



Early warning signals as indicators of cyclostationarity in three-species hierarchies



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ARTICLE INFO

Article history:

Received 18 February 2015

Received in revised form 26 June 2015

Accepted 29 June 2015

Keywords:

Automaton

Patchiness

Early warning signal

Stability

Cyclic

Autocorrelation

Standard deviation

ABSTRACT

Predicting stability from current ecosystem performance is theoretically difficult, but early statistical warning signals (EWS) may enable the anticipation of regime shifts. However, little is known regarding the behavior of EWS in shifts with cyclic dynamics. In this study, we use indicators to assess the stability of a three-species system in a competitive loop similar to a rock–paper–scissors (RPS) hierarchy. In two scenarios, the RPS is simulated using a 3-D automaton whose input matrix combines probabilities of pair-wise dominance with differential reaction frequencies. The first scenario uses the data of a microbial experiment in which the RPS hierarchy is characterized by incomplete dominance within species pairs and differences in reaction frequency between species pairs. The input of the second model was chosen to generate a contrasting scenario: a symmetric RPS interaction gradually subjected to a stressor. The reaction frequency of one species pair was modeled to decay linearly over time. The relative species abundances are monitored spatiotemporally. In the first scenario, abundances oscillate stably despite initial large swings, whereas in the second scenario, one species gradually dominates, eventually resulting in transitivity. In both scenarios, species cluster spatially in patches of single species. In scenario 1, the average patch size remains constant throughout the iterations and possibly contributes to the overall stability; however, in the second scenario, a further homogenization takes place. In the first scenario, EWS reflected the system's stability with species abundances settling into a stable basin. In scenario 1 only one of the EWS indicators detected consistently the loss of resilience. Sensitivity analysis revealed excessive variability in dominance resulted in immediate loss of the RPS hierarchy.

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1. Introduction

Measures that reflect stability were investigated in a variety of research domains, as they have the capacity to anticipate dynamic shifts (Scheffer et al., 2009). To this end, one approach uses statistical indicators, termed early warning signals (EWS), such as autocorrelation and variance, that represent a promising approach to resilience assessment rendering the concept of resilience operational (Rougé et al., 2013; Scheffer, 2010). EWS also meet the criteria

considered crucial for sound ecological indicators, such as ease of calculation and anticipation of reduced system integrity (Dale and Beyeler, 2001). Increases in EWS indicate a slowing down of the system, a phenomenon occurring frequently prior to dynamic shifts (Lenton et al., 2012). In biology EWS have rarely been exploited with the exception of cyclic shifts between alternative states despite their common occurrence in nature (Beninca et al., 2009; van Nes et al., 2007). Such dynamics can result from external cyclic forcing such as glaciations (Petit et al., 1999), or from internal dynamics where, indeed, EWS can predict bifurcations in two-species predator-prey models (Chisholm and Filotas, 2009). To the best of our knowledge, nor have the signals been applied to cases in which more than two species interact in competitive loops, as frequently observed in ecosystems (Petraitis, 1979). However, in other domains, particularly communication and signal processing,

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EWS-type statistical functions have been used extensively to monitor cyclostationarity (Gardner et al., 2006). Scheffer et al. (2009) mention that the dynamics of harmonic systems, aside from having different types of bifurcations, may be expected to slow down before a critical transition and are thus likely to be characterized by EWS when a stressor forces the system to the boundary of its basin of attraction. In addition to autocorrelation and variance, particular spatial heterogeneity can also signal an upcoming regime shift. Although regular spatial patterns persist in environmental heterogeneity, there is a general tendency toward increased spatial coherence – measured as increased cross-correlation among units – with an increase in the size of single-species patches before shifts (Scheffer et al., 2009). It is a fundamental property in different realms: macrobenthos (Burrows and Hawkins, 1998); bacteria (Cordero et al., 2012; Kirkup and Riley, 2004; Morlon, 2012) and vegetation (Scheffer et al., 2009; Rietkerk et al., 2004).

Biological systems are often expressed in the form of networks (Fath, 2004). With only two species, the rule defining their hierarchy is represented by the coin-toss model (Kroese et al., 2011). When three species are present, this opens up the possibility of a competitive cycle in which species pairs follow a defined hierarchy but the entire system is non-transitive (Petraitis, 1979). One of the simplest examples of cyclic dominance is the children’s game rock–paper–scissors (RPS), in which a rock beats a pair of scissors, scissors beat a sheet of paper and paper beats a rock (Frean and Abraham, 2001). RPS systems are of great interest in various disciplines, as they are characterized by dynamically stable oscillations, and as such allow great diversity that is improbable under transitive hierarchies (Frean and Abraham, 2001; Allesina and Levine, 2011). In marine biology, coverage and overgrowth of sessile organisms on rocky shores and Jamaican coral reef showed this type of cyclic competitive interaction (Buss and Jackson, 1979; Burrows and Hawkins, 1998). In bacterial research, RPS interactions studied by combining mobility of species and the frequency of their reactions were found to favor the sustainability of bacterial diversity (Venkat and Pleimling, 2010; Cordero et al., 2012; Morlon, 2012). *In vivo* experiments carried out on the bacterial population of the intestines of caged mice also revealed an RPS interaction (Kirkup and Riley, 2004), where antibiotic interactions generated ecological stability and maintained the importance for microbial biodiversity. Such microbial community stabilization occurs both in structured systems (Cordero et al., 2012) and unstructured ones (Kelsic et al., 2015). The stability of RPS is determined by the pair-wise dominance between species, which can be estimated by the observed proportion of wins of a species against the other. In addition, differences in reaction frequencies between species pairs might move the RPS away from stability as shown for rodents where changes in temperature and humidity altered encounter opportunities (Kausrud et al., 2008).

