1   **Refocusing multiple stressor research around the targets and scales of**

2   **ecological impacts**

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26 **Abstract**

27 Ecological communities face a variety of environmental and anthropogenic stressors acting

28 simultaneously. Stressor impacts can combine additively, or can interact, causing synergistic or

29 antagonistic effects. Our knowledge of when and how interactions arise is limited, as most models and

30 experiments only consider the effect of a small number of non-interacting stressors at one or few scales

31 of ecological organisation. This is concerning because it could lead to significant under- or

32 overestimations of threats to biodiversity. Furthermore, stressors have been largely classified by their

33 source, rather than by the mechanisms and ecological scales at which they act (the target). Here we

34 argue, first, that a more nuanced classification of stressors by target and ecological scale can generate

35 valuable new insights and hypotheses about stressor interactions. Second, that the predictability of

36 multiple stressor effects, and consistent patterns in their impacts, can be evaluated by examining the

37 distribution of stressor effects across targets and ecological scales. Third, that a variety of existing

38 mechanistic and statistical modelling tools can play an important role in our framework and advance

39 multiple stressor research.

Introduction

Habitat loss and degradation; pollution; temperature changes and harvesting are some of the biggest stressors impacting ecosystems around the world[1]. This list of stressors has become standard throughout ecology and conservation, from undergraduate teaching to international policy documents, and broadly groups ecosystem threats by where stressors come from – by their source. This is stated explicitly by current programmes for classifying the effects of different stressors, like the Living Planet Index and the IUCN Threats Classification Scheme, which define threats as "synonymous with sources of stress and proximate pressures" [2,3]. Such 'source-based' classifications of stressors are certainly necessary for understanding the economic space in which mitigation can be applied and policy developed. They are effective, for example, at offering descriptions of how frequently taxa are being impacted by a source of stress which, in turn, can help make it clear where management actions should be targeted. However, they provide little insight into the mechanisms and ecological scales through which stressors act, which, in turn, hinders our ability to identify commonalities in how stressors re-shape ecological communities. Thus, source-based schemes alone, while valuable, may be insufficient to manage and mitigate threats to biodiversity and ecosystem function. Consider the example of pollution and temperature change. These stressors are generally regarded as separate under a source-based classification. However, when considering the mechanisms via which they operate, pollution and temperature might be grouped together as stressors that act primarily by altering the metabolism and physiology of individuals. Such a grouping makes it easier to understand how and why these stressors might interact, leading to more accurate estimates of the prevalence, magnitude and direction of their combined effects.

Improving our understanding of potential interactions between stressors is critical because stressors often co-occur in time and space, resulting in more- or less-than additive effects (synergistic or antagonistic interactions respectively) [2-10]. These interactions can occur as interaction chains, where one stressor increases the level of a second stressor, but the per capita impact of the second stressor does not change (such as habitat loss increasing introduced species abundance). Alternatively, they can occur as interaction modifications, where the per capita impact of a stressor changes with the level of a second

66   stressor (such as habitat loss changing the per capita interaction strength between native and introduced

67   species)[11]. Without quantification of stressor interactions, we risk significantly over- or underestimating

68   threats to biodiversity. Despite their importance, current understanding of stressor interactions is

69   limited, with studies generally only considering one or two stressors at a time, often ignoring interactive

70   effects, and considering only one scale of ecological organisation [12-15]. Measuring the magnitude and

71   distribution of multiple stressor effects across ecological scales thus remains a persistent challenge and

72   a necessary objective. Ideally, we need a way to understand how accurately impacts of many different

73   stressors can be forecasted (*predictability*) and the extent to which there are consistent patterns in

74   stressor impacts in and among ecological scales (*consistency*).

75   Here we argue for classifying stressors by the ecological scales at which they have their impacts, rather

76   than by their source. We use this mechanistic classification of stressors to advocate focusing on the

77   distribution of additive *versus* interactive stressor effects across different scales of ecological

78   organisation (from the physiology of individuals, to populations, communities and whole ecosystems).

79   We argue that thinking about this distribution is a common ground for theorists and empiricists alike,

80   and can be used to quantify the predictability and consistency of multiple stressor effects. Given the

81   difficulty of large-scale experimentation with multiple stressors, we outline a set of criteria we believe

82   the next generation of ecological models must satisfy to generate informative predictions for improving

83   knowledge of the impacts of multiple, interacting stressors. Finally, we review several approaches to

84   building such model frameworks, alongside statistical approaches for analysing their outputs and related

85   empirical data.

86   **The ecological scales of environmental change**

87   In nature, there are many different scales at which stressors generate impacts: metabolism/physiology,

88   individuals, populations, communities and ecosystems (Figure 1). At each of these scales, there are a

89   number of *targets* in which we can detect the effects of stressors. Encompassed by a wide range of

90   ecological theory, these targets include processes regulated by enzymes and metabolic rates at the

91   physiological scale; the life history traits of individuals; the abundance or biomass of a population; or

92   the diversity or structure of a community (Figure 1). Targets are thus both the 'access points' through

93   which stressors enter ecological systems, and the response variables used to quantify the additive or

94   interactive impacts of stressors.

95   This idea of defining properties of organisms and scales as the targets of a stressor is most well

96   developed in ecotoxicology by the 'mode of action' concept [16,17] and the source-pressure-pathway-

97   receptor models in cumulative risk assessment [18]. To a lesser extent, the idea has also been discussed in

98   ecology, with Schäfer and Piggot recognising three stressor modes of action[19], Orr *et al.* suggesting that

99   the similarity of stressor modes of action could generate insight into stressor interactions[7], and Boyd

100   and Brown recognising the different scales at which stressor interactions can occur[20]. Other works have

101   also laid an important foundation for the mode of action approach[21-23], though these tend to be system-

102   or scale-specific.

103   There have also been modelling approaches that have provided frameworks to integrate stressors on the

104   scales of individuals, populations or communities. Such approaches often span ecological scales (e.g.

105   individual, population, ecosystem function), but typically do not represent diverse networks of

106   interacting species and predict and evaluate only a limited set of endpoints (targets). As such, they do

107   not provide the opportunity to assess predictability and consistency. For example, de Laender *et al.*[24]

108   provides a model centred on a single trait (resource uptake), focused on competitive interactions and

109   derived from core theory in plant ecology and productivity-diversity and diversity-stability research.

110   While the study uses a multi-species and multi-stressor model, it is essentially focused on a single

111   trophic level and a narrow set of traits. Goussen *et al.*[25] offer another approach that combines Dynamic

112   Energy Budget (DEB) theory with an Individual Based Model. The study allows several traits defined

113   in the DEB to respond to stressors, but focuses on single species. Finally, Liess *et al.*[26] propose a model

114   focused on a single population level trait (mortality) and propose an additive null model of stressor

115   effects on a concentration-response relationship. While this is a useful approach to dealing with

116   toxicants, it is not generalised across multiple traits, stressors and scales.

