A theoretical approach to understand spatial organization in complex ecologies

Ahmed Roman^{a,b}, Debanjan Dasgupta^c, Michel Pleimling^{b,d,e,*}

^a*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA*

^b*Department of Physics, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0435, USA*

^c*Booz Allen Hamilton, 575 Herndon Parkway, Herndon, Virginia 20170, USA*

^d*Center for Soft Matter and Biological Physics, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0435, USA*

^e*Academy of Integrated Science, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0405, USA*

Abstract

Predicting the fate of ecologies is a daunting, albeit extremely important, task. As part of this task one needs to develop an understanding of the organization, hierarchies, and correlations among the species forming the ecology. Focusing on complex food networks we present a theoretical method that allows to achieve this understanding. Starting from the adjacency matrix the method derives specific matrices that encode the various inter-species relationships. The full potential of the method is achieved in a spatial setting where one obtains detailed predictions for the emerging space-time patterns. For a variety of cases these theoretical predictions are verified through numerical simulations.

Keywords: many species food networks, emerging space-time patterns, matrix approach

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1. Introduction

Understanding the spatial structure of ecological networks is vital in theoretical and experimental biology and ecology (May, 1974; Maynard Smith, 1974; Sole and Bascompte, 2006; Maynard Smith, 1982; Hofbauer and Sigmund, 1998; Nowak, 2006; Weber et al., 2014). The stability of the dynamics of ecological networks is influenced by a variety of factors such as the topology of the network as well as the weights of the links composing the network (see (Knebel et al., 2013) for a recent example of Lotka-Volterra networks). A spatial setting, where individuals interact locally and are mobile, strongly influences the dynamics of

*Corresponding author

Email address: pleim@vt.edu (Michel Pleimling)

the system and also has a large impact on the stability of an ecological network (Reichenbach et al., 2007a; Roman et al., 2013).

The introduction of space gives rise to rich, interaction network dependent, phenomena including pattern formation, cluster coarsening, alliance formation and nested ecological niches. These phenomena have yielded a huge theoretical interest recently, and a variety of techniques (Szabó and Fáth, 2007; Frey, 2010) have been employed to study these intriguing phenomena for symmetric networks, ranging from simple cases with three (Reichenbach et al., 2007a,b; Peltomäki and Alava, 2008; Reichenbach and Frey, 2008; Venkat and Pleimling, 2010; Shi et al., 2010; Wang et al., 2010; He et al., 2010; Winkler et al., 2010; He et al., 2011; Rulands et al., 2011; Wang et al., 2011; Nahum et al., 2011; Jiang et al., 2011; He et al., 2012; Juul et al., 2012; Jiang et al., 2012; Lamouroux et al., 2012; Adamson and Morozov, 2012; Juul et al., 2013; Rulands et al., 2013; Szczesny et al., 2013; Schreiber and Killingback, 2013; Szczesny et al., 2014; Grošelj et al., 2015) and four species (Roman et al., 2012; Szabó and Sznaider, 2004; Szabó et al., 2007a; Szabó and Szolnoki, 2008; Intoy and Pleimling, 2013; Guisoni et al., 2013; Intoy and Pleimling, 2015) to complex situations with an arbitrary number of species (Roman et al., 2013; Szabó and Czárán, 2001a,b; Szabó, 2005; Perc et al., 2007; Szabó et al., 2008; Avelino et al., 2012a,b, 2014a; Mowlaei et al., 2014; Szabó et al., 2007a; Vukov et al., 2013; Kang et al., 2013; Avelino et al., 2014b; Cheng et al., 2014). Realistic ecologies, however, are endowed with complex interaction networks that can not be captured fully by only considering symmetric networks. As such it is important to develop theoretical approaches that allow to understand the dynamics of general networks (Szabó et al., 2007b; Lütz et al., 2013; Provata et al., 1999; Vandermeer and Yitbarek, 2012; Knebel et al., 2013; Dobrinevski et al., 2014; Rulquin and Arenzon, 2014; Varga et al., 2014; Szabó et al., 2015; Daly et al., 2015; Szolnoki and Perc, 2015) and their effects on biodiversity, correlations, and spatio-temporal patterns.

In the following we present an exact method that allows to reveal why species are partitioned in domains and what are the partition sets of the species labels in complex food networks. This information is a necessary first step in order to develop a predictive theory for the fate of ecologies. Our approach predicts the alliance formation between different species and fixes the emerging space-time patterns in many spatial interaction networks. As a consequence, our approach also permits to shed light on the stability of ecological niches by breaking down this stability question into two distinctive parts: the stability of interactions among domains and within domains.

