Ecological Indicators 85 (2018) 991–998

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Review

Merging community assembly into the regime-shift approach for informing ecological restoration

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ARTICLE INFO

Key-words:
Competition
Ecosystem functioning
Facilitation
Hysteresis
Positive feedback
Restoration
State transition

ABSTRACT

Ecosystems that exhibit alternative stable states are a prominent challenge for ecological restoration. So far, alternative stable states have been addressed from two different angles: community assembly studies, which focus on species and their interactions, and regime shift studies, which focus on changes in ecosystem states following environmental change. Here, we propose a synthetic perspective that merges the community assembly with the regime shift approach to effectively inform restoration of ecosystems exhibiting alternative stable states. We show that the community assembly and the regime shift approaches have emphasized different aspects of alternative stable states (i.e., coarse vs fine resolutions of the focal state variable, different sets of feedback mechanisms, and small vs large spatial scales), and consequently have different limitations that influence restoration strategies. Using a simple mathematical model, we illustrate that a more explicit consideration of species identity and composition (i.e., the community assembly approach) can improve our ability to understand regime shifts and restore degraded ecosystems. Finally, we highlight two case studies in which such merging can bring novel insights into alternative stable states and ecological restoration. Understanding the relevant aspects of community assembly (biotic interactions and species identity) will lead to more informed decisions that target future restoration and the prediction of regime shifts in response to global environmental change.

1. Introduction

Natural ecosystems can exhibit sudden, and sometimes unpredictable, state transitions (Scheffer et al., 2001; Suding et al., 2004). In some cases, such transition in the ecosystem state cannot be easily reversed, particularly when human activities have decreased the ecosystem's capacity to return to the original state on its own. The concept of alternative stable states, in which an ecosystem may exist in one of several possible stable states under the same range of environmental conditions, has attracted increasing interest in the literature because of the possible ecological and economic consequences that transitions between the alternative stable states may imply (Beisner et al., 2003).

Two parallel lines of research have used independent frameworks to understand different aspects of alternative stable states. *Community assembly (CA) approaches* have traditionally focused on how communities assemble through interspecific interactions and can lead to divergent species compositions as a result of different histories of community assembly (e.g. Robinson and Dickerson, 1987; Drake, 1991; Chase, 2003; Fukami et al., 2005; Kadowaki et al., 2012; Chang and HilleRisLambers, 2016). On the other hand, *regime-shift (RS) approaches* have focused on sudden transitions and hysteresis of the states of ecosystems and communities due to environmental change (Scheffer and Carpenter, 2003; Suding et al., 2004). Thus, the CA and RS approaches have emphasized different feedback mechanisms for the occurrence of alternative stable states. The CA approach has focused on biotic interactions among species, such as competition (Drake, 1991; Kadowaki et al., 2012), and we therefore refer to the feedbacks typically investigated in the CA approach as "biotic feedbacks". The RS approach has sought to identify possible mechanisms that accelerate the effects of environmental change, generally positive feedback mechanisms due to the modification of the abiotic environment by the biotic community component (e.g. Sasaki et al., 2008; Isbell et al., 2013). We refer to the feedbacks typically investigated in the RS approach as "abiotic feedbacks", because it generally puts more emphasis on abiotic effects such

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https://doi.org/10.1016/j.ecolind.2017.11.035
Received 26 January 2017; Received in revised form 7 October 2017; Accepted 19 November 2017
Available online 01 December 2017
1470-160X/

as environmental modifications than the CA approach. Not all case studies strictly conform to one of these two broad categories of CA vs RS approaches, but this distinction captures most of the relevant differences between the approaches.

Generally, ecological restoration of systems potentially exhibiting alternative stable states requires a joint application of the RS and CA approaches that have focused on different component mechanisms supporting restoration success, i.e., the abiotic and biotic feedback mechanisms respectively. Studies using the RS approach are generally interested in that abiotic feedback mechanisms that can preclude restoration from a degraded state toward the original/desirable state (Suding and Hobbs, 2009). For example, in depression wetlands in south-eastern United States, species-rich herbaceous communities embedded within longleaf pine forests are maintained with prescribed fires (Martin and Kirkman, 2009). Periods of extended fire suppression, however, cause a shift in community structure from an herbaceous ground flora to one dominated by shrubs and hardwood species. After hardwood species dominate, re-introduction of fire alone does not restore previous herbaceous communities because hardwood species impede the spread of fire, which further facilitates hardwood dominance. Here, the restoration of herbaceous communities based on the RS approach involves reinstating prescribed fire (i.e., abiotic management) as well as mechanical and chemical hardwood species removal (i.e., biotic management). Thus, ecological restoration based on the RS approach generally seeks to re-establish the abiotic feedback that was present before the shift and thereby restore the original/desirable state, often by managing both abiotic and biotic factors.

