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# *Alternative stable states, trait dispersion and ecological restoration*

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**Didham et al. suggested that abiotically structured communities showing trait under-dispersion are more likely to exhibit alternative stable states than are competitively structured communities showing trait over-dispersion. We argue that the opposite is the logical expectation, and discuss implications for ecological restoration at local and regional scales.**

There has recently been a renewed interest in alternative stable states of community structure, in particular as a basis for understanding approaches to ecological restoration (Beisner et al. 2003, Suding et al. 2004). Didham et al. (2005) (DWN) make a contribution to this topic by placing alternative stable states within the trait dispersion model of community assembly (Weiher and Keddy 1995). In this note, we suggest that their hypothesis is logically flawed, propose an alternative hypothesis, and discuss implications for restoration.

## Didham et al.'s hypothesis

DWN suggest that "strongly abiotically- or disturbance-structured assemblages, with nonrandom trait under-dispersion (Weiher and Keddy 1995), are more likely to exhibit catastrophic phase shifts [and thus alternative stable states] (insertion by us) in community structure than assemblages which are weakly structured by environmental adversity" (p. 409). They discuss three processes ("propagule limitation," "stochastic priority effects," and "alteration to the regional species pool") to explain the rationale for this hypothesis (p. 411–412). All of the suggested processes involve the following that they present as a causal sequence: (i) "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" (p. 410), and (ii) during community assembly, "these species [having more similar traits] will be more likely to resist displacement by newly arriving propagules that share very similar traits" (p. 411), resulting in alternative stable states.

We believe there is a flaw in linking (i) and (ii) above. The reason for species living in environments with strong underlying abiotic gradients or disturbance regimes to be similar in traits is that only species with a narrow set of traits that enable them to cope with such conditions persist in the community. In this case, species co-occurrence is more likely to be determined by the response of each species to abiotic conditions than by competition or other interspecific interactions. Therefore, it does not make ecological sense to expect competitive displacement of newly arriving species by early colonizers to be likely under these conditions. In fact, it is trait over-dispersion, rather than trait under-dispersion, that process (ii) is expected to produce (Weiher and Keddy 1995). In short, DWN confuse cause and effect.

We also believe that the empirical evidence that DWN cite for their hypothesis (p. 409–410) is not as compelling as they claim. They argue that the majority of the ecosystems that appear to show alternative stable states are influenced more by environmental adversity than by competitive adversity. However, such between-ecosystem comparisons are likely confounded by other differences between ecosystems (Srivastava 1999). DWN do make a few within-ecosystem comparisons (p. 412–413), but there is no evidence indicating that the mechanism behind alternative stable states is trait under-dispersion. In any case, the logical flaw in their hypothesis (discussed above) prevents the hypothesis from being a potential explanation for alternative stable states.

## An alternative hypothesis

We propose the following alternative hypothesis: all else being equal, communities that are "weakly structured by environmental adversity" are more likely to exhibit alternative stable states than are communities that are "strongly abiotically- or disturbance-structured." Here we use the term environmental adversity only to make our hypothesis comparable to DWN's (above) and Weiher and Keddy's (1995) on which DWN's is built. However, environmental adversity is an ambiguous term that can refer to many different things. Below we define environmental adversity with more precise terms in order to explain part of the rationale behind our hypothesis.

First, a key aspect of environmental adversity is disturbance frequency and/or intensity (Fig. 1a). As disturbance frequency and/or intensity decreases, there will be, on average, more time for species to increase in population density in between disturbance events. Under these circumstances (i.e. lower disturbance frequency and/or intensity), effects of interspecific competition on population densities will in general be stronger (Connell 1978, Huston 1994). Theory suggests that priority effects, the main mechanism generating alternative stable states, are more likely to occur when interspecific competition more greatly affects population densities (Hubbell 2001, Chase 2003, Chase and Leibold 2003, van Nes and Scheffer 2004). Under stronger competition, it is also more likely that some species are displaced by other species having similar traits. Therefore, trait over-dispersion, rather than trait under-dispersion, is the expected outcome of community assembly under lower disturbance frequency and/or intensity. Note that, unlike DWN (i.e. causal sequence from (i) to (ii) above), we do not suggest any causal relationship between trait dispersion and alternative stable states. Instead we see both as an outcome of competitive interactions (Fig. 1a).

Second, environmental adversity can also be described in terms of energy and/or nutrient supply (Fig. 1b). Weaker environmental adversity, or greater energy and/or nutrient supply, typically allows more species in the regional species pool to have the potential to survive in local habitats. Theory suggests that the more species that can potentially colonize communities, the greater number of alternative stable states the assembled communities can assume (Law and Morton 1993, Chase 2003, Fukami 2004a), thereby increasing the likelihood of alternative stable states. Moreover, under greater energy and/or nutrient supply, the range of traits that enable species to survive in local habitats is likely to be broadened. The expanded range of possible traits in turn makes trait over-dispersion more likely than trait under-dispersion. Again, we do not invoke any causal relationship between trait dispersion and alternative stable states; instead they are both a result of a common cause, energy and/or nutrient supply (Fig. 1b).