2. Model and examples

Fig. 1 shows some typical two-dimensional space-time patterns that we aim at predicting with the approach discussed in the following. Whereas snapshot (a) shows an example of a system with spirals where every wavefront contains only one species, panel (b) gives an example of a coarsening process with two types of domains where inside every domain spirals are formed, thus yielding non-trivial dynamics inside the coarsening domains. Example (c) reveals

54 a coarsening process where every domain is formed by an alliance of mutually
 55 neutral species. Finally, snapshot (d) shows a case of fuzzy spirals due to the
 56 mixing of different species inside the waves.

Figure 1: (Color online) Four typical types of patterns observed in many species food networks (in all cases the rates were chosen to be species independent): (a) compact spirals in the (5,3) model (with $\gamma = \delta = 1$ and $\alpha = \beta = 0$); (b) coarsening with spirals forming inside the domains in the (6,3) model (with $\gamma = \delta = 1$ and $\alpha = \beta = 0$); (c) coarsening of neutral species domains in the (6,2) model (with $\gamma = \delta = 1$ and $\alpha = \beta = 0$); (d) fuzzy spirals with mixing of species inside the spirals in the (9,3) model (with $\gamma = \delta = 0.5$ and $\alpha = \beta = 0.25$). Systems of 400×400 sites have been simulated.

57 In order to focus our discussion we consider in the following systems of
 58 N species in two space dimensions where individuals of different species have
 59 mutual predator-prey interactions, give birth to off-springs, and are mobile. For
 60 our method the details of the implementation of these interactions do not matter,
 61 with the exception that the predation-prey interactions should be binary, i.e. at
 62 any given event one predator consumes one prey. For the examples in Fig. 1 as
 63 well as for the more complicated cases discussed later we consider the following
 64 general interaction scheme (X_i denotes a member of species i and $\emptyset$ is an empty

65 site):

66 where every lattice site can be occupied by at most one individual, whereas
 67 reactions between different individuals only occur when they are at neighboring
 68 sites. Our approach remains valid when considering in addition self-predation.
 69 The model parameters δ_{ij} , α_{ij} , γ_i , and β_i are the rates at which these reactions
 70 take place. For the examples included in this paper, predation and swapping
 71 rates are always considered to be independent of the prey, i.e. $\delta_{ij} = \delta_i$ and
 72 $\alpha_{ij} = \alpha_i$. The separation of the predation and birth events is needed for the
 73 formation of spirals as those shown in Fig. 1, but is otherwise not relevant in
 74 order to establish the relationships between species. We also allow for various
 75 ways of mobility (swapping of individuals on neighboring sites (3) or diffusion
 76 by jumping to empty sites (4)), in order to be as general as possible.

77 The reaction scheme (1)-(2) contains many known situations as for example
 78 the cyclic N species Lotka-Volterra and May-Leonard models as well as more
 79 complicated situations like the (N, r) models where each species preys on r other
 80 species in a cyclic way (Roman et al., 2013; Mowlai et al., 2014). Whereas the
 81 examples shown in Fig. 1 are those of (N, r) models with symmetric rates (hence
 82 we can drop the labels i, j for the rates, see the figure caption), more general
 83 cases will be discussed below.

84 The matrix approach discussed in the following is valid for rather general
 85 predator-prey networks, provided that no interactions of higher order than sec-
 86 ond order are present. We assume that the species network gives rise to a unique
 87 partition of the species into domains. While we have not encountered a case
 88 where this assumption is not fulfilled, we can not exclude that there exist net-
 89 works of species that exhibit in presence of noise two non-isomorphic partitions
 90 of species into domains. For the cases used to illustrate our approach, we con-
 91 sider rates for which none of the species go extinct before the quasi-steady state
 92 of the dynamics is reached, i.e. the time scale on which the species are forming
 93 alliances and domains is shorter than the extinction time for any of the species.
 94 Notably this requires that the diffusion and mobility rates are not too high so
 95 as to induce rapid extinction of the species, but are still large enough to allow
 96 the formation of species alliances.

97 3. Matrix approach

98 The predation scheme (1) can be represented by a graph where one connects
 99 species i and j by a directed edge if i preys on j . The scheme can also be encoded
 100 in the $N \times N$ *adjacency matrix* $\underline{\mathbf{A}}$ where the element $a_{ij} = 1$ if i preys on j and

0 otherwise. The *square of the adjacency matrix* $\mathbf{B} = \mathbf{A}^2$ contains information about preferred partnership formations based on the maximum protection a species can enjoy while being close to some other species. Indeed, the element b_{ij} counts the number of directed paths of length 2 from vertex i to vertex j , i.e. the number of paths of the form $i \rightarrow k \rightarrow j$ where k is a vertex different from i and j . Following the maxim that "the enemy of my enemy is my friend," species j wants to be in close proximity to that species that attacks most of its predators. Mathematically, this preferred partner of j is obtained from the condition $\max_i b_{ij}$.

