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Navigating the complexity of ecological stability

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1   **Abstract**

2   Human actions challenge nature in many ways. Ecological responses are ineluctably complex,

3   demanding measures that describe them succinctly. Collectively, these measures encapsulate the

4   overall "stability" of the system. Many international bodies, including the Intergovernmental

5   Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), broadly aspire to

6   maintain or enhance ecological stability. Such bodies frequently use terms pertaining to stability

7   that lack clear definition. Consequently, we cannot measure them and so they disconnect from a

8   large body of theoretical and empirical understanding. We assess the scientific and policy literature

9   and show that this disconnect is one consequence of an inconsistent and one-dimensional approach

10   that ecologists have taken to both disturbances and stability. This has led to confused

11   communication of the nature of stability and the level of our insight into it. Disturbances and

12   stability are multidimensional. Our understanding of them is not. We have a remarkably poor

13   understanding of the impacts on stability of the characteristics that define many, perhaps all, of the

14   most important elements of global change. We provide recommendations for theoreticians,

15   empiricists and policymakers on how to better integrate the multidimensional nature of ecological

16   stability into their research, policies and actions.

Introduction

17

18   Species live in a web of prey and other resources, mutualists, competitors, predators, diseases,

19   and other enemies (Montoya *et al.* 2006; Bascompte 2009; McCann & Rooney 2009; Kéfi *et al.*

20   2012; Tilman *et al.* 2012). All encounter a profusion of diverse perturbations in their environment,

21   both natural and human-induced, that vary in their spatial extents, periods, durations, frequencies

22   and intensities (Tylianakis *et al.* 2008; Miller *et al.* 2011; Pincebourde *et al.* 2012; MacDougall *et*

23   *al.* 2013). These multifaceted disturbances precipitate a range of responses that can alter the many

24   components of ecological stability and the relationships among them (Donohue *et al.* 2013). This

25   complexity necessitates a multidimensional approach to the measurement of stability. We examine

26   the extent of our understanding of the multidimensional nature of both disturbances and stability.

27   We find that it is highly restricted. Consequently, our ability to maintain the overall stability of

28   ecosystems for different management and policy goals is limited. If ecology is to support and

29   inform robust and successful policy, we must rectify this.

30   At least three scientific communities use terms that map onto various dimensions of

31   ecological stability. Theoreticians, for example, have developed an extensive literature on whether

32   the population dynamics of multi-species systems will be asymptotically stable in the strict

33   mathematical sense (May 1972; Thébault & Fontaine 2010; Allesina & Tang 2012; Rohr *et al.*

34   2014), or resilient, in the sense of a fast return to equilibrium following a small disturbance (Pimm

35   & Lawton 1977; Okuyama & Holland 2008; Suweis *et al.* 2013), and other well-defined measures

36   (see, for example, Pimm 1984; McCann 2000; Ives & Carpenter 2007). Empiricists observe and

37   manipulate natural systems or variously perturb experimental ones to measure ecological responses

38   in constant or naturally changing environments (Tilman *et al.* 2006; O'Gorman & Emmerson 2009;

39   Grman *et al.* 2010; Carpenter *et al.* 2011; de Mazancourt *et al.* 2013; O'Connor & Donohue 2013;

40   Hautier *et al.* 2014). Finally, many international bodies concerned with environmental conservation

41   aspire to maintain, protect, and sustain nature and avoid altering and degrading it, all for informing

42 decision makers and aspiring to enrich people's lives and well-being (Mace 2014; Díaz *et al.* 2015;

43 Lu *et al.* 2015).

44   We explore whether the associated three scientific literatures engage each other in using the

45 same terms and employ the same meanings for them when they do. Generally, they do not. We

46 must remedy this. International bodies need terms that are simple and flexible, but surely not to the

47 point of being meaningless. Theory cannot advance usefully in isolation from tests of it (Scheiner

48 2013), and theory, experiment, and observation must sensibly inform decision makers at all levels.

49 Most importantly, the multidimensional complexity of natural responses to environmental change

50 needs to be recognised by all communities, both separately and collectively.

51   We suggest solutions to help achieve these goals. For theoreticians, we provide suggestions

52 on where to focus future research to incorporate the sort of complexities commonly encountered in

53 natural systems. Empiricists will find useful our summary of the methodologies developed so far to

54 study the different facets of ecological stability and our recommendations for better assessing

55 stability in collaboration with theoreticians and policymakers. Finally, we provide suggestions for

56 environmental policymakers on how to develop and frame objectives and targets that are not only

57 relevant for policy but at the same time facilitate much closer links with the supporting, and

58 evolving, science.

59

60 **The multifaceted nature of disturbances and ecological responses**

61   Disturbances are changes in the biotic or abiotic environment that alter the structure and

62 dynamics of ecosystems. Although they occur at a variety of scales and vary in their direct and

63 indirect effects on species, all disturbances comprise four key properties; their magnitude, their

64 duration, their frequency and how they change over space and time (Sousa 1984; Benedetti-Cecchi

65 2003; García Molinos & Donohue 2011; Pincebourde *et al.* 2012; Tamburello *et al.* 2013). The

66 magnitude of a disturbance is defined by how much the aspect of environmental change departs

67 from its undisturbed state (*i.e. "a measure of the strength of the disturbing force"*; Sousa 1984). A

68   minor storm versus a once in 100-year hurricane is an example of disturbances that vary in

69   magnitude. Their duration refers to a continuum with instantaneous pulses — short, sharp

70   shocks — and sustained presses — constant, long-term change — at the ends of the spectrum (Fig.

71   1a). A discrete pollution event, such as a chemical spill, is a pulse, and the extinction of a species

72   from an ecosystem is a press. Theoreticians focus primarily on one of these two extremes of the

73   duration gradient (Ives & Carpenter 2007). Empiricists sometimes refer to these extremes as acute

74   and chronic disturbances, respectively.

75   Natural disturbance regimes are clearly more complicated than this. Changes in the

76   magnitude, duration and frequency of disturbances over time or in space can combine to give

77   disturbances directionality (Fig. 1b). Directionality measures the trajectory of change, which can be

78   highly dynamic and variable in terms of its mean and variance. Both can elicit distinct ecological

79   responses (Bertocci *et al.* 2005; Benedetti-Cecchi *et al.* 2006; García Molinos & Donohue 2010,

80   2011; Pincebourde *et al.* 2012; Mrowicki *et al.* 2016). Many of the most globally important

81   disturbances in nature are of this kind (Fig. 1c). Therefore, while a focus on pure pulse or press

82   disturbances provides some important insight into mechanisms that can underpin biological

83   responses to disturbances, the relevance of this to predicting responses to real disturbances in the

84   natural world may be limited.

