Stabilization of biodiversity in the coevolutionary rock-paper-scissors game on complex networks

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The dynamical mechanisms that can stabilize the coexistence of species (or strategies) are of substantial interest for the maintenance of biodiversity and in sociobiological dynamics. We investigate the mean extinction time in the coevolutionary dynamics of three cyclically invading strategies for different evolutionary processes on various classes of complex networks, including random graphs, scale-free and small world networks. We find that scale-free and random graphs lead to a strong stabilization of coexistence both for the Moran process and the local Update process. The stabilization is of an order of magnitude stronger compared to a lattice topology, and is mainly caused by the degree heterogeneity of the graph. However, evolutionary processes on graphs can be defined in many variants, and we show that in a process using effective payoffs the effect of the network topology can be completely reversed. Thus, stabilization of coexistence depends on both network geometry and underlying evolutionary process.

I. INTRODUCTION

Dynamical mechanisms that stabilize cooperation have intrigued scientists from different fields for many decades, and evolutionary game theory has developed from a coining metaphor to a well-established research area with a wide range of applications from biology to behaviour [1–5]. An analogous question addresses the dynamical mechanisms that can stabilize coexistence of (biological) species or (behavioral) strategies [6]. In a biological context: how is biodiversity sustained? Here, cyclic coevolution has been suggested as to support the coexistence of strategies [7–9]. But it already has been reported that cyclic dominance alone is not enough to stabilize coexistence of strategies [8, 10]. While space (or, in ecological setting, niches) provides a means of stabilizing biodiversity, it is not the only mechanism to be taken into account. One additional way of stabilization is the introduction of a non-zero sum game, which also can stabilize finite but sufficiently large populations [11] and results in an exponential scaling of the mean first extinction time [12].

In general, the stability of the coexistence fixed point depends on several instances: firstly, on the payoff matrix [7, 11], secondly, on the population size and the underlying evolutionary process [13, 14], and thirdly, on the spatial structure of the population which can assume interaction topologies with the structure of a lattice or more general graphs. A spatial discretization of coevolutionary dynamics can lead to a stabilization of the coexistence of game theoretical strategies, compared to well mixed populations [7, 8]. This corresponds to the effect of spatial discretization in 2-strategy games, where – despite exceptions [15] – cooperative strategies can be stabilized [16, 17]. In this direction, many works deal with structured versions of the prisoners dilemma [18], where it has been shown that cooperators can coexist with defectors even in parameter regions where cooperation will never be observed in mixed populations [19, 20]. In contrast to these two-strategy evolutionary games, here we analyze the widely known rock-paper-scissors game (RPS) which includes three strategies with cyclic dominance. Such three-strategy models including cyclic dominance are well-known in game theory and related fields [8, 9, 27, 29]. In a spatially extended system, the coexistence of the three cyclically invading strategies is stabilized, even in cases where it is not stabilized in the well-mixed system [27] – but how strong is this stabilization? Are there differences between the stabilization effect on different graphs and for different processes? How does the population size influence the stabilization? To answer these questions, in this paper we examine three different update mechanisms – the frequency–dependent Moran process [30, 31], the local update process [13], and a process adapted from Szolnoki, Perc, and Danku [22] – and a broad range of complex network types as underlying structures, and, for each network type, analyze the mean extinction time (MET), i.e. the average time until one of the three strategies has gone extinct.

II. THE ROCK-PAPER-SCISSORS GAME

We consider a population of $N$ individuals or agents. $N$ is assumed to be constant all the time (although this common assumption is an approximation, and additional effects emerge, e.g., in growing populations [53]). Each individual is placed on one vertex of a graph containing $N$ vertices and can take on one of the three strategies ‘rock’, ‘paper’, or ‘scissors’. As played on schoolyards, ‘rock’ looses against ‘paper’ but wins against ‘scissors’, and cyclically permuted. In game theory, the ‘interaction kernel’ quantifying the outcome of agent collisions is cast into a payoff matrix, which reads for RPS

$$
P = \begin{pmatrix}
0 & -1 & 1 \\
1 & 0 & -1 \\
-1 & 1 & 0
\end{pmatrix},
$$

and we assume that we have a zero-sum RPS game. We now can find the total payoff for a certain individual $i$ playing strategy $S(i)$ by adding all payoffs that $i$ gets from neighbored nodes. With $L$ as the adjacency matrix (whose elements $L_{i,j}$ are 1 if two vertices $i$ and $j$ are connected by a link, and 0 otherwise), we can compute the total payoff $\pi_i$ for an individual
Now we choose a vertex \( i \) by

\[
\pi_i = \sum_{j=1,j \neq i}^{N} L_{i,j} P_{S(i),S(j)}.
\]

(2)

Assume the strategy \( S(i) \) to be \( \alpha \). Let us use the notation \( \beta \) for the strategy dominated by \( \alpha \), and \( \gamma \) for the strategy that dominates \( \alpha \), with \([0, 1, 2]\) as numerical values that represent these strategies. Then using the special structure of our payoff matrix, this term can be simplified to

\[
\pi_i = \sum_{j=1}^{N} L_{i,j} \left( \delta_{S(j),\beta} - \delta_{S(j),\gamma} \right).
\]

(3)

This total payoff can be modified for normalization issues, as we will describe in the next section, because the way of normalization varies in the different update mechanisms, defining rules after which strategy changes occur, depending on \( \pi_i \). Note that this total payoff can vary relevantly from the case of unstructured populations. For example, consider the case of a node \( i \) playing strategy \( \alpha \). Let \( j \) be the only vertex \( i \) is connected to, and let \( j \) be the only vertex that plays strategy \( \gamma \) which may dominate \( \alpha \) so that \( j \) gets a total payoff \( \pi_j = -1 \) although in the whole population there is only one agent that dominates strategy \( \alpha \). This single agent playing strategy \( \gamma \) would only have negligible influence on the payoff of \( i \) in a well mixed population, namely, reduce it by \( 1/(N-1) \).

