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Article

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Biodiversity and resilience of ecosystem functions

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Abstract

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.

Glossary

Beta diversity: Variation in the composition of species communities across locations

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 article, we focus on the proximate biological processes – such as productivity, pest control, pollination – that determine the supply of ecosystem services.

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

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

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.

Resilient ecosystem function: See main text for 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 provision to remain stable in the face of environmental perturbation or the tendency to rapidly return to pre-perturbation levels.

Response traits: Attributes that influence the persistence of individuals of a species in the face of environmental changes.

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

(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, avoid predators or herbivores, or a limited ability to engage in co-operative behaviours.

Alternate 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.

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, 5, 6]. Progress is being made in this area, but a serious issue is that monitoring and modelling 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 which 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, non-linear 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 its function) or collapsed, prompting need for a re-build, 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 whilst 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’ recognising multiple stable states and the ability for systems to resist regime shifts and maintain functions, potentially through internal reorganisation [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 focusses 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 which are the biological foundation of ecosystem services [3]. However, the stability of species composition itself is *not* a necessary pre-requisite for the resilience of ecosystem functions. Turnover in species communities might actually be the very thing that allows for resilient functions. For example, in communities subjected to climatic warming, cold-adapted species are expected to decline whilst 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, then ecosystem functions can suffer unless other species with similar functional roles replace them. In fact, 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 upon 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.

Threats to ecosystem functions.

Environmental change is not unusual (ecosystems have always faced periodic and persistent changes), but anthropogenic activity (e.g. land conversion, carbon emissions, nitrogen cycle disruption, species introductions) is now increasing both the rate and intensity of environmental change to previously unprecedented levels [36-38]. Rapid changes to the abiotic environment might alter local and regional species pools through environmental filtering and disrupting biotic interactions, leading to changes in the suites of traits and interactions that affect ecosystem functioning [39]. The timescales involved tend to be measured with respect to relevant human interventions, i.e. usually over years to decades. The environmental changes may be: rapid onset (e.g. disease), chronic (e.g. habitat loss) or transitory perturbations (e.g. drought; Figure 2a). Some environmental pressures can show complex temporal patterns. For example, climate change includes transitory perturbations due to climatic extremes overlaid on a background of long-term warming, with the potential for rapid onset changes if tipping points are reached [40].

The impacts of environmental perturbations on ecosystem functions will depend on the presence of ecosystem characteristics that confer resilience, involving interacting mechanisms at multiple ecological scales (see next section). These processes govern the form of functional response to environmental change (Figure 2b), and their rates relative to the environmental change driver will govern the resilience and ultimate temoral trends in ecosystem function (figure 2c).

Mechanisms underpinning resilient ecosystem functions

Previous studies have attempted to identify characteristics of resilient systems from a broad socioeconomic perspective [20, 21], but here we focus on the biological underpinnings of the resilience of ecosystem functions, to inform targeted environmental management practices. The resilience of ecosystem functions to environmental change is likely to be determined by multiple factors acting at various levels of biological organisation; namely, species, communities and landscapes (Table 1). These ecological levels are interconnected so that changes at a particular level can cascade to other levels in the same system. For instance, individual species' responses to environmental change mediate changes in the population abundance and resulting interactions with other species, thus affecting community structure and composition as well as the distribution of effect and response traits [39]. These changes can extend to the level of whole ecosystems, but are mediated the ecosystem context, such as landscape level heterogeneity or habitat connectivity, to determine the resilience of ecosystem function.

Here, we provide a new assessment of evidence for the mechanisms underpinning the resilience of ecosystem functions across these ecological levels (Table 1). Our assessment is focussed on promoting general resilience to a range of different primary threats to ecosystem function.

Table 1, Mechanisms underpinning the resistance and recovery of ecosystem functions to environmental perturbation. The abbreviations 'RES', 'REC and 'RES/REC' indicate the importance of each mechanism for resistance, recovery or both respectively.

