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## *Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states?*

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Suding et al. (2004) demonstrate how conceptual advances in alternative ecosystem states theory have led to a greater understanding of why degraded systems are often resilient to restoration management. In their review they pose one (of several) ‘outstanding’ questions (Box 3 in Suding et al. 2004): “Are there predictable characteristics that indicate when a system will follow a successional pathway and/or that indicate the presence or absence of alternative ecosystem states?” We suggest that the persistence of alternative stable states might be predicted from simple consideration of assembly rules for systems structured along a gradient of environmental adversity. We raise the hypothesis that strongly abiotically- or disturbance-structured assemblages, with nonrandom trait under-dispersion (Weiher and Keddy 1995), are more likely to exhibit catastrophic phase shifts in community structure than assemblages which are weakly structured by environmental adversity.

To some extent, perceptions of the importance and prevalence of alternative stable states in restoration ecology stem from the systems perspective within which the authors are based. Suding et al. (2004) consider that restoration efforts have traditionally focused on ways in which to reestablish historical disturbance regimes (both abiotic, such as fire and hydrological regimes, as well as biotic, such as grazing intensity) as a means by which to promote successional revegetation of the site. However, this is only one of two common historical approaches to restoration. The other, and arguably the more frequent, is to reestablish the vegetation cover of the site by reseeding or replanting. In fact, the importance of reinstating former disturbance regimes would not be recognised if some degraded systems were not resilient (sensu Beisner et al. 2003) to addition of native plant propagules (e.g. at the trivial extreme, it is obvious that replanting bog plants in a drained wetland is futile, Whisenant 1999).

When former disturbance regimes are reinstated, some systems follow a simple successional pathway to community reassembly (Mitsch and Wilson 1996, Baer et al.

2002, Copeland et al. 2002), but there are a growing number of examples in which superficially quite similar systems appear to be irreversibly altered (van de Koppel et al. 1997, Anderson et al. 2000). Suding et al. (2004) and other recent reviews (Crespi 2004, Mayer and Rietkerk 2004, Rietkerk et al. 2004, van Nes and Scheffer 2004) make a compelling case for rapid (‘catastrophic’) shifts between multiple stable basins of attraction in community composition that are internally maintained by positive feedbacks between species and environment (hysteresis, sensu Beisner et al. 2003). However, beyond the reductionist, case-by-case arguments for species-specific or context-dependent mechanisms causing the state change in each example (Mayer and Rietkerk 2004), are there any generalisable predictions that can be made about which systems are more likely to exhibit resilient alternative ecosystem states?

Our reading of the literature suggests that the overwhelming majority of cases in which alternative stable states have been detected, and which are resilient to restoration management efforts, come from systems that were historically subject to moderate to extreme abiotic regimes: for example, wetlands (Zedler and Callaway 1999, Zedler 2000), streams (Wootton et al. 1996, Bradley and Ormerod 2002), deserts (Whisenant 1999), arid grasslands or rangelands (van de Koppel et al. 1997, Anderson et al. 2000, van de Koppel and Rietkerk 2004), woodland savannas (Sankaran et al. 2004), salt marshes (Srivastava and Jefferies 1996, van de Koppel et al. 2005), intertidal mud flats (van de Koppel et al. 2001) and so on (see other empirical examples in van de Koppel et al. 1997, Scheffer et al. 2001, Scheffer and Carpenter 2003, Hobbs and Norton 2004, Mayer and Rietkerk 2004, Rietkerk et al. 2004, Suding et al. 2004). This is not to say that *all* abiotically-controlled systems will necessarily exhibit multiple stable states (as the

empirical grassland and wetland examples in Suding et al. 2004, p. 46, make clear), or that systems with weak abiotic gradients or disturbance regimes *never* exhibit alternative states (as is clear from empirical examples of coral reefs: Nyström et al. 2000, Aronson et al. 2004, Bellwood et al. 2004; lakes: van Nes et al. 2002, Martin 2004; and tropical forests: Wilson and Agnew 1992, Sternberg 2001; see also examples in Scheffer et al. 2001, Scheffer and Carpenter 2003, Mayer and Rietkerk 2004), but it does raise the possibility that systems with inherently strong underlying abiotic regimes may (1) be more prone to enter resilient alternative states, (2) switch more readily to an alternative state following a lower level of perturbation, or (3) be more difficult to restore, than systems which are weakly structured by environmental adversity. Here we present this hypothesis in the context of a qualitative model of assembly rules for communities structured along a gradient of environmental adversity, and briefly discuss the empirical basis and management implications of our arguments.