### III. UPDATE MECHANISMS

#### A. The frequency-dependent Moran process on networks

For the first update rule we have adapted the well known frequency-dependent Moran process [30]. For normalization, we divide the total payoff \( \pi_i \) by \( k(i) \) (being the vertex degree, number of neighbors of \( i \)). So the payoff reads

\[
\pi_i = \frac{1}{k(i)} \sum_{j=1}^{N} L_{i,j} \left( \delta_{S(j),\beta} - \delta_{S(j),\gamma} \right).
\]

(4)

Now we choose a vertex \( i \) and another vertex \( j \), for which \( L_{i,j} = 1 \) holds, at random. With probability

\[
\phi_{LU}^{S(j) \rightarrow S(i)} = \frac{1}{2(1 - \omega + \omega \pi_i)}
\]

(5)

the individual on the vertex \( i \) reproduces, and its strategy replaces the strategy of the player on the vertex \( j \). Here \( \omega \) is the strength of selection and

\[
\langle \pi \rangle = \frac{1}{k(i)} \sum_{j=1}^{N} L_{i,j} \pi_j
\]

(6)

is the mean fitness of the relevant subpopulation, in our case, all neighbors of \( i \). Note that in contrast to the Moran process in well mixed populations, \( \langle \pi \rangle \) needs not to be 0 even for the case of zero-sum RPS we have analyzed here (although this still holds for the expectation value \( \langle \pi \rangle \)). Note also that the original definition of the Moran process is slightly different because one should choose an agent \( i \) for reproduction at random proportional to \( \phi_{LU} \). That means we are ensured that there is a real update event in every update step, which is not the case in our definition. Our definition is numerical cheaper because it is not necessary to compute the payoffs for all of the vertices in every time step, and it influences the time scale only by a constant factor.

#### B. Local update process on networks

As the availability of the global information \( \langle \pi \rangle \) to all individuals may often be unrealistic, one should also consider processes where only locally available information is of relevance to the dynamics. In the extreme case, only randomly selected pairs of nodes compete, as in the class of local comparison processes [24, 32–36]. From this class, we have investigated the local update process [13] as well. Here we, again, normalize the payoff of a vertex \( i \) by dividing it by the number of its neighbors. Then we again choose two linked vertices \( i \) and \( j \). With probability

\[
\phi_{LU}^{S(j) \rightarrow S(i)} = \frac{1 - \omega(\pi_a - \pi_b)}{2\Delta \pi_{max}}
\]

(7)

\( j \) changes its strategy to the strategy of \( i \). Here, \( \Delta \pi_{max} \) is the greatest possible payoff difference, that is the difference between the largest and the smallest entry in the payoff matrix.

#### C. SPD-process

As a third update rule we have modified a process introduced by Szolnoki, Perc, and Danku [22] which one could think of as a simplified version of the local update process at the first view. We choose a vertex \( i \) per random and another vertex \( j \) which is connected to \( i \) by a link also per random. In contrast to the Moran and the local update process, both payoffs are modified according to the rule

\[
\pi_{LU} = a\pi_i + (1-a)\pi_j
\]

(8)

(In the case \( a = 0 \) we again have the payoffs like in the other two processes.) Now, only if \( \pi_{LU} > \pi_j \), \( j \) reproduces with probability

\[
\phi_{SPD}^{S(i) \rightarrow S(j)} = \frac{(\pi_{LU} - \pi_j)}{\max(\pi_j - \pi_i)}
\]

(9)

proportional to the difference of the payoffs, and the strategy of vertex \( j \) replaces the strategy of vertex \( i \). The maximum in this term has to be understood as the the maximum of the possible payoff difference that two vertices with degrees \( k(i) \) and \( k(j) \) can have. This ensures the probability to always be in the range of 0 and 1. One can easily compute this maximum, so we can achieve the following:

\[
\phi_{SPD}^{S(i) \rightarrow S(j)} = \frac{\pi_{LU} - \pi_j}{2(1 + a(k_{max} - 1))}
\]

(10)

Here \( k_{max} \) is the maximum of \( k(i) \) and \( k(j) \).
FIG. 1: Realizations of five different types of networks with an average vertex degree of $\bar{k} = 4$ and a total number of vertices of $N = 25$. (a) Square lattice with periodic constraints. The half-links are clear illustrations of the periodic constraints. (b) Random regular graph. Each vertex has the same degree $\bar{k}$. (c) A connected ER-random graph. (d) Scalefree network after Barabási and Albert. The nodes placed on the square in the middle are the $k_0$ starting nodes. (e) Smallworld network after Watts and Strogatz with $p = 0.25$.

IV. INVESTIGATED NETWORKS

All networks used as an underlying topology for such a game should fulfill some common properties. They should be connected, so that we do not have some parts of the population not being linked to the rest of the population. Here, we always consider undirected and unweighted (binary) graphs. To avoid self-interactions of the agents, self-loops should be excluded. A schematic illustration of the network types used in this paper is shown in Fig. 1.

A. Regular lattice

The first step of complexity of placing vertices spatially – beyond the linear chain – is a regular square (or rectangular) lattice. Typically, each node is connected with 4 or 8 nearest neighbors. To eliminate boundary effects, we use periodic boundary conditions. This is a very simple, but in many cases not realistic model, so we have analyzed some other specific types of models that will be presented in the following subsections. For a better comparability with the regular lattice with natural connectivity of 4 or 8, we have restricted ourselves to graphs with an average vertex degree of 4 and 8.

B. Erdős-Rényi random graph

The most frequently used model of real, not lattice-like graphs in the past decades was the Erdős-Rényi (ER) random graph [37]. Here one starts with a graph with $N$ nodes and connects each pair of nodes with probability $p$. In this model the probability of finding a node with degree $k$ follows a Poisson distribution

$$P(k) = \frac{e^{-\lambda} \lambda^k}{k!},$$

where

$$\lambda = N \left( \frac{N-1}{k} \right) p^k (1-p)^{N-1-k}.$$  

The graphs we have investigated are constrained in two ways. On the one hand, they must be connected, what means that there is at least one possibly path from each node to any other so that we don’t have two or more groups of not interrelated agents. On the other hand, we restrict ourselves to networks with a mean vertex degree of 4 or 8 for better comparability with the regular lattice. Because we will need only connected graphs with a certain mean degree $\bar{k}$, and because we would find these networks only with some probability even by adjusting $p$ with respect to the number of nodes, we have used the following algorithm:

1. Start with a graph $G$ with $N$ vertices and no edges.
2. Link randomly chosen vertex pairs if they are not already linked until the total number of edges equals $N \bar{k}$. Now the mean vertex degree will equal $\bar{k}$.
3. If the graph is connected, accept it, otherwise return to step (1).

C. Random regular graph

A compromise between the random graph and the regular lattice is the random regular graph with the same degree $\bar{k}$ for all vertices but a much shorter average shortest path length than in a lattice. For generating the random regular graphs we have used an algorithm proposed by Steger and Wormald [38]. This algorithm ensures to give connected random graphs with equal degree $\bar{k}$ for all vertices:

1. Start with a graph $G$ with $N$ nodes $(1, 2, ..., n)$ and no edges.
2. Repeat the following until the set $S$ is empty: Let $S$ be the set of vertex pairs $\{u, v\}$ of $G$ that are not connected by an edge yet with both having at most degree $\bar{k} - 1$. Then choose a specific pair $\{u, v\}$ out of $S$ with probability proportional to $(\bar{k} - k(u)) (\bar{k} - k(v))$, where $k(u)$ and $k(v)$ are the degrees of $u$ and $v$ in the graph.
generated up to now. Add the edge to $G$. Delete the pair \{u, v\} from $S$.