Species (intraspecific)	**Community (interspecific)**	**Landscape (ecosystem context)**
Sensitivity to environmental change (RES)	Correlation between response and effect traits (RES)	Local environmental heterogeneity (RES)
Intrinsic rate of population increase (RES/REC)	Functional redundancy (RES/REC)	Landscape-level functional connectivity (RES/REC)
Adaptive phenotypic plasticity (RES/REC)	Network interaction structure (RES)	Potential for alternate stable states (RES/REC)
Genetic variability (RES/REC)	-	Area of natural habitat cover at the landscape scale (RES/REC)
Allee effects (RES/REC)	-	-

Species-level mechanisms

Species rarely experience identical impacts of environmental change due to interactions between traits, landscape composition and the scale at which they experience environmental drivers [41, 42]. This variation in response within and between individual species determines both the short-term provision and long-term resilience of ecosystem functions. Below we list five key mechanisms operating at the species level and provide hypotheses for their effects on the resilience of ecosystem functions.

Sensitivity to environmental change: Species vary in their capacity to persist in the face of the environmental perturbations, mediated by a range of behavioural and physiological adaptations (response traits) [43]. Such traits show both interspecific and intraspecific variation. Individuals with traits conferring reduced sensitivity to environmental change will confer higher resistance to ecosystem functions [44]. For example, trees vary in their sensitivity to drought depending on non-structural carbohydrate levels [44], which in turn might affect the resistance of ecosystem functions that they provide. Broader suites of traits, such as the plant resource economics spectrum [45], are also likely to explain variation in sensitivity. Note, however that there might be negative correlations between sensitivity and intrinsic growth rates, with slow-growing species providing more resistant ecosystem functions but with lower capacity to recover if perturbation does occur.

Intrinsic rate of population increase: The capacity of species populations to grow rapidly from low numbers is determined by a suite of related characteristics including generation time, mortality and fecundity rates. Species with a high intrinsic rate of increase will recover more quickly from environmental perturbations [46], or show resistance if this population reinforcement occurs during the perturbation.

Adaptive phenotypic plasticity: Individuals have the capacity to respond to environmental changes through flexible behavioural or physiological strategies which promote their survival [43] and resistance of ecosystem functions. For example, thermoregulatory behaviour appears to be an essential survival tool in many ectotherms that operate in temperature conditions close or beyond their physiological limits [47]. Additionally, adaptations might allow flexibility to maximise resource acquisition and growth rates in changed environmental conditions enabling more rapid population recovery and recovery of ecosystem function.

Genetic variability: Higher adaptive genetic variation increases the likelihood that genotypes which are tolerant to a given environmental perturbation will be present in a population [18]. This reduces the population impacts of environmental perturbations [48] and promotes resistance of ecosystem functions [49]. In addition, the persistence of tolerant genotypes locally means that population recovery rates are likely to be higher, leading to enhanced function recovery rates [48, 50]. Adaptive genotypes can be present in standing genetic variation, which is more likely at higher effective population sizes. Alternatively they can arise locally through mutation or through immigration from other populations [18]. It is also becoming increasingly apparent that epigenetic effects can provide heritable variation in ecologically relevant traits [51].

Allee effects: Allee effects make populations more susceptible to environmental perturbations causing crashes from which it is difficult to recover [52, 53]. Certain species are more susceptible to Allee effects through mechanisms such as an inability to find mates, avoid predators or a limited ability to engage in co-operative behaviours.

Community-level mechanisms

Beyond the tolerance and adaptability of individuals, the composition and structure of the biological community is of particular importance for the resilience of ecosystem functions. Below we list three key underpinning mechanisms.

Correlation between response and effect traits: If the extent of species' population decline following an environmental perturbation (mediated by response traits) is positively correlated with the magnitude of species' effects on an ecosystem function (via effect traits) then this will lead to less resistant ecosystem functions [39, 54]. This might occur if the same traits mediate both response and effects, or through indirect associations between different traits. Correlations and trade-offs are probably a common aspect of traits as a result of biophysical limitations in structure and function [55]. For example, traits such as body size have been linked with both sensitivity to environmental change (response traits) and the maintenance of ecosystem functions (effects traits) such as pollination by bees [56, 57], nutrient recycling by dung beetles [56] and pest control from predatory invertebrates [58, 59]. In contrast, completely uncorrelated response and effects traits cause higher resistance in ecosystem function, since responses of species to environmental change are decoupled from their effects on function [54, 56]. For example, Diaz *et al.* [39] summarise several studies which show no correlation between decomposability in plants (an effect trait for nutrient cycling and soil fertility) and persistence in the seedbank (a response trait to disturbance under agricultural intensification).

