

When are alternative stable states more likely to occur?

A reply to T. Fukami and W. G. Lee

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T. Fukami and W. G. Lee argue that the logical expectation from ecological theory is that competitively-structured assemblages will be more likely to exhibit alternative stable states than abiotically-structured assemblages. We suggest that there are several important misinterpretations in their arguments, and that the substance of their hypothesis has both a weak basis in ecological theory and is not supported by empirical evidence which shows that alternative stable states occur more frequently in natural systems subject to moderate- to harsh abiotic extremes. While this debate is founded in ecological theory, it has important applied implications for restoration management. Sound theoretical predictions about when to expect alternative stable states can only aid more effective restoration if theoretical expectations can be shown to translate into predictable empirical outcomes. If strongly abiotically- or disturbance-structured systems are more likely to exhibit catastrophic phase shifts in community structure that can be resilient to management efforts, then restoration ecologists will need to treat these systems differently in terms of the types of management inputs that are required.

Recently, we raised the hypothesis that strongly abiotically-or disturbance-structured assemblages, with non-random 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 (Didham et al. 2005). Initially, this hypothesis was spurred by our observation that the majority of cases in which catastrophic phase shifts have been detected (and which are resilient to restoration management efforts) appeared to come from systems that were historically subject to moderate to extreme abiotic regimes. To explore this further, we subsequently reviewed all the empirical examples of these putative

‘alternative stable states’ that we could find, including examples of both abiotically-structured and competitively-structured assemblages, within and between systems (Didham et al. 2005), and concluded that abiotically-structured systems did indeed appear to be more likely to enter resilient alternative states following habitat degradation. We attempted to argue a potential mechanistic basis for this empirical, phenomenological observation, rooted in the processes driving community assembly along a gradient from environmentally-enforced to competitively-induced adversity (Weiher and Keddy 1995).

Fukami and Lee (2006) combine an interesting series of (mis-) interpretations of our arguments to reach the conclusion that our hypothesis is “logically flawed”. Instead, they consider that the “logical expectation” from ecological theory would be to find directly the opposite relationship, that competitively-structured assemblages are in fact more likely to exhibit alternative stable states than abiotically-structured systems. However, Fukami and Lee (2006) present no supporting empirical justification for their alternative hypothesis, and in our view their hypothesis stands in direct contradiction to the empirical evidence that we reviewed. Nevertheless, we take this exchange of views as a useful opportunity to clarify important points of our hypothesis, as we believe that a better understanding of the reasons why systems exhibit catastrophic phase shifts is important for both ecological theory and for restoration management.

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No logical flaw in our hypothesis

Fukami and Lee (2006) believe that our hypothesis “does not make ecological sense” because there is a fundamental flaw in our logical reasoning. As far as we can judge, their viewpoint boils down to an erroneous belief that we use a ‘competitive dominance’ argument to reason that abiotically-structured systems are more likely to exhibit alternative stable states than competitively-structured systems. They consider that we raise the following rationale 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” (drawn from p. 410 of Didham et al. 2005), and (ii) that “these species will be more likely to resist displacement by newly-arriving propagules that share very similar traits” (drawn from p. 411), resulting in alternative stable states. Fukami and Lee (2006) have extracted these two quotes out of separate contexts. However, we state quite categorically that we do not raise trait dispersion as a causal mechanism (below). We can also state categorically that we do not raise competition as a primary driver of assembly in abiotically-structured systems. We used the terms “resist displacement” and “resilient to subsequent species replacement”, to indicate situations in which early colonists may become dominant and occupy most of the available space and resources, leaving little opportunity for newly-arriving species to establish, particularly if they have very similar traits. It does not make sense to us to phrase such a process as “competitive displacement of newly arriving species by early colonists” (Fukami and Lee 2006). How and why would it be useful to speak of early colonists as competitively displacing newly-arriving propagules? We believe that Fukami and Lee (2006) have simply misinterpreted our statements. Our phrase “more likely to resist displacement” (under environmental adversity) is the direct equivalent of saying that established individuals are less likely to be competitively displaced by newly-arriving colonists. We feel sure that Fukami and Lee (2006) will agree that competitive displacement should be less likely in abiotically-structured assemblages.

We also suspect that Fukami and Lee (2006) have not clearly considered the fact that competition can be locally strong (between individuals at small spatial or temporal scales), despite it being a weak force in structuring community assembly under strong environmental adversity. For example, propagules of two plant species sharing similar traits allowing them to survive under adverse environmental conditions may face strong competition with each other (for space, light, water, nutrients and so on) if they were to germinate in close proximity to each other, regardless of the fact that competition would be considered a weak determinant of

community structure at larger spatial and temporal scales within the same system.