### A model of community assembly

One model of community assembly (Weiher and Keddy 1995) places communities along an axis of environmentally-enforced to competitively-induced adversity, which at the extremes gives rise to deterministically-structured assemblages with non-random patterns of trait dispersion among species (the abscissa in Fig. 1). Extreme environmental adversity is often associated with comparatively low species diversity and strong directional selection for traits that allow survival under the prevailing conditions. Consequently, the trait complexes of species living in environments with strong underlying abiotic gradients or disturbance regimes all tend to be more similar to each other than expected by chance alone. Conversely, competitive adversity promotes the

coexistence of species with trait complexes that are more different from each other than expected by chance alone (Weiher and Keddy 1995, Chase and Leibold 2003).

Chase and Leibold (2003) consider that “true alternative stable states” exist only when (1) all species have access to the local community, (2) any species could establish if it arrived first, and (3) later colonists are prevented from establishing even though they could have survived if they had got there first (Chase and Leibold 2003, p. 128). This is likely to occur in cases where community assembly is particularly strongly influenced by site or assemblage history, in addition to species interactions (Chase and Leibold 2003). The constraints that trait under-dispersion pose for community assembly, are that there will be fewer species adapted to the strong underlying abiotic conditions prevailing at the site, and these species will, on average, be more similar to each other in their niche requirements than species in communities with random dispersion or over-dispersion of traits. Consequently, historical differences in arrival and establishment will appear more dichotomous among the smaller set of potential colonists, and there will be a greater likelihood of these early colonists reaching dominance and excluding future colonists from establishing.

Interestingly, the central concept of variation in the degree of resilience to restoration management along a gradient of environmental adversity is embodied in Hobbs and Norton’s (2004, p. 75) prior suggestion that “there are a number of different filters (on community assembly) that vary in their importance along relatively easily defined gradients” and “the resistance of degraded systems to restoration (that is, the degree of effort needed to restore the system to a particular state) will vary along these gradients”. Hobbs and Norton (2004, Fig. 5.1) also suggest that phase transitions involving the alteration of abiotic or disturbance regimes result in

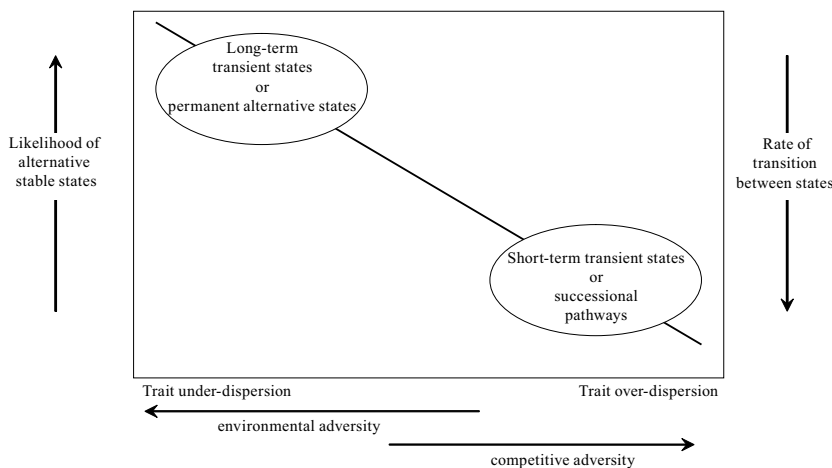


Fig. 1. A qualitative model for the likelihood of alternative stable states in restoration ecology. Ecological perception of the ‘permanence’ of alternative states is a function of the time-scale of observation and the rate of community response to perturbation, and may equally represent an axis from short term to long term transience in community structure. For simplicity, we align trait dispersion along a single axis of environmentally-enforced to competitively-induced adversity (after Weiher and Keddy 1995).

more severe state changes, that are more difficult to restore, than those involving changes in biotic variables. However, they do not formalize the reasoning or potential mechanisms underlying these observed relationships.

