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# Plant functional assemblages as indicators of the resilience of grassland ecosystem service provision

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ABSTRACT

Ecosystems provide a variety of ecosystem services (ES), which act as key linkages between social and ecological systems. ES respond spatially and temporally to abiotic and biotic variation, and to management. Thus, resistant and resilient ES provision is expected to remain within a stable range when facing disturbances. In this study, generic indicators to evaluate resistance, potential resilience and capacity for transformation of ES provision are developed and their relevance demonstrated for a mountain grassland system. Indicators are based on plant trait composition (i.e. functional composition) and abiotic parameters determining ES provision at community, meta-community and landscape scales. First the resistance of an ES is indicated by its normal operating range characterized by observed values under current conditions. Second its resilience is assessed by its potential operating range – under hypotheses of reassembly from the community's species pool. Third its transformation potential is assessed for reassembly at meta-community and landscape scales. Using a state-and-transition model, possible management-related transitions between mountain grassland states were identified, and indicators calculated for two provisioning and two regulating ES. Overall, resilience properties varied across individual ES, supporting a focus on resilience of specific ES. The resilience potential of the two provisioning services was greater than for the two regulating services, both being linked to functional complementarity within communities. We also found high transformation potential reflecting functional redundancy among communities within each meta-community, and across meta-communities in the landscape. Presented indicators are promising for the projection of future ES provision and the identification of management options under environmental change.

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## 1. Introduction

Terrestrial and aquatic ecosystems deliver multiple, interrelated provisioning, regulating, and cultural services that benefit human well-being (Díaz et al., 2015). Ecosystem services (ES) are thereby one of the key linkages between social and ecological systems (Díaz et al., 2015; Reyers et al., 2013), and their steady provision needs to be preserved into the future to sustain societies. However, under increasing anthropogenic pressures threatening ecosystem integrity, the sustainability of ES provision will be determined by ecosystem resilience to combined pressures from land use, changing climate, nitrogen deposition or species invasions (Carpenter and Folke, 2006; Leadley et al., 2014), making the notion of resilience central to forecasting and managing for future human well-being (Spears et al., 2015).

Ecological resilience is defined as the amount of disturbance a system can cope with without shifting to another state (Holling, 1973; Walker et al., 2004). To address social-ecological resilience, which considers interactions between ecosystem properties and social dynamics (Biggs et al., 2012), the definition of resilience can be expanded as the ability of an ecosystem to provide a stable amount of ES while facing management or environmental changes (Carpenter and Folke, 2006; Elmqvist et al., 2003). Considering that the resilience of an ES is maintained through constant dynamics and change (Walker and Salt, 2006), a resilient system will adapt its structure to change while keeping the same dynamic set of states

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and associated ES (Standish et al., 2014; Walker et al., 2004). While a holistic, conceptual assessment of resilience needs to integrate social and ecological dynamics, for the purpose of measurement and indicator development a simplification, and specification of the term 'resilience' is required (Quinlan et al., 2016). In particular, indicators focusing explicitly on the resilience of ES are still missing.

Acknowledging that resistance and resilience are intrinsic properties of all ecosystems, in this paper we propose a conceptual approach that targets the ecological underpinnings of the resilience of ecosystem functions based on ecosystem dynamics (Oliver et al., 2015), and focuses on a measurement approach (*sensu* Quinlan et al., 2016). More specifically, we linked the concept of resilience to the concept of community functional dynamics (Suding et al., 2008) in order to propose quantifiable indicators of ES resilience. Focusing on the resilience of ES requires assessing specific resilience, defined as the resilience of a specific part of the social-ecosystem to a particular disturbance type (Walker and Salt, 2006; Quinlan et al., 2016), rather than system-level, generic resilience (e.g. Carpenter and Brock, 2006; Scheffer et al., 2009). Indeed, we hypothesize that individual ES may have different sensitivities to disturbances and therefore different resilience (Oliver et al., 2015; Scheffer et al., 2001) due to specific critical changes in their underpinning ecological characteristics. We further refer to 'potential' resilience of ES as our approach does not consider the transient dynamics and time lag of returning to the pre-disturbed state which follows once the range of resilience might be exceeded. The 'realised' resilience will depend on additional properties such as species regeneration traits and local contingencies. Our approach is positioned within the broad field of social-ecological resilience; however, we apply a purely ecological perspective to the measurement of ES resilience.

Our framework proposes to assess the specific resilience of an ES by distinguishing the three phases of resilience (Walker and Salt, 2006): first, the initial resistance to change which we define as the range of ES provision under observed environmental fluctuations; second, the maintenance of the current range of ES provision, defined more strictly as resilience, given reversible variations in ecosystem state and processes (Standish et al., 2014); and finally transformation, which implies a shift in system state and associated ecosystem processes (Carpenter and Folke, 2006; Oliver et al., 2015). ES resilience is then quantified by: (1) the observed range of values for an ES, indicating resistance, (2) the potential range of values for the ES within the same ecosystem state, indicating potential resilience *sensu stricto*, and (3) the new potential range of provision after ecosystem transformation to an alternative state.

