Biodiversity and resilience of ecosystem functions

Article

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Biodiversity and resilience of ecosystem functions

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25

26   **Abstract**

27   Accelerating rates of environmental change and the continued loss of global biodiversity

28   threaten functions and services delivered by ecosystems. Much ecosystem monitoring and

29   management is focused on the provision of ecosystem functions and services under current

30   environmental conditions, yet this could lead to inappropriate management guidance and

31   undervaluation of the importance of biodiversity. The maintenance of ecosystem functions

32   and services under substantial predicted future environmental change, (i.e. their

33   'resilience') is crucial. Here, we identify a range of mechanisms underpinning the resilience

34   of ecosystem functions across three ecological scales. Although potentially less important in

35   the short-term, biodiversity, encompassing variation from within-species to across

36   landscapes, may be crucial for the longer-term resilience of ecosystem functions and the

37   services that they underpin.

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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.

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The importance of resilience

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45   Across the globe, conservation efforts have not managed to alleviate biodiversity loss [1],

46   and this will ultimately impact many functions delivered by ecosystems [2, 3]. To aid

47   environmental management in the face of conflicting land use pressures, there is an urgent

48   need to quantify and predict the spatial and temporal distribution of ecosystem functions

49   and services [see Glossary; 4, 5, 6]. Progress is being made in this area, but a serious issue is

50   that monitoring and modelling the delivery of ecosystem functions has been largely based

51   on the *current* set of environmental conditions (e.g. current climate, land use, habitat

52   quality). This ignores the need to ensure that essential ecosystem functions will be provided

53   under a range of environmental perturbations that could occur in the near future (i.e. the

54   provision of *resilient* ecosystem functions). The objective of this review is to identify the

55   range of mechanisms which underpin the provision of resilient ecosystem functions to

56   inform better environmental monitoring and management.

57   A focus on current environmental conditions is problematic because future conditions

58   might be markedly different from current ones (e.g., increased frequency of extreme

59   weather events [7] and pollution [8]), and might therefore lead to rapid, non-linear shifts in

60   ecosystem function provision that are not predicted by current models. Reactive

61   management might be too slow to avert consequent deficits in function, with impacts for

62   societal well-being [9]. An analogy of this situation is the difference between monitoring

63   whether a bridge is either standing (i.e. providing its function) or collapsed, prompting need

64   for a re-build, as opposed to monitoring and repairing damage to prevent the collapse from

65   ever happening. In environmental science, attempts have been made to identify this 'safe

66   operating space' at a global level to ensure that boundaries are not crossed that could lead

67 to rapid losses in ecosystem functions [10, 11]. However, there is a danger that current

68 regional and local assessments of ecosystem functions and management advice do not

69 incorporate such risk assessments. This could result in poor management advice and

70 undervaluation of the importance of biodiversity, because whilst relatively low levels of

71 biodiversity can be adequate to provide current function [12], higher levels might be needed

72 to support similar levels of function under environmental change [2, 13-18]. Therefore,

73 there is a need to identify the characteristics of resilient ecosystem functions and capture

74 these in both predictive models and management guidance.

75

76 **Defining and applying the resilience concept**

77 Resilience is a concept with numerous definitions in ecological [19], social [20] and other

78 sciences [21]. In ecology, an initial focus on the stability of ecosystem processes and the

79 speed with which they return to an equilibrium state following disturbance [recovery or

80 'engineering resilience'; 22] has gradually been replaced by a broader concept of 'ecological

81 resilience' recognising multiple stable states and the ability for systems to resist regime

82 shifts and maintain functions, potentially through internal reorganisation [i.e. their 'adaptive

83 capacity'; 23]. Recent definitions of resilience encompass aspects of both recovery and

84 resistance, although different mechanisms can underpin these, and in some cases there

85 might be trade-offs between them [24]. However, some mechanisms can promote both

86 resistance and recovery depending on the timeframe in which a system is observed (e.g.

87 very rapid recovery can look like resistance). Therefore, we treat resistance and recovery

88 here as two related complementary aspects of resilience [25].