Functional redundancy: When multiple species perform similar functions, i.e., species exhibit some redundancy in their contributions to ecosystem processes, then resistance of an ecosystem function will be higher if those species also have differing responses to environmental perturbations [60, 61]. This gives rise to the 'insurance effect' of biodiversity [62], which is well supported both empirically [14, 15] and theoretically [16, 28]. Underpinning mechanisms include a statistical effect, where averaging across independently fluctuating species populations results in higher resistance ('portfolio effects'), which is enhanced further where there is negative spatial and/or temporal covariance (asynchrony) between species' population sizes, driven by differing responses to environmental change or competition [14-16, 28, 62].

The functional roles of species can be mediated by either continuous or categorical traits [e.g. complementary effect traits such as sward- and ground-active predators for pest control; 63]. Resistance is increased by both more species in total (assuming that there is variation in their response traits) and, for a given total number of species, when they are dispersed equally across effect trait space (Figure 3). In reality, intraspecific variation in traits also occurs and, where this is substantial relative to interspecific variation, it might be relevant to consider redundancy and dispersion of *individuals* across effect trait space [64].

Network interaction structure: The majority of the theory and empirical work discussed above concerns organisms occupying a single trophic level, but interactions between species (e.g. predation, parasitism, mutualism) can have large influences on community responses to environmental change [2, 65]. Loss of highly connected species in interaction networks can cause extinction cascades and reduce network stability [66-68]. If these species are particularly sensitive to environmental change then the resistance of the ecosystem functions they provide will be low [69]. Impacts on ecosystem function will be greater when response and effect traits are correlated and patterned in networks along extinction cascades. For example, body size is linked with both extinction risk and the provision of ecosystem functions in taxa including pollinators [56] and pest control agents [70]. In general, highly-connected nested networks dominated by generalised interactions are less susceptible to cascading extinction effects and provide more resistant ecosystem functions, in contrast to networks dominated by strong specialised interactions [71, 72].

An important consideration is that the impacts of species loss are likely to lead to changes in the abundances of surviving species, so that the presence or absence of density compensation following species loss can be the key predictor of ecosystem function provision [56, 67, 73]. For example, atmospheric deposition of nitrogen can result in species loss from some plant communities, but density compensation of remaining species might support net primary productivity [74].

Landscape-level mechanisms

The intraspecific- and community-level mechanisms described above are influenced by the environmental context of both the local site and wider landscape. The landscape context determines the local and regional species pool and also the abiotic environment which can modify the impacts of environmental perturbations on individuals and communities.

Local environmental heterogeneity: Spatial heterogeneity can enhance the resistance of ecosystem functions by a) facilitating the persistence of individual species under environmental perturbations by providing a range of resources and microclimatic refugia [75-78], and b) increasing overall species richness [79] and, therefore, functional redundancy. These heterogeneity effects can operate at: the fine-scale, for example, through vegetation structural diversity [75]; the medium scale, for example, through topoedaphic diversity [76]; or the larger scale, for example, through diversity of land cover types [77, 78]. Additionally, environmental heterogeneity across locations (promoting beta diversity) has been shown to increase stability of ecosystem functions [27].

Landscape-level functional connectivity: Metapopulation theory suggests that populations in well-connected landscapes will persist better or re-colonise more rapidly following environmental perturbation (the 'rescue effect'). Empirical studies confirming this hypothesis range from mesocosm experiments [80, 81] to landscape-level field studies [82, 83]. This prediction extends to metacommunities and experiments have shown that connectivity enhances community recovery after local perturbations [81, 84]. In a few cases, this recovery of community structure through dispersal has been shown to lead to recovery of ecosystem functions, such as productivity and carbon sequestration, to pre-perturbation levels; a process termed "spatial insurance" [85, 86]

Area of natural habitat cover at the landscape scale: In addition to improving functional connectivity for particular species, larger areas of natural or semi-natural habitat tend to provide a greater range and amount of resources, which promotes higher species richness and larger population sizes of each species [87, 88]. This, in turn, is likely to mean greater genetic diversity, and functional redundancy, both of which promote resistance of ecosystem functions [18, 60, 61].