117   These previous works are highly valuable and lay the foundation from which we argue that only by

118   focusing on targets can we move towards reliably estimating the magnitude and direction of multiple

119   stressor effects at multiple ecological scales. We thus argue for a multi-trait, multi-species, multi-scale

120   approach to detecting interactions and evaluating predictability and consistency. By grounding this in

121   a food web framework we also intrinsically incorporate multiple trophic levels in a community, rather

122   than just one. Such an approach is distinguished from the taxa-, scale- and system- specific attempts

123   above by facilitating generalisation and an evaluation of consistency across systems, stressors and

124   scales.

125   *Visualising the framework*

126   The leftmost column of Figure 1 shows a traditional source-based classification of stressors from the

127   Living Planet Index, where habitat loss and degradation, invasive species, overexploitation, climate

128   change and pollution are treated as separate stressors. Assigning these sources of stress to the ecological

129   scales and targets at which they act reveals several patterns central to understanding the predictability

130   and consistency of multiple simultaneous threats (Figure 1).

131   The first pattern to recognise in Figure 1 is that, because most sources of stress directly impact on many

132   ecological scales[27], the scales and their targets reconcile how disparately defined stressors act via similar

133   mechanisms and on similar targets. This single change in point of view reduces the emphasis on the

134   identity of the stressor and accentuates the long-standing ecological principles by which they have

135   impact. This means that seemingly separate stressors entering at the same scale can be evaluated by the

136   same body of physiological or ecological theory, because the stressors are defined by their targeting of

137   similar properties, traits or biological mechanisms, rather than their source.

138   Relevant bodies of theory include *energy allocation and dynamic energy budgets [13,28], stress physiology*

139   *and ecotoxicology [16] and temperature scaling [29]*, which all underpin our understanding of how sublethal

140   effects of contaminants and temperature alter the abundance of species; *the functional response [30]* which

141   underpins our understanding of how harvesting (e.g. fishing and hunting) impacts directly on the

142 biomass and abundance of species; the concepts of *trait- versus density-mediated effects* [31,32] which link

143 these two collections of theory; *species interactions, trophic indirect effects, trophic cascades and*

144 *stability* [32-34], which underpin our assessment of how perturbations to the numbers of individuals in

145 populations permeate entire communities; *productivity-diversity/stability theory* [35-38], which underpins

146 our understanding of how enrichment of producers or whole trophic levels impacts on community

147 stability and diversity; *disturbance theory, beta-diversity and species distribution theory*, which speaks

148 to the temporal scale that stressors operate on (discrete *versus* continuous stressors events)[39]; and

149 *species distributions and diversity* theory[40-43] which facilitates inference about processes operating on

150 spatial scales.

151 This breadth of theory is fundamental to framing inference about the magnitude, direction and

152 distribution of stressor interactions – the theories define the traits and rationale for when and why

153 interactions arise. As a specific example, consider temperature and sub-lethal concentrations of

154 pesticides. Both stressors ultimately target metabolic processes that mediate the allocation of resources

155 to growth and reproduction. At a lower mechanistic level, temperature is affecting all enzymatic

156 processes while toxins like pesticides are often categorised by reproductive, digestive or neurological

157 modes of action. However, recognising a common ecological scale and a common currency (energy

158 allocation[13]) reveals focused bodies of theory and data on which to frame inference about when and

159 how interactions might arise, their magnitude, and at what scale they may arise[24-26,44,45]. In this case, we

160 might draw on the rich history of resource allocation theory, dynamic energy budget theory and trait-

161 mediated direct and indirect effects theory [46-49] to generate insights that are simply not possible when

162 thinking about stressors in terms of their source alone.

163 The second pattern to recognise in Figure 1 is that most sources of stress act via two pathways: they

164 generate density-mediated effects, that is via directly affecting density and abundance, and trait-

165 mediated effects, that is, 'sub-lethal' effects generating change in the abundance and distribution of

166 organisms via alterations of life history, behavioural traits and traits that define metabolism or

167 physiology. In our framework, trait-mediated effects encompass changes at the individual scale, such

168 as life history and behaviour, and changes at the metabolism/physiology scale, such as enzyme

169 processes, metabolic rate, energe expenditure, immune system status and toxin processing. Thus, for

170 example, oxidate stress is treated as a trait-mediated stressor that affects physiological targets. This link

171 to classic ecological theory synthesises the diversity of ways stressors can exert impacts alone and in

172 interaction. For example, drought can have density-mediated effects via mortality on single populations

173 or multiple populations (the community), or act via trait-mediated effects at the individual or

174 physiological scale, reflecting other outcomes like impaired reproduction, dispersal or diapause. This

175 also highlights that the spatial and temporal scale that a stressor acts on can affect the ecological scale

176 and pathway where the impacts of stressors arise[50]. For example, a discrete extreme heat event might

177 have density mediated effects at the population and community scales, while continuous ongoing

178 warming temperatures might initially have trait-mediated impacts acting at the

179 metabolism/physiological scale.

180 Finally, the third pattern to recognise is that the effects of stressors can manifest at the scales at which

181 they enter an ecological system, but can also drive, via higher-order interactions[51,52], emergent effects

182 at other scales. For example, pesticides can impair the foraging behaviour of bumblebees at the

183 individual scale, which has emergent effects at higher scales by increasing the likelihood of whole-

184 colony failure, impaired pollination services for multiple plant species and, ultimately, the loss of

185 biodiversity [53]. While, in most cases, such emergent effects will occur at higher scales than that where

186 the stressor entered the system, it is also possible for emergent effects to occur at *lower* scales. For

187 example, density effects on populations have been linked to stress hormone levels in surviving

188 individuals with consequences for their behaviour and life history[54-56]. Similarly, the arrival of a

189 specialist invasive species, which enters at the community level by the addition of a new node in the

190 species interaction network, can, for example, have emergent effects on the population-scale targets of

191 a competitor[57].

192 The impact of multiple stressors can be studied and modelled in line with the conceptualisation outlined

193 in Figure 1: embracing the idea that stressors 'enter' ecological systems at different scales, generate

194 responses in targets and, through ecological complexity, also generate responses at lower and higher

195 scales. In other words, grouping stressors by what they do, not what they are, and modelling stressors

196 in terms of the mechanistic targets where they act, not where they have their ultimate effect (e.g.

197 consider modelling climatic variation as a physiological-scale impact that has emergent effects at the

198 population scale, rather than as a term applied directly to a parameter in a population dynamics model[58]).

199 This allows bodies of ecological theory aligned with scales to cut across stressor identities and provide

200 the platform on which to generate hypotheses about how and when stressor interactions arise.

