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Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence

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HIGHLIGHTS

- We assessed evidence for multiple stables states in freshwater ecosystems.
- Evidence was mainly limited to studies of shallow temperate lakes.
- Most studies using such terms lacked convincing evidence or appropriate data.
- There were few reports of freshwater ecosystem recovery from alleviated pressures.
- Inconsistent terminology and vague links with theory lead to its inappropriate use.

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ABSTRACT

The concepts of ecosystem regime shifts, thresholds and alternative or multiple stable states are used extensively in the ecological and environmental management literature. When applied to aquatic ecosystems, these terms are used inconsistently reflecting differing levels of supporting evidence among ecosystem types. Although many aquatic ecosystems around the world have become degraded, the magnitude and causes of changes, relative to the range of historical variability, are poorly known. A working group supported by the Australian Centre for Ecological Analysis and Synthesis (ACEAS) reviewed 135 papers on freshwater ecosystems to assess the evidence for pressure-induced non-linear changes in freshwater ecosystems; these papers used terms indicating sudden and non-linear change in their titles and key words, and so was a positively biased sample. We scrutinized papers for study context and methods, ecosystem characteristics and focus, types of pressures and ecological responses considered, and the type of change reported (i.e., gradual, non-linear, hysteretic or irreversible change). There was little empirical evidence for regime shifts and changes between multiple or alternative stable states in these studies although some shifts between turbid phytoplankton-dominated states and clear-water, macrophyte-dominated states were reported in shallow lakes in temperate climates. We found limited understanding of the subtleties of the relevant theoretical concepts and encountered few mechanistic studies that investigated or identified cause-and-effect relationships between ecological responses and nominal pressures. Our results mirror those of reviews for estuarine, nearshore and marine aquatic ecosystems, demonstrating that although the concepts of regime shifts and alternative stable states have become prominent in the scientific and management literature, their empirical underpinning is weak outside of a specific environmental setting. The

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application of these concepts in future research and management applications should include evidence on the mechanistic links between pressures and consequent ecological change. Explicit consideration should also be given to whether observed temporal dynamics represent variation along a continuum rather than categorically different states.

1. Introduction

Rapid and dramatic change in the structure and function of ecosystems due to human-induced pressures is of major concern to modern society, with high stakes associated with the impacts and management of such change. Of particular recent concern is the increasingly prevalent notion that dramatic ecological change can occur suddenly, and without warning, potentially causing stark or irreversible shifts in ecosystem state (Scheffer et al., 2001a,b; Carpenter, 2003; Mac Nally et al., 2014). Ecologists have conceptualized these ideas with terminology borrowed from engineering and other systems sciences so that non-linear ecological change is typically conceived as a shift in state from one relatively stable 'basin of attraction' or 'regime' to another, usually after an external trigger or disturbance tips the system over an unstable 'threshold'. Internal feedbacks are inferred to maintain ecosystems in particular states with varying degrees of 'resistance' (i.e., capacity to maintain a current state against a rising pressure) and 'resilience' (i.e., the capacity to recover once a pressure is relaxed) to disturbance (Harrison, 1979). The potential for such 'ecological surprises' is often raised to support urgent management action to avoid 'tipping points' and consequent undesirable change (Scheffer and Carpenter, 2003; Lindenmayer et al., 2011). Conversely, terms such as regime shift are often invoked to argue that a system has already exceeded a critical ecological threshold and is residing either in an unstable phase or in an alternative, often novel, regime and therefore requires different management goals and tools (e.g., Walker et al., 2009). The regime-shift metaphor has profound implications for management choices and the development of appropriate aims, methods and interventions. It is vital that the evidence supporting this prominent conceptual framework be thoroughly and critically evaluated so that its relevance to particular ecosystems can be determined.

Ideas of ecological regime shifts, alternative or multiple stable states and thresholds are controversial (e.g., Peterson, 1984; Groffman et al., 2006) and have recently come under increasing analytical scrutiny (e.g., Petraitis, 2013; Mac Nally et al., 2014). Empirical evidence has been evaluated for a range of ecological systems, particularly marine environments and, most recently, in estuaries and nearshore ecosystems (Table 1). These assessments found few instances of regime shifts and multiple stable states, and generally concluded either that methodological approaches to the identification of multiple stable states were inadequate or that the concept was of little practical value (Bertness et al., 2002). The quest for valid evidence of regime shifts and multiple stable states appears to be hampered by three main impediments: (1) terminological proliferation and inconsistency; (2) inadequacy of the temporal and spatial resolution and scope of datasets for evaluating change in relation to the range of system variability; and (3) insufficient demonstration of mechanistic links between pressures and consequent ecological change (Peterson, 1984; Mac Nally et al., 2014). Mac Nally et al. (2014) pointed out that the frequency of non-linear change relative to that of linear change has rarely been considered.

Freshwater ecosystems frequently are cited as exemplars of regime shifts and multiple stable states (Holling, 1973; Carpenter et al., 2011), the classic case being a shift in shallow temperate lakes between clear-water, macrophyte-dominated states and turbid, phytoplankton-dominated states (Scheffer et al., 1993). However, we are unaware of any prior critical evaluation of the evidence for regime shifts and multiple stable states in freshwater ecosystems more generally. Understanding ecological change in freshwater ecosystems is especially important because they are among the world's most altered and damaged ecosystems yet have high socio-ecological interdependence and highly contested resource management and allocation (Vörösmarty et al., 2010; Capon et al., 2013). Freshwater ecosystems are likely to be extremely vulnerable to future changes in climate and other human pressures (Capon et al., 2013; Capon and Bunn, 2015).

We examined the evidence for non-linear ecological change, including regime shifts, ecological thresholds, and multiple or alternative stable states, in freshwater ecosystems. We searched for published papers reporting abrupt ecological change and evaluated these with respect to their context, methods and results. Studies claiming to provide empirical evidence of ecological change were characterized according to the type of ecological change described and were assessed with criteria deemed relevant to establish convincing evidence of non-linear change.

Table 1
Summary of papers examining evidence for ecological regime shifts.

Citation	Description	Ecological system(s)	Findings
Connell and Sousa (1983)	Review of instances cited by theoretical papers	Range	Instances reviewed all found to have at least one of following shortcomings: 1.) physical environment differs between alternative states, 2.) alternative states persist only when artificial controls (pressures) maintained, 3.) evidence simply inadequate
Petraitis and Dudgeon (2004)	Assessment of published experiments against Peterson's (1984) criteria	Marine	Limited evidence found for alternative stable states due to lack of experimental studies in coral reefs, rocky intertidal shores and soft sediment habitats Kelp forests and coralline barrens meet criteria for alternative stable states
Lees et al. (2006)	Assessment of case studies against defining criteria (N.B. lacking criteria for stability or self-maintenance)	Marine	Regime shifts identified but not demonstrated to be pressure-induced or stable
Spencer et al. (2011)	Regime shift detection analysis of over 300 biological time series	Marine	Apparent regime shifts determined to be artifacts of temporal trends rather than true regime shifts
Mac Nally et al. (2014)	Literature review	Estuarine and near-shore	Most instances reviewed lacked evidence of 'stark' ecological changes with most drawing on space for time substitutions rather than time-series data. Eight instances identified with compelling evidence of stark changes.