

A probabilistic approach of flow-balanced network based on Markov chains

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Abstract

We used Markov chains to assess residence time, first passage time, rate of transfers between compartments, recycling index with a general mathematical formalism. Such a description applies to any flow-balanced system that can be modelled as a series of discrete stages or compartments through which matter flows. We derived a general set of equations from a probabilistic approach and applied them to a food web and a physical system derived from the literature. We therefore analysed preferential pathways of matter and behaviour of these systems and showed how it was possible to build up and exploit indices on the basis of a transition probability matrix describing the network, and to characterize with a generic algorithm: (1) the total indirect relationships between two compartments, (2) the residence time of one compartment and (3) the general recycling pathways including the amount of matter recycling and the implication of each compartment in recycling.

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1. Introduction

Ecosystem behaviour is driven by different temporal and spatial scales of biological and physical processes.

Because of the spatial boundaries of a system, any matter (salt or fresh water, carbon, nitrogen or any substance) flowing through it will remain for a period, which depends on the interactions between the process involved and the type of matter. Therefore, assessing matter cycling, pathways and residence time within ecosystem compartments can help in understanding ecosystem properties. For deterministic systems based

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on interactions between compartments, whether this be matter transfer as described by Guangsuo et al. (2002), Thompson et al. (2002), Sivakumar et al. (2005) and Yu and Wehrly (2004), or changes of the system from one state to another as described by Logofet and Lesnaya (2000), probability of transition from one compartment to another can be defined during a given time. Assuming that transition probabilities are time-independent, this corresponds to a Markov chain model, where the state of the system at time $s > t$ can be predicted from the knowledge of the state of the system at time t and does not depend on the situation before t (Markov property, Bailey, 1964). Markov chain models are particularly adapted to the study of succession processes such as forest successions (Logofet and Lesnaya, 2000; Benabdellah et al., 2003), metapopulation dynamics (Moilanen, 2004), or the evaluation of transit times of tracers in various environments. Examples of transit though environments include: transit in a gasifer (Guangsuo et al., 2002), of a particle in a tidal mixing estuary (Thompson et al., 2002), of a solute in an aquifer system (Sivakumar et al., 2005) and of drugs within the body (Yu and Wehrly, 2004).

Description of this type also applies to ecological studies. Odum (1959) defined ecology as “the study of the relationships of organisms with one another and with their non-living environment” and the magnitude of matter and energy flows between the various components of an ecosystem is now regarded as an appropriate measure of such relationships (Szyrmer and Ulanowicz, 1987). A food web is therefore a good method for the quantitative description of an ecosystem (Ulanowicz, 1984). The food web can be seen as a graph, with nodes (the compartments) and quantitative links (the trophic fluxes between them). Such a representation might seem static and non-evolutive, as would a still photograph of the ecosystem. Yet trophic dynamic aspects emerge from such representations (Lindeman, 1942). Once the food web is drawn, this often complex scheme can be transformed into a more synthetic representation which reveals the emergent properties of the system (Ulanowicz, 1986). When studying the interrelations between components of a food web, looking at direct interactions (first passage flows) is not enough and one has also to consider subsequent passage flow from a holistic point of view (Patten, 1995). Hannon (1973) applied Leontief’s input–output analysis (Leontief,

1936, 1951) to ecology, in order to study the interdependence of organisms in an ecosystem. The central element in this theory is the Leontief structure matrix, which is commonly thought to express the total direct and indirect flows between any two compartments of a system (Szyrmer and Ulanowicz, 1987). Two parallel conceptions can be distinguished in input–output analysis. These are Leontief’s backward formalism, which from the outputs of the systems deduces the necessary inputs, and Augustinovicz’s forward formalism, which calculates the fate of outputs from the compartments, thus deducing the transit of the matter from the inputs to the system (Kay et al., 1989). The direct interactions are shown by the two-dimensional matrix of internal exchanges, and much information can be obtained about the indirect links through straightforward operations on the matrix of direct flows (Ulanowicz, 1984). The multiplicity of possible pathways within the food web are translated into indices based on thermodynamics and information theory, such as ascendancy, redundancy and overheads (Ulanowicz, 1986; Ulanowicz and Norden, 1990). By introducing the idea of temporality into this conception, Higashi et al. (1993) gave importance to the biomass of the compartments. In their description, the transfer of matter (energy, carbon, biomass, etc.) from one compartment to another can be delayed by storage in the compartments. Hence, each flow is a possible pathway for matter, which is taken with a certain probability. This describes a Markov process in which matter is transferred or retained in the food web at each time-step, depending only on its previous trajectories. Markov transition probability matrices can be constructed according to the two conceptions of information theory, backward or forward cases (Kay et al., 1989).

Residence time has received a lot of attention as a useful indicator in physical oceanography. Several definitions of residence time can be found in the literature. According to Takeoka (1984a), transit time should be distinguished from residence time. The first deals with the time water particles take to cross an area from entrance to exit. For the second, all the particles contained in the area are considered. In this case, the residence time corresponds to the mean transit time but depends on the initial location of the particles. Takeoka (1984a) showed that the difference between the two mean temporal characteristics could be defined as the age of the particles retained in the area. In a general

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