3. If $G$ is $k$-regular (that means connected and of the same degree $k$ for all vertices), accept it, otherwise return to step (1).

The last step with the return statement is necessary because unfortunately the algorithm does not exclude the possibility of receiving disaggregated graphs (which occurs rarely) or that the last connection possibilities are only self-loops.

D. Barabási-Albert scalefree network

Many real networks, primarily huge ones, are described by the ER-model in an insufficient way. In many of these networks, for instance the internet [39], the WWW [40, 41], the network of power nodes in the west of the United States [42], the network of scientific collaborations [43], or the metabolic network of yeast [44] one observes a degree distribution that (approximately) follows a power law,

$$P(k) \propto k^{-\gamma}. \quad (13)$$

Barabási and Albert [45] have proposed the following algorithm of modelling complex real networks:

1. Start with a small number $k_0$ vertices that are all connected to each other.
2. Add another node and link it to an already present vertex with probability proportional to the degree of this vertex. Add further links in the same fashion until the new vertex has a degree $k < k_0$.
3. Repeat step (2) (until you have reached some value of $N$ you want).

In contrast to the ER-model for random graphs or the likewise frequently used Watts-Strogatz-Modell [42], see next subsection) this model incorporates two main aspects of real networks, growth and preferential attachment. Namely, most real networks do not have a fixed size but grow like the WWW [40, 41]. The WWW is also an example for the preferential attachment: When creating a new website, one will typically try to link it to well known and popular sites to gain more attention for ones own site. Because of that, the Barabási-Albert network has a high density of so-called hubs. These are vertices that are connected with many other nodes with relatively small vertex degree.

E. Small-World-Network after Watts and Strogatz

Another frequently used network model is the Small-World network. The existence of long range connections with simultaneous appearance of a high local cluster coefficient is a phenomenon often obtained in real networks [46]. The notion integrates some slightly different types of networks.

Here we have used the original model of Watts and Strogatz [42]. In their model one starts with a circle of nodes. All of them are connected with $k$ nearest neighbors ($k/2$ in the one direction and $k/2$ in the other). Afterwards, one starts with rewiring the links, beginning with an arbitrary vertex $i$ on the circle. With a certain probability $p$, $i$ is disconnected from its nearest neighbor in clockwise direction and is connected to a randomly chosen vertex $j$ that is not already linked to $i$. In this way one goes on in clockwise direction until all links to nearest neighbors have been checked for rewiring. Then one goes on with the second nearest neighbor, and so on, until all links have been checked for rewiring.

For $p \to 0$ one achieves obviously some kind of regular lattice (that is structured in a different way that the one we have used). In contrast to that, for $p \to 1$ one achieves a graph equivalent to the ER-random graph. But for intermediate values of $p$ one gets networks with high local cluster coefficients like a regular graph (or lattice), but also a small average shortest path length like a random graph [47]. For the sake of clarity, we have used $p = 0.25$ in all cases.

F. Network with Gaussian degree distribution

As a sixth type of networks, we have used a graph with a Gaussian degree distribution. This type is a compromise between the ER-random graph and the random regular graph. To generate these networks we have modified the algorithm used for the random regular graph by making the designated vertex degree $k$ dependent of $i, i = 1, 2, ..., n$. For these $k(i)$ we have used a Gaussian distribution with a standard deviation of $\sqrt{k}/3$, where $\sqrt{k}$ is the designated average vertex degree. By this choice of the standard deviation it is ensured that almost all designated degrees $k(i)$ are positive. We have ignored the few occurring non-positive (negative or 0) degrees by choosing a new designated degree in the case of such a choice.

G. Uncorrelated scalefree graph

To analyze possible effects of the vertex degree distribution in scalefree graphs after Barabási and Albert on the dynamics of our games, we have investigated the dynamics on uncorrelated scalefree graphs as well. For the construction of such networks we have used the algorithm described in the preceding subsection (IV E) with a power law degree distribution identical with the distribution of vertex degrees of the Barabási-Albert scalefree graph instead of a Gaussian distribution. To avoid confusion, we will refer to this graph short as uncorrelated. If we refer to scalefree graphs (without mentioning anything about the correlation) we always consider the Barabási-Albert network.

V. MEAN EXTINCTION TIMES

We have carried out extensive simulations to obtain the mean time until one of the three strategies has gone extinct.
when starting with each of the strategies having the same frequency $N/3$ (this requires that $N$ is an integer multiple of three). After the first strategy has vanished, the game lacks its cyclic dominance, and we return to the two strategy case which is well known and will end up in a much shorter time in a single-strategy steady-state because one of the two remaining strategies definitely dominates the second. Note that we measure time in units of single update steps instead of Monte Carlo steps, where on average each agent has been updated in one time step, so there is a factor of $N$ between these two time scales.

A. Mean extinction time in well mixed populations

First, let us consider the case of well mixed populations for comparison, which is identical to the case of fully connected graphs (that means each vertex is directly linked to any of the $N - 1$ others). We have to distinguish between two cases: the Moran and the local update process on the one hand, and the SPD-process on the other hand.

1. Moran and local update process in mixed populations

In well-mixed populations, the Moran and local update process have been shown in [13] to have the adjusted replicator equation [48] and the standard replicator equation [3] as limits as $N$ goes to infinity. They both have a neutrally stable (for the zero-sum RPS) fixed point in the state space of strategy densities at $(\frac{N}{3}, \frac{N}{3}, \frac{N}{3})$. For any other point inside of the simplex, both replicator equations predict neutrally stable oscillations around this fixed point, but in the case of finite populations the population can run out of the fixed point and the orbits around it because of stochastical fluctuations, and end up on the edge of the simplex $S_1$ which is the boundary of the state space. A point on the edge of this simplex corresponds to the extinction of at least one of the three strategies (there are three points on the boundary corresponding to the survival of only one strategy). So we expect the MET of this system to tend to infinity as $N \to \infty$. But at this point there are still two open questions: What is the exact scaling dependence of the MET on $N$? And how does the selection strength $\omega$ influence this dependence?

