



Predicting the structure and mode of vegetation dynamics: An application of graph theory to state-and-transition models



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ABSTRACT

The recent literature suggests that the network structure of ecological states within a system can determine whether the system's response to environmental changes is reinforced by positive feedback mechanisms (amplification); rapidly propagated throughout the entire network of states (synchronization); or structurally constrained. The purpose of this research was to predict these various modes of system dynamics in the context of vegetation change represented as state-and-transition models (STMs) at a salt marsh of the Danish Wadden Sea. In the STM framework, several different plant communities identified by a classification approach were regarded as multiple alternative "states," with "transitions" defined by observed transformations among the communities over time. Treating these STMs as mathematical graphs, three metrics from algebraic graph theory—*spectral radius*, *algebraic connectivity*, and *S-metric*—were calculated to characterize the degree of amplification, synchronization, and structural constraint, respectively. Results demonstrated that observed vegetation dynamics underwent stronger amplification and synchronization, and weaker constraint than hypothesized benchmark patterns such as linear sequential, cyclic, convergent, and divergent dynamics. These findings indicate that, as marsh development proceeds through vegetation processes, the connectivity among plant communities becomes enhanced, which corresponds to a higher possibility for abrupt and complex system reorganization in response to environmental changes (e.g., gradual sea-level variations and storm surges). In this way, the coupled graph theory and STM approach contributes to identifying holistic properties of an ecological system that are otherwise not evident from the conventional theories (e.g., the continuum concept) and methodologies (e.g., gradient analysis).

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1. Introduction

Ecologists have long sought to understand the extent and mode of ecological systems' response to environmental changes (Parmesan and Yohe, 2003; Harley et al., 2006; Post et al., 2009). The response patterns have often been examined by defining several different ecological states (e.g., savannah vs. woodland) within a system, and studying how these individual states behave in conjunction with environmental variations (Jørgensen and Bendoricchio, 2001). However, a body of recent research suggests that, independently of such states' internal dynamics, the network structure among states can also determine the overall system behavior (e.g., Restrepo et al., 2007). In other words, the dynamics of states such as ecological interactions within a plant community, and the structure of links among them such as community transitions, may influence overall system dynamics independently. Therefore, to get a holistic picture of system dynamics, the study of

ecological processes within communities should be accompanied by looking at the topology of the interaction network among the communities in the form of state transitions.

Recently, Phillips (2011a,b, 2012) has developed a novel approach for examining effects of network structures on ecological dynamics: changes in ecological states are represented via state-and-transition models (STMs), and, by treating the STMs as mathematical graphs, several metrics from algebraic graph theory are employed to quantify the degree of such dynamics (Harary et al., 1965; Hage and Harary, 1983). While graph theory has long been used to analyze spatial patterns in geography and landscape ecology, the combination of STMs and graph theory provides environmental scientists with a new opportunity to understand how effects of environmental changes can be amplified, synchronized or structurally constrained, depending on the pattern of the network structure among ecological states in a system. The use of this combination is still in its infancy, however. It has been employed in only a few studies related to soil and rangeland types (e.g., Phillips, 2011a,b), but not in community ecological research yet. Because STMs are one way of representing vegetation dynamics, and plant communities are a common way of defining alternative ecological

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states, algebraic graph theory may be useful in community ecology more generally.

The purpose of this paper is to investigate relationships between the network structure of transitions among plant communities, and the mode of vegetation dynamics in a coastal salt marsh through time. These communities are identified by a multivariate classification approach. The resulting communities are considered multiple alternative states, with network structure represented via STMs. The system dynamics we are particularly concerned with in this research are amplification of environmental changes, synchronization, and structural constraints (these are discussed in Section 2.2). For each of these items, the relevant graph theory metrics are calculated. The implications of the analysis are then discussed with respect to the contexts of coastal setting and community ecology.

2. Background

2.1. State-and-transition models (STMs)

The application of graph theory to STMs may be of direct interest to community ecologists. STMs were originally developed due to the longstanding dissatisfaction arising from the inability of the so-called climax model (Clements, 1916; Dyksterhuis, 1949) to incorporate complex, multiple pathways of vegetation dynamics observed in nature. In their foundational discussion, Westoby et al. (1989) introduced the framework of STMs, as an alternative to the Clementsian concept of single equilibrium communities and deterministic successional pathways. In STMs, patterns of vegetation dynamics are described by a set of discrete *states* of the vegetation and a set of discrete *transitions* between states. Here, a state is defined as an alternative, persistent plant community. STMs have been developed and most commonly used in range ecology (see overviews by Briske et al., 2005; Bestelmeyer et al., 2009; Derner et al., 2012). However, their robustness is increasingly reported in other systems, including forests, river and riparian corridors, wetlands, and karst landscapes (e.g., van der Wal, 2006; Hernstrom et al., 2007; Czembor and Vesk, 2009; Zweig and Kitchens, 2009; Froend and Sommer, 2010; Lester and Fairweather, 2011; Phillips, 2011a,b, 2012).