5

89   There has been much semantic and theoretical treatment of the resilience concept, but

90   here we are concerned with identifying metrics for real world applications. An ecological

91   system can be defined by the species composition at any point in time [26] and there is a

92   rich ecological literature, both theoretical and experimental, that focusses on the stability of

93   communities [16, 27-29] with potential relevance to resilience. Of course, the species in a

94   community are essential to the provision of many ecosystem functions which are the

95   biological foundation of ecosystem services [3]. However, the stability of species

96   composition itself is *not* a necessary pre-requisite for the resilience of ecosystem functions.

97   Turnover in species communities might actually be the very thing that allows for resilient

98   functions. For example, in communities subjected to climatic warming, cold-adapted species

99   are expected to decline whilst warm-adapted species increase [30]. The decline of cold-

100   adapted species can be limited through management [31], but in many cases their local loss

101   might be inevitable [32]. If these species have important functional roles, then ecosystem

102   functions can suffer unless other species with similar functional roles replace them. In fact,

103   similar sets of functions might be achieved by very different community structures [33].

104   Therefore, while the species composition of an ecosystem is typically the target of

105   conservation, it is ecosystem functions, rather than species composition *per se*, that need to

106   be resilient, if ecosystem services are to be maintained (Figure 1). In this case the most

107   relevant definition of resilience is: *the degree to which an ecosystem function can resist or*

108   *recover rapidly from environmental perturbations, thereby maintaining function above a*

109   *socially acceptable level*. This can be thought of as the ecosystem-functions related meaning

110   of resilience [19], or alternatively as the inverse of ecological 'vulnerability' [34]. Resilience

111   in this context is related to the stability of an ecosystem function as defined by its constancy

112 over time [35], but the approach of using a minimum threshold more explicitly measures

113 deficits of ecological function that impact upon human well-being [e.g. 14]. Note that here

114 we focus on the resilience of individual ecosystem functions, which might be appropriate for

115 policy formulation (e.g. pollination resilience), although ecosystem managers will ultimately

116 want to consider the suite of ecosystem functions supporting essential services in a given

117 location.

118

119 **Threats to ecosystem functions.**

120 Environmental change is not unusual (ecosystems have always faced periodic and persistent

121 changes), but anthropogenic activity (e.g. land conversion, carbon emissions, nitrogen cycle

122 disruption, species introductions) is now increasing both the rate and intensity of

123 environmental change to previously unprecedented levels [36-38]. Rapid changes to the

124 abiotic environment might alter local and regional species pools through environmental

125 filtering and disrupting biotic interactions, leading to changes in the suites of traits and

126 interactions that affect ecosystem functioning [39]. The timescales involved tend to be

127 measured with respect to relevant human interventions, i.e. usually over years to decades.

128 The environmental changes may be: rapid onset (e.g. disease), chronic (e.g. habitat loss) or

129 transitory perturbations (e.g. drought; Figure 2a). Some environmental pressures can show

130 complex temporal patterns. For example, climate change includes transitory perturbations

131 due to climatic extremes overlaid on a background of long-term warming, with the potential

132 for rapid onset changes if tipping points are reached [40].

133   The impacts of environmental perturbations on ecosystem functions will depend on the

134 presence of ecosystem characteristics that confer resilience, involving interacting

135   mechanisms at multiple ecological scales (see next section). These processes govern the

136   form of functional response to environmental change (Figure 2b), and their rates relative to

137   the environmental change driver will govern the resilience and ultimate temoral trends in

138   ecosystem function (figure 2c).

139

140   **Mechanisms underpinning resilient ecosystem functions**

141   Previous studies have attempted to identify characteristics of resilient systems from a broad

142   socioeconomic perspective [20, 21], but here we focus on the biological underpinnings of

143   the resilience of ecosystem functions, to inform targeted environmental management

144   practices. The resilience of ecosystem functions to environmental change is likely to be

145   determined by multiple factors acting at various levels of biological organisation; namely,

146   species, communities and landscapes (Table 1). These ecological levels are interconnected

147   so that changes at a particular level can cascade to other levels in the same system. For

148   instance, individual species' responses to environmental change mediate changes in the

149   population abundance and resulting interactions with other species, thus affecting

150   community structure and composition as well as the distribution of effect and response

151   traits [39]. These changes can extend to the level of whole ecosystems, but are mediated

152   the ecosystem context, such as landscape level heterogeneity or habitat connectivity, to

153   determine the resilience of ecosystem function.