Trait dispersion is not a mechanism

One of the most important clarifications that must be made is that we did not, at any stage in our earlier paper, suggest that trait dispersion is a ‘mechanism’ causing alternative stable states. Fukami and Lee (2006) consider that we “confuse cause and effect”, and that “unlike [Didham et al. 2005] (i.e. causal sequence from (i) to (ii) above), we do not suggest any causal relationship between trait dispersion and alternative stable states”. Again, this is emphatically not correct, as any number of quotes from our earlier paper would suffice to show (e.g. “Hysteresis may be most frequent in ecosystems with strong underlying abiotic regimes, where traits of species are markedly under-dispersed”; Didham et al. 2005, p. 414). Surprisingly, though, when Fukami and Lee (2006) dismiss the validity of our empirical examples, their reasoning for doing so is that these examples provide “no evidence indicating that the mechanism behind alternative stable states is trait under-dispersion”. We presume this is not what Fukami and Lee (2006) intended to say, because obviously trait dispersion is not a causal mechanism. And neither are trait dispersion and alternative stable states both “an outcome of competitive interactions”, as Fukami and Lee put it. Actually, they are both an outcome of the interplay between the relative frequency and intensity of environmental and competitive structuring forces. In any case, we (like Fukami and Lee 2006) know full well that trait dispersion is not a cause, but rather a consequence, of community assembly.

Within-ecosystem versus between-ecosystem comparisons

There are undoubtedly some confounding issues in making cross-ecosystem comparisons, but the title and focus of our earlier paper was explicitly whether *systems* with strong underlying abiotic regimes are more likely to exhibit resilient alternative states. We raised our hypothesis based on the critical observation, across ecosystems, that the frequency of catastrophic phase shifts to community states that are resilient to restoration management efforts appears to be greater in systems that were historically subject to moderate to severe abiotic structuring, such as wetlands, streams, deserts, arid grasslands or rangelands, dry woodland savannas, salt marshes and intertidal mud flats (extensive references given in Didham et al. 2005). Inevitably, there are relatively few within-ecosystem comparisons that offer a gradient in environmentally-enforced to competitively-

induced adversity across which to test the relative frequency of occurrence of alternative stable states. However, we did identify a few key within-ecosystem examples (e.g. van de Koppel 2001), and these empirically supported our contention that abiotically-structured systems appear more likely to enter resilient alternative states following disturbance than competitively-structured communities. We believe that these examples serve to strengthen the inference drawn from the between-ecosystem comparisons. If Fukami and Lee (2006) believe that these patterns are due entirely to confounding extrinsic factors across ecosystems, then we would welcome a critical analysis of what those factors might be. At the very least, the question would have to be asked why observational evidence shows that disparate systems such as wetlands, deserts and arctic tundra (in which assemblages all happen to be abiotically-structured) appear to exhibit resilient alternative states more frequently than a disparate range of other systems such as moist temperate forests, tropical forests or diverse coral reefs (in which assemblages all happen to be more competitively structured).

What empirical evidence is there that competitively-structured assemblages are more likely to enter resilient alternative ecosystem states?

Fukami and Lee (2006) “believe that the empirical evidence that [Didham et al. 2005] cite for their hypothesis (p. 409–410) is not as compelling as they claim”. We would be the first to admit that the observational evidence we presented is far from perfect, and that observational evidence in general is no substitute for experimental manipulations to identify the underlying mechanisms causing putative alternative stable states (Chase 2003a, Schröder et al. 2005). However, we might have more sympathy for Fukami and Lee’s (2006) statement if they had presented empirical evidence supporting their alternative hypothesis. We spent considerable time attempting to find and present examples of competitively-structured systems which were reported to be resilient to restoration management efforts, but we found relatively few (although some that we missed are discussed in Schröder et al. 2005). We believe that the empirical evidence supports the argument that competitively-structured systems are less likely to enter resilient alternative stable states than abiotically-structured systems.

Are we talking at cross-purposes?