85   While the multifaceted nature of disturbances creates a problem for assessing, understanding,

86   and predicting how ecological systems respond (García Molinos & Donohue, 2010; Mrowicki *et al.*

87   2016), the ecological responses themselves are also complex. Ecological stability is a

88   multidimensional concept that tries to capture the different aspects of the dynamics of the system

89   and its response to perturbations. Pimm (1984) reviewed five components of ecological stability

90   that are in common use. *Asymptotic stability* is a binary measure describing whether a system

91   returns asymptotically to its equilibrium following small disturbances away from it. One measures

92   *variability*, the inverse of stability, as the coefficient of variation of a variable over time or across

93   space. *Persistence* is the length of time a system maintains the same state before it changes in some

94   defined way. It is often used as a measure of the susceptibility of systems to invasion by new

95   species or the loss of native species. *Resistance* is a dimensionless ratio of some system variable

96   measured after, compared to before, some perturbation. *Resilience* is the rate at which a system

97   returns to its equilibrium, often measured as its reciprocal, the return time for the disturbance to

98   decay to some specific fraction of its initial value. Systems with shorter (faster) return times are

99   more resilient than those that recover more slowly. Holling (1973) introduced another definition of

100 resilience that is currently in common use, particularly in policy fora (Walker *et al.* 2004; Hodgson

101 *et al.* 2015). It "*is a measure of the persistence of systems and of their ability to absorb change and*

102 *disturbance and still maintain the same relationships between populations or state variables.*" This

103 definition is multidimensional. It integrates persistence, resistance and the existence of local

104 asymptotic stability at multiple equilibria. It has come to mean whether or not a system returns to

105 its former equilibrium following disturbance or moves to another one. This idea may be expanded

106 further to compare systems in terms of what range of disturbances a system can withstand before

107 being shifted to a new equilibrium (Ives & Carpenter 2007). If there is a limit beyond which a

108 system cannot return directly to its former state, this is termed a *tipping point*.

109   The different components of stability are all based in some way on the composition, function

110 and dynamics of communities. They are unlikely to be independent. Furthermore, the strength and

111 even the nature of relationships among stability components can change when communities are

112 disturbed in different ways (Donohue *et al.* 2013). This complexity has critical implications for our

113 understanding of the impacts of disturbances on ecosystems. It means that restricting our focus to

114 single measures of stability in isolation, or to amalgamated ones such as Holling's resilience, when

115 they are used to reduce the multidimensional complexity of stability to a single dimension and its

116 measurement to a single number, risks significantly underestimating the impacts of perturbations. It

117 also risks incomplete understanding of the mechanisms that underpin the overall stability of

118 ecosystems. The multidimensionality of ecological responses demands explicit multidimensional

119 measurement of both disturbances and stability.

120   The definitions of the various components of stability all come with underlying assumptions

121   about the nature of ecosystems and the disturbances that affect them. Measures of variability, for

122   example, commonly assume the presence of stationary fluctuations [*i.e.* without an underlying

123   directional trend (Tilman *et al.* 2006; Loreau & de Mazancourt 2013)]. The ecological definitions of

124   resilience (Quinlan *et al.* 2016) argue for different worldviews, one where a single equilibrium

125   dominates, the other where two or more equilibrium domains are possible, with tipping points

126   between them. The Aichi Targets (UN 2010) that consider "safe ecological limits" may invoke the

127   latter view, as do related concepts, such as planetary boundaries, that are the subject of considerable

128   debate (Box 1). Other definitions may read into a simpler notion of, for example, preventing

129   overexploitation. Irrespective of definitions, theoretical studies of stability are generally based on

130   the dynamics of communities at, or very close to, some form of equilibrial state. Given the highly

131   dynamic nature of the natural world and the strong directionality of many elements of global

132   change, this limits the applicability of existing theory to the real world and creates significant

133   challenges for empiricists trying to test its predictions.

134

135   **What do ecologists measure?**

136   To understand the differences in what theoreticians and empiricists study, we surveyed three

137   high impact multidisciplinary journals and four leading general ecology journals: *Nature*, *Science*,

138   *PNAS*, *Ecology Letters*, *Ecology*, *Oikos* and *American Naturalist*. Using relevant search terms

139   ("ecolog* stability"; "ecolog* resilience"; "ecolog* resistance"; "stability and diversity"), this

140   yielded 894 papers, 354 of which measured ecological stability in one or more ways. About half of

141   these studies were purely theoretical, the other half empirical. Of the latter, there were nearly equal

142   proportions of experimental and observational studies. Only 4% of papers combined both theory

143   and empirical measurement.

144   In our survey, 93% of theoretical studies and 85% of experimental and observational studies

145   focus on a single facet of stability (Fig. 2a). Some 83% of theoretical studies and 80% of

146 experimental and observational studies also focus on only a single disturbance component (Fig. 2b).

147 This demonstrates a restricted, largely one-dimensional, perspective. It means that we have little

148 understanding of either the multidimensional nature of ecological stability or the correspondence of

149 different components of stability to different types of perturbations.

150 There is also a significant disjoint between theoretical and empirical approaches to, and

151 understanding of, ecological stability. The majority (57%) of theoretical studies focus on

152 asymptotic stability, whereas experimental (61%) and observational (72%) studies concentrate

153 primarily on variability (Fig. 3a). In contrast, asymptotic stability comprises the focus of only 4%

154 of empirical studies, while only 18% of theoretical studies quantified variability. Only a small

155 minority of studies, either theoretical or empirical, examine persistence (10% of studies), resilience

156 (7%) or resistance (7%). Within these latter three measures, there are notable differences.

157 Theoretical studies most often examine persistence, resilience and a particular measure of resistance

158 called robustness – the susceptibility to species extinctions, usually caused by the initial loss of a

159 species (Solé & Montoya 2001; Staniczenko *et al.* 2010). Observational studies emphasise

160 resistance, while experimental studies consider resistance and resilience in equal measure. Our

161 survey identified very few empirical studies of robustness. Additional aspects of stability are

162 potentially addressed in more specialized journals than those scanned in our survey. However, the

163 literature we surveyed came from the general ecological journals most probably read by both

164 theoreticians and empiricists, potentially making the divergence we found in terms and concepts

165 even more significant.

166 We found similar disparities between the focus of theory and empirical research on the

167 different types of disturbance durations and frequencies. The majority (70%) of theoretical studies

168 focus on the effects of single pulse perturbations on stability (Fig. 3b). In contrast, 83% of

169 observational studies examine the effects of combined, multiple pulse disturbances (Fig. 1a),

170 usually in the form of natural environmental fluctuations. Experimental studies prioritise the effects

171 of press and multiple pulse disturbances in broadly equal measure (respectively, 38% and 47%).

172   Only 15% of studies we surveyed incorporate the effects of disturbance magnitude. The problem is

173   more acute when we account for different components of stability. For example, our survey

174   identified no theoretical studies of the effects of disturbance magnitude, pulse or multiple pulse

175   disturbance frequencies on ecological resistance. Nor did we find any experimental or observational

176   studies of the effects of pulse disturbances on asymptotic stability (Fig. S1). In spite of its

177   importance to characterising disturbances in the real world, our survey identified only one study

178   (van Nes & Scheffer 2004) that explored the effects of the directionality of a disturbance on

179   ecological stability.

180   Almost exclusively, just two characteristics of communities provide the basis upon which

181   studies measure ecological stability. Population or community biomass comprises the focus of

182   approximately two-thirds (63%) of studies included in our survey, while almost all of the remaining

183   studies (35%) examine the stability of taxonomic composition in some way (Fig. 3c). This pattern is

184   broadly consistent across both theoretical and empirical studies and across all components of

185   stability, except for persistence, where the majority of studies focus on composition, and

186   robustness, whose definition is constrained to community composition (Fig. S2). We found few

187   (six) studies that measured the resilience of community composition.

188   In spite of the strong policy focus on ensuring the sustained provision of ecosystem services

189   (*e.g.* TEEB 2010; Díaz *et al.* 2015), we found remarkably few empirical or theoretical assessments

190   of the stability of related ecosystem functions or processes. Only 2% of studies in our survey

191   examined the stability of an ecosystem function or process, in spite of their importance to the

192   perceived economic value of ecosystems (Armsworth & Roughgarden 2003). Of those, almost all

193   measured the variability of ecosystem function in time or space. We found only one study (Zavaleta

194   *et al.* 2010) that also examined thresholds for the persistence of multiple functions. Our survey

195   identified no studies of the resilience, asymptotic stability or resistance of ecosystem functions.