154   Here, we provide a new assessment of evidence for the mechanisms underpinning the

155   resilience of ecosystem functions across these ecological levels (Table 1). Our assessment is

156   focussed on promoting general resilience to a range of different primary threats to

157   ecosystem function.

158

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)	-	-

162

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.

170

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

175 confer higher resistance to ecosystem functions [44]. For example, trees vary in their

176 sensitivity to drought depending on non-structural carbohydrate levels [44], which in turn

177 might affect the resistance of ecosystem functions that they provide. Broader suites of

178 traits, such as the plant resource economics spectrum [45], are also likely to explain

179 variation in sensitivity. Note, however that there might be negative correlations between

180 sensitivity and intrinsic growth rates, with slow-growing species providing more resistant

181 ecosystem functions but with lower capacity to recover if perturbation does occur.

182

183 **Intrinsic rate of population increase:** The capacity of species populations to grow rapidly

184 from low numbers is determined by a suite of related characteristics including generation

185 time, mortality and fecundity rates. Species with a high intrinsic rate of increase will recover

186 more quickly from environmental perturbations [46], or show resistance if this population

187 reinforcement occurs during the perturbation.

188

189 **Adaptive phenotypic plasticity**: Individuals have the capacity to respond to environmental

190 changes through flexible behavioural or physiological strategies which promote their

191 survival [43] and resistance of ecosystem functions. For example, thermoregulatory

192 behaviour appears to be an essential survival tool in many ectotherms that operate in

193 temperature conditions close or beyond their physiological limits [47]. Additionally,

194 adaptations might allow flexibility to maximise resource acquisition and growth rates in

195 changed environmental conditions enabling more rapid population recovery and recovery of

196 ecosystem function.

197

198   **Genetic variability:** Higher adaptive genetic variation increases the likelihood that

199   genotypes which are tolerant to a given environmental perturbation will be present in a

200   population [18]. This reduces the population impacts of environmental perturbations [48]

201   and promotes resistance of ecosystem functions [49]. In addition, the persistence of

202   tolerant genotypes locally means that population recovery rates are likely to be higher,

203   leading to enhanced function recovery rates [48, 50]. Adaptive genotypes can be present in

204   standing genetic variation, which is more likely at higher effective population sizes.

205   Alternatively they can arise locally through mutation or through immigration from other

206   populations [18]. It is also becoming increasingly apparent that epigenetic effects can

207   provide heritable variation in ecologically relevant traits [51].

208

209   **Allee effects**: Allee effects make populations more susceptible to environmental

210   perturbations causing crashes from which it is difficult to recover [52, 53]. Certain species

211   are more susceptible to Allee effects through mechanisms such as an inability to find mates,

212   avoid predators or a limited ability to engage in co-operative behaviours.

213

214   *Community-level mechanisms*

215   Beyond the tolerance and adaptability of individuals, the composition and structure of the

216   biological community is of particular importance for the resilience of ecosystem functions.

217   Below we list three key underpinning mechanisms.

218

219   **Correlation between response and effect traits:** If the extent of species' population decline

220   following an environmental perturbation (mediated by response traits) is positively

221 correlated with the magnitude of species' effects on an ecosystem function (via effect traits)

222 then this will lead to less resistant ecosystem functions [39, 54]. This might occur if the same

223 traits mediate both response and effects, or through indirect associations between different

224 traits. Correlations and trade-offs are probably a common aspect of traits as a result of

225 biophysical limitations in structure and function [55]. For example, traits such as body size

226 have been linked with both sensitivity to environmental change (response traits) and the

227 maintenance of ecosystem functions (effects traits) such as pollination by bees [56, 57],

228 nutrient recycling by dung beetles [56] and pest control from predatory invertebrates [58,

229 59]. In contrast, completely uncorrelated response and effects traits cause higher resistance

230 in ecosystem function, since responses of species to environmental change are decoupled

231 from their effects on function [54, 56]. For example, Diaz *et al.* [39] summarise several

232 studies which show no correlation between decomposability in plants (an effect trait for

233 nutrient cycling and soil fertility) and persistence in the seedbank (a response trait to

234 disturbance under agricultural intensification).