201 Note that Figure 1 represents just one example of a stressor-target mapping, and that other mappings

202 using different stressor classifications are certainly possible. Additionally, the arrows shown in Figure

203 1 represent all possible *a priori* connections between stressors and scales: statistical analyses can

204 provide valuable information about the relative importance/weighting of each of these arrows and thus

205 a version of Figure 1 incorporating weights or effect sizes for each arrow would likely have substantially

206 fewer significant connections and reveal dominant scales at which stressors act. Figure 2 provides a

207 framework for how such effect sizes can be estimated.

208 Below we extend the interpretation of Figure 1 with examples of how this framework can synthesise

209 understanding of multiple stressor effects by ecological scale and the targets at each of these scales.

210 *Metabolism/Physiology and Individual Scales*

211 These two scales are sub-population scales, focusing attention on traits of individuals. At these scales,

212 ecological theory about trait-mediated effects frames the targets in which we detect how multiple

213 stressors interact and expectations about the patterns of these effects. These scales are vital

214 components of a framework for assessing the magnitude and distribution of interactions among

215 stressors because the strength of these sub-lethal effects is well known to be equal to, or stronger than,

216 density-mediated effects in numerous communities[46,59].

217 The metabolism/physiology and individual scales also generate a substantial coalescence among

218 stressors in disparate source categories (Figure 1). For example, theory about thermal performance

9

219   suggests that temperature change as a stressor makes its effects via altering metabolism [29,60-64]. This

220   focus on metabolism and physiology also encompasses, for example, how sub-lethal concentrations of

221   contaminants can alter physiological processes (e.g. neurological, reproductive and digestive modes of

222   action *sensu* ecotoxicological mode of action;[16]). Responses to these types of stress at these two scales

223   can generate emergent responses at the higher ecological scales of individual [63-65], population [66-68], and

224   community [69-72] [73-77]. For example, temperature or sub-lethal concentrations of pesticides have

225   consequences on species' population dynamics by affecting mortality and birth rates; life history traits,

226   such as growth rates; reproductive performance; community structure; and, potentially, diversity [78-84].

227   *Population Scale*

228   Stressors causing mortality of individuals in specific populations are common and assessments of

229   stressor impacts on the targets of this scale (e.g. density and biomass) receive significant attention. This

230   scale also synthesises among stressors from different sources, integrating classical theory about density-

231   independent or density-dependent sources of mortality on populations [85-87]. Description of stressors at

232   this scale are often more specific, with size- or trait-specific targets within a population. They are

233   usually described as a loss function based on modifications of a functional response [86,87] or reflecting

234   specific equipment (e.g. fishing gear[88,89]). The sources of such stressor effects are most often aligned

235   with the 'overexploitation' source (Figure 1; e.g. hunting or fishing [90]), but are not limited to these

236   sources. Lethal concentrations of pollutants[17] and climate change can also directly generate mortality

237   of individuals. As with the individual and metabolism/physiology scales, indirect consequences of

238   effects at this scale emerge at higher ecological scales [91,92]. For example, abundance changes in producer

239   or predator species are drivers of bottom up and top-down effects, such as trophic cascades, which

240   represent changes in relative abundance among multiple species at the community-scale. As

241   exemplified in the fisheries-induced-evolution literature, the effects of harvesting stressors at the

242   population scale can also emerge at the physiological and individual scale on life history traits[88,89,93].

243   *Community scale*

244 The community scale is defined by a species interaction network, which encompasses species diversity

245 and the distribution of interspecific interactions that define community structure. At this scale, targets

246 include network properties like connectance (network complexity), generalism and related descriptors

247 of degree distributions, modularity, as well as other community-scale targets like the body-size

248 distribution.

249 There are at least three ways to frame the effects of multiple stressors at the community scale. The first

250 frame centres on threats that directly target multiple populations within functional groups or trophic

251 levels, but only indirectly the rest of the community. One example is agricultural nitrogen and

252 phosphorus run-off, which can be classed as acting on entire functional groups or trophic levels that

253 encompass multiple species, such as primary producers (autotrophs), or 'basal species', and

254 decomposers [94,95] (though notably nutrient enrichment can be a dominant stressor at a range of scales

255 [96]). While the source of stress can vary, the targets of such effects are the community-scale distributions

256 of carrying capacity, growth rates and reproductive traits across species comprising the trophic levels

257 or functional groups (e.g. physiology stress *sensu* [13]), rather than the values for just one species

258 population. Such impacts are defined by ecological theory about how enrichment, carrying capacity and

259 productivity ('bottom up' effects) generate impacts on biomass across trophic levels [97,98], ultimately

260 influencing dynamics and community structure (defined by a species interaction network) [94,95,99,100]. For

261 example, fertiliser run-off has contributed to enhanced primary production and a consequent depletion

262 of oxygen in bottom waters, resulting in 'dead zones' in over 400 marine systems [101]. Of course, similar

263 patterns can happen via broad-spectrum chemical stressors causing trophic cascades by reducing grazer

264 abundance[45,102,103].

265 The second frame centres on threats that operate across functional groups and trophic levels, such as

266 habitat loss and fragmentation caused by urbanisation, deforestation, certain types of harvesting (e.g.

267 fishing) or bushfires. Again, the sources vary, but the defining feature of such threats is that populations

268 of several species across functional groups and trophic levels are perturbed or removed from a

269 community. While challenging, the body of ecological theory that helps us evaluate multiple threats

270 centres on the decomposition of the contribution of mortality from multiple stressors on multiple species

271 and the turnover components of beta-diversity [40,104].

272 The third frame is invasive species, which are defined by the arrival of a new species in the community.

273 Invasive species thus operate slightly differently to the majority of community-scale stressors, by

274 initially directly acting on species richness and network structure (a new node being added) with a

275 multitude of indirect emergent effects at other scales, such as decreases in a competitor's fruit set [57].

276 *Ecosystem function scale*

277 Our framework does not include direct effects of stressors on the ecosystem function scale. We define

278 this scale narrowly as comprising targets, such as nutrient cycling and energy fluxes, that only respond

279 to stress indirectly as a function of changes to targets at lower scales. For example, deforestation may

280 change ecosystem-function-level nutrient cycling, but this is an emergent property of a reduction in the

281 abundance, or change in relative abundance, of multiple tree species populations.

282 **Evaluating the predictability and consistency of multiple stressor effects**

283 Having outlined this classification of stressors, we now introduce how we can use this classification to

284 understand the *predictability* and *consistency* of interactive effects.

