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# 1 Biodiversity and resilience of ecosystem functions

2

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24

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26

27 **Abstract**

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

39

40

41

## 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.

46 Across the globe, conservation efforts have not managed to alleviate biodiversity loss [1],  
47 and this will ultimately impact many functions delivered by ecosystems [2, 3]. To aid  
48 environmental management in the face of conflicting land use pressures, there is an urgent  
49 need to quantify and predict the spatial and temporal distribution of ecosystem functions  
50 and services [see Glossary; 4, 5, 6]. Progress is being made in this area, but a serious issue is  
51 that monitoring and modelling the delivery of ecosystem functions has been largely based  
52 on the *current* set of environmental conditions (e.g. current climate, land use, habitat  
53 quality). This ignores the need to ensure that essential ecosystem functions will be provided  
54 under a range of environmental perturbations that could occur in the near future (i.e. the  
55 provision of *resilient* ecosystem functions). The objective of this review is to identify the  
56 range of mechanisms which underpin the provision of resilient ecosystem functions to  
57 inform better environmental monitoring and management.

58 A focus on current environmental conditions is problematic because future conditions  
59 might be markedly different from current ones (e.g., increased frequency of extreme  
60 weather events [7] and pollution [8]), and might therefore lead to rapid, non-linear shifts in  
61 ecosystem function provision that are not predicted by current models. Reactive  
62 management might be too slow to avert consequent deficits in function, with impacts for  
63 societal well-being [9]. An analogy of this situation is the difference between monitoring  
64 whether a bridge is either standing (i.e. providing its function) or collapsed, prompting need  
65 for a re-build, as opposed to monitoring and repairing damage to prevent the collapse from  
66 ever happening. In environmental science, attempts have been made to identify this 'safe  
67 operating space' at a global level to ensure that boundaries are not crossed that could lead  
68 to rapid losses in ecosystem functions [10, 11]. However, there is a danger that current

69 regional and local assessments of ecosystem functions and management advice do not  
70 incorporate such risk assessments. This could result in poor management advice and  
71 undervaluation of the importance of biodiversity, because whilst relatively low levels of  
72 biodiversity can be adequate to provide current function [12], higher levels might be needed  
73 to support similar levels of function under environmental change [2, 13-18]. Therefore,  
74 there is a need to identify the characteristics of resilient ecosystem functions and capture  
75 these in both predictive models and management guidance.

76

### 77 **Defining and applying the resilience concept**

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

90 There has been much semantic and theoretical treatment of the resilience concept, but  
91 here we are concerned with identifying metrics for real world applications. An ecological

92 system can be defined by the species composition at any point in time [26] and there is a  
93 rich ecological literature, both theoretical and experimental, that focusses on the stability of  
94 communities [16, 27-29] with potential relevance to resilience. Of course, the species in a  
95 community are essential to the provision of many ecosystem functions which are the  
96 biological foundation of ecosystem services [3]. However, the stability of species  
97 composition itself is *not* a necessary pre-requisite for the resilience of ecosystem functions.  
98 Turnover in species communities might actually be the very thing that allows for resilient  
99 functions. For example, in communities subjected to climatic warming, cold-adapted species  
100 are expected to decline whilst warm-adapted species increase [30]. The decline of cold-  
101 adapted species can be limited through management [31], but in many cases their local loss  
102 might be inevitable [32]. If these species have important functional roles, then ecosystem  
103 functions can suffer unless other species with similar functional roles replace them. In fact,  
104 similar sets of functions might be achieved by very different community structures [33].  
105 Therefore, while the species composition of an ecosystem is typically the target of  
106 conservation, it is ecosystem functions, rather than species composition *per se*, that need to  
107 be resilient, if ecosystem services are to be maintained (Figure 1). In this case the most  
108 relevant definition of resilience is: *the degree to which an ecosystem function can resist or*  
109 *recover rapidly from environmental perturbations, thereby maintaining function above a*  
110 *socially acceptable level*. This can be thought of as the ecosystem-functions related meaning  
111 of resilience [19], or alternatively as the inverse of ecological ‘vulnerability’ [34]. Resilience  
112 in this context is related to the stability of an ecosystem function as defined by its constancy  
113 over time [35], but the approach of using a minimum threshold more explicitly measures  
114 deficits of ecological function that impact upon human well-being [e.g. 14]. Note that here

115 we focus on the resilience of individual ecosystem functions, which might be appropriate for  
116 policy formulation (e.g. pollination resilience), although ecosystem managers will ultimately  
117 want to consider the suite of ecosystem functions supporting essential services in a given  
118 location.