235

236 **Functional redundancy:** When multiple species perform similar functions, i.e., species

237 exhibit some redundancy in their contributions to ecosystem processes, then resistance of

238 an ecosystem function will be higher if those species also have differing responses to

239 environmental perturbations [60, 61]. This gives rise to the 'insurance effect' of biodiversity

240 [62], which is well supported both empirically [14, 15] and theoretically [16, 28].

241 Underpinning mechanisms include a statistical effect, where averaging across independently

242 fluctuating species populations results in higher resistance ('portfolio effects'), which is

243 enhanced further where there is negative spatial and/or temporal covariance (asynchrony)

244 between species' population sizes, driven by differing responses to environmental change or

245 competition [14-16, 28, 62].

246 　　The functional roles of species can be mediated by either continuous or categorical

247 traits [e.g. complementary effect traits such as sward- and ground-active predators for pest

248 control; 63]. Resistance is increased by both more species in total (assuming that there is

249 variation in their response traits) and, for a given total number of species, when they are

250 dispersed equally across effect trait space (Figure 3). In reality, intraspecific variation in

251 traits also occurs and, where this is substantial relative to interspecific variation, it might be

252 relevant to consider redundancy and dispersion of *individuals* across effect trait space [64].

253

254 **Network interaction structure:** The majority of the theory and empirical work discussed

255 above concerns organisms occupying a single trophic level, but interactions between species

256 (e.g. predation, parasitism, mutualism) can have large influences on community responses

257 to environmental change [2, 65]. Loss of highly connected species in interaction networks

258 can cause extinction cascades and reduce network stability [66-68]. If these species are

259 particularly sensitive to environmental change then the resistance of the ecosystem

260 functions they provide will be low [69]. Impacts on ecosystem function will be greater when

261 response and effect traits are correlated and patterned in networks along extinction

262 cascades. For example, body size is linked with both extinction risk and the provision of

263 ecosystem functions in taxa including pollinators [56] and pest control agents [70]. In

264 general, highly-connected nested networks dominated by generalised interactions are less

265 susceptible to cascading extinction effects and provide more resistant ecosystem functions,

266 in contrast to networks dominated by strong specialised interactions [71, 72].

267   An important consideration is that the impacts of species loss are likely to lead to

268   changes in the abundances of surviving species, so that the presence or absence of density

269   compensation following species loss can be the key predictor of ecosystem function

270   provision [56, 67, 73]. For example, atmospheric deposition of nitrogen can result in species

271   loss from some plant communities, but density compensation of remaining species might

272   support net primary productivity [74].

273

274   *Landscape-level mechanisms*

275   The intraspecific- and community-level mechanisms described above are influenced by the

276   environmental context of both the local site and wider landscape. The landscape context

277   determines the local and regional species pool and also the abiotic environment which can

278   modify the impacts of environmental perturbations on individuals and communities.

279

280   **Local environmental heterogeneity:** Spatial heterogeneity can enhance the resistance of

281   ecosystem functions by a) facilitating the persistence of individual species under

282   environmental perturbations by providing a range of resources and microclimatic refugia

283   [75-78], and b) increasing overall species richness [79] and, therefore, functional

284   redundancy. These heterogeneity effects can operate at: the fine-scale, for example,

285   through vegetation structural diversity [75]; the medium scale, for example, through

286   topoedaphic diversity [76]; or the larger scale, for example, through diversity of land cover

287   types [77, 78]. Additionally, environmental heterogeneity across locations (promoting beta

288   diversity) has been shown to increase stability of ecosystem functions [27].

