Ecological Indicators 70 (2016) 498–506

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original research paper

Indicators and mechanisms of stability and resilience to climatic and landscape changes in a remnant calcareous grassland

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ARTICLE INFO

Article history:
Received 26 January 2016
Received in revised form 25 April 2016
Accepted 18 June 2016

Keywords:
Beta diversity
Raup-Crick index
Dispersal
Resistance
Habitat fragmentation
Rainfall variability

ABSTRACT

When considering the development of conservation strategies for threatened plant communities it is crucial to understand their resilience to environmental change, taking into account current decline and the occurrence of further habitat fragmentation and climatic changes. Many recent works describe resilience character and elements, but there is little focus on the metrics and indices that describe elements of stability and specific resistance or resilience over the community composition matrix. Communities with strong niche selection might be restricted to specific resistance strategies to cope with environmental changes. This would result in a community at greater risk from increasing fragmentation and climatic changes.

In a 35 years survey of relic calcareous grasslands, we looked at measures to identify the resilience mechanisms for stability in the presence and abundance of species. We used techniques of partitioning of temporal beta diversity in nestedness and turnover components, analysis of functional strategy changes and dissimilarity analysis to detect changes in between–plot diversity and exchanges.

Contrary to expectations, we observe strong resilience with different stabilizing mechanisms both at plot level and exchanges between plots. At the scale of our grassland complex, response diversity and environmental stochasticity allow for the maintenance of high biodiversity under natural perturbations and gradual human-induced environmental changes. This highlights the importance of dispersal, recruitment dynamics and microsite diversity.

Community resilience is more than just the sum of species resilience strategies; adaptive management strategies need more emphasis on the variability of conditions, as this can enable or disrupt important community resilience mechanisms.

1. Introduction

The way biotic communities preserve their structure and function in time, is a central point of ecological research in the light of human perturbations (Tilman and Downing, 1994). This focus is topical with the growing concern for climatic change and the difficulty to predict changes or construct adaptive strategies. It is well-acknowledged nowadays that resilience is a useful concept to understand ecosystem change, but that we have to develop a better understanding of the mechanisms involved in community resilience (Reyer et al., 2015b). Many recent works describe resilience character and elements, but little focus is present for the indicators to describe elements of stability and specific resistance/resilience over the community composition matrix. Metrics and indices to describe stability and resilience are often simple species richness or in most cases productivity measures (Isbell et al., 2015; Müller et al., 2015). But productivity measures are directly related to the disturbance and do not allow to distinguish between individual species physiological responses and community responses of resistance and resilience. To infer community assembly mechanisms of resistance and resilience, changes in composition need to be analysed in time, during and after disturbance.

Here, we analyse grassland stability and resilience over an exceptionally long time series, for effects of pulse disturbances of climatic origin – extremely dry or wet years, and a press disturbance of habitat degradation at the landscape scale.

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http://dx.doi.org/10.1016/j.ecolind.2016.06.036
1470-160X/

Calcareous grassland is an ecosystem of high patrimonial value as it is among the richest and most threatened plant communities of Europe. It is believed to be very sensitive to environmental changes of intensifying agricultural practices and fertilizer use (Grime et al., 2000). Understanding its resilience to environmental change is crucial in the perspective of European conservation strategies. Calcareous grasslands are currently suffering from species loss because of the abandonment of traditional agro-pastoral practices. Even though very fragile, they are presumed to be little impacted by predicted temperature increases in the temperate zone, or by drier summers, and thus quite resistant to climatic changes (Carey, 2012). This resistance to climate change is earlier described in terms of stability and resilience, defined as the ability of a community to maintain its composition and biomass in response to environmental stress (Grime et al., 2000). Knowledge of the grasslands' intrinsic resilience to disturbances of different origin is a prerequisite to construct management strategies and adaptive management reckoning with climatic change (Hulme, 2005; Sutherland et al., 2010; Maalouf et al., 2012). Still, sufficiently long data series to analyse these elements prove rare.