196   There is significant bias towards terrestrial ecosystems (52%) among empirical studies of

197   stability, of which most (53%) are from grasslands. Of the remaining studies, 29% are from

198   freshwater ecosystems, while only 16% are from marine systems. Experimental and observational

199   studies are represented approximately equally across all ecosystem types.

200   What are the conclusions we draw from this? Clearly, experimentalists and empiricists can

201   estimate the clearly-defined measures used by theoreticians. The problem is that some things are

202   easy to measure and other things not, a distinction that likely leads to the differences we have noted.

203   The differences are even greater on closer inspection: theory does not always address what

204   empiricists can measure. This is, at least in part, because the mathematics of dynamical systems

205   lacks tools for evaluating quantities of interest to empirical ecologists. Take resilience, for example.

206   Models measuring resilience use the engagingly simple idea of asymptotic stability. They calculate

207   return times over long intervals — when transient changes have decayed — and close to the

208   equilibrium — where one can use linear approximations to the underlying non-linear nature of the

209   system (Pimm 1982). Empiricists, on the other hand, tend to look at short intervals and disturbances

210   far from the equilibrium, where transient effects in the models may be significant (De Vries *et al.*

211   2012; Hoover *et al.* 2014; O'Connor *et al.* 2015). Here, the simplifying mathematics are

212   unavailable, and so are ignored. The models may still provide broadly the right insights, but there is

213   no guarantee that they do. Theoreticians could take the extra step and explore the dynamics of their

214   models over short intervals away from equilibrium, even if only using simulations, to check their

215   generality (*e.g.* Hastings 2004; Ives & Carpenter 2007; Ruokolainen & Fowler 2008). More

216   generally, theoreticians might recognise that certain aspects of their theories are far more likely to

217   be tested — and to be more widely useful — if they addressed metrics that empiricists can more

218   easily measure (Shou *et al.* 2015).

219   A more fundamental problem arises from the lack of exploration of the multidimensional

220   nature of either disturbances or stability. This gap in knowledge limits our ability to understand and

221   predict the effects of disturbances on the overall stability of ecosystems. If the science of ecology is

222   to support and inform robust and successful policy, we should close this gap.

223

224 **The goals of policy and their measurement**

225   Many consequences of human actions on nature are simple and have clearly defined units.

226 For instance, the United Nations Convention on Biological Diversity (CBD) and related

227 conventions sets targets that include the numbers of species and areas of habitat to be protected, and

228 rates of extinction, habitat loss and fragmentation, and overexploitation of fisheries and rangelands

229 to be minimised (UN 1992). Assisting developing countries reduce carbon emissions from

230 deforestation and forest degradation is the simply stated goal of the United Nations REDD

231 (Reducing Emissions from Deforestation and Forest Degradation in Developing Countries)

232 Programme (UN 2008). These may neither be easy to measure in practice nor to manage

233 effectively, but they do not pose conceptual challenges.

234   Much more problematic are associated terms. *Sustainability* is ubiquitous (Bosch *et al.* 2015),

235 and has a large associated literature. For some, it is used in a normative way, that is, as some

236 desired goal or set of goals. Thus, it is part of the mission of the Global Environment Facility

237 (GEF), and about half of the CBD's Aichi Biodiversity Targets for 2010-2020 include the word

238 (UN 2010). IPBES includes conservation and sustainability of ecosystem services to provide long-

239 term human well-being in its conceptual framework (Díaz *et al.* 2015). Responsibilities of the UK

240 Department for Environment, Food and Rural Affairs include sustainable development, which

241 China adopted explicitly as a national strategy in 1996 (Chinese Ministry of Finance *et al.* 2014).

242 Most commercial enterprises now include statements about corporate and environmental

243 sustainability in their mission statements. Normative definitions of sustainability therefore play an

244 important role in policy, and environmental decision makers clearly do not only concern themselves

245 with ecological components of stability. But neither should they ignore them.

246   We defer to the Oxford English Dictionary that defines "sustainable" as "*the quality of being*

247 *sustainable at a certain rate or level*" and environmentally sustainable as "*the degree to which a*

248 *process or enterprise is able to be maintained or continued while avoiding the long-term depletion*

249 *of natural resources*." Following this, we take sustainability (in its non-normative sense) to mean

250 that a particular resource persists, or persists above (or below) some pre-determined level, or is

251 resistant to disturbances. Its translation to ecological concepts is conceptually straightforward.

252   Other terms are less so. For example, the 20 Aichi Targets include: *safe ecological limits*

253 (Targets 4 & 6), *degradation* (Target 5), *function* (Targets 8, 10 & 19), and *integrity* (Target 10)

254 (UN 2010). These terms lack definitions, or have more than one definition, and have no clear units

255 for quantification. This imprecision is unfortunate in itself (Bosch *et al.* 2015; Lu *et al.* 2015). It

256 also denies the integration of the large body of empirical and theoretical literature that deals with

257 broadly similar, but quantifiable, measures of multi-species systems that might provide key

258 insights.

259   Differences among terms used, and in the meanings of common terms (Grimm *et al.* 1992;

260 Grimm & Wissel 1997; Ives & Carpenter 2007; Hodgson *et al.* 2015), are likely a consequence of

261 the different goals of theoretical and empirical ecologists and policymakers and practitioners. They

262 also reflect the fact that ecologists have perhaps less influence on these terms and their use than we

263 might hope. These differences create significant challenges for translating research findings into

264 policy-relevant information, for communication among individuals from different groups, and for

265 dealing with the complexity and multifaceted nature of ecological stability. We now examine the

266 terms used by policymakers and practitioners, then explore the potential for common ground.

267

268 **How do ecologists and policymakers differ in the terms they use?**

269   We surveyed policy targets and mission and vision statements of 42 key international

270 agreements, organisations and agencies (Table 1) that are concerned primarily with the conservation

271 and protection of nature. We searched for terms that are associated positively with stability. The

272 most common terms we found were, by some distance, '*sustain*' and '*sustainability*'. These were

273 present in more than half of the targets and statements examined (Table 2). They occurred almost

274 twice as frequently as the next most common terms, '*conserve*' and '*conservation*'. We identified

275 14 other terms that occurred less frequently across the documents we examined (Table 2). Of all of

276 the terms we identified, only two, '*stabilise*'/'*stable*' and '*resilience*'/'*resilient*', have clear

277 ecological definitions. Unfortunately, their use in the documents implied different meanings to

278 those widely used in ecological theory, relating most strongly to, respectively, variability and

279 resistance.

280   In spite of the widely different terminologies used by ecologists and policymakers and

281 practitioners, all of the terms we identified in policy targets and statements could be associated in

282 some way with at least one, and frequently more than one, component of ecological stability (Table

283 2). In fact, the stability components that associate most strongly with these terms are among the

284 least studied by ecologists (Fig. 3a). For some terms, the link with components of stability was

285 clear, for others less so. For example, to '*constrain impacts*' necessitates increasing the resistance of

286 systems to disturbances. It also implies increasing their resilience (*i.e.* reducing their return times).

287 The fact that the majority of the terms used in policy integrate across different components of

288 ecological stability means that they are also, at least implicitly, multifaceted. '*Sustainable*' is a good

289 example of this. In order to be sustainable, ecosystems must be resistant to disturbances. They must

290 recover quickly from them (*i.e.* have high resilience). This implies that at least some properties (*e.g.*

291 primary production) remain relatively unchanged through time (*i.e.* have high robustness, low

292 variability) even though there may be considerable turnover in other properties (*e.g.* species

293 composition; indeed, it may be the turnover in species composition that results in sustainable

294 primary production).