289

290 **Landscape-level functional connectivity**: Metapopulation theory suggests that populations

291 in well-connected landscapes will persist better or re-colonise more rapidly following

292 environmental perturbation (the 'rescue effect'). Empirical studies confirming this

293 hypothesis range from mesocosm experiments [80, 81] to landscape-level field studies [82,

294 83]. This prediction extends to metacommunities and experiments have shown that

295 connectivity enhances community recovery after local perturbations [81, 84]. In a few cases,

296 this recovery of community structure through dispersal has been shown to lead to recovery

297 of ecosystem functions, such as productivity and carbon sequestration, to pre-perturbation

298 levels; a process termed "spatial insurance" [85, 86]

299

300 **Area of natural habitat cover at the landscape scale:** In addition to improving functional

301 connectivity for particular species, larger areas of natural or semi-natural habitat tend to

302 provide a greater range and amount of resources, which promotes higher species richness

303 and larger population sizes of each species [87, 88]. This, in turn, is likely to mean greater

304 genetic diversity, and functional redundancy, both of which promote resistance of

305 ecosystem functions [18, 60, 61].

306

307 **Potential for alternate stable states:** Alternate stable states are associated with abrupt

308 shifts in ecosystems, tipping points and hysteresis, all of which challenge traditional

309 approaches to ecosystem management [17, 89]. Ecosystem states maintain their stability

310 through internal feedback mechanisms, which confers resistance to ecosystem functions.

311 However, environmental perturbations can increase the likelihood of regime shift leading to

312 a fundamental change in the assemblages of species providing functions [17]. Systems can

313 be more susceptible to environmental stochasticity and transient perturbations close to

314 these critical tipping points leading to sudden changes to a new equilibrium [53]. Some

315 alternative stable states might be unfavourable in terms of ecosystem functions with return

316 to previous states possible only through large and costly management interventions

317 (hysteresis), thereby limiting the recovery capacity of ecosystem function. Alternative states

318 are documented in a wide variety of ecosystems from local to global scales, although how

319 stable and persistent these are remains uncertain [89-91].

320

321 **Managing for resilience**

322 *Applied ecosystem management*

323 Ecosystem services are beginning to be integrated within major land management

324 programmes (e.g. the EU Common Agricultural Policy, REDD+). However, the measurement,

325 monitoring and direct management of ecosystem function resilience in these programmes is

326 lacking [92]. The ecological theory and empirical evidence discussed above suggest that

327 multiple factors will determine ecosystem resilience. However, we do not yet know which

328 will be the most important in determining resilience in particular functions or ecosystems. It

329 is clear that some factors will be more amenable to management (e.g. population-level

330 genetic variability and landscape structure [18, 31]) than others (e.g. environmental

331 sensitivity of individual species, presence of alternative stable states). Additionally, there

332 can be trade-offs and synergies between resilience and the short-term performance of

333 ecosystem functions [49, 93] .

334

335 *Synergies and trade-offs with short-term performance*

336 In some cases there are synergies between the short-term performance of ecosystem

337 functions and their longer-term resilience , e.g. if species richness is associated with higher

338 levels of function under current conditions due to complementarity [13], and with higher

339 resilience of function due to higher functional redundancy [39, 54]. In these cases,

340 management targeted towards short-term performance will also enhance resilience. In

341 other cases, however, trade-offs can occur. For example, maintaining genetic diversity for

342 resilience of ecosystem functions, may conflict with the aim to produce 'best locally adapted

343 phenotype'[49]. Much intensive agricultural management currently focusses on such low

344 diversity systems that produce high levels of provisioning services but which might have low

345 resilience [93]. Furthermore, while habitat heterogeneity can promote the persistence of

346 species through climatic extremes [77, 78], it can, in the shorter term, reduce the availability

347 of specific habitats required by key species. In these cases, short-term management for

348 higher levels of ecosystem function might hinder resilience.

349

350 *Measuring and monitoring resilience*

351 Reporting on ecosystem services has focussed on the short-term [6], despite the

352 acknowledgement of long term resilience in earth systems management [10, 92]. Therefore,

353 a challenge is the development of robust, yet cost-effective, indicators of the resilience of

354 ecosystem functions and services (Box 1). To develop indicators, research is needed into

355 current data availability, feasibility of data collection, and validation of indicator metrics.

356 The subsequent implementation of resilience indicators to inform environmental

357 management will also require significant interdisciplinary research with the socio-economic

358 sciences; for example, in order to ascertain target suites of ecosystem functions in different

17

359 areas and to set socially-acceptable minimum thresholds for functions. An additional

360 challenge will be to identify and balance trade-offs between the resilience of multiple

361 functions. Such research, however, is essential to safeguard the provision of ecosystem

362 functions under the significant environmental perturbations expected within the next

363 century (see Box 2- Outstanding Questions).