119

### 120 **Threats to ecosystem functions.**

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

134 The impacts of environmental perturbations on ecosystem functions will depend on the  
135 presence of ecosystem characteristics that confer resilience, involving interacting  
136 mechanisms at multiple ecological scales (see next section). These processes govern the  
137 form of functional response to environmental change (Figure 2b), and their rates relative to

138 the environmental change driver will govern the resilience and ultimate temporal trends in  
139 ecosystem function (figure 2c).

140

#### 141 **Mechanisms underpinning resilient ecosystem functions**

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

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

159

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

<b>Species (intraspecific)</b>	<b>Community (interspecific)</b>	<b>Landscape (ecosystem context)</b>
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)	-	-

163

164 *Species-level mechanisms*

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

171

172 **Sensitivity to environmental change:** Species vary in their capacity to persist in the face of  
 173 the environmental perturbations, mediated by a range of behavioural and physiological  
 174 adaptations (response traits) [43]. Such traits show both interspecific and intraspecific  
 175 variation. Individuals with traits conferring reduced sensitivity to environmental change will  
 176 confer higher resistance to ecosystem functions [44]. For example, trees vary in their

177 sensitivity to drought depending on non-structural carbohydrate levels [44], which in turn  
178 might affect the resistance of ecosystem functions that they provide. Broader suites of  
179 traits, such as the plant resource economics spectrum [45], are also likely to explain  
180 variation in sensitivity. Note, however that there might be negative correlations between  
181 sensitivity and intrinsic growth rates, with slow-growing species providing more resistant  
182 ecosystem functions but with lower capacity to recover if perturbation does occur.

183

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

189

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

198

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

209

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

214

#### 215 *Community-level mechanisms*

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

219

220 **Correlation between response and effect traits:** If the extent of species' population decline  
221 following an environmental perturbation (mediated by response traits) is positively

222 correlated with the magnitude of species' effects on an ecosystem function (via effect traits)  
223 then this will lead to less resistant ecosystem functions [39, 54]. This might occur if the same  
224 traits mediate both response and effects, or through indirect associations between different  
225 traits. Correlations and trade-offs are probably a common aspect of traits as a result of  
226 biophysical limitations in structure and function [55]. For example, traits such as body size  
227 have been linked with both sensitivity to environmental change (response traits) and the  
228 maintenance of ecosystem functions (effects traits) such as pollination by bees [56, 57],  
229 nutrient recycling by dung beetles [56] and pest control from predatory invertebrates [58,  
230 59]. In contrast, completely uncorrelated response and effects traits cause higher resistance  
231 in ecosystem function, since responses of species to environmental change are decoupled  
232 from their effects on function [54, 56]. For example, Diaz *et al.* [39] summarise several  
233 studies which show no correlation between decomposability in plants (an effect trait for  
234 nutrient cycling and soil fertility) and persistence in the seedbank (a response trait to  
235 disturbance under agricultural intensification).

236

237 **Functional redundancy:** When multiple species perform similar functions, i.e., species  
238 exhibit some redundancy in their contributions to ecosystem processes, then resistance of  
239 an ecosystem function will be higher if those species also have differing responses to  
240 environmental perturbations [60, 61]. This gives rise to the 'insurance effect' of biodiversity  
241 [62], which is well supported both empirically [14, 15] and theoretically [16, 28].

242 Underpinning mechanisms include a statistical effect, where averaging across independently  
243 fluctuating species populations results in higher resistance ('portfolio effects'), which is  
244 enhanced further where there is negative spatial and/or temporal covariance (asynchrony)

245 between species' population sizes, driven by differing responses to environmental change or  
246 competition [14-16, 28, 62].