295   Thus, key terms may lack unambiguous and clear definitions, and are not therefore directly

296 quantifiable. Yet, the widespread use of such holistic terms implies that the multidimensionality of

297 ecological stability is already integrated, even if unconsciously, in the language and targets of

298 policymakers. This observation provides the motivation for closer integration with the science of

299 ecology.

300

301 **Solutions and recommendations**

302   Nature responds to human pressures in complex ways. Conversely, political and governance

303   decisions often demand simplicity (OECD 2001; Harwood & Stokes 2003; Lu *et al.* 2015).

304   Acknowledging this dilemma is a first step towards enhancing the quality of the communication of

305   "stability" at the science-policy interface and within both science and policy. It is incumbent upon

306   ecologists to ensure that this process does not dilute the integrity of the underlying science.

307   The necessary second step involves the definition of terms and their measurement. There is a

308   fundamental need for interdisciplinary discussions about both of these (Box 2). Policymakers have

309   to attach measurable quantities to the terms used in their documents, while scientists must address

310   these concepts directly in their studies. The proliferation of undefined and, indeed, unmeasurable

311   ideals, such as many of the tasks that underpin the recently published United Nations Sustainable

312   Development Goals (SDGs) for the conservation of ecosystems (Goals 14 and 15), hinders progress

313   and is self-defeating. For example, SDG Task 14.2 sets the target that, "*By 2020, (countries will)*

314   *sustainably manage and protect marine and coastal ecosystems and avoid significant adverse*

315   *impacts, including by strengthening their resilience*". This statement is ambiguous to the point of

316   being meaningless. Not a single aspect of this target is measurable. What constitutes "significant"?

317   What does resilience mean in this context? The goals of policy and the terminology used to describe

318   them *always* need to be defined and measurable.

319   Consider two examples from the Aichi Targets that contrast how measureable are their

320   aspirations. First, Aichi Target 11: "*By 2020, at least 17 per cent of terrestrial and inland water,*

321   *and 10 per cent of coastal and marine areas…are conserved through effectively and equitably*

322   *managed, ecologically representative and well connected systems of protected areas*". These goals

323   are explicit and measureable, but those for Aichi Target 6 are not: "*By 2020 all fish and*

324   *invertebrate stocks and aquatic plants are managed and harvested sustainably…so that … fisheries*

325   *have no significant adverse impacts on threatened species and vulnerable ecosystems and the*

326   *impacts of fisheries on stocks, species and ecosystems are within safe ecological limits*". This

327   statement contains three particularly obscure terms that lack clear methods for measurement –

328 *sustainably*, *significant adverse impacts* and *safe ecological limits* – each of which appears to mean

329 two distinct things. As used in this context (see also Table 2), *sustainably* has a compositional

330 aspect – that species present in the system persist – and another related to biomass stability – that

331 variability of biomass at both population and community level is minimised at least to a level that

332 ensures the persistence of species. *Significant adverse impacts* requires that the persistence of both

333 ‘threatened species’ and the functioning of ‘vulnerable ecosystems’ is ensured, while *safe*

334 *ecological limits* requires ensuring the persistence of each of the biomass, composition and

335 functioning of ecosystems, presumably by enhancing their resistance to fishing activities.

336 Removing the obscure terms and replacing them with the clearly defined ones we suggest would

337 make the goal measureable. This would enable closer links with the supporting science and

338 highlight key research needs, which, in turn, make the goal attainable.

339   For their part, scientists need to take a coherent approach to quantifying stability, such as the

340 one we describe here. The field will not advance by publishing more, partly overlapping, definitions

341 of single terms used in isolation within a discipline. We need to employ broadly accepted terms and

342 apply them consistently across different communities. Both theoreticians and empiricists also need

343 to be more explicit about the basis upon which they are measuring stability. Conclusions drawn

344 about the factors that drive biomass resilience, for example, are likely to be very different from

345 those that underpin compositional resilience.

346   The third step is crucial. Both scientists and policymakers need to recognise that the

347 multidimensional nature of environmental change *always* requires a multidimensional assessment

348 of responses. To date, scientists and policymakers alike have tended to assess the response to one

349 driver of change using one aspect of stability or amalgamated concepts such as Holling’s resilience.

350 The hope is that this strategy provides a piece of the jigsaw that, in total, provides insight into the

351 overall complexity of responses. Rather, such simplification blurs the overall picture. For example,

352 increasing temporal variability of algal biomass may indicate transient dynamics in changing lake

353 food-webs (Carpenter *et al.* 2011). It tells us little about any underlying changes in community

354 structure that may be undermining, or indeed enhancing, resistance to different kinds of

355 disturbances. The one-dimensional approach to disturbances and stability means that we

356 underestimate the impacts of perturbations and cannot identify the mechanisms that underpin the

357 overall stability of ecosystem structure or functions. The existence of trade-offs (*i.e.* inverse

358 correlations) between different components of stability exacerbates this situation. Such trade-offs

359 exist in nature (Donohue *et al.* 2013) and there is some theoretical insight into why they occur

360 (Harrison 1979; Loreau 1994; Dai *et al.* 2015). Their existence has profound implications for

361 policymakers and practitioners, necessitating decisions on which aspects of stability to prioritise for

362 different management goals. They also provoke an environmental cost to those decisions, where

363 some aspects of ecological stability are necessarily diminished to enhance others. The lack of

364 exploration of the multidimensional nature of ecological stability means that our ability to *optimise*

365 the overall stability of ecosystems for different management and policy goals is at present

366 extremely limited.

367

368 *What science is needed to support these steps and enhance the efficacy of policy?*

369 We make three recommendations. First, the necessity for improved and mechanistic insight

370 into the multidimensional nature of disturbances and stability requires more realistic theory and

371 experimental designs and an improved ability to integrate across studies from different spatial and

372 temporal scales and different kinds of ecosystem (*e.g.* Peters *et al.* 2011). Even single pulse

373 disturbances (*e.g.*, a chemical spill) often have a legacy (*e.g.*, contamination, loss of rare species)

374 that corresponds to a press disturbance. Pulse and press disturbances likely affect different

375 components of stability in different ways. Likewise, many press disturbances exhibit clear

376 directionality and dynamic variation around the mean, with single extreme events occurring more

377 frequently. For instance, the nature of climate disruption calls for new theory (Ives *et al.* 2010;

378 Stenseth *et al.* 2015) and long-term experiments. These need to consider the incrementally

379 increasing magnitude of, for example, temperature change, and the possibility of including large

380 variability up to extreme climatic events. They must employ stability metrics that do not require

381 strong equilibrium assumptions (*e.g.* fixed point attractors). Moreover, they must be able to

382 evaluate ecosystems in continuous transient dynamics (Fukami & Nakajima 2011). The research of

383 theoretical and empirical ecologists has to include the complex nature of disturbances and stability,

384 and the result of such multidimensional approaches has to inform policymakers.