### **Why should trait under-dispersion increase the likelihood of alternative stable states?**

We argue that communities with strong trait under-dispersion may exhibit resilient alternative stable states more frequently, because at least three of the major processes controlling community assembly are likely to result in greater divergence in compositional states in under-dispersed compared with over-dispersed communities. Under environmental adversity, we predict that propagule limitation, stochastic priority effects, and alterations to the regional species pool will all have much more extreme consequences for community assembly than they would in competitively-structured assemblages.

First, propagule limitation imposes constraints on the outcome of lottery competition during early succession, and on the subsequent trajectory of community assembly (Drake 1990). Even if no extinctions have occurred within the regional species pool, dispersal and propagule supply can be limiting in fragmented landscapes (Hanski 1998; although this depends strongly on species traits, Henle et al. 2004), and these landscapes are most often the prime focus of restoration management. All other factors being equal, the same level of propagule limitation during colonization should have a much greater effect on the outcome of successional processes in systems that are abiotically- or disturbance-driven, because these systems typically contain fewer species that tend to have more similar traits. Consequently, trait under-dispersion should give rise to a relatively small number of alternative community states characterised by different dominant species, and these species will be more likely to resist displacement by newly arriving propagules that share very similar traits. For example, in experiments with two fungal-feeding *Drosophila* species with very similar traits, Shorrocks and Bingley (1994) found that when average arrival time of species was altered (i.e. relative propagule limitation, which they referred to as 'fugitive' situations) then the sequence of arrival had a marked effect upon species coexistence. In simplified ecological niche models, this is akin to saying that species have very similar zero net growth isoclines in relation to the prevailing environmental stresses, and so each discrete combination of species is more likely to represent an uninvincible equilibrium (Chase and Leibold 2003, p. 109).

Second, even if we assume an equal probability of all species reaching the local site (no propagule limitation),

stochastic priority effects can generate discrete assembly trajectories in many communities (Belyea and Lancaster 1999, Weiher and Keddy 1999, Chase and Leibold 2003). The term 'priority effect' is often used informally to denote variation in community assembly that arises from species-specific effects of early colonists on subsequent succession, regardless of whether the sequence of colonization was determined by a significant difference in propagule pressure between species, or by chance events. However, the term is used more formally in the assembly rules literature to refer to the effects of stochastic colonization events on community assembly, when those communities are assembled from a common species pool (i.e. all individuals have an equal probability of reaching the local site, as defined by Chase and Leibold 2003). Examples of such priority effects are discussed in Ehmann and MacMahon (1996), Sunahara and Mogi (2002) and Munday (2004). We use priority effects in the latter sense of the term, and consider that the probability of stochastic priority effects leading to alternative stable states also becomes more likely under strong environmental adversity. In large part, this will be the case because stochastic abiotic effects (e.g. disturbance) will play an increasingly large role over resource and interference competition as mechanisms of community structuring (Drake 1990). For example, both theoretical (Amarasekare 2002) and empirical studies (D'Antonio et al. 2001, Palmer et al. 2002) show that early colonization of a resource can allow an inferior competitor to reach dominance and effectively exclude a superior competitor from establishing. Once again, we predict that chance early colonists will be more likely to reach dominance under conditions of strong environmental adversity and will be much more resilient to subsequent species replacement, because resident and colonizing species all tend to be more similar in their trait complexes than expected by chance alone.

Third, it is likely that most of the catastrophic ecosystem state changes observed recently stem from alterations to the regional species pool (through extinctions and invasions) which collectively have a dramatic effect on the outcome of species interactions and community assembly in degraded landscapes. Ultimately, synergies between pervasive landscape alteration (which changes the metapopulation dynamics of interacting populations; Hanski 1998) and the large number of species invasions in disturbed landscapes (Hobbs and Huenneke 1992, Gurevitch and Padilla 2004, Marvier et al. 2004, With 2004) may explain the widespread appearance of resilient alternative stable states in many different ecosystems. It is perhaps not surprising that many of the examples of resilient alternative states in the restoration literature involve the establishment of invasive species (Zedler 2000, Hobbs and Norton 2004, Suding et al. 2004). Even allowing