STMs are not just a management tool, however, as they represent an application of theoretical frameworks in ecology based on alternative stable states, multiple developmental pathways, path dependence, and nonequilibrium dynamics. Though overlapping, the latter concepts are not identical (c.f. Cattalino et al., 1979; DeAngelis and Waterhouse, 1987; Wilson and Agnew, 1992; Tausch et al., 1993; Hobbs, 1994; Klötzli, 1998; Scheffer et al., 2001; Perry, 2002; Woods, 2007; Wood and Bowman, 2012). However, they all represent alternatives to monotonic progression toward a single end-state. While classical succession can be considered a special case, STMs can accommodate any chronology or network of ecological state transitions. López et al. (2011) explicitly linked the STM formalism to the theoretical concepts of dynamic equilibrium, resistance, resilience, and thresholds, and Phillips (2011b) to the dynamics of ecological amplification of effects of environmental change.

An STM is typically represented as a box-and-arrow diagram, indicating ecological states and transitions between them, respectively. In this research, ecological states imply several discrete plant communities. The conditions driving or favoring the transformations among these communities are identified based on both theoretically and empirically determined probabilities. For example, in terms of the Clementsian theory, state transitions occur along the gradients of marsh surface elevation and/or salinity when critical thresholds are transgressed. Alternatively, in the scenario of disproportionate/nonlinear responses and complex adaptive

systems (e.g., Burkett et al., 2005), transitions occur as a function of complex interactions among sea level, sedimentation, and biota, which create a spatial mosaic, rather than an advancing front, of changes (Phillips, 2011a).

2.2. Amplification, synchronization, and structural constraint

Ecological transitions in response to environmental changes can be reinforced by positive feedback mechanisms or disproportionately amplified because of dynamical instabilities (Wilson and Agnew, 1992; Scheffer et al., 2001; Phillips, 2011b). Salt marshes provide a classic example of a positive feedback amplifier phenomenon: in most cases, the presence of vegetation cover enhances sedimentation processes and prevents substrate erosion, which, in turn, facilitates the growth of the vegetation due to the increase in surface elevation and the consequent reduction of physical stress (Reed, 1990; Srivastava and Jefferies, 1995; van de Koppel et al., 2005; van Wesenbeeck et al., 2008).

At its simplest, synchronization means that things operate simultaneously or in unity; for example, concurrence of particular ecological changes across different locations. This topic has been a central issue mainly in population ecology. For instance, Post and Forchhammer (2004) found that, during the periods of 1810–1865 and 1908–1981, increased spatial autocorrelation in local weather conditions drove the spatially synchronous dynamics in local caribou populations in Greenland. In the community ecological context of this present research, synchronization is addressed as the extent to which transitions among multiple communities occur more or less contemporaneously throughout the marsh system studied, rather than progressively seaward or landward along the sea–land gradient.

Amplification and synchronization can be, independently of types of environmental changes and individual communities' dynamics, significantly influenced by the degree of structural constraints. These constraints inherently exist within a system and are determined by the network structure of ecological states. Low structural constraints indicate that environmental changes or transitions among states are potentially readily amplified or transmitted through the system. A high degree of structural constraint is often associated with a relatively sparse network of connections and/or presence of “sink” states where once transition into a given state has occurred, it is difficult or impossible to move out of it. A low degree of structural constraint is associated with greater connectivity, absence of sink states, and presence of “hub and spoke” type structures where there exist one or more highly connected hub states that facilitate transition. Amplification, synchronization, and structural constraint are measured using metrics derived from algebraic graph theory, as described in detail below.

2.3. Graph theory

The combination of graph theory and STMs begins with transferring the box-and-arrow diagram of an STM into a mathematical graph: plant communities (i.e., boxes) and transitions (i.e., arrows) of the STM correspond to N nodes and m links (or edges) in the graph, respectively. This graph may be directed (transitions are one-directional along any link) or undirected (transitions are possible in both directions). The graphs dealt with in this study are assumed to be undirected, because most STMs in previous studies allowed two-way transitions among pairs of communities. A graph is considered connected when every single node is linked to at least one other node, whereas it is called unconnected if any node is *isolated* without any link to another.

Then, a $N \times N$ adjacency matrix (A) is constructed in which only two entries exist: 1 when any row and column nodes are connected, and zero otherwise. The matrix's diagonal entries are always zero.

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