385   Some existing theoretical approaches may be extended to deal with this range of natural

386 complexity. For example, Floquet theory can be used to explore the stability properties of periodic

387 (cyclical, non-single point equilibrium) systems (*e.g.* Lloyd & Jansen 2004, Klausmeier 2008). This

388 can be developed in a similar way to assess how locally stable, single point equilibria respond to

389 perturbations. Lyapunov exponents can be used to investigate more complex, chaotic intrinsic

390 dynamics in naturally variable systems (Ellner & Turchin 1995). Gao *et al.* (2016) have proposed

391 general methods that can reduce the high dimensionality of multi-species systems to predict the loss

392 of resilience (defined there as the ability to avoid switching from a relatively high to much lower

393 mean value of a focal state variable). In parallel, new theoretical developments are starting to

394 explore links between what empiricists measure (*e.g.* variability) and what theoreticians analyse

395 (*e.g.* asymptotic resilience), showing that some fundamental relationships can be established

396 (Arnoldi et al. 2016). Together, these approaches offer promising new directions for further

397 theoretical research that incorporate the sort of complexities empiricists commonly encounter in

398 their study systems.

399   Second, we need simple, yet scientifically sound, ways to integrate across the multiple

400 dimensions to quantify the overall stability of ecosystems. These methods will need to distil the

401 most important elements of stability and make accurate quantitative measures on each dimension.

402 Only then can we combine them (Fig. 4). These methods also need to be adaptable to the priorities

403 of specific policies. Such adaptation is fundamental to optimising the overall stability of ecosystem

404 structure and/or functioning for different management and policy objectives. Agricultural

405 management, for example, aims to minimise variability of yield production and maximise

406 resistance of biomass to pathogens and insect pests. In contrast, many conservation programs might

407 try to maximise the compositional persistence and resilience of communities (rare species are often

408 the most endangered and they tend to determine the slowest return times of the system). Such semi-

409 quantitative methods of holistic assessment may seem too broad-brush and inaccurate to satisfy

410 many scientists. They may also be too complex for some policymakers. The solution has to be

411 something that sits between the two.

412   Third, we need to evaluate and monitor stability through space and time. Ecologists have

413 experience in doing this for single populations and key functional groups (*e.g.* Ives *et al.* 2008;

414 Carpenter *et al.* 2011) and, more recently, for monitoring changes in the provision of ecosystem

415 goods and services (Tallis *et al.* 2012). Monitoring the dynamic stability of whole networks has

416 largely been the province of economists, among others, with numerous financial stability

417 monitoring programs continuously tracking sources of systemic risk (Adrian *et al.* 2014).

418 Analogous programs for monitoring the dynamic multidimensional stability of whole ecological

419 systems over time and space are essential to help assess the effectiveness of policy and management

420 actions. These programmes are needed to help identify ecosystems whose stability is being

421 compromised in the face of global change.

422

423 **Conclusions**

424   There are policies concerned with the protection of nature that set defined and measurable

425 targets. Aichi Target 5 (UN 2010) constitutes a good exemplar: "*By 2020, the rate of loss of all*

426 *natural habitats, including forests, is (to be) at least halved and where feasible brought close to*

427 *zero*". This statement is clear and unambiguous – progress can be quantified, success or failure

428 evaluated. It exemplifies the only way that policies can effect meaningful change.

429   Such policies are in the minority. Many policy documents describe targets that may appear,

430 on face value, explicit and measurable, yet contain terms that are ambiguous, or have multiple

431 definitions that mean different things to different people. Such targets cannot be connected to

432 measureable ecological processes or properties. Policies aiming to increase "resilience" provide

433 pervasive examples. In fact, the majority of policy documents we surveyed contain goals using

434 terms that lack definition within ecology. Such ambiguity paralyses policy.

435   This incoherence is, at least in part, a consequence of the inconsistent and one-dimensional

436 approach that ecologists have taken to ecological stability. This approach has led to confused

437 communication of the nature of stability and the level of our insight into it. Disturbances and

438 stability are multidimensional. Our understanding of them is not. We have a remarkably poor

439 understanding of the impacts on stability of the characteristics that define many, perhaps all, of the

440 most important elements of global change.

441   The solution requires a range of actions. We need more realistic theory based on measures

442 that are of practical significance and empirically quantifiable. Empiricists need to test this theory at

443 a range of spatial and temporal scales. Policymakers need to use these defined and measurable

444 quantities in their targets. Most importantly, theoreticians, empiricists, policymakers and

445 practitioners each need to incorporate the multidimensional complexity of natural responses to

446 environmental change into their research, policies and actions.

447

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460

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747 **Table 1.** International agreements, organisations and agencies whose policy targets and mission and vision state

748 with ecological stability.

Entity	Stability related term(s) found	Document link
Aichi biodiversity targets (CBD)	'integrity'; 'safe ecological limits'; 'resilience'; 'sustain'; 'conserve'	http://www.cbd.int/sp/targets/
Biodiversity International	'sustain'; 'safeguard'	http://www.bioversityinternational.org/about-us/w
Birdlife International	'sustain'; 'maintain'	http://www.birdlife.org/worldwide/partnership/our
Convention on Biological Diversity	'sustain'; 'conserve'	http://www.cbd.int/convention/articles/default.shtr
Conservation International	'healthy'; 'sustainable'; 'stable'	http://www.conservation.org/about/Pages/default.a
UK Department for Environment, Food & Rural Affairs	'safeguard'	https://www.gov.uk/government/organisations/dep
Diversitas (now rolled into Future Earth)	'secure'; 'conserve'; 'sustain'	http://www.diversitas-international.org/about/miss
Earthwatch	'sustain'	http://eu.earthwatch.org/about/earthwatch-mission
European Environment Agency	'sustainable'	http://www.eea.europa.eu/about-us
European Platform for Biodiversity Research Strategy	'maintain'; 'sustain'; 'conserve'	http://www.epbrs.org
Earth System Science Partnership	'sustainable'	http://www.essp.org
European Union Biodiversity Observation Network	None found	http://www.eubon.eu/show/project_2731/
Food and Agriculture Organisation	'security'; 'sustainable	http://www.fao.org/about/en/
Future Earth	'sustainable'	http://www.futureearth.org
Global Environment Facility	'sustainable'	https://www.thegef.org/gef/whatisgef
GreenPeace	'protect'	http://www.greenpeace.org/international/en/about/
International Association for Landscape Ecology	'altered'	http://www.landscape-ecology.org/index.php?id=1
Intergovernmental platform on biodiversity and ecosystem services	'conserve'; sustain'	http://dx.doi.org/10.1016/j.cosust.2014.11.002
Intergovernmental Panel on Climate Change	None found	http://www.ipcc.ch/organization/organization.shtm
International tropical timber organisation	'sustainable'; 'conservation'	http://www.itto.int/about_itto/
International Union for Conservation of Nature	'conserve'; 'sustain'	http://www.iucn.org
LifeWatch infrastructure for biodiversity and ecosystem research	None found	http://www.lifewatch.eu

