

Population–reaction model and microbial experimental ecosystems for understanding hierarchical dynamics of ecosystems

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ARTICLE INFO

Article history:

Received 17 September 2015

Received in revised form

10 December 2015

Accepted 11 December 2015

Available online 30 December 2015

Keywords:

Ecosystem dynamics

Hierarchical dynamics

Population–reaction model

Microbial experimental ecosystem

High-dimensional and nonlinear dynamic systems

ABSTRACT

Understanding ecosystem dynamics is crucial as contemporary human societies face ecosystem degradation. One of the challenges that needs to be recognized is the complex hierarchical dynamics. Conventional dynamic models in ecology often represent only the population level and have yet to include the dynamics of the sub-organism level, which makes an ecosystem a complex adaptive system that shows characteristic behaviors such as resilience and regime shifts. The neglect of the sub-organism level in the conventional dynamic models would be because integrating multiple hierarchical levels makes the models unnecessarily complex unless supporting experimental data are present. Now that large amounts of molecular and ecological data are increasingly accessible in microbial experimental ecosystems, it is worthwhile to tackle the questions of their complex hierarchical dynamics. Here, we propose an approach that combines microbial experimental ecosystems and a hierarchical dynamic model named population–reaction model. We present a simple microbial experimental ecosystem as an example and show how the system can be analyzed by a population–reaction model. We also show that population–reaction models can be applied to various ecological concepts, such as predator–prey interactions, climate change, evolution, and stability of diversity. Our approach will reveal a path to the general understanding of various ecosystems and organisms.

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1. Introduction

Understanding ecosystem dynamics is crucial in view of the recent degradation of ecosystem services, which support human life (World Resources Institute, 2005); however, we have yet to understand the features of ecosystem dynamics, *i.e.*, how ecosystems have been organized, sustained, and degraded. It is even difficult to explain the dynamics of simplified experimental ecosystems (Fussmann *et al.*, 2005; Hosoda *et al.*, 2011; Kasada *et al.*, 2014; Tsuchiya *et al.*, 1972). One of the most critical gaps in our understanding is how organisms change their phenotype within the ecosystems, such as by evolution or phenotypic plasticity (Ellner, 2013; Shimada *et al.*, 2010). A phenotype can be considered as an interface between two hierarchical levels in ecosystems: the ecological level, composed of various organisms and environmental

factors, and the sub-organism level, composed of tissues, cells, and molecules (Fig. 1A; Holling, 2001; Odum and Barrett, 2005). The sub-organism level changes depending on the status of the ecological level, which, in turn, as the phenotype changes, it affects the changes at the ecological level. Thus, a phenotypic change can determine whether an environmental change is absorbed or amplified to become a considerable impact to the ecosystem. Therefore, to understand how ecosystems change, it is necessary to consider the phenotypic changes that determine and are determined by the interaction between two hierarchical levels (Conrad, 1996; Conrad and Pattee, 1970). In this perspective, we focus on the hierarchy of ecosystems, a core feature that makes ecosystems complex adaptive systems (Levin, 1998) that bring important features such as resilience and regime shifts.

For understanding the features of ecosystem dynamics and their bases, it is effective to conceptualize real systems using a dynamic model, which is a mathematical model that mechanically describes how the system changes over time (Ellner and Guckenheimer, 2006). For our purpose, it is necessary to integrate the internal dynamics into the model of ecological dynamics.

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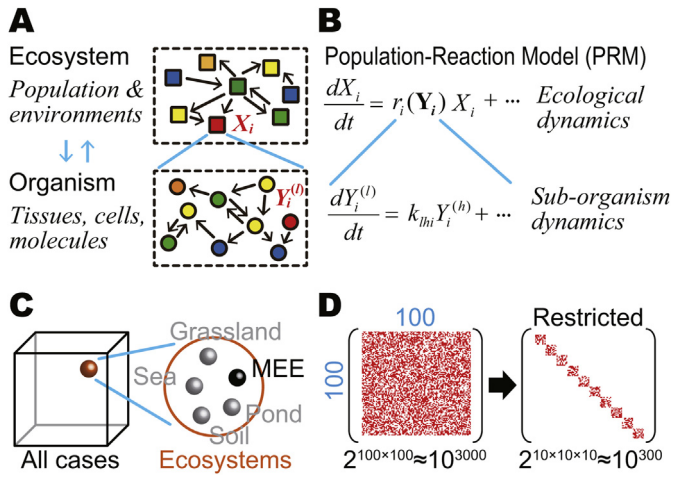


Fig. 1. Ecosystems and population–reaction models. (A) Ecosystem as a hierarchical system. Two hierarchical levels are shown: the ecological level composed of interactions among organisms and environmental components (upper), and the sub-organism level composed of interactions among components inside the organism, such as cells and molecules (lower). (B) Part of the expression of the PRM. X_i and Y indicate the amount of components at the ecological and sub-organism levels, respectively. X_i is the population of the i th organism in the ecosystem, and $Y_i^{(l)}$ is amount of the l th sub-organism component in the i th organism. A phenotype of the i th organism r_i is expressed by the sub-organism components $Y_i = \{Y_i^{(1)}, Y_i^{(2)}, \dots\}$. (C) Schematic presentation of the patterns of the model construction of HNDS. Ecosystems (orange ball) correspond to a tiny fraction among all the mathematically possible cases of HNDS (black cube). Our focus is not on all the cases but the ecosystems (orange ball) including all natural ecosystems and model experimental systems. We consider every MEE (black ball) as one of the ecosystems. (D) Example of a model constraint from hierarchy. Let us consider 10 different organisms, each of which has 10 different sub-organism components, i.e., there are $10 \times 10 = 100$ different sub-organism components in this ecosystem. The logical matrix of the interaction among 100 components is depicted (i.e., a red dot if there is a direct interaction). All the possible cases of the matrix are $2^{100 \times 100} \approx 10^{3000}$. When we add an assumption stating that there is no direct interaction of sub-organism components among different organisms, all the possible cases can be $2^{10 \times 10 \times 10} \approx 10^{300}$, which is one tenth of a whole. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

