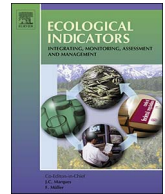


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Identifying best-indicator species for abrupt transitions in multispecies communities

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ABSTRACT

Whereas research primarily focuses on understanding under what conditions sudden transitions in the dynamics and functioning of ecological systems may occur, the scale and complexity of ecosystems limit our capacity to achieve this. Indicators of resilience may help circumvent such limitation by signalling the proximity of ecological systems close to an abrupt transition. However, their successful application strongly depends on the ecosystem under question. Therefore, if we aim to use resilience indicators for ecological management in practice, we need to understand where and how they can be reliably monitored. Here, we test the performance of resilience indicators across species in simple modules of competition to help recognize best-indicator species in a community. We show that differences in species sensitivity to disturbances in a community is affected by the dominant eigenvector of the linearized system at equilibrium. We then use simulated time series to compare trends in variance and autocorrelation across species and at community level. We found high heterogeneity in the strength of the indicators across species, while community-based indicators scored better on average than indicators at species level. Looking at species features, we found that collapsing and invading species showed strongest trends, but we observed no relationship between the number of species interaction links and indicators. Lastly, we explored whether it is possible to identify best-indicator species based on their contribution to community variability using eigenvector decomposition methods. Our results suggest that successfully identifying a best-indicator species for critical transitions in multispecies communities is not an easy task.

1. Introduction

Ecological systems may undergo abrupt transitions to alternative regimes (Scheffer et al., 2001). For instance, the rapid degradation of grazelands due to overgrazing (Rietkerk et al., 2004), trophic cascades due to eutrophication in marine environments (Daskalov et al., 2007), or the boom-and-bust dynamics of overharvested fish stocks (Vert-Pre et al., 2013) are dramatic changes that can impact ecosystem function and lead to huge losses in the provision of ecosystem services. Avoiding such surprises and their negative effects is not an easy task. Proper management requires good knowledge of the underlying ecological processes and on top the potential of intervention to reverse drivers or minimize disturbances that can trigger such transitions. Both requirements, however, are fulfilled only in a handful of cases.

Faced with this challenge, generic resilience indicators have been suggested as an alternative for identifying imminent critical transitions in ecological systems (Scheffer et al., 2015). This alternative is based on the idea that we may indirectly probe the resilience of an ecosystem by

measuring the relative change in its recovery back to equilibrium after a disturbance. This concept of (engineering) resilience (Pimm, 1984) has been long established in the study of ecological stability (Grimm et al., 1997), but recent work has highlighted that slow recovery may also result (and thus be quantified) in specific statistical signatures in time series of systems that are likely to undergo a critical transition. Variance and autocorrelation at-lag-1 (Carpenter and Brock, 2006; Held and Kleinen, 2004), and occasionally skewness (Guttal and Jayaprakash, 2008) have all theoretically been shown to increase prior to critical transitions. Empirical examples have already demonstrated that estimating these statistics as early-warnings of upcoming shifts is more than just a theoretical expectation. Increasing autocorrelation signalled past climatic transitions (Dakos et al., 2008), trophic cascades were preceded by periods of high variance in lake manipulation experiments (Carpenter et al., 2011), and extinction events were announced by rising variability in microcosm zooplankton (Drake and Griffen, 2010) and yeast populations (Dai et al., 2012).

Despite these findings the application of resilience indicators for

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ecosystem management remains challenging. Resilience indicators require extensive monitoring to overcome constraints on data resolution, data length, or observational error (Dakos et al., 2012). Estimating these indicators in some of the best available long-term monitored freshwater systems has revealed inconsistent patterns in their performance as early-warnings (Burthe et al., 2016; Gsell et al., 2016). However, high-frequency monitoring designed specifically to match the relevant time scales of a stressed ecosystem might improve their performance (Batt et al., 2013), as it has been recently demonstrated in a whole lake experiment where resilience indicators helped prevent a transition to an algal bloom (Pace et al., 2016). Nonetheless, even in the presence of the best data, there are types of shifts or conditions where resilience indicators may still fail to flag an approaching transition (Dakos et al., 2015). For example, multiple interacting transitions may muffle indicator patterns (Brock and Carpenter, 2010); transitions between oscillating or chaotic dynamics show no consistent warning (Hastings and Wysham, 2010); and most transitions that correspond to global bifurcations usually occur unannounced (Vandermeer, 2011).

Another growing challenge when it comes to the application of resilience indicators is how to use them for detecting shifts in multicomponent systems (Scheffer et al., 2012). This is especially relevant for detecting species extinctions or invasions in communities driven by climate change (Pimm and Raven, 2000), the collapse of pollination networks due to the die-off of pollinator insects (Burkle et al., 2013), or metapopulation extinctions at the landscape level due to habitat fragmentation or habitat loss (Fahrig, 2003). One reason that detection is challenging in such multicomponent ecosystems is that the dynamics and persistence of these ecosystems depend largely on their topological features (Bastolla et al., 2009; Stouffer and Bascompte, 2011), for which we only now start to learn their effect on the occurrence of critical transitions (Gao et al., 2016; Lever et al., 2014).