Living with Environmental Change	None found	http://www.lwec.org.uk/about
Natural Capital Project	'sustainable'	http://www.naturalcapitalproject.org
Organisation for Economic Co-operation and Development	'sustainable'; 'resilience'	http://www.oecd.org/env/
Rainforest Alliance	'conserve'; 'sustain'; 'safeguard'	http://www.rainforest-alliance.org/about
The Economics of Ecosystems and Biodiversity	None found	http://www.teebweb.org/about/
The Nature Conservancy	'conserve'	http://www.nature.org/about-us/vision-mission/ind
United Nations Reducing Emissions from Deforestation and Forest Degradation	'constrain impacts'	http://www.un-redd.org
United Nations Convention to Combat Desertification	'sustain'; 'secure'	http://www.unccd.int/en/Pages/default.aspx
United Nations Environment Programme	'sustain'	http://www.unep.org/Documents.Multilingual/Def
Kyoto protocol (UNFCCC)	'stabilise'	http://unfccc.int/kyoto_protocol/items/2830.php
United Nations Sustainable Development Goals	'security'; 'sustainable'; 'resilient'; 'conserve'; 'protect'	https://sustainabledevelopment.un.org/post2015/tra
Wetlands International	'resilience'	http://www.wetlands.org/Aboutus/VisionMission/t
World Meteorological Organisation	'safety'	https://www.wmo.int/pages/about/mission_en.htm
World Nature Organisation	'sustainable'	http://www.wno.org/mission
Stern Review on the Economics of Climate Change	None found	http://mudancasclimaticas.cptec.inpe.br/~rmclima/
Worldwatch Institute	'sustainable'	http://www.worldwatch.org/mission
World Wildlife Fund for Nature	'harmony'; 'safeguard'	http://wwf.panda.org/wwf_quick_facts.cfm
York Environment Sustainability Institute	'resilient'; 'maintain'; 'conservation'	http://www.york.ac.uk/media/yesi/downloaddocun
Convention on International Trade in Endangered Species of Wild Fauna and Flora	'survival'	http://www.cites.org/eng/disc/what.php
International Whaling Commission	'conservation'	https://iwc.int/history-and-purpose

750 **Table 2.** Stability-like terms used in policy targets and mission and vision statements of the international agreem

751 highlighted in Table 1, ranked in order of frequency of occurrence, and the components of stability that they ass

752 The use of resistance here incorporates robustness. We assume that the necessity for systems to be asymptoticall

753 limit cycle is implicit in the use of every term.

754

Terms used in policy	Occurrence	Stability component(s) associated most strongly	Other associated stability com
'sustain'/'sustainable'	25/42	Persistence	Resistance, Resilience, Variabili
'conserve'/'conservation'	13/42	Persistence	Resistance, Resilience
'resilience'/'resilient'	5/42	Resistance	Resilience, Persistence
'safeguard'	4/42	Persistence	Resistance
'maintain'	3/42	Persistence	Resistance, Variability
'secure'/'security'	4/42	Persistence	Resistance, Resilience
'stabilise'/'stable'	2/42	Variability	Resistance, Resilience, Persister
'protect'	2/42	Persistence	Resistance
'altered'	1/42	Persistence	Resistance
'constrain impacts'	1/42	Resistance	Resilience
'harmony'	1/42	Variability	
'healthy'	1/42	Resistance	Resilience
'integrity'	1/42	Resistance	Persistence, Resilience
'safety'	1/42	Resistance	Persistence
'survival'	1/42	Persistence	Resistance, Resilience
'safe ecological limits'	1/42	Resistance	Persistence, Resilience, Variabil Multiple locally stable equilibria

755

Figure legends

Fig. 1. Conceptual summary of multifaceted disturbances. Characterisation of pure pulse

and press disturbances (a) that are the focus of most theoretical and experimental studies,

and an intermediate multiple pulse form of disturbance (dotted blue line) that is also

studied frequently, mostly in the form of natural environmental fluctuations in

observational studies. Most disturbances are, however, neither pulse nor press and

instead change in magnitude over time (b), frequently with shifting mean and variance

components. We lack theory and have very limited empirical evidence on the impacts of

these directional aspects of disturbances on ecological stability, yet they represent many

of the most important and widespread aspects of human impacts (c).

Fig. 2. The restricted focus of studies on single components of stability (a) and disturbances

(b). The total number of studies is slightly lower in (b) because some of the studies we

surveyed did not incorporate an explicit disturbance.

Fig. 3. Overview of studies of ecological stability. Number of studies identified by our

survey of the literature that quantified different facets of stability (a), examined the effects

of different components of disturbance on those (b), and that used biomass, taxonomic

composition or ecosystem functioning as a basis for measuring stability (c).

Fig. 4. Integrating across multiple dimensions to quantify overall ecological stability. We

suggest a method that incorporates multiple stability facets and allows for their differential

weighting. This method is based loosely on one developed for the assessment of biodiversity

effects on multiple ecosystem functions (Byrnes *et al.* 2014). A multiple-criteria decision-

making approach would also be suitable here. First, the method identifies which stability

782 facets can be quantified and provides a scoring system for each facet (a). This could be as

783 simple as low, moderate and high, although more sophisticated scoring systems could be

784 developed. It then applies a weighting factor to each score, depending on their perceived

785 relative importance for a given policy or management practice (b). The sum of the weighted

786 scores then corresponds to the stakeholder's value of the stability of the system (c). Even

787 though different facets of stability may be correlated, there is no need to assume this. Trade-

788 offs and synergies among stability metrics can be incorporated, but the method does not

789 assume dependencies.

Box 1: Why the attempt to define planetary boundaries is flawed

790

791   Human actions are changing the biosphere in unprecedented ways. One view is that, given the

792 magnitude and novelty of these impacts, there will be thresholds, beyond which abrupt non-linear

793 change will bring the biosphere to a new and undesirable equilibrium. This view of nature, founded

794 upon Holling's (1973) definition of resilience, explicitly engages policymakers with its invocation

795 of catastrophic tipping points and the conclusion that Earth has already exceeded them. The view is

796 becoming increasingly pervasive in the scientific literature.

797   Certainly, there may be systems that show the tipping points that underpin this worldview.

798 Importantly, there is nothing to suggest they are ubiquitous and so demand their having logical

799 primacy. Nature might work this way sometimes, but there is no compelling argument that it must.

800   In attempting to define global tipping points and, from those, "planetary boundaries",

801 Rockström et al. (2009) have extended this view to circumstances where it is unlikely to operate.

802 We take as an example the variable they deemed already to be outside the planetary boundary

803 arising from our work (Pimm et al. 1995; Pimm et al. 2014): the rate of species extinctions. The

804 metric is simple — a fraction of species going extinct per unit time. The comparison to a natural

805 background rate is also conceptually easy, though there are practical difficulties (De Vos et al.

806 2015). The notion that the current global species extinction rate — about a thousand times higher

807 than background — has exceeded some tipping point where catastrophic ecological changes must

808 follow is problematical in several ways (Mace et al. 2014).

809   First, it is not clear over what spatial and temporal scales extinction rates have exceeded the

810 boundary. For example, how are the locally high rates of plant and animal extinctions on remote

811 Pacific Islands following first contact with Polynesians and later with Europeans supposed to "tip"

812 processes globally or (say) in the Amazon? And over what time period might these catastrophic

813 changes unfold?

814   Subsequent clarifications by Rockström and colleagues (Stockholm Resilience Centre 2012;

815 Steffen et al. 2015) indicate that the proposed 'planetary' boundary for extinctions operates at

816   regional scales, but they are not explicit in defining either the spatial or temporal extents of these

817   regions. This leaves open the vitally important question for policymakers of what scales are most

818   important.