285 Prediction is essential to assess the effects of different threats on ecosystems and to aid policy makers

286 and practitioners in their decision making about ecosystem management [105,106]. A key determinant of

287 the *predictability* of stressor effects is whether stressors combine additively or whether they interact

288 [8,107]. If stressors combine additively, predicting their effects may be comparatively straightforward

289 (though nontrivial in absolute terms), only requiring a relationship between the intensity of individual

290 stressors and their effect size on the target of interest. Conversely, if there are two-, three- or higher-

291 way interactions between stressors, their impacts become substantially more complicated to predict due

292 to high levels of context dependence and whether the interactions can be defined on a linear scale (such

293 as by a linear model). For example, if the effects of temperature on a species' abundance depend on the

294   levels of nitrogen and copper, forecasting is more difficult than if temperature acted independently

295   (additively) of these other stressors. In the context of multiple, simultaneous stressors, we thus define

296   the predictability of a stressor in terms of how many other stressors it interacts with and the statistical

297   order of the interactions: for example, if stressors (S_i) combine additively, this is not an interaction (or

298   is a zero-order interaction; S_1+S_2), and is the most predictable; if two stressors interact, this is a first-

299   order interaction ($S_1 \times S_2$), which is less predictable; if three stressors interact, this is a second-order

300   interaction ($S_1 \times S_2 \times S_3$), and so on. Predictability is thus inversely related to the statistical order of the

301   interactions in which stressors participate.

302   C*onsistency* refers to patterns in how stressor impacts are distributed across ecological scales and

303   among stressors. Below, we introduce three forms of *consistency* in detail. The first is *consistency by*

304   *scale* which refers to whether there are consistent patterns in how stressor impacts are distributed

305   across ecological scales. For example, two-way interactions among multiple stressors may represent

306   the strongest effects at the population scale but additive effects dominate at the community scale. The

307   second form, *consistency by stressor*, relates to whether a stressor has a similar magnitude effect on

308   different targets. For example, temperature having a negative effect of similar magnitude on all targets

309   that it impacts. The third form, *consistency by target*, is where a target is impacted similarly by

310   different stressors: for example, temperature, habitat loss and pollution all having a similar magnitude

311   of impact on species richness.

312

313   *Evaluating predictability and consistency*

314   Evaluating predictability and consistency requires a way to quantify the statistical order (order 0 =

315   additive, order >0 = interactions), magnitude, direction and distribution among scales of stressor

316   impacts. Although the focus of this study is on anthropogenic stress, which are generally considered to

317   have negative impacts, effect sizes allow for both positive and negative impacts of stress (see Figure

318   2). Importantly, because effect sizes act as a common, standardised currency, they allow comparisons

319   to be made among scales, within or between studies, or between theoretical predictions and field

320   observations. Here we have separated the *use* of effect size from the *estimation* of effect size, and we

321   focus on their use first (See Box 1 for estimation).

322   Readers are referred to Figure 2 for a set of caricatures of a three-stressor (temperature, nitrogen,

323   hunting), three ecological scale (population, community, ecosystem) example to complement the

324   following paragraphs. Note that we focus on three scales purely for visual simplicity; in a real analysis,

325   the metabolism/physiology and individual scales are also important to include. We chose these three

326   scales because targets at these scales (e.g. abundance, richness) are the ones most often used in the

327   context of stressor effects on ecosystems and conservation. It is also important to note that, as shown in

328   Figure 1 and discussed above, the targets at the ecosystem scale capture emergent responses rather than

329   being directly impacted by stressors. In Figure 2 we use very broad stressors, such as 'temperature'. In

330   a real use case, it would be necessary to be more specific about the spatial and temporal extent of

331   stressors; for example, clearing a single path of habitat might be distinguished from ongoing habitat

332   fragmentation, or an individual bushfire might be distinguished from a fire regime (discrete *versus*

333   continuous stress, see [50]).

334   *Predictability* can be seen in Figure 2 in cases where effect sizes for additive effects (stressors occurring

335   by themselves in columns 1-3) are greater than (darker) those for interactive effects (columns 4-7). For

336   example, the pattern in Figure 2a suggests that responses at the population scale are more predictable

337   than at community or ecosystem scales because effect sizes are clustered as additive stressor impacts at

338   the population scale, but as interactive stressor impacts at higher ecological scales. This extreme

339   clustering in Figure 2a also defines a strong pattern of *consistency by scale*: all responses at the

340   population scale are additive, all community responses are two-way interactions and all ecosystem

341   responses are three-way interactions. The clustering in Figure 2a also suggests that temperature might

342   be classed as a 'dominant driver' at the population scale, due to its strong effect sizes. Note that this

343   figure is a caricature to demonstrate different forms of consistency and, while Figure 2a shows

344   interactive effects only at the community and ecosystem scales, but not the population scale, in nature

345   interactive effects may occur at all scales[22].

346   In contrast, Figure 2b shows *consistency by stressor*. This is where a column – in this case Nitrogen –

347   has a similar impact across scales and stressor combinations. Regardless of whether Nitrogen is acting

348   additively, or interacting with other stressors, it consistently generates a strong negative effect size

349   across targets and scales (in Figure 2b, all columns involving Nitrogen have a strong negative effect

350   size). Figure 2c shows *consistency by target*, where impacts on a particular row (i.e. a particular target)

351   are similarly strong for all stressors or interactions. For example, the abundance of species 3 is

352   particularly vulnerable to all three stressors combining additively, while species richness is particularly

353   sensitive to two-way interactions between stressors, and ecosystem biomass is not affected by any of

354   the stressors. Figure 2d, in contrast to the others, displays limited evidence of *predictability* or

355   *consistency*; it lacks discernible structure in the distribution of effect sizes either vertically or

356   horizontally.

357   We believe that thinking about the distribution, magnitude and direction of stressor impacts on targets

358   in this way will enable important inferences to be made about the predictability and consistency of

359   multiple stressor effects and interactions, that are relevant to both basic science and applied

360   management. For example, if a stressor is responsible for strong interactions at multiple scales

361   (consistency by stressor; e.g. Nitrogen in Figure 2b), this consistency helps to prioritise and target the

362   allocation of scarce resources to mitigate impacts by focusing on this stressor. Alternatively, if one

363   target, such as the abundance of a particular species, is consistently affected by multiple stressors

364   (consistency by target; e.g. Species 1 or 3 in Figure 2c), then conservation action may be directed at

365   that species.

366   *Absolute Predictability and Consistency*

367   By definition, predictability and consistency may vary with the number and identity of stressors

368   considered. This means that determining an 'absolute' value of the predictability or consistency of

369 stressors would require a study that encompasses all main sources of ecosystem stress, such as the LPI

370 sources in Figure 1. This is particularly feasible in a modelling context. Alternatively, synthesising

371 across studies with different combinations of stressors can also lead to absolute conclusions about

372 predictability and consistency. For example, if stressors A and B are found to interact across many

373 studies, each of which considers a different set of stressors alongside A and B, then this could be

374 evidence of an 'absolute' interaction between A and B, and thus an 'absolute' lower level of

375 predictability than if the stressors combined additively. Similarly, if a stressor, A, is shown to have a

376 consistent negative impact on a particular target across different studies, each evaluating different sets

377 of stressors, this could also be evidence of 'absolute' consistency. If the different studies consider the

378 same sets of stressors, then results are comparable and this can be useful to establish consensus across

379 space and time.