Given the above comments, it might appear at first reading as if there is little common ground to be reached

on two such highly contrasting alternative hypotheses. This may be true, but we cannot help but entertain the possibility that we might be talking slightly at cross-purposes with Fukami and Lee (2006). In a recent review, Schröder et al. (2005) identified four conceptual approaches to determining if alternative stable states are present: (1) the existence of differing parameter thresholds for the back- and forward transitions between states (a test for discontinuity), (2) whether there are state transitions following perturbation (a test for non-recovery), (3) the sensitivity of the stable end state to differing initial conditions (which Schröder et al. 2005 call a test for divergence, but which we believe would be better called a test for lack of convergence), and (4) the degree of stochastic divergence, or unexpected transitions to contrasting states, despite identical initial conditions (a test for random divergence). In our earlier article (Didham et al. 2005), we phrased our arguments within the framework of approach 2, testing for non-recovery following perturbation. This has been the approach of greatest application to restoration ecology, with a growing number of examples of systems showing catastrophic phase shifts to alternative states that are resilient to restoration management (Suding et al. 2004). Our impression is that Fukami and Lee (2006) phrase their arguments (and their recent research) predominantly within the framework of approach 3, testing for the (lack of) convergence of assemblage composition when community assembly is initiated with differing species composition or differing colonization histories (under identical environmental conditions). In their review of 35 experimental studies, Schröder et al. (2005) did find that a larger proportion of ‘appropriate’ experimental tests (six of eight) using approach 3 reported conclusive evidence for the existence of alternative stable states, compared with only three of eight experimental studies using approach 2, although this difference is not statistically significant (chi-square test of relative frequencies across the four differing experimental approaches, ignoring inappropriate experimental tests, as detailed in Table 2 of Schröder et al. (2005), ($\chi^2 = 3.51$, $df = 3$, $P = 0.319$). Whether these different conceptual approaches to the identification of alternative stable states affect the conclusions drawn about the relative frequency of alternative stable states along a gradient of environmental adversity is an open question.

Nevertheless, there is the possibility (although we consider it to be small) that the mismatch between predictions from recent theoretical models and small-scale microcosm experiments using approach 3, on the one hand, versus the conclusions drawn from observational studies using approach 2 on the other hand, may simply stem from abiotically-structured natural systems showing very long transient dynamics which give the appearance of resilient alternative states. We explored

this possibility in our earlier article (Didham et al. 2005, p. 414 and right-hand y-axis in Fig. 1 on p. 410), but this would only serve to mask a non-significant relationship between environmental adversity and frequency of alternative stable states, and would not account for the paucity of empirical examples of alternative stable states in competitively-structured systems.

We do, however, strongly disagree with Fukami and Lee (2006) in their contention that it “has already been proposed and justified in depth” that “environmentally structured communities are less likely to show alternative stable states”. Certainly, the two references they cite (Booth and Larson 1999 and Chase 2003a) give this as a verbal argument, but there is little in the way of empirical justification. In fact, Chase (2003a, p. 493) is the first to admit that he “cannot directly assess whether the patterns of community compositional similarity [in his observational data from natural ponds] arise because of single or multiple stable equilibria, because...the history of these environments” is unknown. The contention of Fukami and Lee (2006) also stands in direct contrast to one of the main conclusions of Schröder et al. (2005) that experimental systems dominated by small, short-living and fast-reproducing organisms (almost exclusively in laboratory experiments) may be more likely to exhibit alternative stable states, compared to systems with long-living, slow-reproducing organisms.

Exploring theoretical arguments that competitively-structured assemblages are more likely to exhibit alternative stable states

The theoretical reasoning that Fukami and Lee (2006) use to argue that competitively-structured assemblages are more likely to exhibit alternative stable states closely follows the reasoning and arguments of Chase (2003a), centred on experimental approaches 3 and 4 of Schröder et al. (2005): essentially, “multiple stable equilibria are more likely in systems with large regional species pools, low rates of connectance, high productivity and low disturbance” (Chase 2003a, p. 489) because “there are more species in the regional species pool that can coexist in any local community, and that many species in the regional species pool possess similar traits” (Chase et al. 2003a, p. 491), resulting in greater likelihood of priority effects (which Fukami and Lee (2006) consider to be the main mechanism generating alternative stable states). We have two main comments on this line of reasoning. First, the most frequently cited evidence for the frequency of alternative stable states increasing with species richness comes from mathematical modeling studies involving very few species, notably Law and Morton (1993). However, the substantive basis to this is that alternative stable states were more frequent in a five species food

chain model (occurring in ca 6000 out of 100 000 simulation runs), than in a four species food chain model (ca 1000 out of 100 000 simulation runs) with simple Lotka-Volterra dynamics and no spatial or temporal heterogeneity (Law and Morton 1993). Most model assemblages collapsed to only one or two species (Law and Morton 1993), and the same holds true in experimental microcosm tests of these models. In their review of direct experimental tests for alternative stable states, Schröder et al. (2005) found no conclusive support for the hypothesis that larger regional pools are more likely to exhibit alternative stable states. For example, Schröder et al. (2005) cited studies by Warren et al. (2003) in which seven species were used (in laboratory cultures) and no alternative stable states were found, whereas Drake (1991) and Sait et al. (2000) did find alternative stable states with only three species each. Consequently, the validity of this line of reasoning is open to question, and the applicability of these simple model scenarios to natural systems is unproven.