Our simulations give clear and short answers for both questions: In the zero-sum RPS game, the MET is proportional to $N^2$ (in single birth-death update steps, corresponding to $N$ Monte Carlo steps), and independent of $\omega$ (both is different in the non zero-sum RPS case). For both processes, Moran and local update process as well, we have found the mean extinction time $t_{ext}$ to scale as [12]

$$\langle t_{ext} \rangle = 0.54(\pm 0.02)N^2.$$  \hspace{1cm} (14)

2. SPD-process in mixed populations

As this process has never been defined for unstructured populations let us use the complete graph as a model for the mixed population for simplicity, so that we do not have the risk of making any alterations to this update rule if re-defining it. Now we find that, when starting with $(\frac{N}{3}, \frac{N}{3}, \frac{N}{3})$, each node has as many neighbors of the dominating strategy as of the dominated one, namely $N/3$. Because of the structure of the payoff matrix the fitness is identical to zero for every strategy and node. So the condition that the second chosen vertex has a greater fitness than the first is never fulfilled, and one will never observe a change in the strategy densities. For this reason the MET becomes infinite even in finite populations (at least when starting in the point $(\frac{N}{3}, \frac{N}{3}, \frac{N}{3})$; even when starting in some neighbourhood point in the state space we would only achieve some conditional mean extinction time).

B. Moran process on networks

From the results of our simulations (see Fig. 2), there are two immediate main observations: First, for some networks biodiversity is greatly stabilized as the MET increases exponentially with $N$, while for other networks biodiversity is only slightly stabilized or even destabilized. Second, the MET is no longer independent of the selection strength $\omega$ even in the zero-sum RPS case that we have considered here. Stabilizing effects of the underlying structure are more distinct for greater $\omega$.

Great stabilization of the biodiversity is only observed for networks with a heterogenous degree distribution and strong selection, while for networks with homogenous degree distribution we have no such strong stabilization. In fact, the networks with homogenous degree distribution can even lead to a slight destabilization of biodiversity for strong selection, as the MET grows slower than $N^2$, as we can see for the random regular graph. Even in the cases of the small world and the Gaussian network, which both have a small heterogeneity in their degree distribution, we have such a destabilization. Only for the square lattice we have a stabilization (although the lattice has a homogenous degree distribution, of course), but the stabilization is much weaker than in case of the random graph or the two scalefree networks. For the stabilization on the lattice, the large average shortest path length might play a role (which is proportional to $\sqrt{N}$ instead of $\log N$ as for random networks [49]).

For small $\omega$, there is not a great change in the behaviour of the MET on all networks compared to unstructured populations (Fig. 2). Also, the correlation strength of the network degrees has only minor effect of the stabilization of biodiversity. The MET for an uncorrelated scalefree graph is, in all cases considered here, somewhat smaller than for the Barabási-Albert scalefree graph, but in comparison to the other effects, mainly the enormous stabilization impact of scalefree networks, this is negligible.
FIG. 2: (Color online.) Mean extinction times of the Moran process on networks. The plots are semi-logarithmic over $N$, and the MET is divided by $N^2$ for a better comparison with the result of well mixed populations and to better discern stabilizing effects. Red circles: $\bar{k} = 4$, $\omega = 0.05$, orange squares: $\bar{k} = 4$, $\omega = 0.40$, green rhombi: $\bar{k} = 8$, $\omega = 0.05$; blue triangles: $\bar{k} = 8$, $\omega = 0.40$, black points: well mixed population. Red circles on the upper edge of a plot in connection with a curve of a different colour mark are only marks that the curve is going on further, but it isn’t depicted for a better presentation. Averages are taken over a sample of 100 runs ($N > 400$) or 1000 runs ($N = 1000$).
**C. Local update process on networks**

One of our main points of interest was whether the evolutionary process itself influences the MET in the case of a networked population. The corresponding results for the Local Update are shown in Fig. 3. There is no qualitative difference between the results in the Moran process and in the Local Update process. Same as for the Moran process, heterogeneous degree distributions cause an enormous stabilization of the biodiversity for strong selection (the MET grows exponentially with $N$), while homogenous degree distributions do not. The MET is now dependent on the selection strength as well, and for small $\omega$ it is proportional to $N^2$ as in the neutral case. The only difference is that stabilizing effects are not as strong as in the Moran process for the same or even a bit larger $\omega$.

**D. SPD-process on networks**

The SPD-process behaves completely different, as shown in Fig. 4. We recall that for this update rule the quite general observation that spatial discretization can lead to a stabilization of biodiversity does not hold. Even ignoring this and taking a MET scaling for large $N$ like the $N^2$ scaling from Moran process and Local Update as reference, for all studied graphs except the lattice we have a destabilization, and the MET grows slower than $N^2$ with only small differences between the different networks. Only in the lattice case the MET grows exponentially with $N$.

Changing the parameter $\alpha$ has minor influence on the properties of the MET than the selection strength $\omega$ in the Moran and the Local Update process. For degree homogenous networks, the MET is even independent of $\alpha$. For networks with a strong heterogeneity in the degree distribution the MET grows with $\alpha$ for the same value of $N$.

There is also some influence of the correlation of network degrees. For the uncorrelated scalefree network, the influence of the parameter $\alpha$ on the MET is not as great as for the Barabási-Albert network, and the METs for the same $N$, but different $\alpha$ and $\beta$ are closer together. But compared to the other effects, this is again negligible.

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**VI. THEORETICAL APPROACH**

**A. Moran process**

1. **General case**

For a version of the RPS game with constant reaction rates it has already been shown that networks with heterogeneous degree distribution effect a stabilization of biodiversity [50]. This corresponds with our simulation results so we have adapted the approach from [50] to underpin the shown behaviour theoretically.

First let us define the probability density of the strategy $\alpha$ on all nodes with degree $k$ as $\rho_{\alpha,k}$, where $\alpha = (0, 1, 2)$. Here we again use the notation $\alpha$ for an arbitrary strategy, $\beta$ for the strategy dominated by $\alpha$, and $\gamma$ for the dominating strategy. Then the probability $\theta_{\alpha'}$ that a neighbored node of an arbitrary vertex plays strategy $\alpha'$ reads

$$\theta_{\alpha'} = \sum_{k'} k' p_{k'} \rho_{\alpha'}/\langle k \rangle. \quad (15)$$

Here $p_k$ is the probability of finding a vertex with degree $k$. Dividing by the average vertex degree, $(k) = \sum_k k p_k$, assures the standardization. Further, by the conservation of the total density one of the quantities $\rho_{\alpha,k}$ and of $\theta_{\alpha}$ is given so that we can eliminate $\rho_{2,k}$ and $\theta_2$ using $\rho_{0,k}$ and $\rho_{1,k}$ as variables, or $\theta_0$ and $\theta_1$, respectively

$$\rho_{2,k} = 1 - \rho_{0,k} - \rho_{1,k} \quad (16)$$

$$\theta_2 = 1 - \theta_0 - \theta_1 \quad (17)$$

The average payoff of a player of strategy $\alpha$ on a node with degree $k$ is then given by

$$\pi_{\alpha,k} = \theta_\beta - \theta_\gamma \quad (18)$$

We find that the average payoff is independent of the vertex degree $k$ so we can drop the index $k$. $\pi_{\alpha,k} = \pi_\alpha$. With this we can compute the average payoff of neighbours of a vertex

$$\langle \pi \rangle = \sum_{\alpha=0}^2 \sum_k \pi_{\alpha} p_{k} k \rho_{\alpha,k}/ k = \frac{2}{\sum_{\alpha=0}^2 \sum_{k'} \pi_{\alpha} p_{k'} k' \rho_{\alpha,k'}}$$

$$= \sum_{\alpha=0}^2 \sum_{k'} (\theta_\beta - \theta_\gamma) k' p_{k'} \rho_{\alpha'}/\langle k \rangle$$

$$= \sum_{\alpha=0}^2 (\theta_\beta - \theta_\gamma) \theta_{\alpha}. \quad (19)$$