364

365 **Conclusions**

366 In this review we have highlighted mechanisms by which biodiversity, at different

367 hierarchical scales, can influence the resilience of ecosystem functions. We hope that a

368 focus on resilience rather than short-term delivery of ecosystem functions and services, and

369 the consideration of specific underpinning mechanisms, will help to join the research areas

370 of biodiversity-ecosystem function and ecological resilience, and ultimately aid the

371 development of evidence-based, yet flexible, ecosystem management. Further work will

372 also need to draw significantly upon other disciplines in order to develop appropriate

373 indicators for the simultaneous resilience of multiple ecosystem functions.

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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.
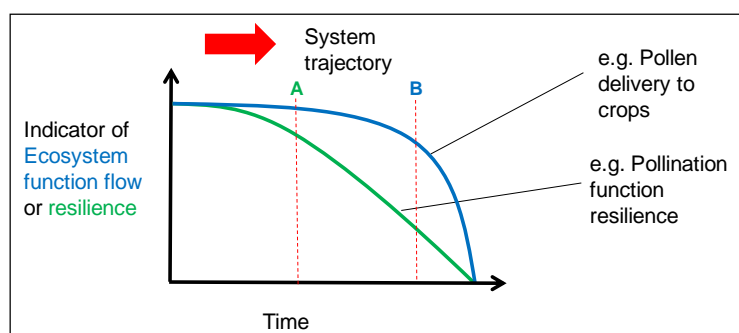

Figure 4 Hypothetical example of indicator values for an ecosystem function flow (pollen delivery to crops) or resilience of that function (pollination under environmental perturbations) as an ecosystem is degraded over time. The thresholds to initiate management action (red dotted lines) differ depending 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.

