Ecological Complexity 27 (2016) 12–16

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original Research Article

Algebraic structures generating reaction-diffusion models: The activator-substrate system

Marcella Palese *

Department of Mathematics, University of Torino, via C. Alberto 10, I-10123 Torino, Italy

ARTICLE INFO

Article history:
Received 30 January 2015
Received in revised form 27 November 2015
Accepted 22 January 2016
Available online 19 February 2016

Keywords:
Reaction-diffusion
Activator-substrate
Integrability
Algebraic structure
Nonlinear model
Skeleton
Tower

ABSTRACT

We shall construct a class of nonlinear reaction-diffusion equations starting from an infinitesimal algebraic skeleton. Our aim is to explore the possibility of an algebraic foundation of integrability properties and of stability of equilibrium states associated with nonlinear models describing patterns formation.

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1. Introduction

In his famous paper, Turing suggested that a system of chemical substances reacting together and diffusing through a tissue, could describe the main phenomena of morphogenesis (Turing, 1952). In particular, in his work it was emphasized that patterns could appear if one of the substances diffuses much faster than the other.

Nonlinear reaction-diffusion systems have then been proposed to answer the question about how cells, under the influence of their common genes, could produce spatial patterns, see *e.g.* Koch and Meinhardt (1994) and references therein. They consist in models describing generation of patterns from an initially homogeneous state taking into account the relevance of chemical gradient in biological systems, in particular nonlinear interaction of two chemicals and their diffusion. Patterns formation turns out then to be the output of *local self-enhancement* such as local autocatalysis and *long range inhibition*. A simple model proposed by Koch & Meinhardt is the activator-substrate systems (constituted by a self-enhanced reactant and a depleted reactant which plays the role of the antagonist). In the simplest mathematical form, only few relevant parameters characterize the model: the normalized *diffusion constant* and the normalized *cross-reaction coefficient*.In particular, the inhibition due to the substrate reactant can be effective if the normalized diffusion constant is $\ll 1$ (that means the diffusion constant of the activator should be much lesser than the diffusion constant of the substrate), a necessary condition for the generation of stable patterns.

Recent studies pointed out how, beside being a universal principle explaining regular pattern formation in chemical, physical and biological morphogenesis systems, Turing's activator-inhibitor principle is also at the basis of regular pattern formation in a variety of ecosystems. In particular, the scale-depending feedback is a unifying ecological principle playing a key rôle and mainly consisting in short-range ecological facilitation such as local modification of the environment and long-range competition for resources; see *e.g.* Rietkerk and van de Koppel (2008) whereby *the prerequisite of long-distance negative feedback is proposed as a basic principle for regular pattern formation in ecosystems*.

In this paper, we show that this condition can be recognized as a condition on the internal symmetry properties of a system. This perspective, concerned with the action of a group of transformations on the space of possible configurations ('fields'), will be exploited in Section 2 and detailed in the Appendices.

In particular, in Section 3 we shed new light on the long-range negative feedback condition by a case study exploiting the internal symmetry algebra of *twisted* reaction-diffusion equations *with a null basic production term*. We observe that, in the limit of a null

* Tel.: +39 0116702889; fax: +39 0116702878.
E-mail address: marcella.palese@unito.it

http://dx.doi.org/10.1016/j.ecocom.2016.01.003
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normalized diffusion constant, such a condition is related with the existence of soliton solutions – *i.e.* travelling waves remaining stable after interactions. We can see that requiring the normalized diffusion constant being null corresponds to look for specific symmetry properties of the associated system; indeed this integrable case can be seen as a limiting case of the internal symmetry algebra (see Appendix 2).

As a major result, in Section 3.2 we recover *activator-substrate systems* by performing a slight modification of the internal symmetry algebra of twisted reaction-diffusion equations. We obtain as a byproduct that the necessary condition for the generation of stable patterns for such a system, besides being related with general integrability properties in the limit of a null normalized diffusion constant, can also be formulated in terms of 'closeness' properties within the symmetry algebra vector space.

This moreover suggests the possibility to enhance the interplay of the two different approaches to the study of stability: the qualitative study based on the analysis of the stability of equilibrium configurations and global integrability properties related with existence of stable solutions such as travelling waves or solitons.

The scope of this work is therefore to propose an intrinsic algebraic form of the local mechanisms expressed by reaction-diffusion partial differential equations. Our considerations are based on the well known duality between linear differential forms and tangent vector fields on manifolds, and make use of algebraic and geometric techniques developed within a theoretical physics framework, see *e.g.* Estabrook (1982), Palese and Winterroth (2002, 2011, 2012), Pirani et al. (1979), in particular suitable generalization of the structure equations of a Lie group. In the present note, we show that the appearing and the significance of parameters in a model can be characterized within an algebraic-geometric formulation in terms of integrable "towers with infinitesimal algebraic skeletons" (see Appendix 1), which generalizes that of integrable connections on spaces of configurations with symmetries.

2. Underlying algebraic skeletons

Concerning real ecosystems in homogeneous landscapes, establishment and survival of organisms can be inhibited by limited resources or other stress factors: it is an empirical evidence that, although the organisms can acts only locally, the effects have influence at distance and therefore are of global nature, showing a dependence on density of the organisms themselves (Rietkerk and van de Koppel, 2008).