Grime et al. (2008) sum up a series of elements of resilience to climate change taken from a 13-year experiment: (*i*) constancy in the relative abundance of growth forms and maintained dominance by long-lived, slow-growing grasses, sedges, and small forbs; (*ii*) immediate but minor shifts in the abundance of several species that have remained stable over the course of the experiment; (*iii*) no change in productivity; and (*iv*) only minor species losses in response to drought and winter heating. Classic ecological theory assumes that conservation management activities (such as regular mowing) and drought events should increase diversity in calcareous grassland communities (Maalouf et al., 2012). Still, high species diversity not necessarily entails high ecosystem resilience or vice versa (Ruijven and Berendse, 2007). Indeed, species-rich areas may be highly vulnerable to environmental change. Especially when they are highly structured by environmental processes (deterministic response), changing environmental conditions can drastically alter community richness (Elmqvist et al., 2003). Resilience to environmental changes and/or natural perturbations can find its origin in mechanisms present in the local community, or at cross-scale level through functional redundancy or in exchanges at metacommunity level driven by dispersal mechanisms. Local community resilience is present as resistance traits of species, and also in variable responses to meteorological events in terms of productivity and biotic interactions (competition, facilitation), facilitated by microsite diversity. Cross-scale resilience is present as response diversity and metacommunity dynamics.

As we define resilience to environmental change as the ability to preserve community composition and structure in time, we can test the actually proposed measures for stability and resilience (Table 1). As yet, most of the existing analyses are restricted to either looking at only one driver of change (f.i. temperature in the experiment of Grime and colleagues), or one measure (drought resistance traits (Vogel et al., 2012)). We hypothesize the different measures for resilience of stability in structure and composition give consistent signals in a same community subsisting several perturbations.

A second hypothesis is that for this community composed of species with little resilience strategies, stability is driven by local mechanisms of resistance. In this context we also refer to the reported sensitivity of communities highly structured by environmental processes (Elmqvist et al., 2003). The cross-scale mechanisms (ruled by dispersal or functional reorganization) are only operational to safeguard local biodiversity in case of communities with many resilience strategies. For our strongly 'environment sensitive' and species sorting driven calcareous grassland community we expect to find only local resistance strategies, with little supra-site resilience. Based on its composition and structure it can typically be defined as a low-resilient community, governed by species with a short-lived seed bank, little ruderal strategy and low regenerative and dispersion capacities.

So, we hypothesize for low resilience to perturbations and little exchange with surroundings. The only source of resilience that we expect is present in the richness both in species as functionality, together with the described resistance elements. This distinction for resistance or resilience predominating can be translated for either continuity and stability in a local community, with compensation in time only at the site level, or a higher scale community stability, combined over sites, driven by exchange processes. This can be tested in comparison with temporal composition changes at plot and between-plot level; this hypothesis would result in higher stability in local plots than over a range of plots. The higher scale resilience can reveal the potential of landscape level processes of dispersal and exchange to sustain the metacommunity richness.

Observing consistent community changes and predicting global change effects require long-term analyses. Where mesocosm and model experiments are well explored nowadays, patterns of community changes in real ecosystems under environmental change still require attention (Gilman et al., 2010). We conducted a long-term series analysis of annually sampled calcareous grassland sites employing standardized methods, spanning over three decades. Starting from the described vulnerability and resistance to changes, resilience measures are constructed and tested to identify drivers and strength of community changes and resilience to environmental change. Calcareous grasslands are documented to be resistant to temperature change, but strongly influenced by annual precipitation regimes of droughts and wet spring seasons. So, in our infertile grasslands with continuous management, we investigated the relevant meteorological data to identify perturbations that could reveal shifts and for which community resilience might be relevant. Further environmental change that might incite resilience is the habitat fragmentation occurring regionally. As our relic calcareous grassland is supposed to be strongly local condition bound, questions arise as for the role of exchange with the surroundings and the resilience to environmental perturbations of climatological or managerial origin.

2. Methods

2.1. Calcareous grassland series

Calcareous grassland is found on shallow, well-drained soils, rich in bases which formed by the weathering of chalk and other types of limestone. It supports a very rich flora, including many rare and scarce species. The 'Thier de Lanaye' is part of a complex of small calcareous grasslands in an isolated and fragmented calcareous region near Maastricht at the Belgian-Dutch border. This long term permanent quadrat (PQ) plot research started up as a test for the introduced nature reserve management. Four PQ's of 3 × 3 m were set out over the large grassland complex, with intervals of minimum 50 m (maximum distance between PQ1 and PQ4 300m), and inventoried in summer by the authors. Thanks to the larger surface of these plots (9m^2), they are well-representative for the local vascular plant community, and with this continuous annual sampling we can treat them as individual plot time series. Furthermore are they within reasonable distances to assume dispersal potentially taking place among them. The Braun-Blanquet recording scale (Braun-Blanquet, 1964) is applied, only taking account of higher plants (angiosperms). For the analysis the Braun-Blanquet scaling was transformed into a decimal scale according to van der Maarel (1979). Plot soils show a mixture of chalk and sandy gravel, with a gradient of richer lime stone soils in plots PQ1-2 that are