

1 Operationalising the concept of ecosystem collapse for
2 conservation practice

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18 **Running Headline:** Operationalisation of ecosystem collapse

19

20 **Abstract**

21 Concern is growing about ecosystem collapse, namely the abrupt decline or loss of an
22 ecosystem resulting from human activities. While efforts to assess the risk of ecosystem
23 collapse have developed at large spatial scales, less attention has been given to the local
24 scales at which conservation management decisions are typically made. Development of
25 appropriate management responses to ecosystem collapse has been limited by uncertainty
26 regarding how collapse may best be identified, together with its underlying causes. Here we
27 operationalise ecosystem collapse for conservation practice by providing a robust definition
28 of collapse, in a form that is relevant to the scale of conservation decision-making. We
29 provide an overview of different causes of collapse, and then explore the implications of this
30 understanding for conservation practice, by examining potential management responses.
31 This is achieved through development of a decision tree, which we illustrate through a series
32 of case studies. We also explore the role of indicators for the early detection of collapse and
33 for monitoring the effectiveness of management responses. Ecosystem collapse represents
34 a significant challenge to conservation practice, as abrupt changes in ecosystem structure,
35 function and composition can occur with little warning, leading to profound impacts on both
36 biodiversity and human society. The risks of ecosystem collapse are likely to increase in
37 future, as multiple forms of environmental change continue to intensify. We suggest that
38 selection of management responses should be based on an understanding of the causal
39 mechanisms responsible for collapse, which can be identified through appropriate monitoring
40 and research activities.

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42 **Keywords:** ecosystem collapse, biodiversity loss, conservation, environmental
43 management, degradation, regime shift

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48 **Introduction**

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Recent events such as the mass bleaching of the Great Barrier Reef, unprecedented fires in regions including California, southern Australia, Indonesia and the Amazon, and the sudden loss of ice habitat in polar regions, have increased international concerns about ecosystem collapse (Newton, 2021; Vincent and Mueller, 2020). The phenomenon is increasingly being referred to in the international media, partly as a result of advocacy by high-profile individuals such as Greta Thunberg and David Attenborough (Dasgupta, 2021; Newton, 2021). At the same time, ecosystem collapse is receiving increasing attention from conservation researchers, as illustrated by a rapid recent increase in the number of publications on the topic (Bergstrom et al., 2021; MacDougall et al., 2013; Newton, 2021; Sato and Lindenmayer, 2017). This growth in interest reflects a number of intensifying concerns: the scale of the ecological changes that are currently occurring in the world's ecosystems; the fact that these changes can sometimes occur rapidly, with little warning; and the magnitude of the potential impacts on both biodiversity and human society.

Trends towards increased recognition of ecosystem collapse have been given particular impetus by the recent development of the IUCN Red List of Ecosystems (RLE), which represents the first systematic attempt to assess the conservation status of different ecosystem types that is appropriate for use at the global scale. The RLE specifies collapse as the endpoint of the process of ecosystem degradation, and employs "Collapsed" as a category in the assessment, in an analogous way to which the IUCN Red List of Threatened Species (RLTS) includes "Extinct" as a category for species (Bland et al., 2017a; IUCN, 2012). While the RLTS has had a major influence on the identification of priorities for conservation action and protection, and has been widely incorporated into policy, the RLE of ecosystems is currently at a much earlier stage of implementation. To date, around 60 assessments have been published, drawn from more than 20 countries or regions. One ecosystem, the Aral Sea, has been classified as 'Collapsed', whereas a number of others have been assessed as 'Critically Endangered' such as the gnarled mossy cloud forest on Lord Howe Island of Australia, the Coorong lagoons of Australia, and the Gonakier forests of Senegal and Mauritania (RLE, 2021). These initial outputs of the RLE are already informing global environmental assessments, such as the Global Biodiversity Outlook (Secretariat of the Convention on Biological Diversity, 2020) and the Global Environment Outlook (GEO-6, UN Environment, 2019), together with their associated policy initiatives. Such global assessments have been further supported by development of the IUCN Global Ecosystem Typology (Keith et al., 2020).

85 The primary focus of the RLE is to assess risk of collapse throughout the entire geographic
86 range of an ecosystem, to support conservation prioritisation (Bland et al., 2017a,b, 2018;
87 Keith et al., 2013, 2015). However, there is also a need to consider ecosystem collapse at
88 the more local scales at which conservation management decisions are typically made. The
89 RLE guidelines note that an ecosystem may undergo a transition to a collapsed state in
90 some parts of its distribution before others; such areas might be described as 'locally
91 collapsed' (Bland et al., 2017a). Despite this, the assessment and analysis of local-scale
92 collapse was not explicitly considered by the RLE. Such collapse may be widespread. For
93 example, in their assessment of 19 Australian ecosystems, Bergstrom et al. (2021) found
94 evidence of local-scale collapse in every ecosystem type, although none had collapsed
95 throughout their entire distribution. In his review of the links between biodiversity and
96 economic development, Dasgupta (2021) notes that the local collapse of an ecosystem can
97 be catastrophic for the human communities that are dependent on it. Furthermore, the
98 impacts are likely to be unequal across different income groups owing to variation in
99 dependence on natural assets and ecosystem services. This highlights the need for actions
100 to reduce the risk of ecosystem collapse at the local scale, both to protect human livelihoods
101 and to benefit wildlife.