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

254

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

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

274

#### 275 *Landscape-level mechanisms*

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

280

281 **Local environmental heterogeneity:** Spatial heterogeneity can enhance the resistance of  
282 ecosystem functions by a) facilitating the persistence of individual species under  
283 environmental perturbations by providing a range of resources and microclimatic refugia  
284 [75-78], and b) increasing overall species richness [79] and, therefore, functional  
285 redundancy. These heterogeneity effects can operate at: the fine-scale, for example,  
286 through vegetation structural diversity [75]; the medium scale, for example, through  
287 topographic diversity [76]; or the larger scale, for example, through diversity of land cover  
288 types [77, 78]. Additionally, environmental heterogeneity across locations (promoting beta  
289 diversity) has been shown to increase stability of ecosystem functions [27].

290

291 **Landscape-level functional connectivity:** Metapopulation theory suggests that populations  
292 in well-connected landscapes will persist better or re-colonise more rapidly following  
293 environmental perturbation (the ‘rescue effect’). Empirical studies confirming this  
294 hypothesis range from mesocosm experiments [80, 81] to landscape-level field studies [82,  
295 83]. This prediction extends to metacommunities and experiments have shown that  
296 connectivity enhances community recovery after local perturbations [81, 84]. In a few cases,  
297 this recovery of community structure through dispersal has been shown to lead to recovery  
298 of ecosystem functions, such as productivity and carbon sequestration, to pre-perturbation  
299 levels; a process termed “spatial insurance” [85, 86]

300

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

307

308 **Potential for alternate stable states:** Alternate stable states are associated with abrupt  
309 shifts in ecosystems, tipping points and hysteresis, all of which challenge traditional  
310 approaches to ecosystem management [17, 89]. Ecosystem states maintain their stability  
311 through internal feedback mechanisms, which confers resistance to ecosystem functions.  
312 However, environmental perturbations can increase the likelihood of regime shift leading to  
313 a fundamental change in the assemblages of species providing functions [17]. Systems can

314 be more susceptible to environmental stochasticity and transient perturbations close to  
315 these critical tipping points leading to sudden changes to a new equilibrium [53]. Some  
316 alternative stable states might be unfavourable in terms of ecosystem functions with return  
317 to previous states possible only through large and costly management interventions  
318 (hysteresis), thereby limiting the recovery capacity of ecosystem function. Alternative states  
319 are documented in a wide variety of ecosystems from local to global scales, although how  
320 stable and persistent these are remains uncertain [89-91].

321

## 322 **Managing for resilience**

### 323 *Applied ecosystem management*

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

335

### 336 *Synergies and trade-offs with short-term performance*

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

350

### 351 *Measuring and monitoring resilience*

352 Reporting on ecosystem services has focussed on the short-term [6], despite the  
353 acknowledgement of long term resilience in earth systems management [10, 92]. Therefore,  
354 a challenge is the development of robust, yet cost-effective, indicators of the resilience of  
355 ecosystem functions and services (Box 1). To develop indicators, research is needed into  
356 current data availability, feasibility of data collection, and validation of indicator metrics.  
357 The subsequent implementation of resilience indicators to inform environmental  
358 management will also require significant interdisciplinary research with the socio-economic  
359 sciences; for example, in order to ascertain target suites of ecosystem functions in different

360 areas and to set socially-acceptable minimum thresholds for functions. An additional  
361 challenge will be to identify and balance trade-offs between the resilience of multiple  
362 functions. Such research, however, is essential to safeguard the provision of ecosystem  
363 functions under the significant environmental perturbations expected within the next  
364 century (see Box 2- Outstanding Questions).

365

### 366 **Conclusions**

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

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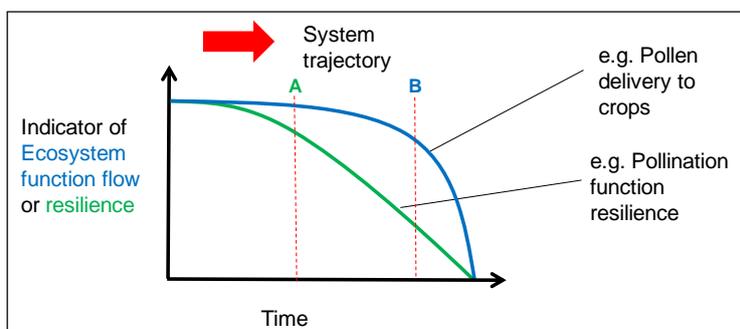
382