The empirical estimation of the strength of competition and the assessment of the degree of competitive intransitivity in nature has proven difficult (Ulrich et al., 2014). The use of automata to simulate the stability of networks is well established (Baianu, 1985). For species associations of 3 up to 25, automata simulations showed that the (a) symmetry of the hierarchy due to differences in competitiveness relates to the stability of the systems (Laird and Schamp, 2006). The input for a cellular automaton derived from 45-year monitoring of the interaction of furoids, barnacles and limpets allowed the study and simulation of their RPS evolution (Burrows and Hawkins, 1998). Experimental data on bacterial diversity in petri-dish and mice intestines are also consistent with simulations by a 2-D automaton (Kerr et al., 2002; Durrett and Levin, 1998). The objective of this paper is to test to what extent EWS are effective in detecting cyclostationarity and the loss of it. For this purpose the cyclic dynamics of RPS hierarchies are used in two contrasting scenario’s modeled in 3D automata. The first scenario simulates

a microbial experiment characterized by RPS while in the second scenario the starting conditions were chosen to generate a gradual loss of resilience. The research hypothesis explored is that trend in autocorrelation and standard deviation would discriminate both scenario’s as theoretically predicted by the early warning signal theory.

2. Materials and methods

2.1. The automaton model

Two three-species spatially structured hierarchies are considered in an automaton consisting of a $27 \times 27 \times 27$ cube. Inside this array, $25 \times 25 \times 25$ compartments each contains one of three species. Starting with a checkerboard pattern, the species react through iterations along the coordinates of the array with their six neighbor species (Fig. 1).

The reactions are computed according to probability rules set forth in the matrices defined below.

Take three species 1, 2 and 3, competing pair-wise $\{u\}$ versus $\{v\}$, where $\{u\}$ and $\{v\}$ can be species 1, 2 or 3. The probability of any species replacing another species is determined by two factors:

- (a) The rule $r_{u,v}$ is the probability of $\{u\} > \{v\}$, given the occurrence of a reaction between $\{u, v\}$. Hence, $r_{u,v} = 1 - r_{v,u}$.
- (b) The reaction frequency $f_{u,v}$ weighs the rules by defining how often a given pair $\{u, v\}$ reacts, relative to the average reaction rate. Hence $f_{u,v} = f_{v,u}$ and the average frequency of the reactions line $\{u\}$, column $\{v\}$, of the matrix is thus set to one.

For three species, this can be represented mathematically by two matrices: $R = |r_{u,v}|$ and $F = |f_{u,v}|$:

$$R = \begin{vmatrix} 1 & r_{1,2} & r_{1,3} = 1 - r_{3,1} \\ r_{2,1} = 1 - r_{1,2} & 1 & r_{2,3} \\ r_{3,1} & r_{3,2} = 1 - r_{2,3} & 1 \end{vmatrix} \quad (1)$$

$$F = \begin{vmatrix} 1 & f_{1,2} & f_{1,3} = f_{3,1} \\ f_{2,1} = f_{1,2} & 1 & f_{2,3} \\ f_{3,1} = 3 - f_{1,2} - f_{2,3} & f_{3,2} = f_{2,3} & 1 \end{vmatrix} \quad (2)$$

If adjacent species are identical, the same species will inherently occupy the compartment after a reaction, hence a probability of 1 in the diagonal of the R matrix. This is independent of the reaction frequency; hence, by convention, the diagonal of F is also set to 1.

Multiplying matrix F element-wise by matrix R sets the probability of the possible interactions: six reactions within different species pairs and three same-species interactions (diagonals). The elements of the matrix are divided by 6 to sum up to a probability of 1:

$$P = \begin{vmatrix} \frac{1}{6} & \frac{f_{1,2}r_{1,2}}{6} & \frac{f_{1,3}r_{1,3}}{6} \\ \frac{f_{2,1}r_{2,1}}{6} & \frac{1}{6} & \frac{f_{2,3}r_{2,3}}{6} \\ \frac{f_{3,1}r_{3,1}}{6} & \frac{f_{3,2}r_{3,2}}{6} & \frac{1}{6} \end{vmatrix} \quad (3)$$

In the automaton, the probability that a given species will remain or be replaced is a function of the surrounding species and the fitness matrix P .

The probabilities of species x_i at iteration T in compartment i being one of the three species a_1, a_2 or a_3 sum up to 1:

$$Pr(x_i^T = a_1) + Pr(x_i^T = a_2) + Pr(x_i^T = a_3) = 1$$

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