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103 Identification of appropriate conservation management interventions to reduce the risk of
104 ecosystem collapse requires an understanding of how and why it occurs, and what the
105 potential consequences of it might be. Development of this understanding has been limited
106 to date, reflecting a lack of consensus regarding the scientific foundations on which the RLE
107 is based. Specifically, Boitani et al. (2015) highlighted a number of problems with the
108 concept of ecosystem collapse presented by Keith et al. (2013), as the definition of an
109 ecosystem might vary dependent on scale or ecological context, and according to the
110 specific features under consideration. Further, Boitani et al. (2015) noted that the collapse of
111 an ecosystem is not equivalent to the extinction of a species; while the latter has a clear
112 theoretical endpoint, the endpoints for an ecosystem can be far more ambiguous. An
113 ecosystem undergoing degradation might exhibit a range of different endpoints, and there
114 may be no consensus on which are desirable or undesirable (Boitani et al., 2015). Progress
115 in developing an understanding of the mechanisms responsible for ecosystem collapse has
116 also been limited to date. Various elements of dynamical systems theory have dominated
117 the literature on ecosystem collapse and on related phenomena such as tipping points,
118 critical transitions, resilience, regime shifts and alternative stable states (Andersen et al.,
119 2009; Bland et al., 2017a, 2018; Keith et al., 2013, 2015; Scheffer, 2009). While there has
120 been substantial theoretical development in this area, not all of these ideas are accessible in
121 a form that can be readily used by conservation practitioners. In addition, theoretical

122 predictions relating to ecosystem collapse have not always been supported by empirical
123 evidence (Hillebrand et al., 2020; Newton, 2021). Consequently there is a need to
124 understand under which situations different theoretical ideas are likely to apply, and
125 therefore which mechanisms are likely to be responsible for causing the collapse, so that
126 appropriate management responses can be identified.

127

128 In this paper, we examine how the concept of ecosystem collapse might be operationalised
129 for use by conservation practitioners. Firstly we consider how ecosystem collapse might best
130 be defined in a way that is relevant to the scale of conservation decision-making. Secondly
131 we provide an overview of current understanding of the mechanisms of collapse in relation to
132 some of the theoretical ideas that have been proposed, and with reference to available
133 empirical data. Thirdly we explore the practical implications of this understanding for
134 conservation practice, by examining potential management options and responses. This is
135 achieved through development of a decision tree and by consideration of a series of case
136 studies.

137

138 **Defining ecosystem collapse**

139

140 Development of an appropriate definition is a key step towards operationalising any
141 ecological concept (Peters, 1991). The term 'ecosystem collapse' was apparently first
142 employed by palaeontologists in the 1980s, in reference to large-scale extinction events
143 detected in the fossil record, although no explicit definition of the term was provided
144 (Newton, 2021). It is only during the last decade that formal definitions of ecosystem
145 collapse have been proposed, most notably in the context of the RLE (Table 1).

146

147 Table 1. Definitions of ecosystem collapse available in the scientific literature.

148

A change from a baseline state beyond the point where an ecosystem has lost key defining features and functions, and is characterised by declining spatial extent, increased environmental degradation, decreases in, or loss of, key species, disruption of biotic processes, and ultimately loss of ecosystem services and functions.	Bergstrom et al. (2021)
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<p>A transformation of identity, a loss of defining features, and a replacement by a different ecosystem type.</p> <p>An ecosystem is collapsed when all occurrences lose defining biotic or abiotic features no longer sustain the characteristic native biota, and have moved outside their natural range of spatial and temporal variability in composition, structure and/or function.</p>	Bland et al. (2017a)
<p>A transition beyond a bounded threshold in one or more indicators that define the identity and natural variability of the ecosystem. Collapse involves a transformation of identity, loss of defining features, and/or replacement by a novel ecosystem. It occurs when all ecosystem occurrences (ie patches) lose defining biotic or abiotic features, and characteristic native biota are no longer sustained.</p>	Bland et al. (2018)
<p>A theoretical threshold, beyond which an ecosystem no longer sustains most of its characteristic native biota or no longer sustains the abundance of biota that have a key role in ecosystem organisation (e.g. trophic or structural dominants, unique functional groups, ecosystem engineers, etc.).</p> <p>Collapse has occurred when all occurrences of an ecosystem have moved outside the natural range of spatial and temporal variability in composition, structure and function. Some or many of the pre-collapse elements of the system may remain within a collapsed ecosystem, but their relative abundances may differ and they may be organised and interact in different ways with a new set of operating rules.</p>	Keith et al. (2013)
<p>An abrupt and undesirable change in ecosystem state.</p>	Lindenmayer <i>et al.</i> (2016)
<p>Major changes in ecosystem conditions [that] are either irreversible or very time- and energy-consuming to reverse.</p>	Lindenmayer and Sato (2018)