### 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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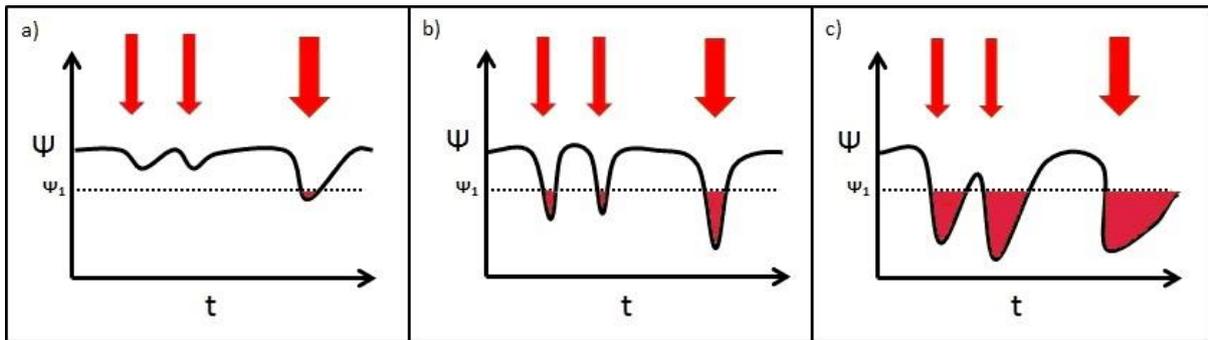
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398 **Acknowledgements**

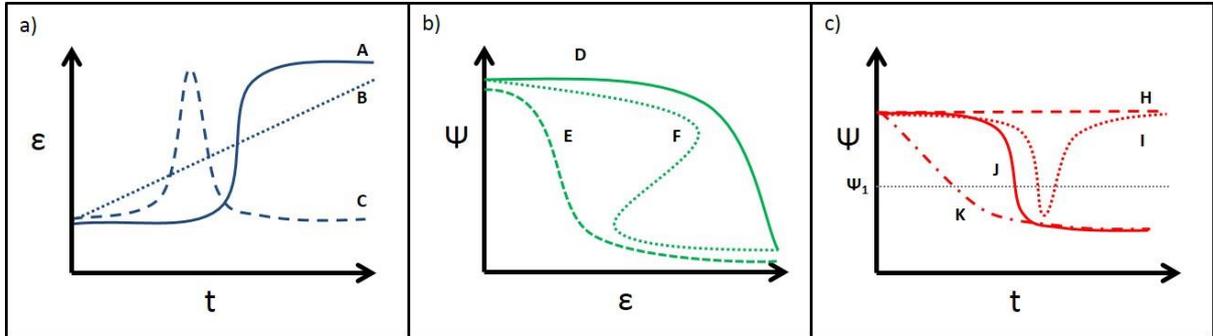
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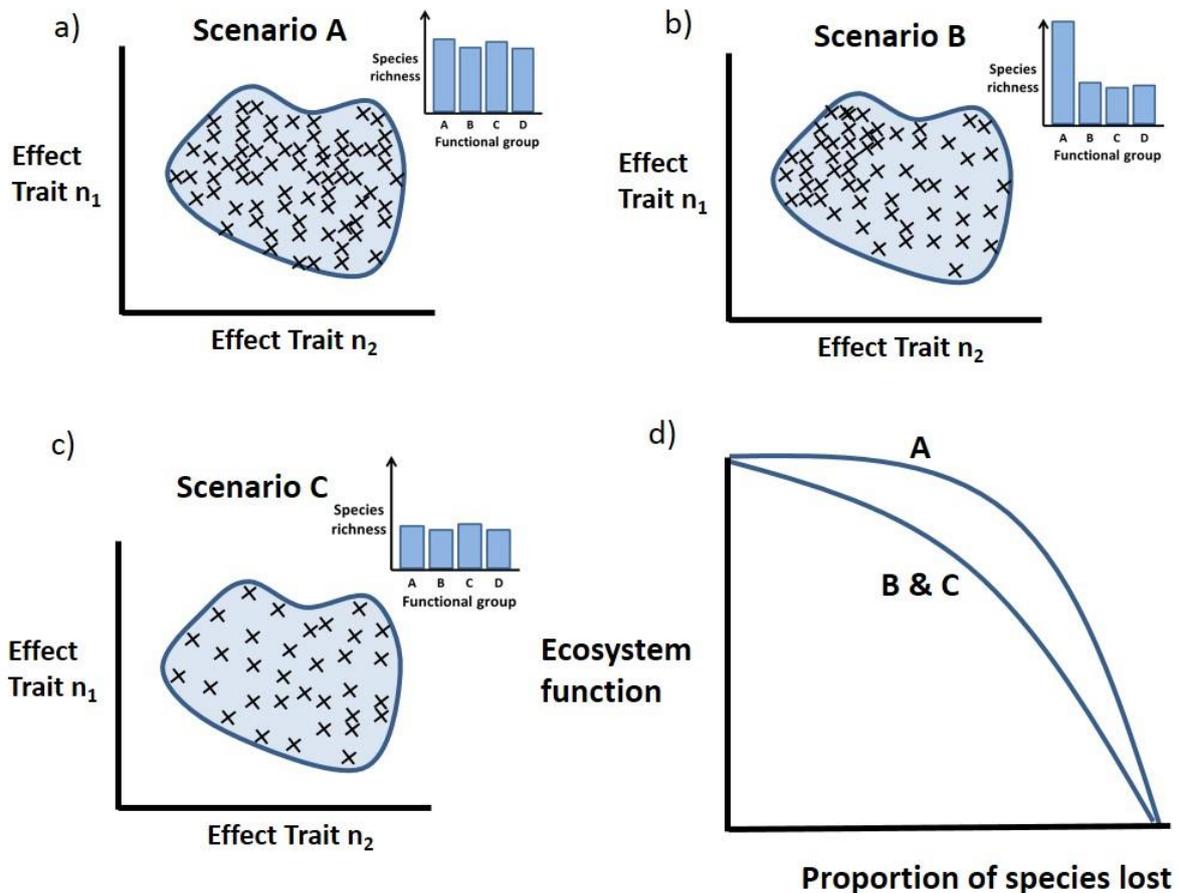
## Figures