In the following, we first present the conceptual framework for ES resilience assessment, and associated indicators based on community functional composition. We then illustrate this concept through an application to grassland ecosystems using data from differently managed grassland states in the central French Alps (Lavorel et al., 2011). Subsequently, we analyse the implementation of indicators using quantitative criteria. We end by discussing challenges we faced when using the concept in practice, general restrictions and implications for future research.

## 2. Conceptual approach

As ecological processes supporting ES provision are determined by land cover and by specific management (Bennett et al., 2009; Allan et al., 2015), an increasing number of studies have attempted to quantify ES provision by considering changes in ecological parameters in response to management in grasslands (Lavorel et al., 2011), agricultural areas and forests (Raudsepp-Hearne et al., 2010), or aquatic systems (Barbier et al., 2011). Each ES provided by a given ecosystem state then varies spatially (and temporally) according to local environmental (e.g. topography, soil characteristics), biotic (community composition), and management characteristics (e.g. nitrogen input, disturbance regime) (Bennett et al., 2009; Díaz et al., 2007b; Lavorel et al., 2011; Quétier et al., 2007). Our concept for quantifying ES resilience is based on the notion of *operating ranges* (OR) of an ES, defined as its range of values in a given ecosystem state (Pereira e Silva et al., 2013), for instance certain management conditions, given environmental and biotic variation. Further, changes in climate, management, species invasion, or species extinctions can lead successively to variation in environmental and biotic parameters within the same ecosystem state and to transformation to another state.

Among available conceptual models describing ecosystem dynamics, and specifically resilience, *state-and-transition models* (STM) (Fig. 1a) have proven particularly successful in capturing linear and nonlinear changes in ecosystem structure and function and their causal mechanisms (e.g. Lavorel et al., 2015; Prober et al., 2014). They can be used to characterize alternative states depending on land use and drivers of specific transitions such as climate, natural disturbance regimes, management, and their interactions. STM are also one of the tools that might be specifically suitable for the identification of changes and resilience of ES under uncertain futures such as climate change (Lavorel et al., 2015). We therefore believe that they are a possible tool to advance the conceptualization and quantification of ES resilience by analysing OR and transitions in biodiversity and ecosystem functioning.

Different approaches, based for instance on taxonomic units (e.g. species) or functional traits exist to model community dynamics. Here, we focus on the re-assembly of functional trait composition (Suding et al., 2008), as ecosystem processes, and thus ES, are primarily influenced by species functional roles, i.e. traits (Cardinale et al., 2012; Díaz et al., 2007b; Lavorel et al., 2011; Oliver et al., 2015). ES resilience indicators are therefore linked to community dynamics within the functional trait pool. Specifically, following Quétier et al. (2007) and Lavorel et al. (2015) we propose to use STM that are formulated in terms of *functional composition (FC)*, i.e. the presence and abundance distribution of plant functional trait values (Díaz et al., 2007a), so as to link ES resilience and transitions to specific mechanisms and to gain predictive power (Standish et al., 2014). The focus on the functional rather than the taxonomic composition of communities provides the ability to explain current ES provision based on functional effect traits, as well as to project future ES provision depending on functional responses and community assembly (Allan et al., 2015; Díaz et al., 2007b).

Combining the concepts of OR, STM, and FC for characterizing resilience, we define our indicators of resilience as OR which can be evaluated at different scales according to dynamic relations between ecosystem states. Consistent with hierarchy theory (O'Neill et al., 1989) ecological systems are structured as nested levels of organisation, each associated with specific spatial and temporal scales of states and processes. Each hierarchical level is linked to certain environmental characteristics (e.g. nutrient availability, pH) constraining the OR of community composition, ecosystem functioning and thus ES provision. However, environmental limits may alter over time inducing a shift to an altered OR (O'Neill et al., 1989). We consider the scaled structure of ecological systems by determining four indicators of resilience for individual ES within a landscape (Fig. 1b): The *Normal Operating Range* (NOR) and the *Community Potential Operating Range* (Com-POR) are applied to the scale of the community (i.e. ecosystem state). The *Meta-Community Potential Operating Range* (Meta-Com-POR) encompasses ecosystem states linked by possible management- or environmentally-driven transitions (Leibold et al., 2004). The highest hierarchical level is considered by the *Landscape Potential Operating Range* (Landscape-POR) representing the functional pool and environmental characteristics of the entire landscape. Here-

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