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150

151 Ecosystem collapse can be considered as the result of environmental degradation, which
152 IPBES (2018) defines as “*the persistent decline or loss in biodiversity and ecosystem*
153 *functions and services that cannot fully recover unaided within decadal timescales*”. This
154 describes a state that is persistent, because ecological recovery has been impeded or
155 impaired. We suggest that this provides a basis for developing a working definition of an
156 ecosystem that has collapsed, although ‘land’ should be extended to include ‘water’, so that
157 marine and freshwater ecosystems are incorporated. Further, following Lindenmayer et al.
158 (2016) we propose that the term ‘ecosystem collapse’ should be limited to those ecosystems
159 that have been degraded rapidly, and that have undergone abrupt change. This is consistent
160 with standard dictionary definitions of the word “collapse”, which generally refer to a

161 relatively sudden or abrupt event. Given that biodiversity, ecosystem function and services
162 do not necessarily covary (Hansson et al., 2005), a collapsed ecosystem could therefore be
163 defined as follows:

164

165 “A degraded ecosystem state that results from the abrupt decline and loss of
166 biodiversity, ecosystem functions and / or services, where these losses are both
167 substantial and persistent, such that they cannot fully recover unaided within decadal
168 timescales”.

169

170 This definition could be applied at a variety of scales, including the local or landscape scales
171 relevant to practical conservation management. The choice of timescale by which “abrupt”
172 might be defined is essentially arbitrary, but following IPBES (2018) “decadal timescales”
173 might be considered appropriate, both in terms of collapse and recovery. This would ensure
174 relevance to the timescales typical of conservation planning. Reference to “substantial”
175 losses also represents a subjective judgement, which could be viewed as equivalent to the
176 “major changes” referred to by Lindenmayer and Sato (2018) in their definition (Table 1).

177

178 Our proposed definition differs from that employed by the RLE (Bland et al., 2017a, Table 1)
179 in a number of ways. First, it does not require replacement by a different ecosystem type; it
180 could just refer to a loss of defining features, without necessarily involving a transformation
181 of identity. Second, it could be applied to individual occurrences of an ecosystem, such as
182 those located within a particular area, and would not need to apply to all occurrences of a
183 particular ecosystem type. Third, as noted above, it specifies that decline is abrupt, whereas
184 the RLE definition includes situations where ecosystem decline is gradual. These differences
185 partly reflect the fact that the RLE is designed to enable risk assessments to be conducted
186 throughout the geographical range of an ecosystem. We do not follow Lindenmayer et al.
187 (2016) in suggesting that ecosystem collapse will necessarily be “undesirable”; it is possible
188 that a collapsed ecosystem could itself be considered to be of some conservation value, for
189 example when a forest ecosystem is replaced by a grassland or shrubland composed of
190 native species. Further, we do not follow Lindenmayer and Sato (2018) in suggesting that
191 ecosystem collapse will necessarily be “widespread”, as it could be an entirely local-scale
192 phenomenon. The definition provided by Bergstrom et al. (2021) (Table 1) also does not
193 specify that decline need be abrupt; furthermore, slight or temporary changes of an
194 ecosystem would qualify as collapsed according to their definition, but not to ours.

195

196 We note that some previous definitions of ecosystem collapse (Table 1) refer to the amount
197 of ecosystem change that has occurred relative to a baseline value (Bergstrom et al., 2021)

198 or to the “natural range of spatial and temporal variability” (Bland et al., 2017a). We accept
199 that comparison of ecosystem characteristics with some form of reference value will likely be
200 essential to establish whether or not collapse has occurred, an issue that we explore further
201 below. However, we have omitted direct reference to these approaches in our proposed
202 definition, as the results obtained are likely to be highly context specific. This is a point made
203 forcefully by Boitani et al. (2015) in their critique of the definition offered by Keith et al. (2013)
204 (Table 1). While noting that it is difficult to quantify the natural range of temporal variability of
205 an ecosystem, Boitani et al. (2015) indicate that collapse will often need to be defined
206 separately for each ecosystem considered, using a variety of different attributes and
207 threshold values. This is because ecosystems are dynamic systems that change in time and
208 space; both the structure and composition of ecosystems can change rapidly, together with
209 the ecosystem processes with which they are associated. Ecosystem properties can
210 sometimes change substantially with small variations in the biotic component, while in other
211 situations, the converse may be true (Boitani et al., 2015). The fact that ecosystem collapse
212 is context-specific limits the scope for developing standardised protocols that could be used
213 to compare ecosystems at large spatial scales, as proposed by the RLE (Boitani et al.,
214 2015). However, this does not prevent the concept of ecosystem collapse from being
215 usefully applied at the local scale, so long as local context is taken into account.