However, this could make the model unfruitfully complex unless supporting empirical or experimental data are available because understanding high-dimensional and nonlinear dynamics is challenging (Blasius et al., 2007; Strogatz, 1994). Currently, the use of microbial systems allows consideration of the molecular basis of the phenotype (Egbert et al., 2010; Karr et al., 2012). Likewise, microbial experimental ecosystems (MEEs) enable us to obtain experimental data from both the ecological and sub-organism levels (Germond et al., 2013; Hosoda et al., 2014; Momeni et al., 2011; Song et al., 2014; Yu et al., 2012). Currently, large amounts of molecular and ecological data are increasingly accessible, and it is worthwhile to consider ecosystems as complex hierarchical systems.

Here, we propose an approach that uses both MEE and a novel framework of dynamic modeling termed as population–reaction model (PRM; Fig. 1B). PRMs are simple fusion of conventional models in population ecology and reaction kinetics, and they consider the amount of components in both ecological and sub-organism levels. Briefly, the phenotype, which has been conventionally expressed as rate constants in the Lotka–Volterra equations, is not a constant but a function of the amount of the sub-organism components in the PRMs. In PRMs, a change at the ecological level affects the changes in the sub-organism level and vice versa. PRMs are primitive and intuitive because they are based on a conventional way. In addition, they can be compared with experiments of MEEs directly because they include the amount of components in both levels. Our proposed approach using MEEs and PRMs has 3 steps: (i) a MEE is constructed as a real system, (ii) the dynamics

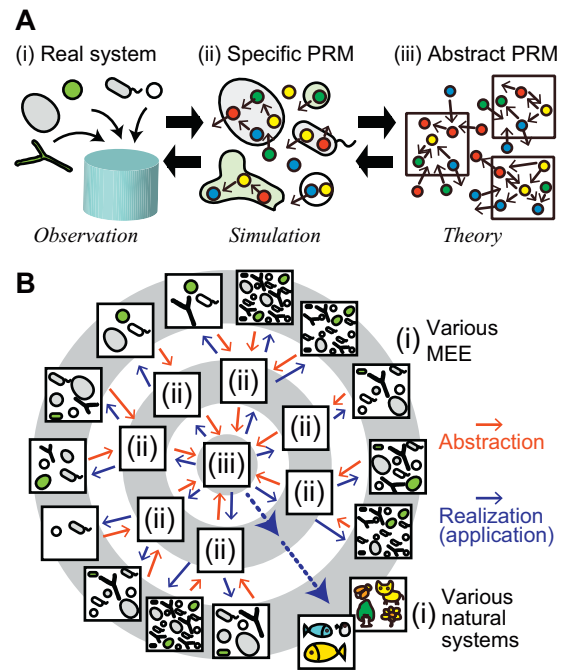


Fig. 2. Proposed approach. The three steps of our strategy. See the text for explanation.

of the MEE is analyzed by a specific PRM, and (iii) an abstract PRM is constructed to highlight the common features of the ecosystem dynamics from the knowledge of various MEEs (Fig. 2, see below). Because the abstract PRM is based on various specific PRMs that correspond to real systems, the consequent theory grasps the real systems with generality. Below, we describe key challenges, our proposed approach, and examples of PRMs.

2. Challenges

Here, we outline the general challenges for understanding complex dynamics using dynamic models. It is challenging to manage high-dimensional (“high” means greater than 5–10; Kaneko and Tsuda, 2003; Smale, 1976) and nonlinear (having nonlinear terms such as predator–prey terms of the Lotka–Volterra equations) dynamic systems (HNDS; Blasius et al., 2007; Strogatz, 1994). Non-linear systems cannot be understood solely as a sum of simple parts; instead, they requires us to consider the “system as a whole” comprehensively even it is high dimensional in contrast to linear systems where the entire system is the same as the sum of the parts. High dimensionality requires us to consider vast numbers of options in the model construction (known as the curse of dimensionality, e.g., in a dynamic model of 100 component, $2^{100 \times 100} \approx 10^{3000}$ of possible interaction patterns exist even if we only consider binary pairwise interactions), despite the fact that small differences in the model assumptions could result in partially contradictory conclusions (May, 1972; Mougi and Kondoh, 2012). Hence, we usually try to decrease the dimensions of the dynamic model by considering only a few components of interest, on the assumption that the other components are negligible. This procedure is effective to understand certain aspects of complex HNDS. Indeed, HNDS can partially show ordered (as opposed to chaotic) phases that can be approximately explained by a few effective dimensions; however, various small changes accumulate as history in other unnoticeable dimensions, and HNDS can suddenly change its state to another phase depending on its history (Kaneko and Tsuda, 2003). Such sudden changes depending on its history can be interpreted as remarkable events in ecosystems such

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