Potential for alternate stable states: Alternate stable states are associated with abrupt shifts in ecosystems, tipping points and hysteresis, all of which challenge traditional approaches to ecosystem management [17, 89]. Ecosystem states maintain their stability through internal feedback mechanisms, which confers resistance to ecosystem functions. However, environmental perturbations can increase the likelihood of regime shift leading to a fundamental change in the assemblages of species providing functions [17]. Systems can be more susceptible to environmental stochasticity and transient perturbations close to these critical tipping points leading to sudden changes to a new equilibrium [53]. Some alternative stable states might be unfavourable in terms of ecosystem functions with return to previous states possible only through large and costly management interventions (hysteresis), thereby limiting the recovery capacity of ecosystem function. Alternative states are documented in a wide variety of ecosystems from local to global scales, although how stable and persistent these are remains uncertain [89-91].

Managing for resilience

Applied ecosystem management

Ecosystem services are beginning to be integrated within major land management programmes (e.g. the EU Common Agricultural Policy, REDD+). However, the measurement, monitoring and direct management of ecosystem function resilience in these programmes is lacking [92]. The ecological theory and empirical evidence discussed above suggest that multiple factors will determine ecosystem resilience. However, we do not yet know which will be the most important in determining resilience in particular functions or ecosystems. It is clear that some factors will be more amenable to management (e.g. population-level genetic variability and landscape structure [18, 31]) than others (e.g. environmental sensitivity of individual species, presence of alternative stable states). Additionally, there can be trade-offs and synergies between resilience and the short-term performance of ecosystem functions [49, 93] .

Synergies and trade-offs with short-term performance

In some cases there are synergies between the short-term performance of ecosystem functions and their longer-term resilience , e.g. if species richness is associated with higher levels of function under current conditions due to complementarity [13], and with higher resilience of function due to higher functional redundancy [39, 54]. In these cases, management targeted towards short-term performance will also enhance resilience. In other cases, however, trade-offs can occur. For example, maintaining genetic diversity for resilience of ecosystem functions, may conflict with the aim to produce 'best locally adapted phenotype'[49]. Much intensive agricultural management currently focusses on such low diversity systems that produce high levels of provisioning services but which might have low resilience [93]. Furthermore, while habitat heterogeneity can promote the persistence of species through climatic extremes [77, 78], it can, in the shorter term, reduce the availability of specific habitats required by key species. In these cases, short-term management for higher levels of ecosystem function might hinder resilience.

Measuring and monitoring resilience

Reporting on ecosystem services has focussed on the short-term [6], despite the acknowledgement of long term resilience in earth systems management [10, 92]. Therefore, a challenge is the development of robust, yet cost-effective, indicators of the resilience of ecosystem functions and services (Box 1). To develop indicators, research is needed into current data availability, feasibility of data collection, and validation of indicator metrics. The subsequent implementation of resilience indicators to inform environmental management will also require significant interdisciplinary research with the socio-economic sciences; for example, in order to ascertain target suites of ecosystem functions in different areas and to set socially-acceptable minimum thresholds for functions. An additional challenge will be to identify and balance trade-offs between the resilience of multiple functions. Such research, however, is essential to safeguard the provision of ecosystem functions under the significant environmental perturbations expected within the next century (see Box 2- Outstanding Questions).

Conclusions

In this review we have highlighted mechanisms by which biodiversity, at different hierarchical scales, can influence the resilience of ecosystem functions. We hope that a focus on resilience rather than short-term delivery of ecosystem functions and services, and the consideration of specific underpinning mechanisms, will help to join the research areas of biodiversity-ecosystem function and ecological resilience, and ultimately aid the development of evidence-based, yet flexible, ecosystem management. Further work will also need to draw significantly upon other disciplines in order to develop appropriate indicators for the simultaneous resilience of multiple ecosystem functions.