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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 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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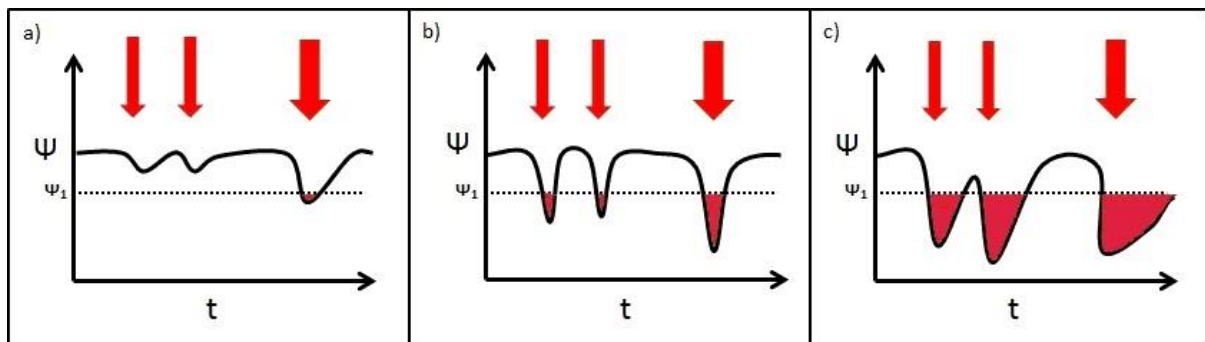
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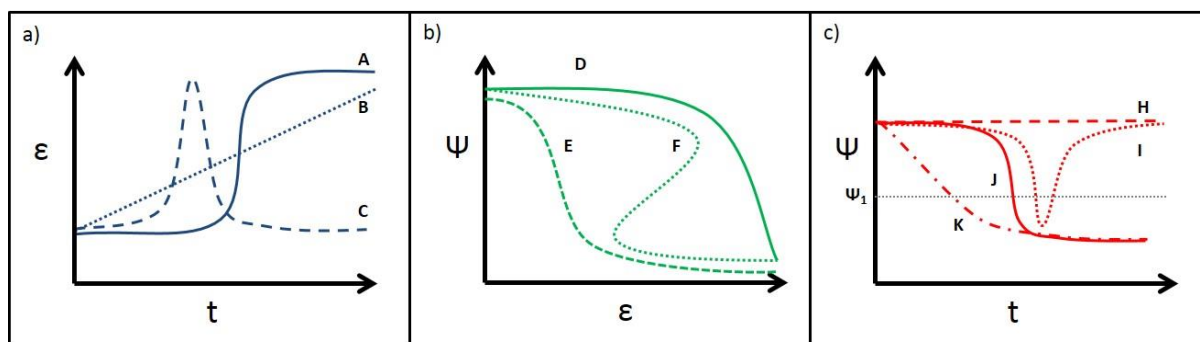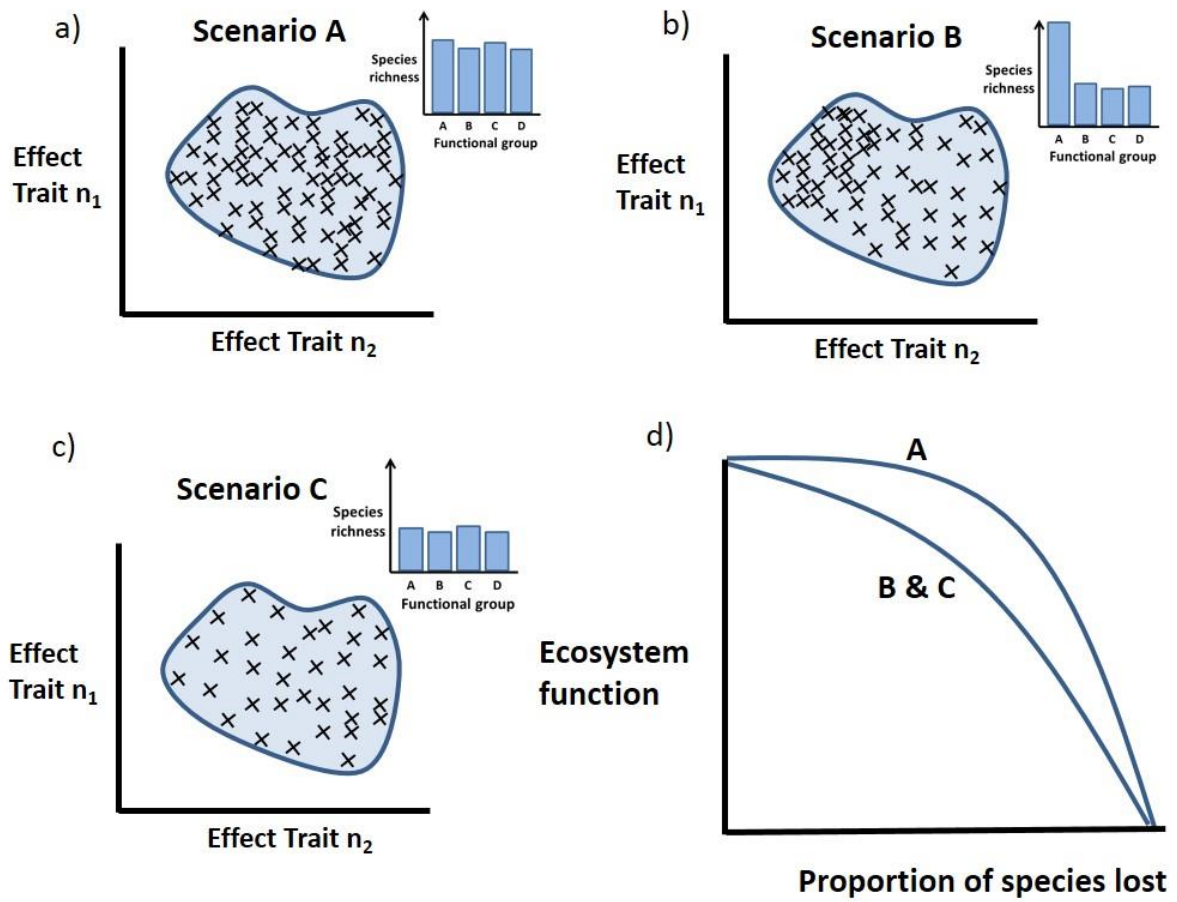
Figure 1

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