Second, the reason given for species-rich assemblages being more likely to exhibit alternative stable states is that there are a greater number of species with similar traits in the regional pool and therefore there should be a greater likelihood of priority effects. This is essentially a variant of the same trait-based priority effect argument we used in our earlier article (Didham et al. 2005), but varying in the conditions under which greatest trait-similarity of colonists is likely to occur. Small-scale experimental evidence does exist for larger, more species-rich microcosm ecosystems showing more pronounced historical effects on final assemblage composition than in smaller microcosms (Drake 1991), although this is not always the case (for example, Fukami 2004 showed greater priority effects in smaller ecosystems). Certainly, we agree that in an absolute sense there may be more species that share similar traits in a larger species pool, but is this what is most important in assessing the likelihood of any given colonist establishing at a local site? Because of the strong ‘abiotic filtering’ (Hobbs and Norton 2004) processes operating in harsh environments, there may well be a lower total number of species with similar traits (than in a larger species pool), but proportionally-speaking, out of the potential colonists that arrive at a site, the average interspecific encounter will be between individuals of two species with a higher average similarity in trait complexes. Therefore, we argue that the new colonist (sharing similar traits) will be less likely to be able to establish, coexist with or displace the established individual (should space be limiting).

In the context of their argument that more species-rich assemblages should exhibit greater priority effects and therefore more frequent alternative stable states, it would seem more logical for Fukami and Lee (2006) to argue for a greater likelihood of alternative stable states at intermediate levels of productivity or disturbance (a la

the hump-backed productivity-diversity relationship and the intermediate disturbance hypothesis). In this vein, some mathematical models have predicted that alternative stable states should be more prevalent at intermediate levels of environmental driving parameters (e.g. productivity; Chase 1999a,b, Diehl and Feiel 2000, Shurin et al. 2004), with limited empirical evidence supporting this for a simple predator-prey system in which alternative stable states only occurred at intermediate productivity levels (Chase 2003b) and speculation that alternative stable states should be more likely at sites with intermediate wave action in a rocky intertidal ecosystem (Bertness et al. 2002). As Schroder et al. (2005, p. 11) put it “spatial or temporal heterogeneity in natural disturbance patterns may explain local community states that differ in which competitor is present, while the endpoint in the absence of disturbance would be competitive exclusion at the regional scale (Kennelly 1987)”. In other words, under strong competitive adversity deterministic community convergence would be the expected outcome, regardless of the number of species in the regional pool or differing assembly histories (which contrasts with the expected outcome of models presented in Fig. 1 of Fukami and Lee 2006).

Again, any (or all) of these theoretical and empirical patterns may well hold true in some situations, but whether this equates to a general prediction that alternative stable states should be more frequent under particular levels of environmental versus competitive structuring forces is obviously still contentious. As we made clear in our Forum article (Didham et al. 2005), there is no expectation that alternative stable states will be found exclusively in abiotically-structured systems, nor that they will never be found in competitively-structured systems. It is the relative frequency of occurrence of alternative stable states across systems that is of greatest interest, and we still consider the weight of evidence to point to systems structured by moderate to strong environmental adversity.

Sound theoretical predictions to aid restoration management

We agree with Fukami and Lee (2006), that it is important for ecologists to “provide sound theoretical predictions about when to expect alternative stable states”, but surely these can only “aid more effective restoration” if theoretical expectations can be shown to translate into predictable empirical outcomes? We do not see this in Fukami and Lee (2006) and so we find it difficult to understand how their alternative hypothesis can have applied implications for restoration management (whether we agree with their viewpoint or not). The one valuable point we did draw from their ‘Implications for restoration’ section was that if systems did

naturally exist in multiple stable states prior to habitat degradation (whatever the underlying processes are which caused this), then restoration must take into account not just the underlying abiotic regimes or pre-disturbance species composition, but also the need to recreate the conditions under which spatial or temporal transitions between alternative states might occur.

In an applied context, the importance of this debate (Didham et al. 2005, Fukami and Lee 2006, this paper) lies in its implications for restoration ecology. The restoration of severely degraded systems requires an understanding of the factors that have caused degradation (Hobbs and Norton 1996). If strongly abiotically- or disturbance-structured systems are more likely to exhibit catastrophic phase shifts in community structure that can be resilient to management efforts, then restoration ecologists will need to treat these systems differently to systems that are competitively-structured in terms of the types of management inputs that are required. While this debate is founded in ecological theory, it has strong implications for restoration management, and it is important that these issues are rigorously debated and that the arguments are grounded on good empirical data.

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