380 Importantly, determining 'absolute' predictability or consistency may not always be an appropriate aim:

381 all stressors do not co-occur in all places at all times, and thus, in the context of managing a particular

382 site for conservation, it may be more useful to understand predictability or consistency *in situ*, by just

383 considering the set of stressors occurring at a particular site. Moreover, it is valuable in its own right to

384 understand the context dependence of predictability and consistency. For example, are particular

385 stressors always hard to predict, or only in the presence of other particular stressors? Or, does a

386 particular stressor consistently generate negative impacts on a target, or does this only happen when a

387 certain set of stressors are present? Again, answering questions like these can generate essential insights

388 for conservation and resource management under environmental change.

389 **Simulation models for studying multiple stressor effects**

390 The framework shown in the first section (Figure 1) outlines conceptually how a modelling approach

391 for evaluating the impacts of multiple simultaneous stressors could work: stressors enter the system at

392 a range of ecological scales, with emergent effects on targets at a range of scales. Here, we build on this

393 framework and propose seven criteria (Figure 3; central box) that simulation models must satisfy to be

394 able to represent stressors and biology in this way. These criteria are motivated by a recent specification

395   of several critical attributes for predictive models [108] and more general guidance about modelling

396   ecological communities that can be useful for multiple stressor research [109]. As a point of reference, we

397   also outline in Figure 3 the extent to which several current modelling tools meet our criteria.

398

399   Models that meet the seven criteria are the platform for generating robust, simulated data for improving

400   knowledge of the impacts of multiple, interacting stressors (though they must also be linked to empirical

401   data and experiments, see Box 2). The seven criteria are specifically associated with modelling that

402   generates times series of biomass or abundance for multiple individuals or species who are embedded

403   in some representation of a community. This means that the simulated data can be analysed to produce

404   effect sizes that populate the statistical and graphical framework presented in Figure 2; thus, the

405   simulated data are central to generating theory about predictability and consistency. Ultimately, the

406   predictability and consistency framework detailed by Figure 2 emerges from statistical analysis of

407   simulated time series produced by a model (or empirical data). Models can be parameterised, for

408   example, based on allometries and known environment response curves (such as temperature), and then

409   used in numerical, fully-factorial, *in silico* experiments about effects of multiple simultaneous stressors

410   [13,70,71,110]. While the Figure 2 framework can be used with either empirical or simulated data, the

411   difficulty of large-scale empirical experimentation with multiple stressors (e.g. combinatorial explosion

412   of stressor combinations and difficulty in detecting biotic interactions) means that simulation models

413   play a key role in improving understanding, generalisations and developing theory.

414

415   A common feature of all models in Figure 3, is that they meet criterion 1, which encompasses the ability

416   of stressors to impact targets at different ecological scales (Figure 3, 'access' row in the table). This is

417   a particularly important feature because quite often stressors have been modelled generically, acting at

418   scales that are different to how they may actually enter ecosystems. For example, environmental

419   perturbations might be modelled by adding stochastic noise terms to population dynamics equations,

420   even if these perturbations are meant to represent stressors that primarily act at lower or higher scales.

421   Such a decision may limit inference about how and why interactions arise because the biology through

422   which two stressors interact (e.g. how higher order interactions emerge) is not defined.

423   We note that no model in Figure 3 currently incorporates adaptive foraging processes that allow species

424   to rewire their connections in the network as the biomass of resources change or species go extinct or

425   arrive, such as through invasion (criterion 4) [111-114]. The central hypothesis is that species that can adjust

426   their diets might persist and buffer ecological communities against stress. There exist several rewiring

427   models for food webs that could be incorporated into existing modelling frameworks. Historically,

428   rewiring has been explored via rules of thumb, inspired by concepts of foraging biology [115,116]. More

429   recently, optimal foraging theory has emerged as a formal principle for wiring and rewiring networks,

430   specifically via The Allometric Diet Breadth Model [113,117,118]. The ADBM uses optimal foraging theory

431   and allometries of foraging variables to predict food web structure. The model predicts which resources

432   a consumer should choose based on which food items maximise energy intake, subject to foraging

433   constraints, such as encounter rates and handling times. The model performs well on empirical data,

434   correctly predicting up to ~85% of links [119], and has been used in topological modelling of primary and

435   secondary extinctions [113].

436   The Allometric Trophic Network Model and Size Spectra models both meet all criteria except

437   incorporating rewiring (criterion 4), and thus offer extensive opportunities. The bioenergetic food web

438   model [120] is an established, mechanistic model of biomass dynamics of species in food webs that

439   integrates metabolism, body size, intraspecific density-dependence and interspecific interactions. In the

440   model, parameters specifying metabolism, production of biomass (reproduction, population growth)

441   and consumption are determined by body size via a set of allometries (each with a constant and

442   exponent). These parameters determine rates of change in species' populations – modelled as

443   collections of biomass – via a set of ordinary differential equations solved numerically. Size-spectrum

444   models offer a size-structured alternative and are primarily used in the marine environment [121-123]. A

445   size spectrum is the relationship between log individual size (body mass) and log abundance, which is

446   roughly –1. Size spectrum models thus conceptualise food webs as a gradient of individuals, organised

447   by size and other traits, where individuals grow by eating smaller individuals and die by being eaten by

448   larger individuals [121,124]. The core of the model is a set of equations (partial differential equations) that

449   model the density per unit mass per unit volume for organisms of mass m at time t. Both these modelling

450 platforms are temporally resolved and structured around some characterisation of multi-species

451 community structure. This mix of temporal resolution and structure is central to making inference about

452 predictability and consistency and for developing theory about the effects of discrete versus continuous

453 stress outlined by Jackson *et al*. [50] (such as the distinction between the gradual increase in mean

454 temperature change and extreme temperature events).

455

456 Finally, we note that relying on a single model to generate theory and inference about predictability and

457 consistency of multiple stressor effects can be risky; it may be beneficial to amalgamate inference from

458 an ensemble of models to establish consensus. Many of the models discussed in Figure 3 can share

459 common state variables and thus could be used as part of an ensemble modelling approach. Ensemble

460 modelling helps deal with three main forms of uncertainty: process uncertainty, caused by the variation

461 and stochasticity inherent to ecosystems; model uncertainty, related to the components of a particular

462 model; and future/scenario uncertainty, related to predictions being made, such as from uncertainty

463 about future conditions[109]. Ensemble modelling has recently been gaining traction in ecology and has

464 already been used to evaluate the impacts of multiple stressors on particular targets, including explicitly

465 building relationships between stressors into the models [125,126]. To capture a final type of uncertainty,

466 known as parameter uncertainty (uncertainty related to the parameter values used in a model[109]),

467 ensemble modelling can be combined with global sensitivity analysis. Global sensitivity analyses can

468 help understand the sensitivity of results and conclusions to changes in model parameters by, for

469 example, running models with parameter values obtained from bootstrap resampling from parameter

470 distributions[109,127]. Thus, ensemble modelling could potentially have a large part to play in multiple

471 stressor research in the future.

