuals of species 1 moving according to Attack, Anticipation, and Safeguard directional tactics, respectively. Solid lines and dashed lines show the results for $R = 2$ and $R = 4$, respectively.