Of course, a given species does not want to undergo a close partnership with one of its predators. Adding this important information yields the *alliance matrix* $\mathbf{S}$ whose elements s_{ij} provide information on the best possible allies j for each species i :

$$s_{ij} = \delta_{b_{ji}, m_i} \delta_{0, a_{ji}} , \quad (5)$$

where $m_i = \max_j b_{ji}$. The first condition selects those species j that are preferred partners of i as they provide the best protection by attacking the largest number of its predators, whereas the second condition makes sure that j is not itself a predator of i , yielding a matrix with elements $s_{ij} = 1$ for the best possible allies of species i and zero otherwise.

In order to fully understand space-time patterns as those shown in Fig. 1, one needs to further distinguish between preferred allies of species i that are hunted by species i and preferred allies towards which species i has a neutral approach. This information is encoded by the two matrices $\mathbf{P}$ (*prey-allies*) and $\mathbf{N}$ (*neutral allies*) with elements

$$p_{ij} = s_{ij} \wedge a_{ij} = \delta_{s_{ij}, a_{ij}} \quad (6)$$

$$n_{ij} = s_{ij} \wedge \neg a_{ij} = \delta_{s_{ij}, (1-a_{ij})} \quad (7)$$

with the binary operators AND ($\wedge$) and NOT ($\neg$).

The two matrices $\mathbf{P}$ and $\mathbf{N}$ allow to understand (and predict) many of the space-time patterns that can emerge in predator-prey systems governed by the reactions (1)-(2). A matrix element $p_{ij} = 1$ means that species i seeks the protection of species j , while at the same time preying on species j . As a result single species waves will form where a wave containing individuals of species i will follow one formed by species j . On the other hand $n_{ij} = 1$ represents non-aggressive coexistence where species i is protected by a neutral species j (i.e. i does not prey on j). As a result i will mix with j in order to enjoy the enhanced protection by its preferred ally. If $n_{ij} = n_{ji} = 1$, then the two mutually neutral partners will form neutral domains and protect each other.

Inspection of Fig. 1d reveals a case that is not yet covered by the matrices given above, namely that of 'fuzzy' waves where three species mix to some degree. Consider three given species i , j , and k . The above situation is encountered when species i and j are mutually neutral and species j and k are mutually neutral, while at the same time species i preys on species k . This means that the following conditions have to be fulfilled simultaneously: $n_{ij} = 1$, $n_{jk} = 1$, and $a_{ik} = 1$. As a result, i chases species k while both mix with

the intermediate species j , giving fuzzy looking waves as those seen in Fig. 1d.
 Defining the matrix elements of a matrix $\underline{\mathbf{F}}$ as

$$f_{ij} = \theta \left(\left(\sum_{k=1}^N \delta_{n_{ij},1} \delta_{n_{jk},1} \delta_{a_{ik},1} \right) - 1 \right), \quad (8)$$

with $\theta(x) = 1$ for $x \geq 0$ and zero otherwise, we have that $f_{ij} = 1$ if j acts as a neutral intermediary between species i and some other species, whereas $f_{ij} = 0$ otherwise.

4. Examples

Let us first look at the four cyclic (N, r) games of Fig. 1 in order to see how to work with the different matrices.

For the $(5, 3)$ game shown in Fig. 1a the relevant matrix is

$$\underline{\mathbf{P}} = \begin{pmatrix} 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (9)$$

whereas $\underline{\mathbf{N}} = \underline{\mathbf{F}} = \underline{\mathbf{0}}$. We readily obtain from the prey-allies matrix $\underline{\mathbf{P}}$ that species 1 wants to ally with its prey species 2, species 2 wants to ally with its species 3, etc. This yields single species spirals where the species follow each other in the order $1 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 5 \rightarrow 1$.

The $(6, 3)$ in Fig. 1b is characterized by a similar looking 6×6 matrix

$$\underline{\mathbf{P}} = \begin{pmatrix} 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (10)$$

where again $\underline{\mathbf{N}} = \underline{\mathbf{F}} = \underline{\mathbf{0}}$. This time, however, two family of spirals (or teams) are formed, one with the ordering $1 \rightarrow 3 \rightarrow 5 \rightarrow 1$, the other with the ordering $2 \rightarrow 4 \rightarrow 6 \rightarrow 2$. As every member in a team has both a prey and a predator in the other team, these two family of spirals compete against each other, which yields a coarsening process with a three-species rock-paper-scissors game within each domain.