Box 1- Indicators of short-term ecosystem function flows versus resilience

The development of indicators for ecosystem functions is hampered by a lack of primary data and there is strong reliance on proxy measures such as habitat extent [94, 95]. These proxy measures are currently used to inform on spatial and temporal trends in ecosystem function for the reporting and management of biodiversity change [4-6]. Such models use abiotic variables such as land cover, topography and climate data as explanatory variables in spatially-explicit statistical correlative models [96, 97] or process models [98, 99] in order to predict the provision of ecosystem functions and services. However, because models are parameterised and validated (where undertaken) on the *current* set of environmental conditions they are often only suitable for producing indicators of short-term ecosystem function flows rather than *resilience* under environmental perturbations (Figure 4).

Attempts at developing resilience indicators for ecological functions have been limited mostly to 'early warning systems' [53, 92]. These focus on emergent properties of systems that might precede impending critical state transitions, e.g. 'critical slowing down' [53]. However, these properties only occur before critical transitions in a subset of cases and thus are likely to be poor general predictive indicators of resilience [91]. A focus on emergent properties of systems also ignores the mechanisms that underpin resilience and therefore has limited ability to inform management advice.

Therefore, assessments of the resilience of ecosystem functions and services are currently severely lacking. The development of robust, yet cost-effective, indicators is likely to be dependent on proxy measures that can be both derived from existing monitoring [4] and shown to covary with resilience. For example, an attempt to assess importance and feasibility of resilience indicators based on expert opinion for coral reef systems is provided by McClanahan et al. [100]. Validation of practicable proxy measures is then important to ensure they are reliable.

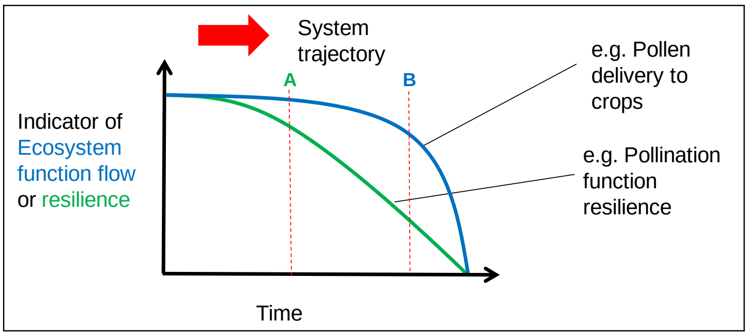

Figure 4 Hypothetical example of indicator values for an ecosystem function flow (pollen delivery to crops) or resilience of that function (pollination under environmental perturbations) as an ecosystem is degraded over time. The thresholds to initiate management action (red dotted lines) differ depending on which indicator is used (A for resilience indicator, B for the ecosystem function flow indicator). Given remedial management takes time to put in place and become effective, unacceptable losses of ecosystem function might occur if ecosystem function flow indicators are solely relied upon. These losses can be costly for society and difficult to reverse.

Box 2- Outstanding questions

The following research questions have particular priority for advancing research into the management of resilient ecosystem functions:

1. Are there thresholds that should be avoided to prevent sudden collapse of ecosystem functions? If so, how quickly are systems moving towards these thresholds and do the thresholds themselves move?

2. How exactly can each of the mechanisms identified in this article and any others be used to inform applied management to enhance resilience of ecosystem functions?

3. How can the relevance and feasibility of these mechanisms be assessed in order to develop robust indicators for the measurement and monitoring of resilience?

4. Given that values people give to ecosystem services are likely to be context-dependent over space and time, how do we decide which services and the underpinning functions are priorities in a given area and what the minimum thresholds are?

5. Given that ecosystem services are the products of both natural capital (i.e. ecosystem functions) and other socioeconomic capitals, what is the relative contribution of resilient ecosystem functions to the maintenance of different ecosystem services over time?

