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# A theoretical approach to understand spatial organization in complex ecologies



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#### HIGHLIGHTS

• A method is presented that allows to understand correlations among species.

• The method derives matrices that encode the various inter-species relationships.

• The full potential of the method is achieved in a spatial setting.

• For some cases these theoretical predictions are verified through simulations.

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#### 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.

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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 Basecompte, 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 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, 2011; He et al., 2010, 2011, 2012; Winkler et al., 2010; Rulands et al., 2011; Nahum et al., 2011; Jiang et al., 2011, 2012; Juul et al., 2012, 2013; Lamouroux et al., 2012; Adamson and Morozov, 2012; 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; Perc et al., 2007; Szabó et al., 2008; Szabó et al., 2007a, 2008; Avelino et al., 2012a,b,

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2014a,b; Mowlaei et al., 2014; Vukov et al., 2013; Kang et al., 2013; Cheng et al., 2014). Realistic ecologies, however, are endowed with complex interaction networks that cannot 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, 2015; 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; 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 into 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





**Fig. 1.** 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.

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