472

473 **BOX 1: Estimation of effect sizes**

474 Calculating the effect sizes necessary to populate the grid framework in Figure 2 can be accomplished

475 with a variety of approaches, outlined below. The capacity for the Figure 2 grid to deliver inference on

476 predictability and consistency, however, requires attention to two details. First, the targets (row names)

477 must be well defined and be distributed across multiple ecological scales. Second, the effect sizes must

478 capture both magnitude and directionality.

479 One approach builds from Piggott et al.'s[8] directional classification system of stressor interactions

480 through to specific null model frameworks, such as the use of ecotoxicological null models of

481 concentration addition and independent action[19,129]. There are several examples of the use of the

482 response ratios that define these null models to analyse empirical experiments[13]. For example, Galic et

483 al.[13] present an example of how these effect sizes can be used to make inference about the predictability

484 and generality of multiple stressor effects. They used an Individual Based Model (IBM) to explore the

485 impacts of multiple 'physiological' stressors on individual traits with consequences estimated at

486 biomass and ecosystem function scales. This framework typically requires an *a priori* experimental

487 design that allows response ratios to be constructed using appropriate null models or control conditions.

488 It is useful for both empirical and simulated *in silico* experiments.

489 An alternative to experimental approaches is to use effect sizes from standardized coefficients of linear,

490 generalised linear and mixed effects models. For example, Tabi, et al. [130] combined this approach with

491 the Piggott, et al. [8] framework to analyse the combined effect of temperature and productivity, aligning

492 classic statistical definitions of interactions with estimations of effect sizes from coefficients. Meta-

493 analyses are another approach, where studies can be synthesised to estimate interaction effect sizes. For

494 example, and O'Brien *et al.*[131] use meta-analysis to estimate interactions between two stressors detected

495 in targets classified by structure and function.

496 Multivariate Auto-Regressive State Space (MARSS) models[132-135] offer an additional toolbox for

497 empirical time series data, empirical spatial data or data derived from stochastic simulations. MARSS

498   models fit multiple regression equations simultaneously to each response variable, using the values of

499   other variables (e.g. species) and environmental covariates (the stressors) from previous time steps as

500   predictors. A matrix of environmental covariate effect sizes (main and interactions) on response

501   variables is recovered. These effect sizes are, by definition, associated with main effects of, and

502   interactions among, stressors and thus are suitable for use in the Figure 2 grid concept. The MARSS

503   models have an additional advantage in that they are good at partitioning uncertainty to understand its

504   specific sources.

505   Didham *et al*. [11] and Geary *et al*. [136] have argued for expanding our understanding of the mechanisms

506   of stressor interactions – beyond simply additive, synergistic or antagonistic – to also include different

507   interaction pathways. The main two pathways are chain interactions, where one stressor alters the

508   prevalence of another stressor directly, and modification interactions, where one stressor changes the

509   prevalence and per capita effect of another stressor. Geary *et al*. [136] put forward additional statistical

510   tools we can use to understand these pathways in the form of the 'threat web' approach, which uses a

511   network approach to understand co-occurrence patterns among threats. The co-occurrence network can

512   be analysed to gain quantitative insight into stressor-stressor interactions, and their causative or

513   coincidental associations. In turn, this can frame our understanding of spatial and temporal threat co-

514   occurrence [136].

515

BOX 2: The models - experiments interface

Model development (where models are defined as simulation models like those discussed in 'Simulation models for studying multiple stressor effects') must be linked with empirical data and experiments. While there is a rich history of empirical work linked to such efforts on multiple stressors (see Introduction), there remains a substantial set of biases along with major differences in semantics and design constraints that often limit the contribution of empirical work to these kinds of models [7,14]. We suggest that recognising at least three facets of the model-experiments interface can help reduce these biases, generate common semantics and maintain a strong relationship between models and data.

One facet of the interface between models and experiments focuses on experiments that produce data to parameterise models. Experiments help evaluate assumptions made by modelling and refine the identity and functional forms of mechanisms embedded in models. This is embodied, for example, in recent meta-analyses and synthesis of data on metabolism and functional response parameters, which are then directly used by simulation models [29,137,138].

A second facet of the interface is to align model predictions with experiments. Our grid approach in Figure 2 requires effect sizes to populate the matrix elements. These effect sizes can be generated by analysing data produced by experiments and by simulation models. For experimental data to be compatible with our approach, we have four key recommendations. First, experiments must incorporate three or more stressors. Second, they must incorporate three or more scales of ecological organisation. These two recommendations are an essential progression beyond the one scale and two stressors studies that currently dominate[14]. Third, studies must adopt a multifactorial experimental design that examines different stressor combinations. Fourth, the experiment must be based around time series, as these are necessary to capture population dynamics which are then analysed to calculate the effect sizes required by the grid framework in Figure 2. This also allows different stressor temporal trends to be incorporated, such as sudden *versus* ongoing changes in temperature[50].

540   Recent work suggests that experiments are increasing in design complexity and the number of stressors

541   and scales evaluated [139,140]. There are already a number of studies which adopt our recommendations

542   and which would be suitable for our framework. For example, Rillig, et al. [139] experimentally

543   manipulated soil communities, applying up to 10 stressors. They found complex changes in soil

544   properties, soil processes, and microbial communities (i.e. multiple scales of response) and decreasing

545   predictability as the number of stressors increased (interactions were pervasive). Tabi, et al. [130]

546   experimentally manipulated temperature and productivity in microbial communities, where targets at

547   multiple scales were monitored through time. The authors combined this experiment with an effect size

548   analysis of the multiple stressor effects to estimate predictability and consistency across scales.

549   Experiments like these are critical to match similar advances occurring in the mathematical modelling.

550   A third facet relates to 'fitting models to data' which can prove challenging, but beneficial, in cases

551   where the complexity of the required experiments to estimate parameters is high. There are emerging

552   methods that link large-scale empirical survey data with models to help parametrise them. These include

553   'inverse methods' or state-space models[141,142] (often now Bayesian with priors to appropriately capture

554   uncertainty). This is perhaps the least developed sphere of the model-experiment interface for the

555   models in Figure 3. However, it is also one with great potential as we move toward leveraging the

556   insight from models to help manage natural resources and biodiversity in the future.