**Figure 1, Schematic showing varying resilience levels of an ecosystem function ( $\Psi$ ) 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  $\Psi_1$ ), 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 in the least resilient system (panel 'c').



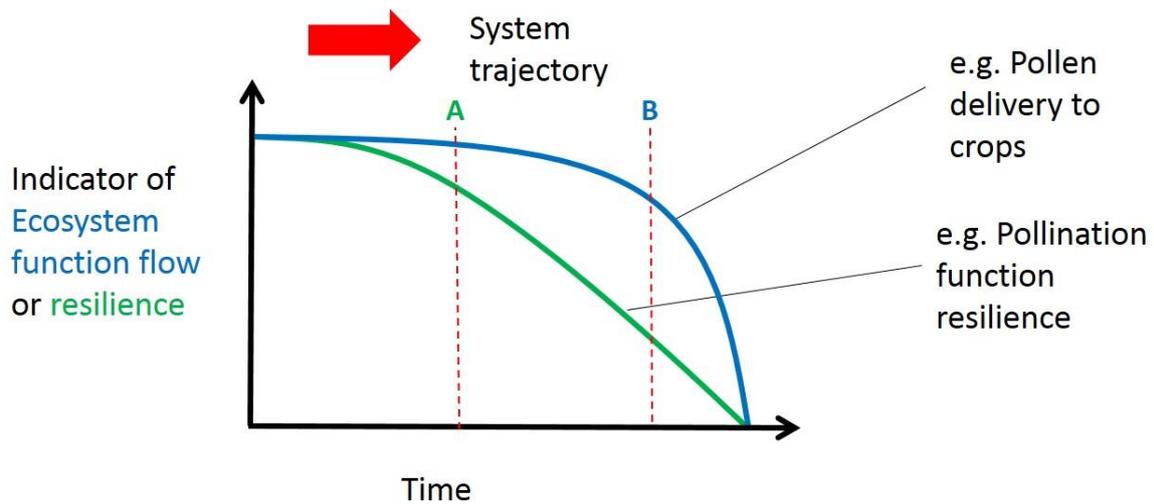
**Figure 2, Different possible relationships between environmental change ( $\epsilon$ ), time ( $t$ ) and level of ecosystem function provided ( $\Psi$ ).** Panel 'a' shows three types of environmental change: rapid onset (A), chronic (B) and transitory perturbation (C). Panel 'b' shows ecosystem function 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  $\Psi_1$  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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