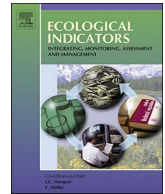




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Spatially heterogeneous stressors can alter the performance of indicators of regime shifts

Alexandre Génin^{a,1}, Sabiha Majumder^{b,1}, Sumithra Sankaran^{c,1}, Florian D. Schneider^{a,d}, Alain Danet^a, Miguel Berdugo^e, Vishweshha Guttal^c, Sonia Kéfi^{a,*}^a ISEM, CNRS, Univ. Montpellier, IRD, EPHE, Montpellier, France^b Department of Physics, Indian Institute of Science, Bengaluru 560012, India^c Center for Ecological Sciences, Indian Institute of Science, Bengaluru 560012, India^d Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany^e Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, C/Tulipán s/n, Móstoles 28933, Spain

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ABSTRACT

Mathematical models together with empirical tests suggest that it may be possible to detect leading indicators, or early warnings, of approaching shifts in ecosystems. Previous studies have often relied on ecological systems where the stressor (e.g. temperature, precipitation) is assumed to act homogeneously in space. Many ecological systems are, however, prone to spatially heterogeneous stresses (or ‘spatial stressors’), such as grazing, whose strength varies as a function of local vegetation patchiness. Here, we employed three well-studied spatially explicit ecological models to investigate how spatial stressors influence (a) the dynamics and resilience of ecosystems and (b) the robustness of early warnings of approaching ecosystem shifts. Mean-field and numerical simulations of the models suggested that spatial stressors could affect the stability and the number of equilibria of the system. Trends of spatial and temporal indicators were broadly consistent with the theory, i.e. they exhibited increasing trends as the system approached ecosystem shifts. However, in two of the three models, at high levels of spatial stress, spatial indicators could either exhibit trends opposite to those expected by the theory, or show no signals at all. Our results suggest that spatial stressors can interfere with the spatial patterns and thereby with the theoretically expected trends of early warning signals of ecosystem shifts. This highlights, once again, the importance of having a good knowledge of the ecosystem under study to be able to accurately interpret the indicator trends observed.

1. Introduction

In some ecosystems, small changes in external conditions may provoke abrupt changes (or shifts) in their states (Scheffer et al., 2001). For example, shallow lakes can switch from a clear water to a turbid state (Scheffer et al., 2001), drylands can become deserts and lose most of their perennial vegetation (Rietkerk et al., 2004), and fish stock can collapse because of overfishing (Hare and Mantua, 2000). Because of the potential negative consequences of such shifts, both from ecological and economic perspectives, extensive efforts were devoted to identifying indicators of approaching shifts (Scheffer et al., 2009), and quantitative indicators were devised based on the phenomenon of ‘critical slowing down’ (Wissel, 1984). Critical slowing down occurs as a dynamical system approaches a tipping (or critical) point, i.e. a point

at which the stability of a system changes qualitatively (Wissel, 1984). Specifically, as a dynamical system approaches a critical point, it takes increasingly long to recover from small perturbations (i.e. it slows down). This results in increased variance, skewness and autocorrelation in the temporal dynamics of the system (Carpenter and Brock, 2006; Van Nes and Scheffer, 2007; Guttal and Jayaprakash, 2008). Moreover, spectral properties of the temporal series show reddening in the vicinity of critical points (Kleinen et al., 2003). These statistical indicators have been referred to as generic temporal indicators (Dakos et al., 2012).

The spatial equivalents to these statistics are expected to show signatures of approaching critical points as well (Guttal and Jayaprakash, 2009; Carpenter and Brock, 2010; Dakos et al., 2011, 2010; Kéfi et al., 2014). The so-called generic spatial indicators – spatial variance, spatial skewness, near-neighbor spatial correlation and spatial

* Corresponding author.

E-mail address: sonia.kefi@umontpellier.fr (S. Kéfi).¹ These authors contributed equally to the study..<https://doi.org/10.1016/j.ecolind.2017.10.071>Received 15 January 2017; Received in revised form 19 October 2017; Accepted 27 October 2017
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spectral density – are all expected to increase as a system moves towards a critical point. These relatively simple statistical indicators have attracted a lot of attention in the literature because they can be measured directly by monitoring ecosystem characteristics in the field (e.g. vegetation cover), and this regardless of the ecological details of the system (Scheffer et al., 2009). Various empirical studies have demonstrated the validity of the temporal, and to a lesser extent of the spatial, indicators of approaching ecosystem shifts (Kéfi et al., 2007a; Dai et al., 2012, 2013; Cline et al., 2014; Benedetti-Cecchi et al., 2015; Scheffer et al., 2015; Eby et al., 2017).

Despite the generality of the underlying phenomenon of critical slowing down, the generic temporal and spatial indicators have been shown to have limitations in various types of ecological systems, such as those with chaotic and long transient phenomena (Hastings and Wysham, 2010), those with multiple dynamic species or variables (Guttal and Jayaprakash, 2008; Chisholm and Filotas, 2009), those with time-delays (Guttal et al., 2013), those driven by stochasticity (Benedetti-Cecchi et al., 2015; Sharma et al., 2015; Guttal et al., 2016) as well as in ecosystems exhibiting spatial patterns (Dakos et al., 2011). In the case of spatially structured ecosystems, such as drylands, studies have suggested that the generic indicators may fail (Dakos et al., 2011), but that metrics based on other aspects of the distribution of organisms in space were likely to offer alternative and potentially more reliable indicators of degradation (Kéfi et al., 2007a; Kéfi et al., 2014).