By using $k' p_{k'} \rho_{\alpha'}/\langle k \rangle$ instead of $p_{k'}$ we consider that is more likely to have a vertex with a high degree as a neighbour than one with a smaller degree if both are equally frequent. Thus we find the probability for a player with strategy $\alpha$ sitting on a node with degree $k$ to reproduce as

$$w_{\alpha,k} = \frac{1}{2} p_k \rho_{\alpha,k} \frac{1 - k - \omega + \omega \pi_{\alpha}}{1 - \omega + \omega \langle \pi \rangle}. \quad (20)$$

and the rate with that a player of strategy $\alpha$ sitting on a vertex with degree $k$ conveys his strategy to a node with degree $k'$, which has played strategy $\alpha'$ before, reads

$$T_{\alpha' \rightarrow \alpha}^{k,k'} = \frac{p_k \rho_{\alpha',k'}}{\langle k \rangle} w_{\alpha,k}$$

$$= \frac{1}{2} \frac{p_k \rho_{\alpha,k'}}{\langle k \rangle} p_k \rho_{\alpha,k} \frac{1 - k - \omega + \omega \pi_{\alpha}}{1 - \omega + \omega \langle \pi \rangle}$$

For $p_k = \delta_{k,k_0}$ ($\delta_{k,k_0}$ is the Kronecker symbol) this reduces to

$$\frac{1}{2} T_{\alpha' \rightarrow \alpha} = \rho_{\alpha} \rho_{\alpha'} \frac{1 - k - \omega + \omega \pi_{\alpha}}{1 - \omega + \omega \langle \pi \rangle}. \quad (22)$$
FIG. 3: (Color online.) Mean extinction times of the local update process on networks. The plots are semi-logarithmic over $N$, and the MET is divided by $N^2$ for a better comparison with the result of well mixed populations and to better discern stabilizing effects. Red circles: $\overline{k} = 4$, $\omega = 0.05$, orange squares: $\overline{k} = 4$, $\omega = 0.50$, green rhombi: $\overline{k} = 8$, $\omega = 0.05$, blue triangles: $\overline{k} = 8$, $\omega = 0.50$, black points: well mixed population. Red circles on the upper edge of a plot in connection with a curve of a different colour marks that the curve is going on further, but it isn’t depicted for a better presentation.
FIG. 4: (Color online.) Mean extinction times of the SPD-process on networks. The plots are semi-logarithmic over $N$, and the MET is divided by $N^2$ for a better comparison with the result of the other processes. Red circles: $\overline{\kappa} = 4$, $\alpha = 0.0$, orange squares: $\overline{\kappa} = 4$, $\alpha = 1.0$, green rhombi: $\overline{\kappa} = 8$, $\alpha = 0.0$, blue triangles: $\overline{\kappa} = 8$, $\alpha = 1.0$. 

Here we have omitted any $k$-indices because there is only one degree left. The payoffs reduce to $\pi_\alpha = \rho_\beta - \rho_\gamma$ and $\langle \pi \rangle = \sum_{\alpha=0}^{2} \pi_\alpha \rho_\alpha$, and one obeys the hopping rates for the Moran process in well mixed populations [11] independent of $k_0$. This rate describes how likely it is that a player with strategy $\alpha'$ is replaced by a copy of another player with strategy $\alpha$ in a single time step.

Let us now consider a heterogenous degree distribution. In the simplest case, such a distribution consists of only two degrees $k_1$ and $k_2$ with frequencies $p_1 = p$ and $p_2 = 1 - p_1 = 1 - p$, respectively. The replicator equation that we obtain from the master equation in the limit $N \to \infty$ for the changing of the frequency of the strategy 0 on nodes with degree $k_1$ reads (for the methodology see e.g. [13 51 52]):

$$\dot{\rho}_{0,k_1} = T_{k_1 \to 0} \rho_{k_1} + T_{k_1 \to 0} \rho_{k_1} - T_{0 \to k_1} \rho_{k_1} - T_{0 \to k_1} \rho_{k_1} + T_{k_1 \to k_2} \rho_{k_1} - T_{k_1 \to k_2} \rho_{k_1} - T_{k_2 \to k_1} \rho_{k_1} - T_{k_2 \to k_1} \rho_{k_1}.$$

Inserting our special degree distribution, after a longish but straightforward calculation we find

$$\dot{\rho}_{0,k_1} = \rho_{0,k_1} \frac{k_1 p^2}{2(k_1 + (\langle \pi \rangle_1)} (\pi_0 - (\pi)_1) + \frac{k_1 p(1-p)}{2(k_1 + (\langle \pi \rangle_1)} (\pi_0 - (\pi)_1) + \rho_{0,k_2} \pi_0 - \rho_{0,k_1} (\pi)_2.$$

Here $\Gamma = \frac{1 - \omega}{\omega}$ is the background fitness, $\langle \pi \rangle_1 = \pi_0 \rho_{0,k_1} + \pi_1 \rho_{1,k_1} + \pi_2 \rho_{2,k_1}$ is the mean fitness of all players on vertices with degree $k_1$, and $\langle \pi \rangle_2$ correspondingly for $k_2$. Then one can compute the other equations in an analytical way or by cyclically permuting the indices. For each vertex degree, one of the equations of motion needs not to be taken into account by the constraint $\rho_{0,k_1} + \rho_{1,k_1} + \rho_{2,k_1} = 1$. For $k_1 = k_2$ or alternatively $p = 1$ this flattens to the well known adjusted replicator equation in the case of well mixed populations, as expected [13 14]. Likewise, the fixed point of this replicator equation at $\langle \pi \rangle_1$ does not alter, we now just have two densities for every strategy. But now the velocity of the reaction is directly dependent of $\omega$ because it is no longer possible to absorb the strength of selection by a dynamical rescaling of time, as it is possible for well mixed populations.