Alternatively, many restoration efforts involving the introduction or removal of a species aim to re-establish the biotic feedback mechanism that steers community assembly (Young et al., 2005; Baer et al., 2015). For example, Baer et al. (2015) shows that, in tallgrass prairie, a former agricultural land may be restored to a high plant species diversity effectively by removing clonal plant species. Clonal plant species could decrease the positive influence of environmental heterogeneity on plant species coexistence and inhibit the establishment of new species that can exploit niches that may become available during community assembly. Thus, consideration of competition (i.e., biotic feedbacks) with clonal plant species that can limit seedling establishment is required to restore species-rich tallgrass prairie ecosystems (Baer et al., 2015). Thus, ecological restoration based on the CA approach aims to leverage the biotic feedbacks that maintain the original species composition of ecological community through removal or reintroduction of species.

Our distinction between the CA and the RS approaches builds on previous reviews (Beisner et al., 2003; Petraitis, 2013; Chang and HilleRisLambers, 2016), in which the CA perspective has dealt with the state transitions through community assembly under fixed environments, whereas the RS perspective has shown the effect of environmental change on state transitions. Notably, these two approaches have often been a source of confusion in uses and meanings of alternative stable states (Walker et al., 2012), sometimes dealt with as if they reflected a dichotomy in ecological thinking (Didham and Norton, 2007). Although several studies have distinguished the CA and RS approaches (Beisner et al., 2003; Petraitis, 2013; Chang and HilleRisLambers, 2016), these independent approaches have rarely been synthesized into a theoretical and practical framework for ecosystem management and restoration (but see Young et al., 2001, 2005 for exceptions).

In this article, we show that the CA and RS approaches have emphasized different aspects of alternative stable states, and consequently have different limitations that influence restoration strategies. Because ecological restoration should accompany value judgement (such as desirable versus undesirable state in terms of anthropogenic use) (Hobbs, 2007; Hobbs and Cramer, 2008) and involve ongoing environmental changes (Scheffer and Carpenter, 2003; Suding et al., 2004), both of which are key properties of the RS approach, we use the RS approach as a foundation approach. In what follows, we first present the key differences between the CA and RS approaches. We then highlight the potential for integration of relevant aspects of the CA approach into the RS approach to develop a more complete framework for ecological restoration. We illustrate this point using a simple mathematical model and case studies from the literature.

2. Key differences between the CA and RS approaches

We summarize the four key differences between the CA and RS approaches, all of which are relevant for developing integrated perspectives for ecological restoration: (i) the resolution of the state variables studied, (ii) the types of perturbation considered, (iii) the relevant interaction types, and (iv) the spatial scales of the studies. Note that these four aspects are strongly related, and collectively characterize the two approaches to informing restoration.

2.1. The type and resolution of the state variables studied

State variables can be defined in a number of ways (e.g., population abundance, spatial coverages, organic and inorganic quantities) (Beisner et al., 2003; Petraitis, 2013), and importantly, the CA and RS approaches have used different resolutions of the state variables to represent alternative stable states (Fig. 1 top row). While CA studies often use different species compositions to represent alternative stable states (Chase, 2003; Fukami et al., 2005; Fukami, 2015), RS studies often summarize the ecosystem state using a single aggregated variable, namely functional groups or aggregated community properties such as total density or cover (Tomimatsu et al., 2013; Kéfi et al., 2016). For instance, an RS approach investigating desertification may define two alternative stable states between positive vegetation cover and zero vegetation cover (e.g., Kéfi et al., 2007); a CA approach investigating desertification may focus on transitions between different types of plant communities, so they may be different sets of alternative stable states along the transition to desertification, e.g. tree-and-grass vs grass only, and grass only vs desert; and there may even be alternative stable states between different abundances of grass. Thus far, the RS approach conventionally evaluates state variables at a coarser resolution than the CA approach.

2.2. Types of perturbations studied

Studies of the CA vs RS approaches have focused on different types of perturbations when making temporal observations of ecological dynamics (Fig. 1, middle row). RS studies typically evaluate the outcomes of abiotic environmental change that gradually decreases the system's ability to return to the original state (press perturbation) and abiotic pulse perturbation, such as a hurricane (Graham et al., 2015) and nutrient loading (Ling et al., 2009; Isbell et al., 2013; Sasaki et al., 2015). For instance, rangeland desertification may result from a mixture of intensified stock grazing (press perturbation) and drought (pulse perturbation) (van de Koppel et al., 1997) Conversely, the CA approach follows successional dynamics after a pulse perturbation (not including a press perturbation) up to the equilibrium of populations and communities (Young et al., 2001; Chang and HilleRisLambers, 2016) and then asks whether species' immigration history can cause differences in the final equilibrium states of species composition under certain environments (Fig. 1; priority effects or historical contingency in community assembly; Chase, 2003; Fukami, 2015). For example, Fukami et al. (2005) experimentally manipulated initial species composition (but not environmental conditions) and then tracked community structure in abandoned grasslands. As a whole, the RS approach tends to consider pulse and press perturbations acting in concert, whereas the CA approach typically often deals with species dynamic history after pulse perturbations (Beisner et al., 2003; Petraitis, 2013; Fig. 1). We illustrate that the community assembly history can determine the success or failure of ecosystem recovery in the next section (see upcoming 3. Illustration using a toy model).