In this paper we propose an approach which is based on the study of global properties of partial differential equations such as internal symmetries and invariance properties having however an issue in dynamics. The underlying idea is that transformations of configurations of a system can be globally studied by means of the theory of the action of Lie groups on manifolds. Differential equations therefore are an issue of the differential content carried by a Lie group (and its Lie algebra) and by its structure equations providing connections on the space of configurations.

Although such mathematical tools could appear of a quite abstract nature, nevertheless they are the right tools to deal with global properties at large scales, being natural tools for connecting local data to global ones. In particular they implement the concept of 'positional information' (Wolpert, 1969). In Appendix 1 the general context is sketched and appropriate references to the abstract theory are given.

It is well known that, looking for invariance properties, a "prolongation" algebra can be associated with a given system of nonlinear partial differential equations. Nonlinearity, then, results in a quite intriguing algebraic structure which is "only partially" a Lie algebra (we speak of an 'open' Lie algebra structure) (Wahlquist and Estabrook, 1975). By an inverse procedure based on the intrinsic duality between Lie algebras and differential systems (Estabrook, 1982), open Lie algebraic structures can 'generate' whole families of different nonlinear systems bound by the same internal symmetry structure.

We show that a slight modification of the internal symmetry properties generates *new* models which can contain possible integrable subcases. As an example, by a modification of the symmetry algebra associated with a model for pattern formation on the shells of molluscs (Meinhardt and Klingler, 1987) we shall recover the activator-substrate reaction-diffusion model proposed by Koch & Meinhardt. In both models the necessary condition for the generation of stable patterns, *i.e.* the prerequisite of long-distance negative feedback, can be interpreted already at a symmetry level, as a "closeness condition" in the symmetry space (see the concluding Remark).

Our results are based on the observation that two fundamental aspects are involved in pattern formations: symmetries on the one side (algebraic content) and changes in time and space on the other side (differential content). In particular, to keep account of the 'interaction' of both aspects, we act effectively with open Lie algebraic structures by using their refined structure: we need to introduce, a notion which generalizes the concept of a homogeneous space, *i.e.* that of an *algebraic skeleton* $\boldsymbol{E} = g \oplus \boldsymbol{V}$ on a finite-dimensional vector space $\boldsymbol{V}$, with g a possibly infinite dimensional Lie algebra (see Appendix 1).

Consider then the following infinite dimensional vector space $\boldsymbol{E} = g \oplus \boldsymbol{V}$

$$
\begin{aligned}
&[\psi_1,\psi_2]=0, \quad [\psi_1,\psi_3]=0, \quad [\psi_1,\psi_4]=0, \quad [\psi_1,\psi_5]=?,\\
&[\psi_1,\psi_6]=0, \quad [\psi_1,\psi_7]=0, \quad [\psi_1,\psi_8]=0\ldots\\
&[\psi_2,\psi_3]=-2\mathcal{D}\psi_6, \quad [\psi_2,\psi_4]=2\mathcal{D}\psi_7, \quad [\psi_2,\psi_5]=?, \quad [\psi_2,\psi_6]=-2\mathcal{D}\psi_2,\\
&[\psi_2,\psi_7]=0, \quad [\psi_2,\psi_8]=[\psi_4,\psi_6]+[\psi_3,\psi_7]\ldots\\
&[\psi_3,\psi_4]=2\mathcal{D}\psi_8, \quad [\psi_3,\psi_5]=?, \quad [\psi_3,\psi_6]=2\kappa\mathcal{D}\psi_3,\\
&[\psi_3,\psi_7]=[\psi_2,\psi_8]-[\psi_4,\psi_6], \quad [\psi_3,\psi_8]=0\ldots\\
&[\psi_4,\psi_5]=0, \quad [\psi_4,\psi_6]=\mathcal{D}[\psi_1,\psi_5], \quad [\psi_4,\psi_7]=[\psi_2,\psi_5]-2\mathcal{D}\psi_2,\\
&[\psi_4,\psi_8]=\mathcal{D}[\psi_3,\psi_5]\ldots\\
&[\psi_5,\psi_6]=[\psi_2,[\psi_3,\psi_5]]-[\psi_3,[\psi_2,\psi_5]], \quad [\psi_5,\psi_7]=[\psi_4,[\psi_2,\psi_5]],\\
&[\psi_5,\psi_8]=[\psi_4,[\psi_3,\psi_5]]\ldots\\
&[\psi_6,\psi_7]=2\mathcal{D}\psi_7-[\psi_1,[\psi_2,\psi_5]], \quad [\psi_6,\psi_8]=-2\kappa\mathcal{D}\psi_8-\mathcal{D}[\psi_3,[\psi_1,\psi_5]]\ldots\\
&[\psi_7,\psi_8]=[\psi_4,[\psi_3,\psi_7]]-[\psi_3,[\psi_4,\psi_7]]\ldots
\end{aligned}
$$

where $\mathcal{D}$, κ are real parameters and '?' denotes undefined commutators.

Note that the commutators $[\psi_1, \psi_5]$, $[\psi_2, \psi_5]$, $[\psi_3, \psi_5]$ are not defined and in particular that even introducing new generators ψ_9, ψ_{10}, ψ_{11}, the algebra anyway does not close as a Lie algebra and is

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