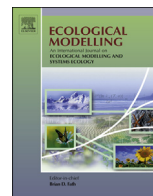




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# The robustness of chronosequences

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### ARTICLE INFO

Article history:  
Available online xxx

Keywords:  
Robustness  
Path stability  
Chronosequence  
Coevolution  
Earth surface systems

### ABSTRACT

Chronosequences are a fundamental tool for studying and representing change in Earth surface systems. Increasingly, chronosequences are understood to be much more complex than a simple monotonic progression from a starting point to a stable end-state. The concept of path stability is introduced here as a measure of chronosequence robustness; i.e., the degree to which developmental trajectories are sensitive to disturbances or change. Path stability is assessed on the basis of the largest Lyapunov exponent ( $\lambda_1$ ) of an interaction matrix consisting of positive, negative, or zero entries based on whether existence of a given system state or stage promotes or facilitates (positive), prevents or inhibits (negative), or has no significant effect on transitions to another state. Analysis of several generic chronosequence structures represented as signed, directed, unweighted graphs indicates five general cases: Path-stable reversible progressions ( $\lambda_1 < 0$ ); neutrally path-stable irreversible progressions ( $\lambda_1 = 0$ ); path unstable with very low divergence ( $0 < \lambda_1 < 1$ ); path unstable with low divergence ( $\lambda_1 = 1$ ); and complex multiple pathways ( $\lambda_1 > 1$ ). Path stability is probably relatively rare in chronosequences due to the directionality inherent in most of them. A complex soil chronosequence on the lower coastal plain of North Carolina was analyzed as described above, yielding  $\lambda_1 = 0.843$ , indicating very low divergence. This outcome is consistent with pedological interpretations, and derives largely from the presence of self-limiting early stages, and a few highly developed states that inhibit retrogression back to many of the earlier stages. This kind of structure is likely to be common in pedological and hydrological sequences, but this suggestion requires further testing.

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## 1. Introduction

Earth surface systems (ESS) are often characterized by tightly woven interconnections among soil, hydrological, ecological, and geomorphological features and processes. All of these may be profoundly influenced by external forcings and boundary conditions of climate, geology, and human agency.

These factors coevolve, both on the shorter timescales of, e.g., ecosystem development and landscape transformation, and on the longer timescales of biological and geological evolution. Because in many cases the time span of ESS development is too long for direct observation, a critical tool for understanding and interpreting change over time is a chronosequence. This paper is concerned with the robustness and path stability of chronosequences.

Chronosequence analysis is a form of ergodic (space-for-time substitution) reasoning (Paine, 1985; Fryirs et al., 2012), although chronosequence is sometimes used more loosely to refer to any historical or successional sequence. In pedology, a chronosequence is a spatial sequence of soils in which the only factor of soil formation that is significantly variable is time, representing the age of

the soil or of the geomorphic surface on which the soil was formed. Thus a sequence of moraines or alluvial terraces, for instance, with similar parent material, climate, topography, etc., could be treated as a chronosequence to determine pathways, rates and stages of pedogenesis. Reviews, syntheses, and critiques of chronosequence approaches in pedology and soil geomorphology are given by Vreeken (1975), Schaetzl et al. (1994), Huggett (1998), and Sauer (2010). Chronosequences have also been used extensively in ecology, and were important in, e.g., development of some of the earliest and most influential ideas on ecological succession (Cowles, 1899). Ecological chronosequence concepts and applications are reviewed and critiqued by Foster and Tilman (2000), Johnson and Miyanishi (2008), Walker et al. (2010), and Dickie et al. (2013).

Path stability is an expansion of stability concepts to the domain of networks of state changes. Existing stability concepts include mechanical stability or similar concepts of *resistance*. These include various notions of resistance to change, or proximity to critical thresholds. Examples include factor-of-safety evaluations of hill-slopes, design of stable channels in engineering hydraulics, and ecological resistance to disturbance. In general, these involve some notion of comparing forces or drivers of change to strength, resistance, or absorption capacity. A second notion is dynamical stability (sometimes called ecological or system stability). This relates to *resilience*—the ability to recover, or return toward the previous

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state, following a disturbance or perturbation. Dynamical stability is directly related to sensitivity to small perturbations and minor variations in initial conditions, and thus to chaotic dynamics. Examples include studies of ecological resilience, sensitivity of hydrologic systems to small disturbances and spatial variations, and chaotic dynamics of soil systems. Path stability complements existing stability concepts of resistance and resilience with an assessment of *robustness*, the tendency to maintain a developmental pathway or mode of operation in the presence of environmental fluctuations. While resistance and resilience apply to individual ESS components or to the network of relationships among system components, robustness or path stability applies to a network of changes in system states, such as that represented by a chronosequence.

Johnson and Miyanishi (2008) are strongly critical of chronosequences used to study ecological succession, particularly because most violate the “critical assumption that all sites have traced the same history” (p. 427). This assumption is also frequently violated in soil chronosequences, simply because the time scales of pedogenesis often transcend climate and other environmental changes and disturbances. Pedologists and geomorphologists recognize this as a handicap. However, space-for-time methods are often the only option if detailed historical reconstructions at a single location are not possible or feasible, so the utility of soil and landform chronosequences, despite their flaws, has not been seriously challenged (see, e.g., Mills, 2005).