The $(6, 2)$ case of Fig. 1c is a case where the prey-allies matrix $\underline{\mathbf{P}}$ vanishes whereas the neutral allies matrix $\underline{\mathbf{N}}$ is non-zero:

$$\underline{\mathbf{N}} = \begin{pmatrix} 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \end{pmatrix}. \quad (11)$$

Inspection of $\underline{\mathbf{N}}$ reveals the formation of three teams composed of two mutually neutral species (1 and 4, 2 and 5, 3 and 6), resulting in a coarsening process with three different types of domains.

167 Finally, the $(9, 3)$ game in Fig. 1d provides us with an example where both
 168 $\underline{\mathbf{N}}$ and $\underline{\mathbf{F}}$ are non-zero:

$$\underline{\mathbf{N}} = \underline{\mathbf{F}} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \end{pmatrix}, \quad (12)$$

169 whereas $\underline{\mathbf{P}} = \underline{\mathbf{0}}$. It follows from this that species 5, which is the preferred
 170 ally of species 1, acts as an intermediary between species 1 and 9. As species
 171 9 preys on species 1, this yields a wavefront of the type $9 \xrightarrow{[5]} 1$ where $[\dots]$
 172 indicates a neutral intermediary. As this happens in a cyclic way, one observes
 173 the emergence of fuzzy spirals, with the ordering $1 \xrightarrow{[6]} 2 \xrightarrow{[7]} 3 \xrightarrow{[8]} 4 \xrightarrow{[9]} 5 \xrightarrow{[1]} 6$
 174 $6 \xrightarrow{[2]} 7 \xrightarrow{[3]} 8 \xrightarrow{[4]} 9 \xrightarrow{[5]} 1$.

175 Let us now look at the two more involved examples shown in Figs. 2 and 3
 176 where the interaction scheme is no longer cyclic.

Figure 2: (Color online) Six-species model defined by the adjacency matrix (13) and the rates (14). Red: species 1, green: species 2, blue: species 3, yellow: species 4, cyan: species 5, pink: species 6. The system size is 500×500 . Times are measured since preparing the system, where one time step corresponds to 500×500 proposed updates.

177 The snapshots in Fig. 2 result from a six-species model with an interaction
 178 scheme described by the matrix

$$\underline{\mathbf{A}} = \begin{pmatrix} 0 & 1 & 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 1 & 1 \\ 1 & 0 & 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 \end{pmatrix} \quad (13)$$

179 and rates given by

$$\begin{pmatrix} \delta_1 & \alpha_1 & \gamma_1 & \beta_1 \\ \delta_2 & \alpha_2 & \gamma_2 & \beta_2 \\ \delta_3 & \alpha_3 & \gamma_3 & \beta_3 \\ \delta_4 & \alpha_4 & \gamma_4 & \beta_4 \\ \delta_5 & \alpha_5 & \gamma_5 & \beta_5 \\ \delta_6 & \alpha_6 & \gamma_6 & \beta_6 \end{pmatrix} = \begin{pmatrix} 0.9 & 0.08 & 0.8 & 0.16 \\ 0.43 & 0.46 & 0.8 & 0.16 \\ 0.9 & 0.08 & 0.8 & 0.16 \\ 0.43 & 0.46 & 0.8 & 0.16 \\ 0.9 & 0.08 & 0.8 & 0.16 \\ 0.43 & 0.46 & 0.8 & 0.16 \end{pmatrix}. \quad (14)$$

180 Following the construction explained above, we get the matrices

$$\underline{\mathbf{P}} = \begin{pmatrix} 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}; \quad \underline{\mathbf{N}} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (15)$$

181 which, together with the fact that $\underline{\mathbf{F}} = \underline{\mathbf{0}}$, allow us to predict the alliances
 182 and space-time pattern appearing in this system. In the present case, both the
 183 prey-allies and neutral allies matrices are non-zero, so that we can expect the
 184 formation of both neutral alliances as well as of alliances where the partners
 185 remain in a predator-prey relationship. Indeed, from the matrix $\underline{\mathbf{P}}$ we obtain
 186 that species 1, 3, and 5 form a three-species cyclic game that results in the
 187 formation of compact wavefronts with the following ordering of the species:
 188 $1 \rightarrow 3 \rightarrow 5 \rightarrow 1$. On the other hand, from the matrix $\underline{\mathbf{N}}$ follows that the species
 189 2, 4, and 6 form a neutral alliance. As a result, two types of domains should form,
 190 one composed of three neutral partners and one composed of three partners that
 191 undergo a cyclic rock-paper-scissors game, resulting in a coarsening process with
 192 different internal dynamics inside the domains.