But what about the stability of this inner fixed point? Within a linear stability analysis, let us linearize the replicator equation around its fixed point

$$\dot{\rho} = A \rho,$$

with $\rho = (\rho_{0,k_1}, \rho_{1,k_1}, \rho_{0,k_2}, \rho_{1,k_2})$ and $A$ being the Jacobian of the system with $A_{ij} = \frac{\partial \rho_i}{\partial \rho_j} |_{\rho=0}$. In our case, we find $A$ as

$$A = \begin{pmatrix} k_1 (p-1)p & k_1 p^2 & k_1 (p-1)p & k_1 p^2 \\ 2(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) & 2(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) \\ k_1 p^2 & k_1 p^2 & k_1 p^2 & k_1 p^2 \\ 6(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) \\ k_2 (p-1)p & k_2 (p-1)p & k_2 (p-1)p & k_2 (p-1)p \\ 2(k_1 + (\langle \pi \rangle_1)) & 2(k_1 + (\langle \pi \rangle_1)) & 2(k_1 + (\langle \pi \rangle_1)) & 2(k_1 + (\langle \pi \rangle_1)) \\ k_1 k_2 (p-1)p & k_1 k_2 (p-1)p & k_1 k_2 (p-1)p & k_1 k_2 (p-1)p \\ 6(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) & 6(k_1 + (\langle \pi \rangle_1)) \end{pmatrix}.$$

To reason about the stability we need to know the signs of the real parts of the eigenvalues $\lambda_i$ of this matrix, but for these eigenvalues we derive quite complicated terms, the signs of which cannot be easily designated (but see Appendix A). The Routh-Hurwitz criterion as an alternative solution does not simplify the situation considerably.

Approximating an upper bound of the real parts of all eigenvalues, it is possible to compute a region in the parameter space where the inner fixed point is guaranteed to be asymptotically stable, namely, for

$$0.5 \leq p < \frac{k_{\max} + k_{\min}}{k_{\max} + k_{\min} + 3 k_{\min}}, \quad (27)$$

For a given value of $p$ this determines the ratio of $k_{\max}$ and $k_{\min}$, or, the other way round, if we want to build up a network with chosen values for $k_{\max}$ and $k_{\min}$, this inequality tells us what frequencies of both vertex degrees are necessary to stabilize biodiversity. So, for example, if we choose $k_1 = 4$ and both vertex degrees should be equally frequent, $k_2$ must be at least 7 to fulfill this inequality. If a higher frequency of $k_1$ is desired, $k_2$ must even be larger.

But as this is just a rough approximation, by inserting numerical values we have found that almost all eigenvalues are $< 0$, except for the trivial cases $k_1 = k_2$, $p = 0$ or $p = 1$. So for all values except these mentioned cases, we have found the fixed point to be asymptotically stable. Here, we have found numerically that the real parts of the eigenvalues become more negative as the difference of $k_1$ and $k_2$ grows in absolute size, and both vertex degrees become equally likely to be found in the network. This explains as well why the stabilization of biodiversity is greater in the case of the scale-free graphs than for the ER-random graph, or it is in both cases greater than for the network with a gaussian degree distribution, which has only as small heterogeneity in its degree distribution.

### 2. Small selection limit

As we have seen in the previous section, for small $\omega$ the MET is almost proportional to $N^2$ as in the well mixed case, and depends only marginally on the underlying network structure. We can intuitively understand this as follows: If $\omega$ is small, than every transition probability is $\approx \frac{1}{2}$, and the corresponding replicator equation in our system reads

$$\dot{\rho}_{\alpha,k} = 0 \quad (28)$$

for all values of $\alpha$ and $k$. Hence, each point of the state space is a neutrally stable fixed point in the limit $N \to \infty$. Therefore there should be no stabilization impact compared to the well mixed case, as there each point in the simplex belongs to a neutrally stable limit cycle, so in both cases a perturbation is neither expected to decay nor to grow in time.

### 3. Local update process

Following the same scheme as for the Moran process, one can derive similar results (see Appendix B for details). As in
are too byzantine for catching the signs of the real parts easily. In the case of both chosen vertices having the same degree, the probability for the node \(i\) to change its strategy to the strategy of \(j\) simplifies to

\[
W_{S(i)\rightarrow S(j)}|_{a=0} = \frac{\pi_j - \pi_i}{2k_{max}}.
\]

(29)

So for the lattice and the random regular graph, where all vertex degrees are the same, any dependence of \(a\) drops out. Note that in this equation and in this whole subsection, when talking about \(\pi_i\) we consider the not modified payoffs. For \(a = 1\) one achieves the same term as in the case of degree homogeneous networks (eq. 29), independent of the network, while for \(a = 0\) we find

\[
W_{S(i)\rightarrow S(j)}|_{a=0} = \frac{\pi_j - \pi_i}{2k_{max}}.
\]

(30)

or

\[
W_{S(i)\rightarrow S(j)}|_{a=0} = \frac{p_{ij}}{k_{max}} - \frac{\pi_i}{2k(i)},
\]

(31)

respectively, depending on which of the vertex degrees is greater. If we compare the probabilities for \(a = 1\) and for \(a = 0\) by computing the ratio of both, we can analyze the impact of the parameter \(a\) and the underlying network structure on the MET. We find

\[
\frac{W_{S(i)\rightarrow S(j)}|_{a=1}}{W_{S(i)\rightarrow S(j)}|_{a=0}} = \frac{k(j)(\pi_i - \pi_j)}{k(j)\pi_i - k_{max}\pi_j},
\]

(32)

FIG. 5: (Color online.) A plot of a numerical solution of the replicator equation for the local update process on a network with only two different vertex degrees (eq. 32) with \(p = 0.5\), \(k_1 = 4, k_2 = 8, \omega = 0.4, \rho_{0,k_1}(0) = 0.65, \rho_{1,k_1}(0) = 0.3, \rho_{0,k_2}(0) = 0.3, \rho_{1,k_2}(0) = 0.1\), red for the density of strategy 0 on nodes with degree \(k_1\), black for the corresponding value on vertices with degree \(k_2\).

C. SPD-process

For this update process, we will use a simpler method to achieve a theoretical understanding of some of the numerical results. In the case of both chosen vertices having the same degree, the probability for the node \(i\) to change its strategy to the strategy of \(j\) simplifies to

\[
W_{S(i)\rightarrow S(j)}|_{h(i)=h(j)} = \frac{\pi_j - \pi_i}{2k_{max}}.
\]

(33)

Hence on degree-heterogenous networks the MET should be greater for \(a = 1\) than for \(a = 0\), as it is confirmed by the simulation results (Fig. 4).