for differences in native versus invader propagule availability and stochastic priority effects, it is likely that the presence and persistence of alternative stable states are contingent upon the identity of the invader. Some invaders will be superior competitors under a wide range of conditions, whereas others may only exclude or displace native species in disturbed (not fully restored) habitats (Lonsdale 1999). For example, Corbin and D'Antonio (2004) have shown that invasion of exotic propagules alone was not sufficient to cause the transition of California coastal prairie grasslands from native perennial to exotic annual grass dominance in the 19th century, without the synergistic effects of changes in land use and climate. More importantly, Mack and D'Antonio (1998) provide plausible positive feedback mechanisms by which an increased abundance or biomass of some invaders may alter the disturbance regime of a system, promoting further invasion, and triggering the transition to an alternative state. Although Mack and D'Antonio (1998) compile a large number of empirical examples of such effects, there are few cases where this has proven to result in stable states that are resilient to the reinstatement of the former abiotic or disturbance regime through restoration management.

Once again, it is likely that the impact of invasive species will be stronger in communities structured by environmental adversity, because in these harsh environments natives and invaders will tend to share traits that allow them to survive under the prevailing abiotic or disturbance regime and will be much more similar in their niche requirements than species in communities with random-dispersion or over-dispersion of traits. We are not aware of any direct comparative tests of this supposition, but many empirical studies in the contentious diversity-invasion resistance debate are founded on gradients from low-nutrient or environmentally adverse conditions to high productivity conditions. For example, Lindig-Cisneros and Zedler (2002) showed that reed canary grass, *Phalaris arundinacea*, invaded more readily under low-diversity native plant canopies subject to adverse disturbance conditions, than under low-diversity native plant canopies subject to favourable conditions for native plant growth. In another example, Lennon et al. (2003) showed that *Daphnia lumholtzi* invaded experimental mesocosms with low nutrient availability more readily than it invaded high-nutrient mesocosms. In these and other (sometimes contrasting) cases, the emerging realisation is that species-specific dominance effects of resident species (facilitation or inhibition) may account for differential diversity-invasion relationships (Hodgson et al. 2002, Smith et al. 2004), and the exact nature of the relationship depends critically on the cause of the underlying species richness gradient (Moore et al. 2001).

## Empirical evidence for the relative frequency of alternative stable states along a gradient in environmental adversity

The classical example of a system switching to a resilient alternative stable state is the over-grazing of arid grasslands, in which reduced vegetation cover causes a decrease in water infiltration rate into the soil, that further limits plant growth rates (Rietkerk and van de Koppel 1997). Ultimately, this positive feedback mechanism can lead to irreversible desertification of arid grasslands (van de Koppel et al. 1997). Similarly, Srivastava and Jefferies (1996) found that a positive feedback between high-intensity snow goose grazing on arctic salt marsh vegetation and increased soil salinity following vegetation removal, caused an irreversible shift to uncolonisable bare soil. While these, and numerous other, case studies show that alternative stable states are frequently observed in abiotically harsh environments (Whisenant 1999, Zedler and Callaway 1999, Anderson et al. 2000, Zedler 2000, Scheffer et al. 2001, Bradley and Ormerod 2002, Scheffer and Carpenter 2003, Hobbs and Norton 2004, Mayer and Rietkerk 2004, Sankaran et al. 2004, Suding et al. 2004, and most notably Rietkerk et al. 2004), there has been no comprehensive comparative analysis of the relative frequency of hysteresis across systems varying in environmental adversity (but see Genkai-Kato and Carpenter 2005).

The few studies available that do compare stable states across multiple sites or systems, provide some support for our hypothesis. The most compelling example comes from the intertidal mudflat system of van de Koppel et al. (2001), in which there is a positive feedback between benthic diatom cover and the stabilization of silt under the force of increasing wave erosion. Even though diatoms secrete substances that stabilize the silt and clay sediments that are essential for their growth, current velocities above a threshold value can still impose bottom shear stress on the substrate and cause rapid erosion (van de Koppel et al. 2001). The resulting low silt fraction in the substrate inhibits diatom growth and sediment binding, so that further erosion occurs more readily at lower current velocities, and the system does not recover. Importantly, van de Koppel et al. (2001) found that in sites with intermediate to high bottom shear stress, there was a significant bimodal distribution of benthic silt content and diatom cover, indicating that the tidal flat system exhibited two (co-occurring) alternative stable states. Conversely, in sites with low bottom shear stress the system exhibited only unimodal silt content and diatom cover distributions, indicating that only a single stable state existed (van de Koppel et al. 2001).