Figure 3: (Color online) Five-species model defined by the adjacency matrix (16) and the rates (17). Red: species 1, green: species 2, blue: species 3, yellow: species 4, cyan: species 5. The system size is 400×400 . Times are measured since preparing the system, where one time step corresponds to 400×400 proposed updates.

193 The five-species model shown in Fig. 3 is defined by the adjacency matrix

$$\underline{\mathbf{A}} = \begin{pmatrix} 0 & 1 & 1 & 1 & 1 \\ 1 & 0 & 1 & 1 & 0 \\ 1 & 0 & 0 & 1 & 0 \\ 1 & 0 & 0 & 0 & 1 \\ 1 & 1 & 0 & 0 & 0 \end{pmatrix}. \quad (16)$$

194 For the time evolution shown in Fig. 3 we used the rates

$$\begin{pmatrix} \delta_1 & \alpha_1 & \gamma_1 & \beta_1 \\ \delta_2 & \alpha_2 & \gamma_2 & \beta_2 \\ \delta_3 & \alpha_3 & \gamma_3 & \beta_3 \\ \delta_4 & \alpha_4 & \gamma_4 & \beta_4 \\ \delta_5 & \alpha_5 & \gamma_5 & \beta_5 \end{pmatrix} = \begin{pmatrix} 0.5 & 0.4 & 0.8 & 0.16 \\ 0.7 & 0.24 & 0.8 & 0.16 \\ 0.3 & 0.56 & 0.8 & 0.16 \\ 0.8 & 0.16 & 0.8 & 0.16 \\ 0.3 & 0.56 & 0.8 & 0.16 \end{pmatrix}. \quad (17)$$

195 From $\underline{\mathbf{A}}$ we readily obtain

$$\underline{\mathbf{P}} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 \end{pmatrix}; \quad \underline{\mathbf{N}} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \end{pmatrix}, \quad (18)$$

196 whereas $\underline{\mathbf{F}} = \underline{\mathbf{0}}$ (i.e. no fuzzy wavefronts are formed). The matrices immedi-
 197 ately yield all the relevant information regarding the partnerships forming in
 198 this system. As $n_{11} = 1$, species 1 wants to self-segregate, which is a direct
 199 consequence of the fact that all the other species are both its predators and
 200 preys. The neutral allies matrix $\underline{\mathbf{N}}$ also indicates that species 3 and 5 form
 201 a neutral alliance, in order to fight off their corresponding predators. Finally,
 202 the prey-allies matrix $\underline{\mathbf{P}}$ reveals that the three species 2, 4, and 5 tend to form
 203 an active three-species alliance with the following ordering of the wave fronts:
 204 $2 \rightarrow 4 \rightarrow 5 \rightarrow 2$. Our method therefore predicts the formation of three types
 205 of domains (pure species 1 domains, domains of the neutral alliance between
 206 species 3 and 5, as well as domains where species 2, 4, and 5 undergo a cyclic
 207 game), where, remarkably, species 5 is involved in *two* different alliances. All
 208 these predictions are indeed verified when inspecting the snapshots in Fig. 3.

209 Knowing the partnerships and the resulting space-time pattern is an im-
 210 portant step in order to better understand the fate of an ecology. This alone,
 211 though, is not enough to predict whether a given species will go extinct, as the
 212 survival of a species also depends on the rates of its interactions with the other
 213 species. The reliability of our predictions at least for the (N, r) model with
 214 symmetric rates is confirmed via exact agreement with the theoretical predic-
 215 tions in (Mowlai et al., 2014) obtained using the complex Ginzburg Landau
 216 approach. Comprehensive numerical studies are required to fully understand
 217 the parameter regimes for which the presented ad-hoc methods are valid. We
 218 leave such calculations for future investigations.

219 5. Summary

220 We have presented a theoretical approach that allows to predict partnership
 221 formation and emerging space-time patterns in many-species food networks.

While our emphasis was on predator-prey systems, the proposed use of various matrices, derived from the adjacency matrix, to understand alliances and spatio-temporal pattern formation can be straightforwardly expanded to other systems, ranging from ecology to social sciences (Maynard Smith, 1982; Hofbauer and Sigmund, 1998; Nowak, 2006; Hauert et al., 2002; Gokhale and Traulsen, 2014), governed by binary interactions between different 'species'.

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