6. How can the measures to promote resilience be justified to when, under stable environmental conditions and in many decision-making relevant time-scales, they lead to apparent redundancy?

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Figure Legends

Figure 1, **Schematic showing varying resilience levels of an ecosystem function (Ψ) to environmental perturbations (red arrows)**. Panel 'a' shows a system with high resistance but slow recovery; panel 'b' shows a system with low resistance but rapid recovery; panel 'c' shows a system with both low resistance and slow recovery. Lack of resilience (vulnerability) could be quantified as the length of time that ecosystem functions are provided below some minimum threshold set by resource managers (this threshold shown with the symbol Ψ_1), or the total deficit of ecosystem function (i.e. the total shaded red area). Note that, in the short-term, mean function is similar in all systems but in the longer term mean function is lower and the extent of functional deficit is higher is the least resilient system (panel 'c').

Figure 2, Different possible relationships between environmental change (ε), time (t) and level of ecosystem function provided (Ψ). Panel 'a' shows three types of environmental change: rapid onset (A), chronic (B) and transitory perturbation (C). Panel 'b' shows ecosystem function might be relatively resistant to increasing levels of environmental change (D), less resistant (E) or demonstrate hysteresis (F). Panel 'c' shows the four qualitatively different outcomes for how ecosystem function varies over time, whether the system is fully resistant to an environmental change (H), shows limited resistance but full recovery (I); or shows limited- (J) or low- resistance (K) with no recovery of function. The horizontal line at Ψ_1 indicates some minimum threshold for ecosystem function that is set by resource managers. In both panels 'a' and 'c', short-term stochasticity about trends is omitted for clarity.

Figure 3, Functional redundancy and effects on resilience of ecosystem functions. Complementary effect trait space occupied by all species in a community can be characterised by an *n*-dimensional hypervolume for continuous traits (main panels a-c), or as discrete functional groups for categorical traits (inset panels a-c). A high density of species spread evenly across complementary trait space (panel a, shown for two of *n* possible traits) leads to higher resistance of ecosystem functions. This is shown in panel d (scenario A) which shows the hypothetical average impact on ecosystem function as species are lost from a community under increasing environmental perturbation. The same number of species less evenly dispersed across complementary effect trait space (i.e. a more 'clumped' distribution, panel b) leads to less resistant ecosystem functions (panel d, scenario B). Similarly, fewer species that are evenly, but thinly, spread across complementary effect trait space (panel c), also leads to less resistant ecosystem functions. In both cases, the communities are said to have lower 'functional redundancy'. The exact rate of loss of ecosystem function will be context dependent (e.g. depending on initial number species, ordering of species extinctions and degree of species clustering in trait space).

Figure 4 Hypothetical example of indicator values for an ecosystem function flow (e.g. estimates of pollen delivery to crops) or resilience of that function (e.g. pollination under environmental perturbations as measured by some combination of the mechanisms highlighted in this paper) as an ecosystem is degraded over time. The thresholds to initiate management action (red dotted lines) differ depending on which indicator is used (A for resilience indicator, B for the ecosystem function flow indicator). Given remedial management takes time to put in place and become effective, unacceptable losses of ecosystem function might occur if ecosystem function flow indicators are solely relied upon. These losses can be costly for society and difficult to reverse.