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217 In their critique, Boitani et al. (2015) also highlight the difficulty of defining an ecosystem.
218 Given that the ecosystem is considered to be the most important concept in ecology (Willis,
219 1997), it is surprising that there is still a lack of consensus regarding how this concept should
220 be defined (Fitzsimmons, 1996). Contrasting views regarding the nature of ecosystems are
221 rooted in different philosophical standpoints that extend back to the scientific origins of
222 ecology (Kirchhoff et al., 2010). Furthermore, concepts of ecosystems have evolved over
223 time; while they are now often seen as dis-equilibrial, open, hierarchical, spatially patterned
224 and scaled (O’Neill, 2001), alternative views still persist in the literature. For example from a
225 ‘bio-ecological’ perspective, an ecosystem is flexible in time and space, depending on the
226 location of the organisms of interest. In contrast, from a ‘geo-ecological’ perspective, an
227 ecosystem is a specific area of the Earth’s surface, defined by abiotic factors such as
228 landforms, topography and climate (Rowe and Barnes, 1994).

229
230 As a consequence of such contrasting views, Boitani et al. (2015) suggest that there is no
231 means by which ecosystems can be consistently defined for conservation management.
232 However, Post et al. (2007) provide valuable guidance for operationalising the ecosystem
233 concept, by highlighting the overriding importance of understanding ecosystem boundaries,
234 which may be either structural or functional and either well-defined or diffuse. Specifically,

235 the boundaries of an ecosystem in time and space need to relate to the ecological features
236 or processes being studied, which may show little correspondence with physical boundaries.
237 Here we follow Bland et al. (2017a) in supporting the use of the proxies for ecosystems that
238 are widely used in conservation assessments, such as ecological communities, habitats,
239 biotopes, and vegetation types. As these can usually be mapped, they can be readily used
240 as a basis of developing conservation management plans. However, it should be
241 remembered that such “tangible” boundaries do not always coincide with the ecological
242 processes of interest, highlighting the need to use them with care (Post et al., 2007).

243

244 **Causes of ecosystem collapse**

245

246 Conservation practitioners are well versed in the factors that can cause loss of biodiversity,
247 which are commonly referred to as threats or threatening processes, most of which are
248 attributable to anthropogenic pressures. The most significant of these threats at the global
249 scale, according to a recent review (IPBES, 2019), are (in declining order of importance)
250 land/sea use change, direct exploitation, climate change, pollution and invasive alien
251 species. Other threats that have been widely implicated in biodiversity loss include a change
252 in the fire regime owing to human intervention, and habitat fragmentation. Each of these
253 threats could potentially cause or contribute to ecosystem collapse, but their relative
254 importance will vary according to the characteristics of the threat and the ecosystem
255 concerned. For example, Salafsky et al. (2008) identified three categories of threat, namely
256 those that can cause: (i) elimination of an ecosystem through direct and complete
257 conversion (e.g. clear-cutting a forest and converting to agriculture, eliminating a stream,
258 removing a coral reef); (ii) degradation of an ecosystem through direct damage to an
259 ecosystem’s biotic and / or abiotic condition (e.g. pollution, selective removal of species,
260 removal of top predators, altered fire or hydrological regime); (iii) indirect damage to an
261 ecosystem (e.g. fragmentation or isolation of an ecosystem, impacts on the food resources
262 of a species). It is also useful to differentiate between the different dimensions of threat, such
263 as the immediate threat or pressure *versus* underlying drivers. For example, the immediate
264 threat of an introduced exotic species to a marine ecosystem might be attributable to the
265 underlying driver of increasing global trade and an associated increase in international
266 shipping (Balmford et al., 2009).