This is not the case in ecology, where Johnson and Miyanishi (2008), expanding on earlier critiques, concluded that the chronosequence approach is not a valid method for studying vegetation dynamics. These criticisms are based on whether the all-other-things-equal assumption of chronosequences are met, the failure of some ecological chronosequences to identify clear trends, and the application of other methods to classic chronosequence locations that do not support the space-for-time studies (Johnson and Miyanishi, 2008). Walker et al. (2010) did not dispute those specific critiques, but maintained that under certain circumstances chronosequences are appropriate in studies of ecological succession and soil development. As is often the case in pedology and Earth sciences, Walker et al. (2010) are willing to live with the flaws of the approach when no better alternative is available. Specifically, they find ecological chronosequences most appropriate for systems with low biodiversity, following convergent trajectories, with rapid turnover and low disturbance frequency (and least appropriate for the converse). Similarly, Dickie et al. (2013) specifically called for additional chronosequence studies to elucidate relationships between ecosystem development and mycorrhizal communities.

Criticisms of chronosequence studies are often based on the inability of space-for-time methods to identify monotonic developmental trends in many cases (c.f. Foster and Tilman, 2000; Johnson and Miyanishi, 2008). Such criticisms are of limited relevance, however, when the goal is to identify and understand patterns of environmental change, whether or not multiple pathways and outcomes are present. Thus, while Walker et al. (2010) are correct that divergence in a chronosequence makes the identification of monotonic trends problematic, a divergent chronosequence may have its own intrinsic value in understanding, e.g., pedological, hydrological, and ecological change.

Most chronosequence studies have utilized single or mean characterizations of the stage or state of the system at each time increment. However, chronosequences by definition have spatial as well as temporal dimensions. Thus it is possible for several different states (e.g., soil types) to exist during the same time period. A few pedological chronosequence studies explicitly address, or at least acknowledge, variations within time periods and changes in variability or diversity over time (Sondheim and Standish, 1983; Thompson, 1983, 1992; Barrett and Schaeztl, 1993; Phillips, 1993a,

2001; Eppes and Harrison, 1999; Barrett, 2001; Toomanian et al., 2006; Caldwell et al., 2012). For the most part (but not entirely), these studies show an increase in soil richness over time, indicating pathways more complex than a linear successional sequence. Langley-Turnbaugh and Bockheim (1997) and Gracheva et al. (2001) also studied chronosequences exhibiting more than one distinct soil type at a given stage. Zilioli et al. (2011), Botha and Porat (2007) and Gracheva et al. (2001) showed how soil chronosequences may involve distinctly different pedogenetic pathways. An alluvial soil chronosequence from the Virginia coastal plain showed that not all soil properties exhibited similar directions, much less rates, of development, and that transitions between stages were sometimes marked by reversals in the direction of soil evolution (Howard et al., 1993).

Similarly, space-for-time studies in geomorphology have been dominated by identification of characteristic forms at different stages rather than increasing or decreasing spatial variability or multiple evolutionary paths. However, there are some exceptions. Increases in topographic roughness over time were documented in a glacial moraine chronosequence by Elliott (1989). Klaar et al. (2009) specifically addressed increases in hydraulic and geomorphic complexity in a 200-year chronosequence of recently formed proglacial streams, and an ergodic approach led Leyland and Darby (2008) to a multipath model of gully evolution.

Divergence in the form of multiple plant communities at the same age or chronological stage has been found in a number of ecological chronosequences (e.g., Olson, 1958; Gersmehl, 1976; Matthews, 1979; Fastie, 1995; Johnson and Miyanishi, 2008; Williamson et al., 2012). The discovery of multiple pathways and stable states in chronosequences, and other studies of succession, has led to a number of alternative frameworks such as community assembly, state-and-transition models, and alternative stable state models.

Space-for-time substitutions are rare in hydrology, but several studies specifically address changes in soil hydrologic properties along a chronosequence (Peñuela and Drew, 2004; Young et al., 2004; Bens et al., 2007; Hart and Davis, 2011).

Rather than lamenting or circumventing divergence in chronosequences, another approach is to embrace or exploit it. Divergence (or convergence) in historical sequences has been promoted and used as a method for identifying chaos and dynamical instability in biogeography and geomorphology (Phillips, 2004a, 2006). Noting that some of the most species-rich plant communities occur on older, highly weathered soils, Laliberte et al. (2013) recently proposed exploiting soil chronosequences specifically to explore links between pedogenesis and divergent ecosystem development.

As chronosequences are not all single-path historical sequences where one stage or system state replaces another in a predictable sequence, understanding hydrological and other environmental changes should involve understanding the patterns of changes in ESS states over time, including in some cases the complexity of these patterns. Given the possibility of multiple developmental pathways and convergent or divergent evolution, a key question is the extent to which an observed sequence or an identified network of potential transitions is robust to environmental changes. For example, a path-unstable, convergent chronosequence could indicate equifinality, whereby different processes or histories lead to similar results. By contrast, a divergent, non-robust sequence is indicative of dynamical instability and deterministic chaos.

## 2. Theory and methods

A chronosequence can be represented as a network. A set of discrete system states or developmental stages comprise the nodes of

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