VII. CONCLUSIONS

Cyclic coevolutionary dynamics manifests an interesting class of dynamical systems that are discussed as models to explain long-term stabilization of coexistence of species or strategies. In this paper we have shown that, for the coevolutionary RPS game on complex networks, there are considerable differences in the mean extinction time (MET) between different networks, and for different processes as well. The simple statement “Spatial discretization stabilizes biodiversity” must be refined in a more sophisticated way. While for example in the Moran and in the local update process degree-heterogenous networks preserve biodiversity (the MET grows exponentially with the number \(N\) of players), in the SPD-process they do not, and even degree-homogeneous networks may destabilize while the lattice still stabilizes. In summary, we have shown that, for the cyclic evolutionary RPS on networks, there is a striking influence on the mean extinction time characteristics of the spatial structure and the update rule as well.
Appendix A: Eigenvalues of the Jacobian in equation (20)

With the help of (e.g.) Mathematica™ one can easily compute the eigenvalues $\lambda_i$ of the Jacobian in equation (20):

$$\lambda_1 = -\frac{1}{12(k)^2\Gamma} \left( i \left( k^2_1(p-1)^2 + k^2_2p^2 \right) \right)$$  \hspace{1cm} \text{(A1)}

$$-3(k_1 + k_2)(p-1)p\Gamma + \sqrt{c_1 - ic_2}$$

$$\lambda_2 = \frac{1}{12(k)^2\Gamma} \left( -i \left( k^2_1(p-1)^2 + k^2_2p^2 \right) \right)$$  \hspace{1cm} \text{(A2)}

$$+3(k_1 + k_2)(p-1)p\Gamma + \sqrt{c_1 - ic_2}$$

$$\lambda_3 = \frac{1}{12(k)^2\Gamma} \left( ik^2_2(p-1)^2 + 3k_2(p)\Gamma(p-1) \right)$$

$$+k_1p(ik_1p + 3(k)(p-1)\Gamma) - \sqrt{c_1 + ic_2}$$  \hspace{1cm} \text{(A3)}

$$\lambda_4 = \frac{1}{12(k)^2\Gamma} \left( ik^2_2(p-1)^2 + 3k_2(p)\Gamma(p-1) \right)$$

$$+k_1p(ik_1p + 3(k)(p-1)\Gamma) + \sqrt{c_1 + ic_2}$$  \hspace{1cm} \text{(A4)}

with the abbreviations

$$c_1 = \left( k^2_1(p-1)^2 + k^2_2p^2 \right)^2$$  \hspace{1cm} \text{(A5)}

$$+9(k_1 + k_2)^2(k)(p-1)^2p^2\Gamma^2$$

$$c_2 = 6k(p-1)p(p^2k_1^2 + k_2(p-2)p)k^2$$  \hspace{1cm} \text{(A6)}

$$+k_2^2(p - 1)k + k_2^2(p-1)^2 \Gamma.$$

The real parts $\Re \lambda_i$ of these eigenvalues are then given by

$$\Re \lambda_1 = \frac{k_1p^2}{4(k)} + \frac{k_2p^2}{4(k)} - \frac{k_1p}{4(k)} - \frac{k_2p}{4(k)} \cos \left( \frac{1}{2} \arg(c_1 - ic_2) \right) \sqrt{c_1^2 + c_2^2}$$ \hspace{1cm} \text{(A7)}

$$\Re \lambda_2 = \frac{k_1p^2}{4(k)} + \frac{k_2p^2}{4(k)} - \frac{k_1p}{4(k)} - \frac{k_2p}{4(k)} \cos \left( \frac{1}{2} \arg(c_1 + ic_2) \right) \sqrt{c_1^2 + c_2^2}$$ \hspace{1cm} \text{(A8)}

$$\Re \lambda_3 = \frac{k_1p^2}{4(k)} + \frac{k_2p^2}{4(k)} - \frac{k_1p}{4(k)} - \frac{k_2p}{4(k)} \cos \left( \frac{1}{2} \arg(c_1 + ic_2) \right) \sqrt{c_1^2 + c_2^2}$$ \hspace{1cm} \text{(A9)}

$$\Re \lambda_4 = \frac{k_1p^2}{4(k)} + \frac{k_2p^2}{4(k)} - \frac{k_1p}{4(k)} - \frac{k_2p}{4(k)} \cos \left( \frac{1}{2} \arg(c_1 + ic_2) \right) \sqrt{c_1^2 + c_2^2}$$ \hspace{1cm} \text{(A10)}

Here, $\arg(z)$ is the argument of the complex number $z$. The sum of the first four terms negative in each case because $0 < p < 1$ and for this reason $p^2 < p$. The problem is the last summand, but it is possible to make a rough approximation of where all real parts are negative. As $\sqrt{c_1^2 + c_2^2} > 0$ and

$$-1 \leq \cos(x) \leq 1,$$ all real parts are smaller than

$$\frac{k_1p^2}{4(k)} + \frac{k_2p^2}{4(k)} - \frac{k_1p}{4(k)} - \frac{k_2p}{4(k)} + \sqrt{c_1^2 + c_2^2}$$  \hspace{1cm} \text{(A11)}$$

Inserting $c_1$ and $c_2$ and assuming $p \geq 0.5$ without loss of generality, one can approximate the fourth root in the last term by

$$\sqrt{c_1^2 + c_2^2} = (36\delta^2(1-p)^2\Gamma^2 + (-2 + p)$$

$$pk_1^2k_2 + (1 + p^2)k_1k_2 + (1 - p)^2k_2^2)$$

$$+ (-k^2(1-p)^2\Gamma^2(k_1 + k_2)^2$$

$$+ (p^2k_1^2 + (1 - p)^2k_2^2)^2) \frac{1}{2}$$

$$< (36\delta^2(1-p)^2\Gamma^2 + (p^2k_1^2 + (2 + p)$$

$$pk_1^2k_2 + (1 + p^2)k_1k_2 + (1 - p)^2k_2^2)$$

$$+ ((k^2(1-p)^2\Gamma^2(k_1 + k_2)^2$$

$$+ (p^2k_1^2 + (1 - p)^2k_2^2)^2) \frac{1}{2}$$

$$< 36\delta^2(1-p)^2\Gamma^2(k_1 + k_2)^2$$

$$+ 9k_1^2k_2^2\Gamma^2(2k_{max})^2 + (2p^2k_{max}^2)^2 \frac{1}{2}$$

$$< (36\cdot 144\delta^2(1-p)^2\Gamma^2 + (36\delta^2 + 4)p^2k_{max}^2 \frac{1}{2}$$

$$= p^2k_{max}^2 \sqrt{36\cdot 144\delta^2 + (36\delta^2 + 4)^2}$$  \hspace{1cm} \text{(A12)}$$