267

268 To date, there has been no systematic assessment of the association between different
269 threats and the risk of ecosystem collapse; this clearly merits further research. On the face
270 of it, those threats associated with ecosystem conversion, as identified by Salafsky et al.
271 (2008), would be more likely to cause ecosystem collapse than those associated with

272 degradation or indirect damage to an ecosystem. However, this difference could simply
273 reflect the different timescales involved; while ecosystem conversion could be very abrupt,
274 continuous degradation over a longer period could result in a similar outcome. Newton
275 (2021) reviewed empirical evidence of ecosystem collapse in relation to available theory,
276 and reached the following conclusions regarding its potential causes:

- 277 • Ecosystem collapse often occurs when ecosystems are subjected to multiple
278 anthropogenic pressures, especially if there are positive interactions between these
279 pressures.
- 280 • Ecosystem collapse can be caused by extrinsic factors (i.e. anthropogenic pressures
281 or threats) acting in isolation, but it can also be caused by a combination of extrinsic
282 factors and those that are intrinsic to the system (i.e. the internal ecological
283 processes influencing the dynamics of the ecosystem, such as competition and
284 predation).
- 285 • Ecosystem collapse can occur when species are lost that are highly connected to
286 many others in ecological networks. These might include generalist species, and
287 those at the top or bottom of food chains.
- 288 • Ecosystem collapse is often associated with situations where ecological recovery is
289 impeded, typically by chronic anthropogenic disturbance; this can increase the
290 persistence of degraded ecosystem states.

291
292 Collapse of an ecosystem can therefore result from an abrupt change in an anthropogenic
293 pressure or its underlying drivers, from an interaction between different pressures, or from
294 an abrupt change in the state of the ecosystem with a small or smooth change in a pressure
295 (Andersen et al., 2009; Newton, 2021; Watson et al., 2018). An example of the latter is
296 provided by coral bleaching events, where symbiotic algae associated with corals are
297 expelled when sea temperatures exceed a threshold value. In some cases, abrupt changes
298 in ecosystem state that occur when a pressure reaches a threshold value are driven by
299 feedbacks between intrinsic ecological processes; such 'critical transitions' have attracted
300 particular interest from theoreticians (Scheffer et al., 2009, 2015).

301
302 The relative frequency of these different mechanisms of ecosystem collapse is currently
303 unknown, as it has not been investigated systematically. However, much of the recent
304 literature relating to transitions between ecosystem states has focused on application of
305 different elements of dynamical systems theory, particularly bifurcation theory, catastrophe
306 theory and theories of alternative stable states (Petraitis, 2013; Scheffer, 2009). Some
307 authors have explicitly linked ecosystem collapse to these theoretical ideas (e.g. Keith et al.,

308 2015; Lindenmayer et al., 2016). Although different states of ecosystems can be widely
309 observed in nature, it is not always clear whether these correspond to the alternative stable
310 states postulated by theory (Newton, 2021; Petraitis, 2013). In fact, this suggestion has been
311 challenged in a variety of different ecosystem types, for example in coral reefs (Dudgeon et
312 al., 2010), freshwater ecosystems (Capon et al., 2015) and savannas (Lloyd and
313 Veenendaal, 2016), the very same ecosystems that are most often cited in support of the
314 theory (Scheffer, 2009). This is partly because key assumptions of the theory have often not
315 been met in field situations (e.g. Bruno et al., 2009; Möllmann and Diekmann, 2012; Capon
316 et al., 2015; Newton and Cantarello, 2015). For example, transitions between ecosystem
317 states are often associated with a change in environmental conditions, which is not
318 consistent with theory relating to alternative stable states (Petraitis and Dudgeon, 2004;
319 Dudgeon et al., 2010). Furthermore, according to theory, such transitions are driven by
320 feedbacks among intrinsic ecological processes rather than by extrinsic factors acting in
321 isolation. These theoretical ideas are therefore not relevant to situations where ecosystem
322 collapse has been entirely caused by extrinsic factors, such as those examples involving
323 complete and direct ecosystem conversion (Newton, 2021). As indicated earlier, this
324 currently comprises the principal form of ecosystem collapse.

325

326 Another concept associated with dynamical systems theory that has been widely linked to
327 ecosystem collapse is a “regime shift” (or “phase shift”) (Bergstrom et al., 2021; Cooper et
328 al., 2020; Scheffer and Carpenter, 2003). Some authors (e.g. Rocha et al., 2018) consider
329 regime shifts to be equivalent to critical transitions between alternative stable states; in other
330 words, they are driven by intrinsic feedback mechanisms. In fact, the term “regime shift”
331 refers to any abrupt change, regardless of mechanism (Scheffer, 2009). Whereas a regime
332 shift represents a change in the state of a system in response to a persistent change in
333 environmental conditions, alternative stable states represent different configurations of a
334 system under the same environment (Dudgeon et al., 2010). Some examples of ecosystem
335 collapse could therefore be considered to be regime shifts. However, regime shifts reflect
336 transitions between system states that are equilibrating with different environmental conditions
337 (Dudgeon et al., 2010). The different states associated with ecosystem collapse do not need
338 to be equilibrating in order to meet our definition of collapse, and could (for example) be
339 equivalent to the non-equibrating “alternative transient states” of Fukami and Nakajima (2011).
340 It is therefore inappropriate to consider ecosystem collapse as equivalent to a regime shift,
341 as some authors have implied (e.g. Cooper et al., 2020).