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Figure 1

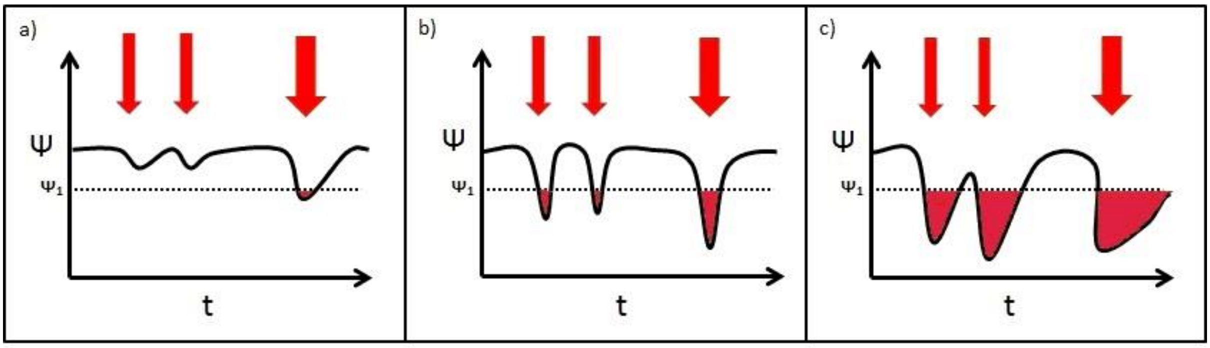


Figure 2

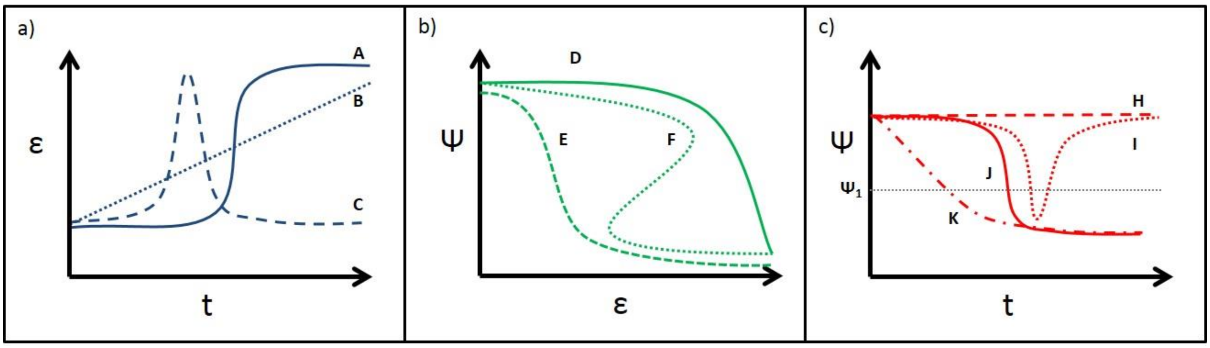
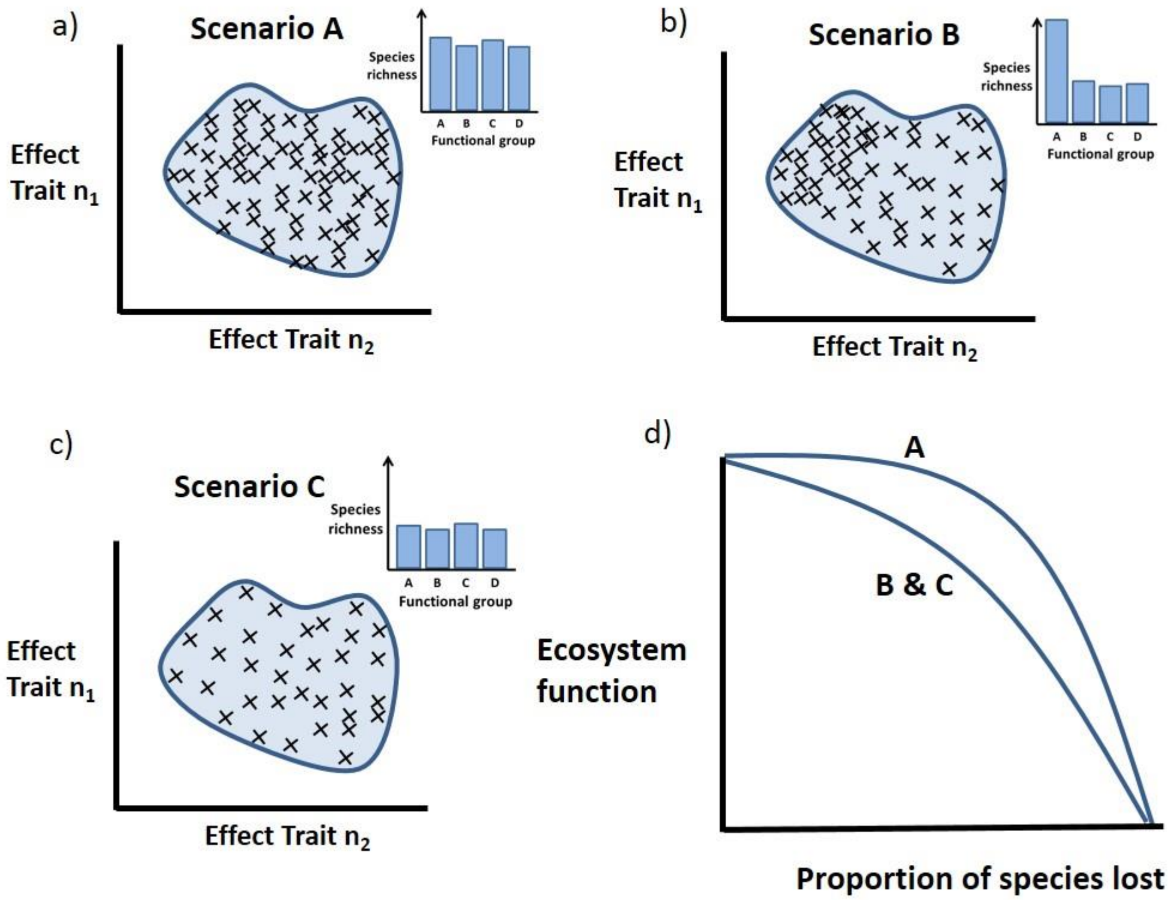
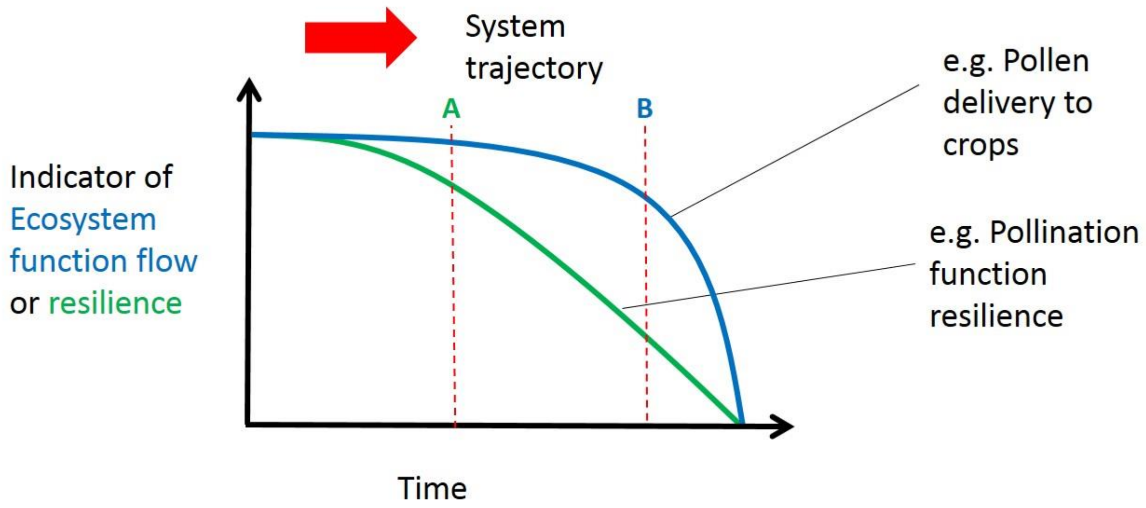


Figure 3



a)
Scenario A
Species richness
A B C D
Functional group
Effect Trait n_1
Effect Trait n_2
b)
Scenario B
Species richness
A B C D
Functional group
Effect Trait n_1
Effect Trait n_2
c)
Scenario C
Species richness
A B C D
Functional group
Effect Trait n_1
Effect Trait n_2
d)
A
B & C
Ecosystem function
Proportion of species lost

Figure 4


System
trajectory
A
B
e.g. Pollen
delivery to
crops
Indicator of
Ecosystem
function flow
or resilience
e.g. Pollination
function
resilience
Time