A less explored reason, however, is that it is hard to a priori define which species (or functional group) in a community, or which patch in a habitat network can provide the best information for detecting a system wide transition. In a model of a simple lake food web it has been shown that indicators estimated from phytoplankton dynamics can signal a transition to planktivorous dominance two levels higher in the food web (Carpenter et al., 2008). On the other hand, in a food web model of a predator and a stage-structured prey, only the dynamics of the juvenile prey could signal the upcoming collapse of the predator, while the dynamics of the adult prey and predator provided no warning (Boerlijst et al., 2013). Resilience indicators derived from modelling empirical mutualistic networks demonstrated that not all species in a community provide the same signal strength for the upcoming transition (Dakos and Bascompte, 2014). In the best-case scenarios, differences like the above can be dealt with by collecting same quality information for each species in the community. But what if that is not possible? How do we know that we measure the right variable?

Here, we test the performance of resilience indicators across species in competition modules to help recognize best-indicator species in a community. We first explain how differences in recovery times between species can be explained by the structure of the dominant eigenvector of the linearized Jacobian at equilibrium. We, then, simulate critical transitions in simple competition module communities by gradually changing environmental conditions. We compute resilience indicators at species level and community level (variance and autocorrelation at lag-1) to explore whether differences in species features have an effect on the performance of the indicators. Lastly, we propose how eigenvector decomposition may help to identify best-indicator species in a community approaching a critical transition.

2. Critical slowing down and the sensitivity of species to disturbance prior to critical transitions

Mathematically, the underlying reason for the emergence of resilience indicators lies in the fact that a broad class of critical transitions

corresponds to local bifurcations where an equilibrium becomes unstable or ceases to exist. Before such local bifurcations the dominant eigenvalue of the linearized system decreases gradually to zero giving rise to the phenomenon of ‘critical slowing down’ (Kuehn, 2011; Wissel, 1984) that is responsible for the increasingly slow recovery of the system from external perturbations. In theory, critical slowing down should affect all components of a system, like a multispecies community, and resilience indicators derived from any species should signal the approaching transition.

In fact, it has been shown that this might not be necessarily the case. In a model of a predator feeding on a stage-structured prey, a slow increase in the predator mortality rate leads to the sudden collapse of the predator and the abrupt increase of the juvenile population (Boerlijst et al., 2013). However, only indicators measured in the dynamics of the juvenile population flagged the upcoming transition; predator and adult prey dynamics showed no signs. This discrepancy can be understood in terms of the eigenvectors that govern the direction of change in the system. In the stage-structured model, there are three eigenvectors and corresponding eigenvalues (equal to the dimensionality of the system). Among the three populations in the model, only juveniles are closely aligned to the eigenvector of the dominant eigenvalue: that is the eigenvalue that causes critical slowing down. For this reason, it is only the dynamics of the juvenile population that reflect the proximity to transition in the resilience indicators.

We can generalize this observation and show that we can identify the sensitivity of a system component i (i.e. a species in a community) using the dominant eigenvalues and eigenvectors in the neighborhood of the equilibrium state. We present a proof of this generalisation in Appendix A (Supplementary material) for the more mathematically inclined reader, while here we provide a layman’s summary together with an example. Disturbances around equilibrium in the direction of the dominant eigenvector \mathbf{r} (that is related to the dominant eigenvalue) give rise to the slowest exponential convergence of the linearized system back to equilibrium. Species i that is closest to the dominant eigenvector \mathbf{r} inherits the slowest exponential recovery rate compared to all other species. Therefore, species i will have the slowest recovery in the entire community and its difference in the expected recovery times compared to an arbitrary species k will be:

$$\Delta_{ik} = \frac{\log|r_{i1}| - \log|r_{k1}|}{|\lambda_1|} \quad (1)$$

Here, λ_1 is the maximum eigenvalue for the linearized system, and r_{i1} and r_{k1} are the projections of the eigenvector \mathbf{r}_1 onto species i and k respectively (Lemma 5 Appendix A in Supplementary material).

We exemplify this approximation in a two species Lotka-Volterra competition model. Fig. 1a shows that a decrease in the carrying capacity of species 1 leads to the classical result of outcompetition of species 1 and the invasion of species 2. Along this path eigenvalue λ_2 (dominant eigenvalue) gradually grows to 0 implying the rise of critical slowing down in the system (Fig. 1b). At the same time, the direction of the eigenvectors that are associated to the two eigenvalues is also changing (colored areas in Fig. 1c). In Fig. 1b, we quantify how close the two species are to the two eigenvectors. We find that species 2 is closer to the dominant eigenvector 2 than species 1 (the projection of the dominant eigenvector on species 2 is greater than the projection on species 1). This implies that the effect of critical slowing down should be stronger in species 2 than species 1. Indeed, we find that the difference in the numerically estimated recovery time between the two species matches closer the approximation of eq1 when we consider the projection of eigenvector 2 than the projection of eigenvector 1 (Fig. 1d). This result suggests that in multispecies communities there will be differences in the response rates of species to disturbances close to critical transitions. In what follows, we explore how these differences may affect the performance of resilience indicators across species in simple modules of competition communities.

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