342

343 Research on dynamical systems theory has been of particular value in drawing attention to
344 the potential role of feedbacks as a mechanism of ecosystem collapse, in situations where

345 the ecosystem has not been completely eliminated by the threatening process. There are
346 important differences between threats in their propensity to generate such feedbacks.
347 In particular, fire and herbivory can create positive feedbacks with vegetation, as some plant
348 species are adapted to these forms of disturbance. It is significant that some of the most
349 persistent examples of ecosystem collapse, such as those of New Zealand and Madagascar,
350 were initially driven by increased fire frequency (Newton, 2021). However, this is not the only
351 reason why a change in the fire regime is so damaging to some terrestrial ecosystems; it can
352 also cause persistent edaphic changes, for example in soil structural, chemical and physical
353 properties (Kitzberger et al., 2005). Further research is therefore needed on the feedbacks
354 associated with different threats, and their relative contribution to ecosystem transitions.
355 There is also a need to understand why some threats appear to be more significant causes
356 of collapse than others in particular types of ecosystem, for example invasive species in
357 freshwater ecosystems and hypoxia in benthic marine environments (Newton, 2021).

358
359 In this context, it is important to recognise the overriding importance of climate change.
360 While climate change is currently not considered to be the principal cause of biodiversity loss
361 at the global scale (IPBES, 2019; Maxwell et al., 2016; Noss et al., 2012), it clearly has the
362 potential to become the principal cause of collapse in most, if not all, types of ecosystem.
363 This is illustrated by its consistent association with mass extinction events observed in the
364 fossil record (Barnosky et al., 2011). Reasons for this importance include: (i) its scale of
365 impact; while many threats operate at local or landscape scales, climate change can affect
366 all of the ecosystems in entire regions; (ii) rather than comprising a single threat, climate
367 change encompasses change in a range of different variables (e.g. total rainfall, rainfall
368 distribution, mean temperature, maximum temperature, etc.), each of which can individually
369 influence different ecosystem attributes (Peters et al., 2011); (iii) unlike most other threats,
370 climate change can alter some of the abiotic components of an ecosystem, such as the
371 availability, temperature or acidity of water; (iv) climate change can interact with all other
372 threats; (v) as species respond individualistically to climate change, reflecting variation in
373 life-history traits (Bellard et al., 2012, Schloss et al., 2012; Urban, 2019; Warren et al., 2018),
374 climate change can cause the disassembly of ecological communities and the formation of
375 new communities (Walther, 2010; Williams and Jackson, 2007; Keith et al., 2009).

376
377 Ecosystem collapse can also usefully be considered in terms of the impact of threatening
378 processes on interactions among species, and specifically the structure and dynamics of
379 ecological networks. Based on a literature review, Bascompte and Stouffer (2009) found that
380 ecological networks are relatively robust to the loss of the most specialised species, but are
381 more vulnerable to the loss of more generalised species; and that network collapse can be

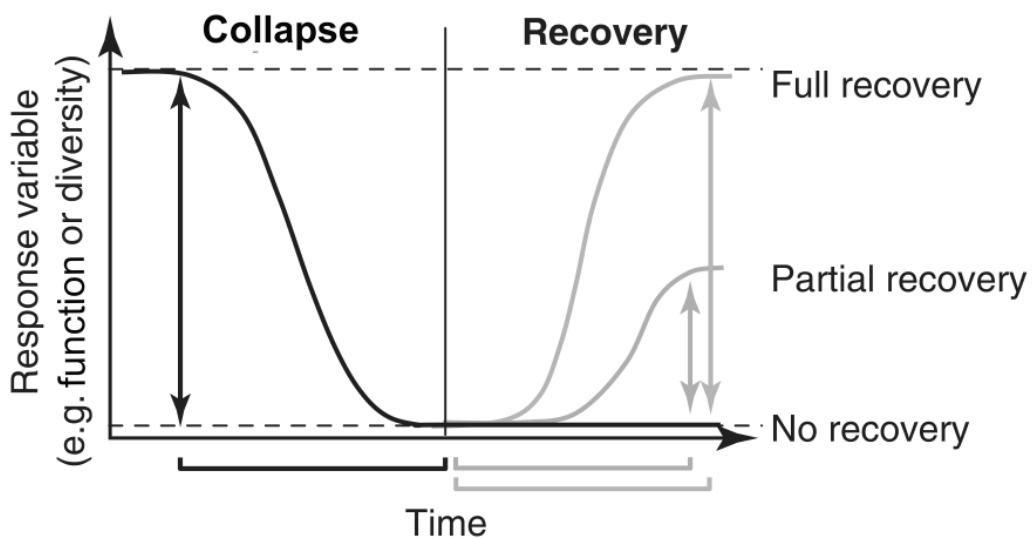
382 non-linear, as secondary extinctions cascade through the network. In other words, once
383 highly connected species begin to be removed from a network, a threshold is exceeded,
384 after which the network collapses much more rapidly. This therefore provides a mechanism
385 for an abrupt collapse of an ecosystem. However, not all studies have obtained this result;
386 for example in their study of pollination networks, Memmott et al. (2004) observed a linear
387 decline in plant species diversity with simulated species loss. Further analyses have shown
388 that the structure of ecological networks, such as connectance or nestedness, can also
389 influence their tolerance of species loss (Dunne et al., 2002; Memmott et al., 2004). The
390 position of a species in a network, for example as a network hub, also influences the risk of
391 collapse (Olesen et al., 2007). However, it should be noted that most previous research in
392 this area has focused on the use of models; very few field-based empirical studies have
393 documented the disassembly of ecological networks (Rodriguez-Cabal et al., 2013). The
394 relevance of model-based analyses to real-world situations is therefore somewhat uncertain.
395 Nonetheless, cascading secondary extinctions provide an example of how intrinsic
396 ecological processes can contribute to ecosystem collapse.