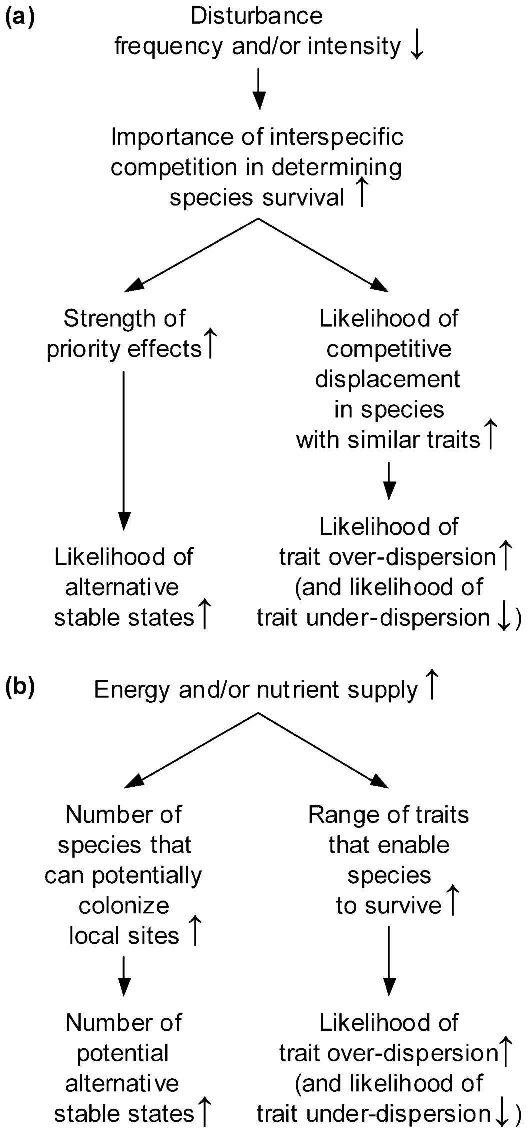

Fig. 1. Hypotheses on how environmental conditions affect the likelihood of alternative stable states and trait dispersion. Downward and upwaid arrows following phrases represent the decrease and increase, respectively, in the factor specified by the phrase.

That environmentally structured communities are less likely to show alternative stable states than competitively structured communities, has already been proposed and justified in depth (Booth and Larson 1999, Chase 2003). Although this prediction has not previously been explicitly linked to trait dispersion, Chase (2003) provided several lines of empirical support for the prediction. His data come from within-ecosystem comparisons, which are more powerful than between-ecosystem comparisons in understanding patterns across environmental gradients, because they are affected by fewer confounding factors (Srivastava 1999, p. 4).

## Implications for restoration

The concept of alternative stable states may provide a useful conceptual framework for ecological restoration (Suding et al. 2004, Temperton et al. 2004, Young et al. 2005). It is largely for this reason that the concept is currently receiving a renewed interest. Our alternative hypothesis has two implications for restoration. First, it may not be possible to restore anthropogenically altered communities to a historical state only by re-establishing the original environmental conditions. That is, because of hysteresis caused by the presence of alternative stable states in naturally undisturbed communities, restoration may also require altering community structure directly (by planting, weeding, etc.) in addition to passive recolonization of restoration sites. This implication has already been discussed extensively (Fig. 2c in Suding et al. 2004).

Our second implication concerns biodiversity restoration at the regional scale. Regional diversity can be greatly enhanced when the presence of alternative stable states increases beta diversity (Chase 2003). Because of variation in assembly history, local communities in a region can assume alternative stable states, each with a different set of locally coexisting species, collectively contributing to regional species diversity. However, our hypothesis suggests that anthropogenic disturbance can drive local communities to assume a single species-poor state, thereby decreasing overall regional diversity. In such cases, restoring original environmental conditions may not be enough for recovering regional biodiversity in anthropogenically altered systems. Therefore at regional and local scales it may be necessary to directly manipulate the composition of at least some of the local communities to restore alternative stable states that cannot be otherwise reached. Additionally, it may be necessary to restore original disturbance regimes that allow local communities in the region to move between alternative stable states.

## But are they stable?

As DWN recognize, alternative "stable" states may not in fact be stable, but instead represent long-term transient states (Fukami 2004b, Hastings 2004). The prevalence of transient states compared to of stable states in many natuial systems has been widely recognized (Pickett and White 1985). DWN propose that "the rate of transition between community states will simply be much slower [i.e. the duration in which ecosystems are in transient states will be much longer] (insertion by us) under strong environmental adversity (e.g. in arid ecosystems), giving rise to the perception of alternative stable states" (p. 414). But they follow this statement by discussing competitively structured communities also showing long-term transients. We suggest that whether state transitions are slower in environmentally or competitively structured communities will depend on the relative influence of abiotic vs biotic factors in slowing community changes (Huston 1994). However, the strength and interactions of these factors remain to be fully investigated and may prove to be case-specific. We believe that understanding these – as well as understanding the limitations and potentials of the alternative stable states models in guiding ecological restoration when transient states are more common in reality – will be crucial in order to better link community theory and restoration practice.

## Conclusion

We have argued that, all else being equal, competitively structured communities, which may show trait over-dispersion, are more likely to exhibit alternative stable states than are environmentally structured communities, which may show trait under-dispersion. However, we do not mean to suggest that knowledge of trait dispersion, or alternative stable states for that matter, is necessarily important to the success of ecological restoration. Trait under-dispersion and over-dispersion are themselves unresolved issues, with respect to what to measure and how, how to build null models to test them, and most importantly, how general they may be in natural systems (Franzen 2004). The same is true with alternative stable states. What is important is for ecologists to provide sound theoretical predictions about when to expect alternative stable states to aid more effective restoration.

*Acknowledgements* – We thank Evan Weiher and two anonymous reviewers for comments. The Japan Society for the Promotion of Science (Research Fellowship for Young Scientists) and the Royal Society of New Zealand (Marsden Fund) supported this work.

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