557

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Competing interests

The authors declare no competing interests.

Figure legends

Figure 1: Conceptual diagram of the ecological scale-target-based classification of stressors to quantify the

impact of multiple simultaneous stressors on ecological communities. We align the Living Planet source-based

categories of stressors with a classical view of ecological scales and the target metrics at each scale. The

framework (and models, see below) highlights targets and ecological scales that coalesce the impacts of stressors

by what they do, not what they are. For example, pollution and climate stressors both can generate direct effects

on species' abundance by killing individuals, but also via trait-mediated effects acting on growth and

reproduction. As different ecological scales are connected by higher-order interactions, outputs at higher and

lower levels of ecological organisation can emerge. Note that we define the effects of a stressor at the individual

scale as those that act within, rather than between, individuals. Thus, a harvesting process, such as hunting, can

have individual-scale effects by altering stress hormone levels in individuals, which has consequences for

demography and thus the population. However, hunting primarily acts by killing individual animals or plants,

which affects directly properties of the population (abundance/biomass), not properties of the individual. Note,

this figure is a first attempt designed to illustrate our framework and is by no means comprehensive.

Figure 2: *A framework for assessing the consistency and predictability of stressors. Rows represent targets at*

different scales of ecological organisation. These are the variables that may be of interest when assessing the

response of ecosystems to multiple, simultaneous stressors. Columns represent different stressors or their

combinations. When a stressor is by itself (for example, Temperature), this means that the stressor combines

additively with other stressors. When a stressor occurs with another (for example, Temperature × Nitrogen), this

means the effects of one stressor depend on the other (interaction). Colours represent the magnitude and direction

of the effect of a stressor, or combination of stressors, on each target. (a) Stressors are more predictable at the

population scale because they all combine additively, whereas prediction may be harder at the community and

ecosystem scales due to complex two- and three-way interactions. Consistency by scale *is also visible: at a given*

scale, all stressors combine in the same way. For example, all stressors combine additively at the population

scale, and all stressors are involved in two-way interactions at the community scale. (b) Shows consistency by

stressor, *where a stressor has a similar effect on targets, whether combining additively or interactively with other*

stressors. In this case, nitrogen consistently has a strong negative effect (all columns involving the nitrogen

stressor have the same strongly negative effect size). (c) Consistency by target, *where targets are affected similarly*

by different stressors. For example, the abundance of species 3 is similarly affected by temperature, nitrogen and

hunting. (d) No pattern of consistency or predictability. Note that this figure is a caricature to demonstrate

different forms of consistency and there is no intention to suggest the specific patterns shown are likely to occur

in nature. For example, interactive effects can occur at all scales, not just at the community and ecosystem scales

as shown in Figure 2a. Moreover, we focus on three scales purely for visual simplicity; in a real analysis, the

*metabolism/physiology and individual scales are also important to include.*

957 ***Figure 3:*** *We propose seven criteria (central blue) that models must satisfy to generate informative, simulated*

958 *data from which effect sizes can be estimated to quantify the impacts of multiple, interacting stressors. Models*

959 *that meet these seven criteria provide a platform for developing a general theory for the predictability and*

960 *consistency of multiple stressor effects. The criteria are motivated by a recent specification of several critical*

961 *attributes for predictive models* [108]. *We are currently unaware of any model that meets all seven criteria; here*

962 *we present four that have been used to evaluate multiple stressor effects on ecological communities and that*

963 *possess several of the criteria. The Allometric Trophic Network (e.g. Bioenergetic Food Web Model* [120]*) and the*

964 *Size-Spectra modelling frameworks* [123] *are two that offer extensive opportunities because they meet many of the*

965 *criteria and may also potentially accommodate rewiring – the re-allocation of network links associated with*

966 *loss or gain of species in the network (see text). The Trophic Network and IBM examples are notable because of*

967 *the detail specified on how various stressors might impact at different ecological scales. Motivating references*

968 *for each criteria: Access* [120]*; Biodiversity* [120,128]*; Interaction Diversity* [120,128]*; Rewiring* [111,113,114,116]*; Scalable* [120]*;*