397

398 In contrast, a substantial body of empirical evidence is available for trophic cascades, where
399 loss of a species at one trophic level leads to further losses of species at other trophic levels
400 (Ripple et al., 2016). Trophic cascades have been observed throughout the world, in a
401 variety of terrestrial, freshwater, and marine systems (Estes et al., 2011). For example, in
402 some systems (such as the sea otter/kelp forest system in the North Pacific Ocean), loss of
403 a top predator can reduce plant production, by increasing populations of herbivores.
404 Conversely in other ecosystems (such as North American lakes), loss of top predators can
405 increase plant production (Estes et al., 2011). Results of a meta-analysis of 114 studies
406 suggested that the strongest cascades occurred in association with invertebrate herbivores
407 and vertebrate predators (Borer et al., 2005), whereas Shurin et al. (2002) found that the
408 effects of predators were strongest in lentic and marine benthos and weakest in marine
409 plankton and terrestrial food webs. Other factors that have been identified as contributing to
410 strong trophic cascades include high system productivity, distinct metabolic requirements of
411 organisms within a system, and high nutritional quality of primary producers (Casey et al.,
412 2017). The widespread evidence of trophic cascades suggests that loss of top predators
413 could lead to major changes in ecosystem composition, structure and function, and therefore
414 provides a potential mechanism for ecosystem collapse (Bland et al., 2018). Although trophic
415 cascades (and their 'bottom-up' analogues) could potentially lead to cascading secondary
416 extinctions, few examples have actually been recorded; most of the effects that have been
417 documented are changes in species abundance (Brodie et al., 2014).

418

419 Ecosystem collapse can also usefully be considered from the perspective of recovery
 420 (Figure 1). According to our proposed definition, to qualify as collapse, any decline in an
 421 ecosystem would need to be persistent. This implies that the processes of ecological
 422 recovery have somehow been impeded. A wide variety of different ecological processes
 423 contribute to recovery of an ecosystem following disturbance; these can vary in importance
 424 not only between different types of ecosystem, but between different examples of the same
 425 ecosystem type. Recovery is critically dependent on intrinsic factors, namely interactions
 426 between organisms and with the physical environment. Key processes can include
 427 reproduction, dispersal, establishment, growth, succession, competition, predation, nutrient
 428 dynamics, and development of critical mutualisms (Clewell and Aronson, 2013). Often, some
 429 elements of an ecosystem recover more rapidly than others, indicating that recovery does
 430 not have a single dimension. A lack of ecological recovery is most often caused by ongoing
 431 chronic pressure, such as repeated burning or herbivory, or recurrent harvesting of animals
 432 or plants (Newton, 2021). However, dynamical systems theory has again focused attention
 433 on the role of feedbacks, specifically the stabilising feedback processes that can maintain an
 434 ecosystem in a degraded state. While such feedbacks have been identified in a number of
 435 field situations (Suding, 2011), it is not clear how widespread they are. In fact, the reasons
 436 for a lack of ecological recovery are often unclear, and this impedes the development of
 437 appropriate management responses. In some situations, for example if key species have
 438 been extirpated or environmental conditions have changed, recovery may be impossible.
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 443 Figure 1. Simple schematic for illustrating the relationship between ecosystem collapse and
 444 recovery. Full recovery within a limited timescale could be considered part of the natural

445 variation of an ecosystem. Only if collapse is persistent, because recovery has been
446 impeded, might it necessitate some form of conservation management response. Note that
447 the trajectories of collapse and recovery may be more complex than those illustrated here
448 (Bergstrom et al., 2021, Bullock et al., 2011), and that lack of recovery may be associated
449 with transformation into another ecosystem type. Adapted from Lotze et al. (2011).