819   Second, there are models of the consequences of losing species and how many more species

820   will be lost consequently at local and regional scales (Pimm 1991). None shows the kind of

821   runaway processes that Rockström and colleagues imagine. Certainly, there is both an extensive

822   theoretical and empirical literature on how species richness (as opposed to its rate of change) affects

823   a variety of ecosystem functions including primary productivity and nutrient cycling (Loreau *et al.*

824   2001; Cardinale *et al.* 2012). This literature shows degradation as species numbers decline

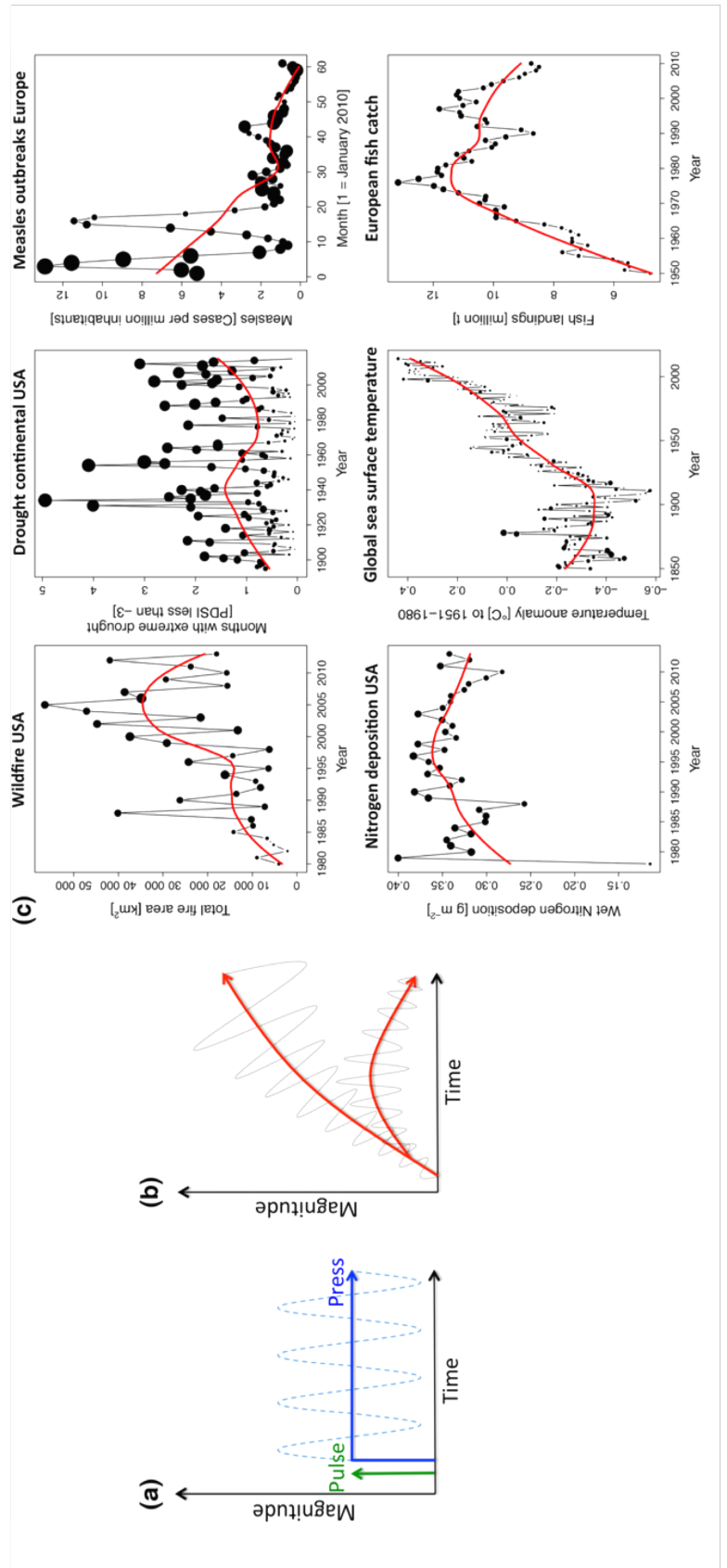825   (Cardinale *et al.* 2011), but no clear thresholds.

Box 2: Learning from experience: biodiversity-ecosystem functioning and service provision

826

827 Even when theoreticians and empiricists converge in what they quantify, there is no guarantee

828 of immediate and successful translation into the policy and management arena. Research on

829 Biodiversity-Ecosystem Functioning (BEF) and Biodiversity-Ecosystem Services (BES)

830 relationships exemplifies this and, as such, we can learn from it.

831 A large body of experiments (> 600 since 1990) developed in close relation with

832 mathematical theory and showed how genetic, species and functional diversity of organisms

833 regulate basic ecological processes – functions – in ecosystems (Cardinale *et al.* 2012). As a result,

834 there is now unequivocal evidence supported by theory that biodiversity loss reduces biomass

835 production, decomposition and recycling of essential nutrients, and the efficiency at which

836 ecosystems capture biological resources. In parallel, a strong policy impulse developed trying to

837 guarantee the provision of ecosystem services to society, now under the umbrella of the recently

838 established Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

839 (IPBES; Díaz *et al.* 2015). Despite the mechanistic understanding of the effects of biodiversity on

840 functioning provided by theoreticians and empiricists, the mechanistic links between biodiversity

841 and ecosystem services are far from being established. This disconnect effectively impairs the

842 distillation of conclusions to inform policy on how biodiversity loss will affect service provisioning

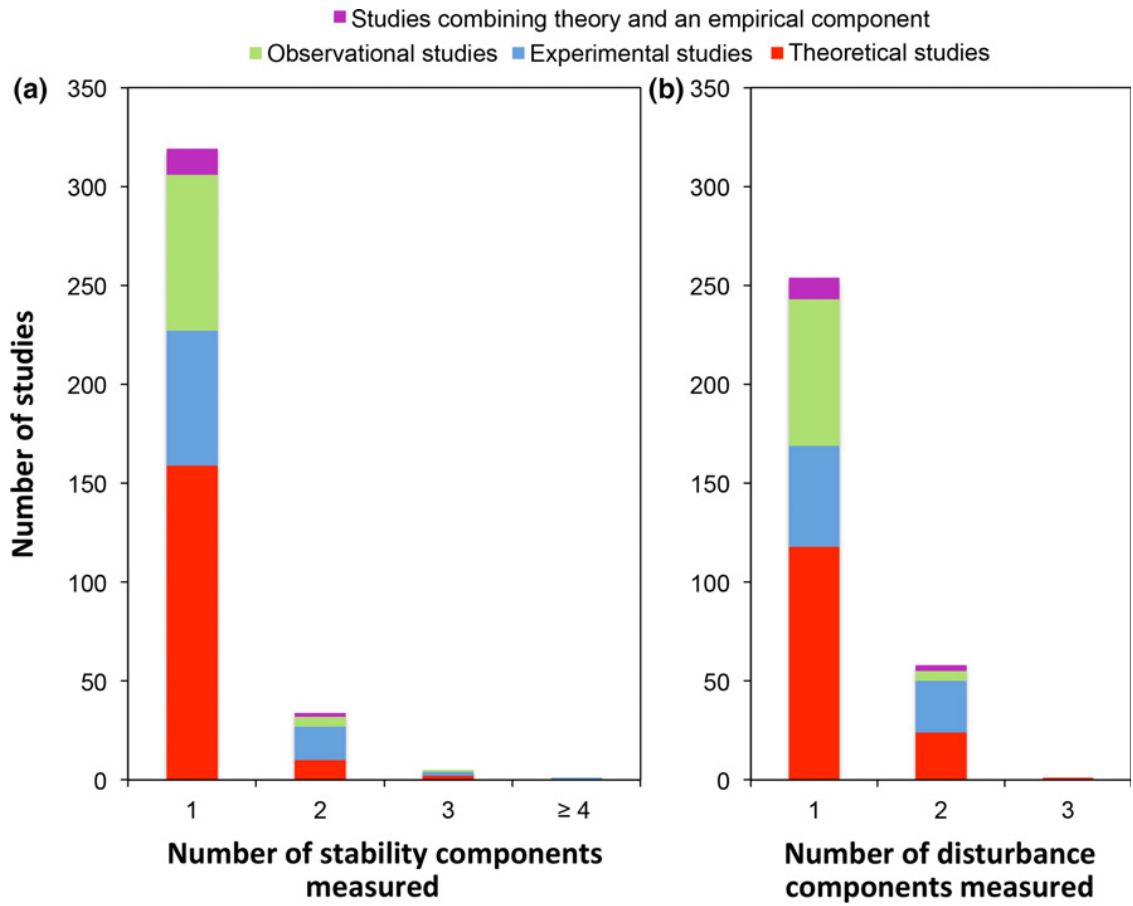843 and regulation and, ultimately, human wellbeing.