969 *Predictions* [13,71,110]*; Feedback* [120,128]*.*

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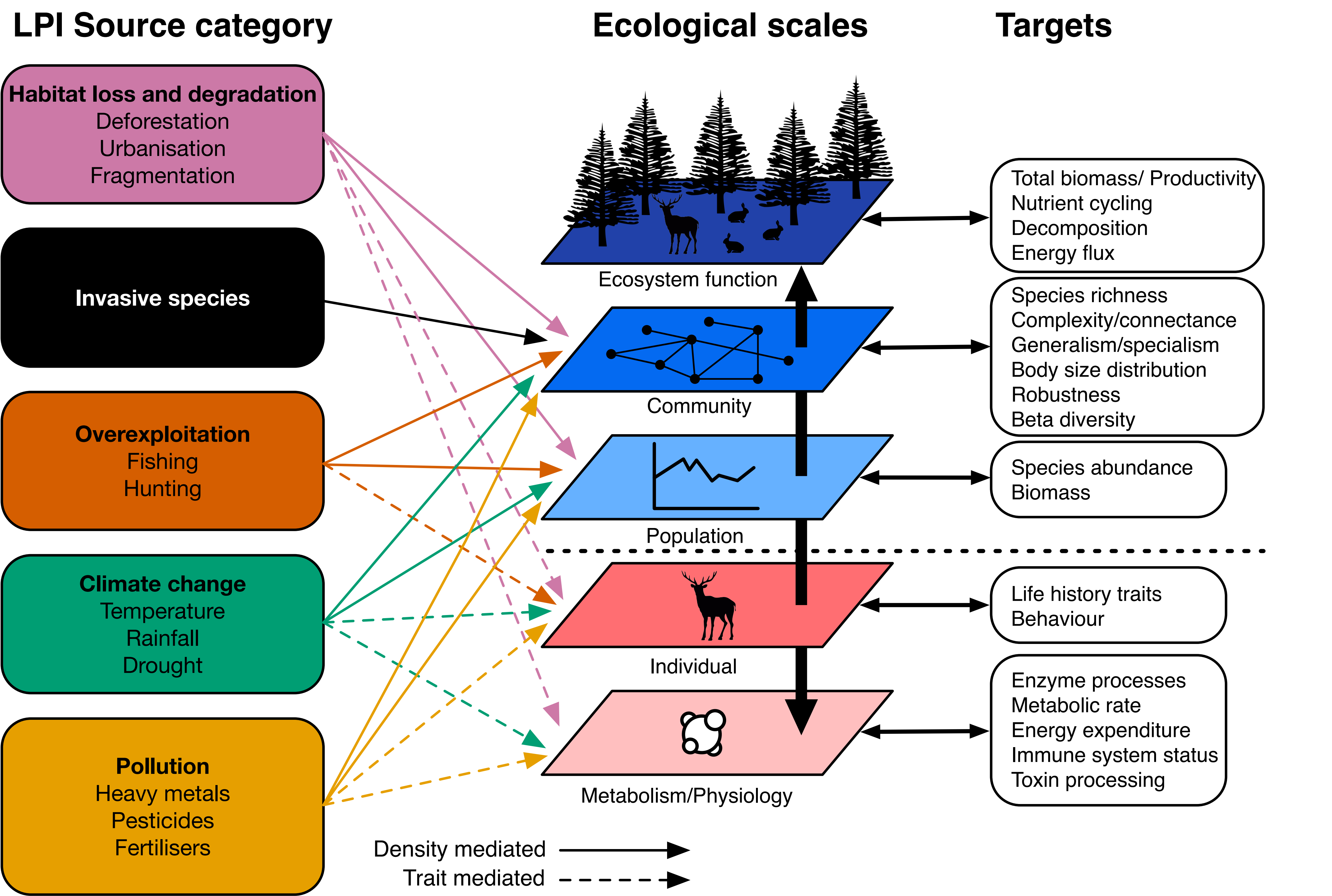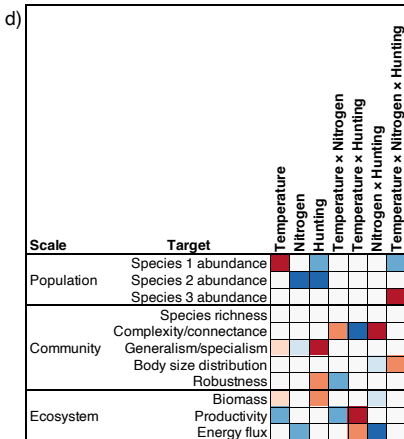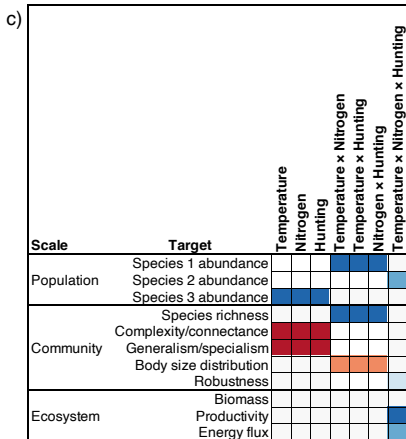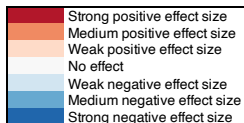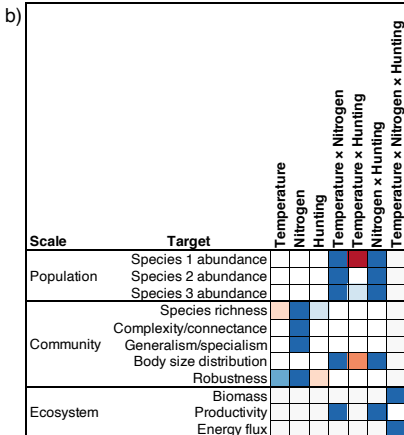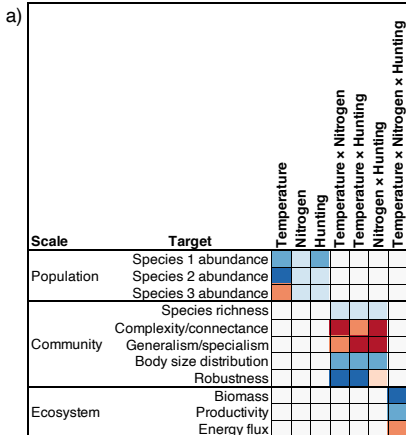
Allometric Trophic Network Model

Example: The Bioenergetic Food Web Model (Delmas et al, Williams et al)

Mechanistic model of biomass dynamics of species in food webs; links metabolism, growth and consumption with body size; temperature scaling is considered

Access	Stressors have access points at metabolism/physiology, individual, population and community scales
Biodiversity	Species, trophic, metabolic class and feeding group diversity represented
Interaction Diversity	Interspecific predation, intraspecific competition/density dependence, indirect effects
Rewiring	NA
Scalable	Allometry allows a few equations to represent high-diversity communities
Predictions	Combined effects of stressors are emergent properties at a variety of ecological scales
Feedback	Feedback between body size distribution, structure and dynamics

IBM/Dynamic Energy Budget

Example: Galic et al 2018

Individual based, dynamic energy budget model; often focused on physiological mode of action

Access	Stressors have access points at metabolism/physiology, individual, population and community scales (limited)
Biodiversity	NA
Interaction Diversity	Physiology and infraspecific density dependence
Rewiring	NA
Scalable	NA
Predictions	Combined effects of stressors are emergent properties at a variety of ecological scales
Feedback	NA

The Seven Criteria

1. Access	Possess multiple access points or targets for stressors to generate their effects
2. Biodiversity	Represent multiple species, size classes or metabolic classes, spanning multiple trophic or feeding groups
3. Interaction Diversity	Represent multiple types of interaction types, direct (e.g. predation/competition) and indirect (e.g. trophic cascades) effects
4. Rewiring	Allow species losses or insertions to drive mechanistic change in the distribution of links among species as resource options change.
5. Scalable	Represent high diversity systems with a small number of equations, e.g. through allometry
6. Predictions	The combined effects of stressors generate responses at the scales they enter and at higher or lower ecological scales
7. Feedback	Allow changes in, and feedback between, traits, structure and dynamics

Trophic Network Model

Example: Rosenblatt et al 2017

Mechanistic model of tri-trophic biomass dynamics; links metabolism, growth and consumption to temperature and CO_2 scaling

Access	Stressors have access points at metabolism/physiology, individual, population and community scales
Biodiversity	Three trophic levels (limited)
Interaction Diversity	Interspecific predation, intraspecific competition/density dependence, indirect effects
Rewiring	NA
Scalable	NA
Predictions	Combined effects of stressors are emergent properties at a variety of ecological scales
Feedback	NA

Size Spectra

Example: mizer (Scott et al 2014)

Mechanistic model of density per unit mass per unit volume for organisms of mass m at time t; integrates metabolism, body size, consumption and growth; temperature scaling is considered

Access	Stressors have access points at metabolism/physiology, individual, population and community scales
Biodiversity	Size spectra maps on to species diversity and trophic groups; species-resolved versions exist
Interaction Diversity	Interspecific and intraspecific predation, intraspecific competition/density dependence, indirect effects
Rewiring	NA
Scalable	Allometry allows a few equations to represent high diversity communities
Predictions	Combined effects of stressors are emergent properties at a variety of ecological scales.
Feedback	Feedback between body size distribution, structure and dynamics