More precisely, in spatially structured ecosystems, the clusters (i.e. set of contiguous occupied cells connected through their nearest neighbours) can be described quantitatively in terms of the distribution of their sizes, commonly termed the patch size distribution. Previous studies have suggested that patch size distributions are generally expected to fit heavy-tailed functions, such as a power-laws (Pascual et al., 2002; Kéfi et al., 2011), but when an ecosystem is subjected to stress, the patch size distributions would become increasingly truncated and eventually reach an exponential distribution before the collapse of the ecosystem (Kéfi et al., 2007a; Kéfi et al., 2011; Kéfi et al., 2014). Only a few studies have tested those patch-based indicators on actual ecological data so far (but see e.g. Kéfi et al., 2007a; Lin et al., 2010; Berdugo et al., 2017), and despite promising results there does not seem to be a consensus yet about their detectability and usefulness as indicators of approaching ecosystem shifts (Maestre and Escudero, 2009, 2010; Kéfi et al., 2010a; Lin et al., 2010; Moreno-de las Heras et al., 2011; Xu et al., 2015; Weerman et al., 2012).

In sum, a number of indicators of approaching ecosystem shifts have been suggested in the literature so far, but our understanding of their reliability is still limited, in particular for spatially structured ecosystems (Dakos et al., 2011; Kéfi et al., 2014). Most of the studies investigating indicators of ecosystem shifts have focused on cases where the external stress is considered homogeneous in space. There are, however, a number of real situations where stressors are spatially heterogeneous (e.g. waves, wind, grazing). For example, in a meadow with a fragmented vegetation cover, the grazing pressure might not be the same everywhere in the landscape but depends, among other things, on the movement of the grazers and where they decide to eat (Adler et al., 2001). Such a spatial heterogeneous stress is expected to affect the size and shape of the vegetation clusters and thereby the detectability and reliability of at least the indicators based on spatial patterns (see Schneider and Kéfi, 2016 for a study of the patch-based indicators in a grazing system). This naturally raises the question that we aimed to address in this manuscript: How does spatially heterogeneous stress affect the spatial patterns in the ecosystems and what does that mean for the performance of the temporal and spatial indicators of ecosystem shifts (Dakos et al., 2012; Kéfi et al., 2014)? Remarkably, the behavior of the generic temporal and spatial indicators of ecosystem shifts currently available in the literature has not been studied in spatially structured ecosystems submitted to a spatially heterogeneous stress so far. Such knowledge could help improve our ability to anticipate ecosystem degradation in spatially structured ecosystems.

Here, we addressed this gap in our understanding using, as examples, models of three ecological systems subjected to spatially heterogeneous stress: mussel bed patterns caused by wave-induced disturbance (Guichard et al., 2003), vegetation of a dryland ecosystem under the influence of grazing (Schneider and Kéfi, 2016), and forest gaps created by disturbances such as fire or wind (Kubo et al., 1996). In previous studies, these lattice-based models, nonlinear and stochastic, have been shown to exhibit spatial patterns in the form of clusters of individuals (i.e. patches) as well as power law scaling in the geometry of these clusters (Pascual et al., 2002; Roy et al., 2003). We subjected these model ecosystems to increasing stress levels. We conducted mean-field analyses, i.e. discarding the spatially explicit aspects of the models, to describe the relationship between the equilibrium state of the ecosystems and the stress level, based on which we obtained expected trends of all the generic indicators along the gradient of stress. We then investigated whether the generic (temporal and spatial) and patch-based indicators provided early warning signals of approaching critical points in the three models.

2. Methods

We adopted the following approach to address our research questions. We investigated three spatially-explicit models representing three ecological systems. Each of these three models includes both a spatially homogeneous and a spatially heterogeneous stress. For each model, we performed a mean field analysis, which consists of simplifying the models by ignoring their spatial aspects (see upcoming paragraph on ‘Mean field approximation’ for more details). As a consequence of this simplification, relatively simple dynamical equations can be written and solved to obtain the stable and unstable equilibria along gradients of stress (i.e. bifurcation diagrams). This allowed us to make predictions about expected trends of the indicators. We then ran spatially explicit simulations of the models along gradients of homogeneous stressors and this for different values of the heterogeneous stressors. We calculated the generic and patch-based indicators along these gradients and compared the behavior of the indicators for different values of the heterogeneous stressor in the three models.

2.1. The models

We analyzed three spatially-explicit models representing three ecological systems exhibiting spatial patterns due to different underlying ecological mechanisms.

(i) The first model describes mussel dynamics where wave disturbance creates gaps in the mussel bed (Guichard et al., 2003) (hereafter referred to as the ‘mussel bed model’). In the mussel bed model, mussels are disturbed by strong waves that create gaps; the edges of the gaps consist of mussels that lost their byssal thread attachment to some of their neighbors and to the substratum (i.e. disturbed mussels). As a consequence, the edges of newly formed gaps are temporarily unstable and more susceptible to disturbance; this means that the disturbance spreads via the unstable edges in this model (by making neighboring mussels become themselves perturbed). The disturbance is decomposed in two stresses in this model: the spatially homogeneous stress is the probability that a mussel taken anywhere in the system becomes perturbed (density-independent probability), and the spatially heterogeneous stress is related to the spread of the disturbance to near-neighbors (i.e. the probability that a mussel which has at least one disturbed neighbor becomes disturbed itself).

(ii) The second model describes vegetation dynamics in semi-arid ecosystems, where plants are eaten by grazers (Schneider and Kéfi, 2016) (hereafter referred to as the ‘grazing model’). In the grazing model, droughts are assumed to affect the recruitment probability of new individuals everywhere in the landscape (spatially homogeneous stress); grazing affects plant mortality, but plants with more neighbors mutually benefit from their investment in protective structures, such as thorns, and

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