844 An example is Payment for Ecosystem Services (PES), where beneficiaries of nature's

845 services pay owners or stewards of ecosystems that generate those services. Naeem *et al.* (2015)

846 suggested recently that few PES studies get the science right, with most projects based on weak

847 scientific foundations. The main reason for this was poor interdisciplinary communication and

848 coordination. The absence of unifying definitions and associated metrics, baseline data, monitoring,

849 recognition of the dynamic nature of ecosystems, and poor interdisciplinary communication and

850 coordination helps to explain this gap. The BEF community measures functions without linking

851 those to known services. The BES community commonly describe services without linking them to

852   their underlying ecological function. A more active communication and convergence on what to

853   measure and at what scale, and how to monitor over space and time is needed (Cardinale *et al.*
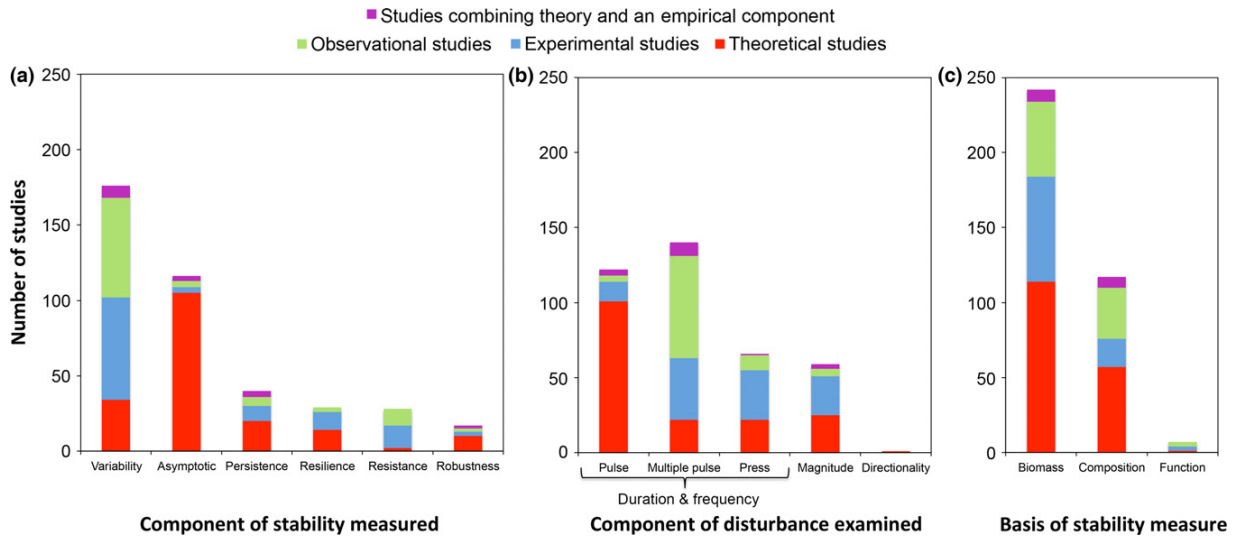
854   2012; Naeem *et al.* 2015).
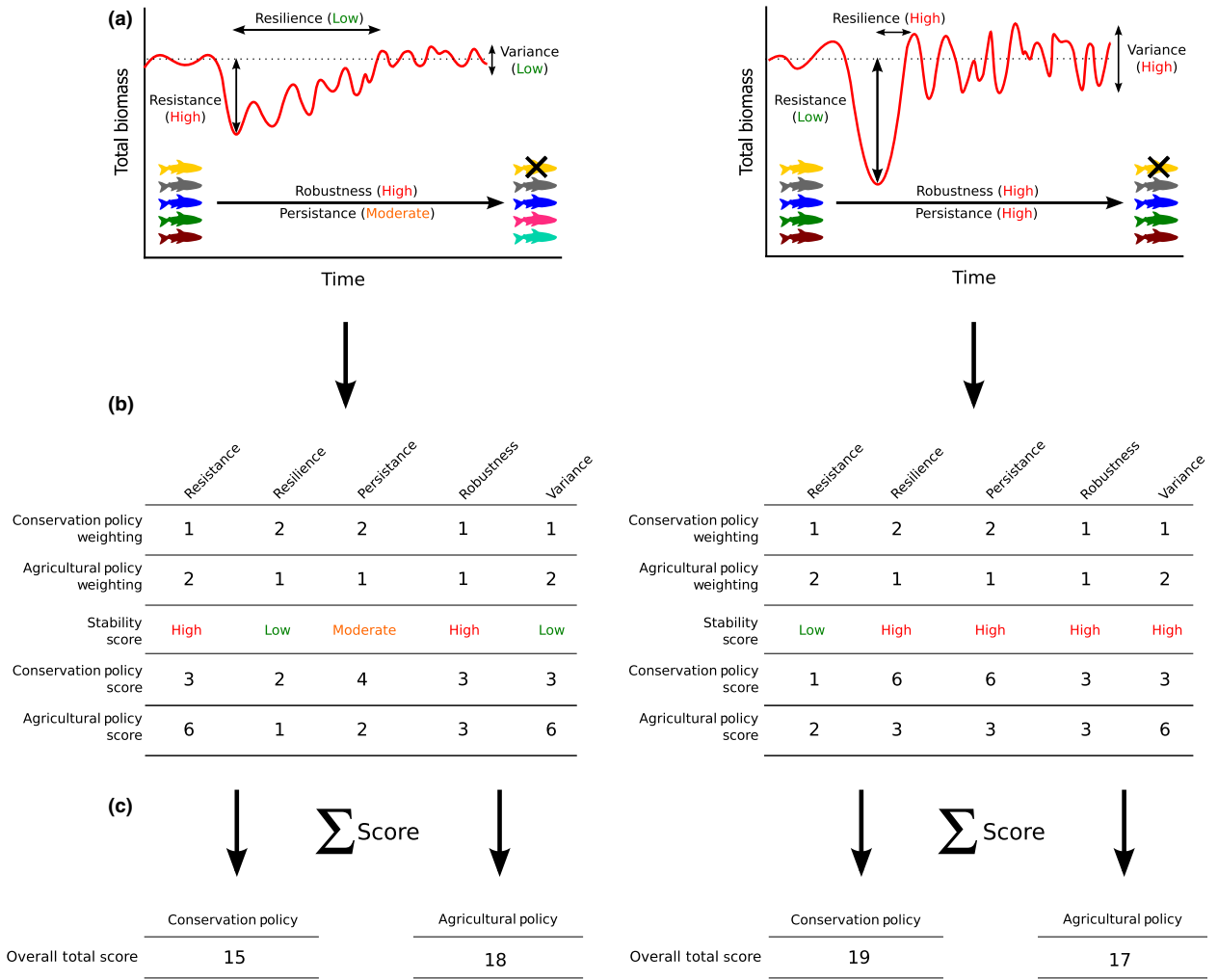
Figure 2

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860

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Figure 3

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(a)

(b)

(c)

$\sum$Score

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Figure 4

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