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Review

Biodiversity and Resilience of Ecosystem Functions

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Accelerating rates of environmental change and the continued loss of global biodiversity threaten functions and services delivered by ecosystems. Much ecosystem monitoring and management is focused on the provision of ecosystem functions and services under current environmental conditions, yet this could lead to inappropriate management guidance and undervaluation of the importance of biodiversity. The maintenance of ecosystem functions and services under substantial predicted future environmental change (i.e., their 'resilience') is crucial. Here we identify a range of mechanisms underpinning the resilience of ecosystem functions across three ecological scales. Although potentially less important in the short term, biodiversity, encompassing variation from within species to across landscapes, may be crucial for the longer-term resilience of ecosystem functions and the services that they underpin.

The Importance of Resilience

Across the globe, conservation efforts have not managed to alleviate biodiversity loss [1], and this will ultimately impact many functions delivered by ecosystems [2,3]. To aid environmental management in the face of conflicting land-use pressures, there is an urgent need to quantify and predict the spatial and temporal distribution of **ecosystem functions** and **services** (see Glossary) [4–6]. Progress is being made in this area, but a serious issue is that monitoring and modeling the delivery of ecosystem functions has been largely based on the current set of environmental conditions (e.g., current climate, land use, habitat quality). This ignores the need to ensure that essential ecosystem functions will be provided under a range of environmental perturbations that could occur in the near future (i.e., the provision of **resilient ecosystem functions**). The objective of this review is to identify the range of mechanisms that underpin the provision of resilient ecosystem functions to inform better environmental monitoring and management.

A focus on current environmental conditions is problematic because future conditions might be markedly different from current ones (e.g., increased frequency of extreme weather events [7] and pollution [8]) and might therefore lead to rapid, nonlinear shifts in ecosystem function provision that are not predicted by current models. Reactive management might be too slow to avert consequent deficits in function, with impacts for societal well-being [9]. An analogy of this situation is the difference between monitoring whether a bridge is either standing (i.e., providing

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its function) or collapsed, prompting need for a rebuild, as opposed to monitoring and repairing damage to prevent the collapse from ever happening. In environmental science, attempts have been made to identify this 'safe operating space' at a global level to ensure that boundaries are not crossed that could lead to rapid losses in ecosystem functions [10,11]. However, there is a danger that current regional and local assessments of ecosystem functions and management advice do not incorporate such risk assessments. This could result in poor management advice and undervaluation of the importance of biodiversity, because while relatively low levels of biodiversity can be adequate to provide current function [12], higher levels might be needed to support similar levels of function under environmental change [2,13–18]. Therefore, there is a need to identify the characteristics of resilient ecosystem functions and capture these in both predictive models and management guidance.

Defining and Applying the Resilience Concept

Resilience is a concept with numerous definitions in ecological [19], social [20], and other sciences [21]. In ecology, an initial focus on the stability of ecosystem processes and the speed with which they return to an equilibrium state following disturbance (**recovery** or 'engineering resilience' [22]) has gradually been replaced by a broader concept of 'ecological resilience' recognizing multiple stable states and the ability for systems to **resist** regime shifts and maintain functions, potentially through internal reorganization (i.e., their 'adaptive capacity' [23]). Recent definitions of resilience encompass aspects of both recovery and resistance, although different mechanisms can underpin these and in some cases there might be trade-offs between them [24]. However, some mechanisms can promote both resistance and recovery depending on the timeframe in which a system is observed (e.g., very rapid recovery can look like resistance). Therefore, we treat resistance and recovery here as two related complementary aspects of resilience [25].

There has been much semantic and theoretical treatment of the resilience concept, but here we are concerned with identifying metrics for real-world applications. An ecological system can be defined by the species composition at any point in time [26] and there is a rich ecological literature, both theoretical and experimental, that focuses on the stability of communities [16,27–29] with potential relevance to resilience. Of course, the species in a community are essential to the provision of many ecosystem functions that are the biological foundation of ecosystem services [3]. However, the stability of species composition itself is not a necessary prerequisite for the resilience of ecosystem functions. Turnover in species communities might be the very thing that allows resilient functions. For example, in communities subjected to climatic warming, cold-adapted species are expected to decline while warm-adapted species increase [30]. The decline of cold-adapted species can be limited through management [31], but in many cases their local loss might be inevitable [32]. If these species have important functional roles, ecosystem functions can suffer unless other species with similar functional roles replace them. Indeed, similar sets of functions might be achieved by very different community structures [33]. Therefore, while the species composition of an ecosystem is typically the target of conservation, it is ecosystem functions, rather than species composition *per se*, that need to be resilient if ecosystem services are to be maintained (Figure 1). In this case the most relevant definition of resilience is the degree to which an ecosystem function can resist or recover rapidly from environmental perturbations, thereby maintaining function above a socially acceptable level. This can be thought of as the ecosystem functions-related meaning of resilience [19], or alternatively as the inverse of ecological 'vulnerability' [34]. Resilience in this context is related to the stability of an ecosystem function as defined by its constancy over time [35], but the approach of using a minimum threshold more explicitly measures deficits of ecological function that impact on human well-being (e.g., [14]). Note that here we focus on the resilience of individual ecosystem functions, which might be appropriate for policy formulation (e.g., pollination resilience), although ecosystem managers will ultimately want to consider the suite of ecosystem functions supporting essential services in a given location.

Glossary

Alternative stable states: when an ecosystem has more than one stable state (e.g., community structure) for a particular set of environmental conditions. These states can differ in the levels of specific ecosystem functions.

Beta diversity: variation in the composition of species communities across locations.

(Demographic) Allee effects: where small populations exhibit very slow or negative growth contrary to the rapid growth usually expected. Explanations range from an inability to find mates or avoid predators or herbivores to limited ability to engage in cooperative behaviors.

Ecosystem functions: the biological underpinning of ecosystem services. While ecosystem services are governed by both ecological and social factors (e.g., business demand–supply chains), in this review we focus on the proximate biological processes – such as productivity, pest control, and pollination – that determine the supply of ecosystem services.

Ecosystem services: outputs of ecosystem processes that provide benefits to humans (e.g., crop and timber production).

Effect traits: attributes of the individuals of a species that underlie its impacts on ecosystem functions and services.

Functional redundancy: the tendency for species to perform similar functions, such that they can compensate for changes in each other's contribution to ecosystem processes. Functional redundancy arises when multiple species share similar effect traits but differ in response traits.

Phenotypic plasticity: gene-by-environment interactions that lead to the same genotypes expressing changed behavior or physiology under different environmental conditions.

Resilient ecosystem function: see main text for a history of the term resilience. The definition used here is the degree to which an ecosystem function can resist or recover rapidly from environmental perturbations, thereby maintaining function above a socially acceptable level.

Resistance/recovery: in the context used here, these refer to the tendency of ecosystem function