Few other examples are as clear-cut as van de Koppel et al. (2001), but application of the same general perspective to systems not traditionally considered to

be abiotically controlled (i.e. lakes, tropical forests and coral reefs) may prove instructive in explaining the occurrence of alternative stable states. For lake systems, the rapid shift from oligotrophic to eutrophic conditions has been an important (Scheffer et al. 2001) and costly (Martin 2004) management issue worldwide. However, it is already well recognized that eutrophication is not a problem for all lakes in general, but for a specific subset of shallow to intermediate depth lakes (Scheffer et al. 2001, van Nes et al. 2002, Genkai-Kato and Carpenter 2005), due to high phosphorus input but limited sediment storage and stability (compared to deep lakes), as well as differences in horizontal lake mixing as a function of lake depth (van Nes et al. 2002). In the context of our model, shallow to intermediate depth lakes may represent systems with a higher degree of abiotic- or disturbance control (compared to deep lakes) and are thus more prone to enter an alternative stable state following a similar degree of perturbation.

For tropical forests, there are only two studies that we are aware of that refer to alternative stable states following perturbation (Wilson and Agnew 1992, Sternberg 2001), as compared to the much larger number of examples from arid woodlands. Importantly, both of these studies involved systems where water availability was seasonally limiting and the maintenance of plant community structure was marginal under altered hydrological conditions. For example, Sternberg (2001) predicted that savanna-forest hysteresis in the Amazon basin would only occur following deforestation in specific areas with marginal dry season precipitation (moisture stress). In regions with a more even seasonal distribution of precipitation, hysteresis was not predicted to occur (Sternberg 2001).

Substantial recent interest in alternative stable states has focused on the collapse of reef systems from coral-dominated to algal-dominated reefs over very short time intervals (Nyström et al. 2000, Scheffer et al. 2001, Aronson et al. 2004, Bellwood et al. 2004). Arguably, coral reefs are the archetypal example of diverse, competitively-structured assemblages that under our hypothesis would be expected to be the systems least likely to show hysteresis. There has been intense debate about whether recent changes to reef communities indicate rapid threshold shifts between states (Nyström et al. 2000), or whether they are simply the cumulative outcome of massive multiple stressors over the past hundred years (Pandolfi et al. 2003). In principle, of course, if any system is disturbed hard enough, for long enough, it will change so dramatically that it may be considered to be in an alternative ecosystem state. Scheffer and Carpenter (2003) make a persuasive case that sudden, often dramatic, regime shifts stem from a series of events that incrementally decreased the resilience of a system. Whether this condition is permanent, or recovery is simply very slow, remains to be seen (for

example, some reefs have eventually recovered over several decades without management input; Edmunds and Carpenter 2001). The most important point seems to be that "a disturbance that could previously be buffered by a diverse functional group...became the trigger that caused an ecosystem with reduced resilience to shift from a coral-dominated state to one dominated by algae" (Nyström et al. 2000, p. 414). However, as Bellwood et al. (2004) point out, reef collapses have not occurred uniformly throughout the world. Instead, the low-diversity Caribbean reefs have been much more susceptible to collapse than the high-diversity Indo-Pacific reefs. Bellwood et al. (2004) contend that lower species diversity within functional groups in the Caribbean gave these systems an inherently lower resilience to anthropogenic disturbances. From the perspective of our model, it could therefore be suggested that low-diversity Caribbean reefs are analogous to systems that are more abiotically-structured than high-diversity Indo-Pacific reefs. The general inference is that systems with inherently low functional (trait) diversity may be more prone to enter alternative states and may be more resistant to recovery (Bellwood et al. 2004), as we would also predict under environmentally adverse conditions.