As the have checked numerically, the remaining root divided by $\sqrt{36\cdot 144\delta^2 + (36\delta^2 + 4)^2}/\Gamma < 9$ for $\omega < 0.45$ (which is necessary to have mathematically meaningful probabilities between 0 and 1), so

$$\frac{\sqrt{c_1^2 + c_2^2}}{12(k)^2\Gamma} < \frac{3p^2k_{max}^2}{4(k)}$$  \hspace{1cm} \text{(A13)}$$

and therefore all real parts are negative if

$$k_{max} + k_{min} > p \left( k_{max} + k_{min} + \frac{k_{max}^2}{k} \right),$$  \hspace{1cm} \text{(A14)}$$

or noted in a simplified way and remembering the assumption at the beginning of this approximation,

$$0.5 \leq p < \frac{k_{max} + k_{min}}{k_{max} + k_{min} + \frac{k_{max}^2}{k}}.$$  \hspace{1cm} \text{(A15)}$$

Appendix B: Theoretical approach: local update process on networks

Similar as in the Moran process, in the local update process on networks the rate with which vertices with degree $k$ and strategy $\alpha$ carry this strategy over to nodes with degree $k'$ and strategy $\alpha'$ is given by

$$T_{k,k'}^{\alpha\rightarrow\alpha'} = \frac{Dk'k\rho_{\alpha,k'\alpha,k}}{\langle k \rangle} \left( \frac{1}{2} + \frac{1}{2} \frac{\pi_{\alpha} - \pi_{\alpha'}}{\Delta \pi_{\alpha}} \right).$$  \hspace{1cm} \text{(B1)}$$
which does not vary from the results in well mixed populations in the case of homogenous degree distribution. The replicator equation for the model system of a heterogenous degree distribution with only two vertex degrees reads

\[ \dot{\rho}_{0,k_1} = \frac{\psi k_1 p^2}{\langle k \rangle} \rho_{0,k_1} (\pi_0 - \langle \pi \rangle) \]  

(B2)

\[ + \frac{k_1 p (1 - p)}{2k} (\rho_{0,k_1} (1 + \psi (\pi_0 \langle \pi \rangle))) \]

\[ - \rho_{0,k_1} (1 + \psi (\langle \pi_2 \rangle - \pi_0))) \]  

with \( \psi = \omega/\Delta \pi_{max} \). The other equations are obtained analogously. Here again the position of the fixed point is not changed compared to the well mixed case. But again it is no longer possible to absorb the selection strength \( \omega \) by a rescaling of time.

A linear stability analysis leads to the matrix \( A \)

\[
\begin{pmatrix}
\frac{k_1 (p - 1)p}{2k} & \frac{k_2 (p - 1)p}{2k} & \frac{k_1 k_2 (p - 1)p^2}{2k} \\
-\frac{k_1 (p - 1)p}{2k} & \frac{k_1 k_2 (p - 1)p}{2k} & \frac{k_2 (p - 1)p^2}{2k} \\
\frac{k_1 k_2 (p - 1)p^2}{2k} & \frac{k_2 (p - 1)p^2}{2k} & \frac{k_1 k_2 (p - 1)p^2}{2k}
\end{pmatrix}
\]

(B3)

The eigenvalues of this matrix are again given by

\[ \lambda_1 = -\frac{1}{12(k_1 k_2)} (3k_1 k_2 (p - 1)p) \] 
\[ + 2i (k_2^2 (p - 1)^2 + k_1^2 p^2) \psi + \sqrt{c_1 - ic_2}) \]  

(B4)

\[ \lambda_2 = \frac{1}{12(k_1 k_2)} (3k_1 k_2 (p - 1)p) \] 
\[ - 2i (k_2^2 (p - 1)^2 + k_1^2 p^2) \psi + \sqrt{c_1 - ic_2}) \]  

(B5)

\[ \lambda_3 = \frac{1}{12(k_1 k_2)} (2ik_1^2 p^2 + 3k_1 (p - 1)p) \] 
\[ + k_2 (p - 1)(3k_1 p + 2ik_2 (p - 1) \psi) - \sqrt{c_1 + ic_2}) \]  

(B6)

\[ \lambda_4 = \frac{1}{12(k_1 k_2)} (2ik_1^2 p^2 + 3k_1 (p - 1)p) \] 
\[ + k_2 (p - 1)(3k_1 p + 2ik_2 (p - 1) \psi) + \sqrt{c_1 + ic_2}) \]  

(B7)

with the abbreviations

\[ c_1 = 9(k_1 + k_2)^2 (k_1^2 (p - 1)^2 p^2) \] 
\[ - 4 \left( k_2^4 (p - 1)^2 + k_1^2 p^2 \right)^2 \psi \]  

(B8)

\[ c_2 = 12(k_2 (p - 1)^2 + k_2 (p - 2)p k_1^2 \] 
\[ + k_2 (p^2 - 1) k_1 + k_2 (p - 1)^2 \psi \]  

(B9)

The real parts of this eigenvalues are given by

\[ \Re \lambda_1 = \frac{k_1 p^2}{4(k_1)} + \frac{k_2 p^2}{4(k_1)} - \frac{k_1 p}{4(k_1)} - \frac{k_2 p}{4(k_1)} \] 
\[ - \cos \left( \frac{1}{2} \arg (c_1 - ic_2) \right) \sqrt{c_1^2 + c_2^2} \]  

(B10)

\[ \Re \lambda_2 = \frac{k_1 p^2}{4(k_1)} + \frac{k_2 p^2}{4(k_1)} - \frac{k_1 p}{4(k_1)} - \frac{k_2 p}{4(k_1)} \] 
\[ + \cos \left( \frac{1}{2} \arg (c_1 - ic_2) \right) \sqrt{c_1^2 + c_2^2} \]  

(B11)

\[ \Re \lambda_3 = \frac{k_1 p^2}{4(k_1)} + \frac{k_2 p^2}{4(k_1)} - \frac{k_1 p}{4(k_1)} - \frac{k_2 p}{4(k_1)} \] 
\[ - \cos \left( \frac{1}{2} \arg (c_1 + ic_2) \right) \sqrt{c_1^2 + c_2^2} \]  

(B12)

\[ \Re \lambda_4 = \frac{k_1 p^2}{4(k_1)} + \frac{k_2 p^2}{4(k_1)} - \frac{k_1 p}{4(k_1)} - \frac{k_2 p}{4(k_1)} \] 
\[ + \cos \left( \frac{1}{2} \arg (c_1 + ic_2) \right) \sqrt{c_1^2 + c_2^2} \]  

(B13)

which is very similar to the corresponding result in the Moran process (it varies only slightly in \( c_1 \) and \( c_2 \)). Searching for an upper bound for the real parts of the eigenvalues, we even derive the same inequality as for the Moran process

\[ 0.5 \leq p < \frac{k_{max} + k_{min}}{k_{max} + k_{min} + 3 \frac{\pi_{max}}{(k_1 k_2)}} \]  

(B14)

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