### **Determining the scale or extent of abiotic structuring in assemblages**

An intrinsically difficult problem in trying to determine the relative extent of abiotic structuring of assemblages, is that the spatial scale of the study or system is crucially important. For example, at some spatial or temporal scales coral reefs may be considered to be competitively structured, and at others they may be considered to be abiotically structured. Two studies that we are aware of give empirical examples of alternative stable states that were 'entrained' by removal of biotic interactions (predation); one in an intertidal system (Paine and Trimble 2004) and one in a meadow system (Schmitz 2004). Both systems, from the perspective of the small scale experiments conducted by the observers, would be considered to be biotically structured. However, at larger scales Paine's intertidal system is heavily structured by disturbance (wave action), and Schmitz's meadow system was surrounded on all sides by hardwood forest, and presumably represented one point along a continuum of successional revegetation following past disturbance. Quantifying the strength of abiotic drivers across multiple scales will be one of the central challenges in attempting a comprehensive, comparative assessment of the relative frequency of alternative stable states across systems varying in environmental adversity (Rietkerk et al. 2004).

## Alternative stable states or long-term transients?

One of the most important unresolved questions is whether alternative 'stable' states are in fact permanent in their own right (Petraitis and Latham 1999). While constraints on propagule access and stochastic priority effects have fundamental effects on community assembly, these are better thought of as generating transient alternative states where succession (to the restoration goal) might proceed only slowly without increased natural or artificial propagule addition over time (assuming competitive hierarchies are maintained). Consequently, propagule limitation and priority effects do not necessarily result in permanent alternative stable states. Even with alteration to the regional species pool through extinctions and invasions, it may be difficult to distinguish between long term transients and permanent states. Of course, Fukami (2004) suggests that long term transient community dynamics can still make assembly history important for community structuring, even in the absence of alternative stable states. However, the question is really how to determine the time scale of transience if the rate of 'succession' grossly exceeds the time frame of human observation. In particular, long term transients could confound comparison of the frequency of hysteresis across systems. For instance, we expect that in most cases the rate of transition between community states will simply be much slower under strong environmental adversity (e.g. in arid ecosystems), giving rise to the perception of alternative stable states (Fig. 1). Furthermore, the rate of transition is likely to be proportional to the lifespan of the dominant organisms. Even in some communities that might commonly be considered to be competitively structured, rather than abiotically structured, community transition can be extraordinarily slow. For example, in their rocky intertidal community, Paine and Trimble (2004) found that experimental removal of top-predator starfish from 5 m<sup>2</sup> plots allowed mussels to become dominant over canopy-forming algae, yet even at this small spatial scale it took 20–30 years of continuous monitoring before it was clear that plots would return to an algal-dominated state following star-fish reintroduction. At the other extreme, long lag times in community responses to perturbation can actually mask the existence of threshold changes in community composition (Milchunas and Lauenroth 1995).

Transience versus permanence of alternative ecosystem states would appear to be crucial to long term perspectives on the need for management action in a given situation (Beisner et al. 2003). However, the distinction may be a moot point if even short term transients are unacceptable for ecological, social or aesthetic reasons (Hobbs and Norton 2004), especially in the face of potentially rapidly changing global conditions.

## Conclusion

We suggest that the measurement of trait dispersion may prove to be of key importance in predicting the prevalence and persistence of long term transient and alternative stable states in restoration ecology (Fig. 1). Hysteresis may be most frequent in ecosystems with strong underlying abiotic regimes, where traits of species are markedly under-dispersed (e.g. wetlands and arid ecosystems). Clear resolution of management options will require discrimination of propagule limitation, stochastic priority effects and alteration of the species pool as determinants of short term and long term state changes in community assembly. Unfortunately, synergistic interactions between landscape change and species invasion in degraded systems (Gurevitch and Padilla 2004, Marvier et al. 2004, With 2004) are likely to introduce threshold effects on the probability of successful management solutions to local restoration problems (Hobbs 2001, Hobbs and Norton 2004, Suding et al. 2004). We agree with Bellwood et al. (2004) that the solution does not lie in the conservation of focal species or focal processes, but instead in enhancing the resilience of critical functional groups to future disturbance. Nowhere will this be more important than in systems structured by moderate to strong environmental adversity, which appear to be much more prone to catastrophic regime shifts.

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