450

451 **Assessing the risk of ecosystem collapse**

452

453 The IUCN RLE is the only formal assessment protocol that has been explicitly designed to
454 assess the risk of ecosystem collapse. The approach closely parallels that developed for
455 species in the RLTS, with five rule-based criteria (A-E) used to assign ecosystems to a risk
456 category, ranging from Not Evaluated to Collapsed. Two of the criteria assess spatial
457 symptoms of ecosystem collapse, namely declining distribution (A) and restricted distribution
458 (B), whereas two criteria assess functional symptoms of ecosystem collapse, namely
459 environmental degradation (C) and disruption of biotic processes and interactions (D). The
460 final category (E) is based on producing quantitative estimates of the risk of collapse using
461 an appropriate modelling approach (Bland et al., 2017a). Each ecosystem type is assessed
462 against all of the RLE criteria, subject to available data. This involves application of a series
463 of thresholds, which are used to assign an ecosystem to a particular category. For example,
464 a reduction in geographic distribution over a 50 year interval (including the past, present
465 and/or future) of $\geq 80\%$ would classify an ecosystem as Critically Endangered (CR); $\geq 50\%$
466 as Endangered (EN); and $\geq 30\%$ as Vulnerable (VU) (Bland et al., 2017a). Typically the
467 assessment is undertaken in consultation with stakeholders and experts, and key threats are
468 identified, while making use of existing data and assessments available for the ecosystem.

469

470 As noted earlier, the RLE is designed for use at a range of scales, including global
471 assessments that consider all occurrences of an ecosystem type throughout the world.
472 Although RLE assessments are also possible at sub-global scales, no thresholds are
473 presented that are explicitly designed to apply at the local scale (Bland et al. 2017a). In their
474 assessment of Australian ecosystems, Bergstrom et al. (2021) described an alternative
475 approach that might be more appropriate for assessing collapse risk at local scales. The
476 approach was based on use of expert knowledge, supported by analysis of available
477 quantitative and qualitative data. This included collation of evidence of past (baseline) and
478 current states of each ecosystem spanning at least the last ~200 years, focusing on change
479 over the last 30 years. The pressures and underlying drivers responsible for collapse were
480 also identified, and characterised by their scale (time and/or space) and origin. The
481 approach involved construction of generalised trajectories, referred to as 'collapse profiles'.

482 These illustrate potential ecosystem responses to disturbance events, and provide insights
483 into the ability to withstand stress (i.e. the capacity to absorb pressure, often referred to as
484 resistance), as well as recovery potential (i.e. the likely capacity of an ecosystem to return to
485 its baseline state when the pressure is removed) (Bergstrom et al., 2021). Other methods
486 that could potentially support this approach include evaluation of the vulnerability of
487 ecosystems to environmental change, which can be achieved using spatial analysis and
488 modelling approaches (Li et al., 2018; Wilson et al., 2005).

489

490 Conservation practitioners might also value early-warning indicators of collapse, to help
491 detect it at an early stage. Much of the research in this area has focused on the use of
492 ecosystem models that represent dynamical systems theory. According to theory, there are
493 three features of such models that might provide advance warning of a transition between
494 system states (Hastings and Wysham, 2010): (i) an increase in variance around the mean
495 population size or some other measure, (ii) an increase in skew, or (iii) critical slowing down,
496 which is a decreasing rate of recovery from small perturbations. There have been relatively
497 few field-based tests of such indicators. The limited evidence available suggests that often
498 they are not effective in field situations (Dakos et al. 2015), as illustrated by cases from
499 drylands (Bestelmeyer et al., 2013) and marine ecosystems (Lindegren et al., 2012).

500 Clements and Ozgul (2018) suggest that such failures may often be attributed to the inherent
501 complexity and low signal-to-noise ratios of ecosystems. Consequently, in their review
502 Spears et al. (2017) conclude that confidence in early-warning indicators is currently too low
503 to support their wide-scale practical application. Nevertheless, there are examples where
504 indicators have been successfully tested (e.g. Wang et al., 2012), and this remains a very
505 active research area that could make a significant contribution to practical conservation
506 management in the future (Scheffer et al., 2009, 2015).

507

508 Alternatively, rather than using theory and models, early-warning indicators can potentially
509 be developed through analysis of empirical data (Boettiger and Hastings, 2013), for example
510 using multivariate analysis (Burthe et al., 2016). As illustration, Lindenmayer and Sato
511 (2018) proposed a set of early-warning indicators for Mountain Ash forests in Australia,
512 based on the results of their field observations. These include: (i) rates of decline of key
513 ecosystem structures (e.g. large, old trees), (ii) rates of decline of shorter-lived species
514 dependent on these key ecosystem structures (e.g. arboreal marsupials), and (iii) the spatial
515 extent of key ecosystem structures (e.g. stands of old growth forest). Similar results were
516 obtained by Evans et al. (2019) along gradients of forest collapse in the UK, where structural
517 variables such as basal area were found to correlate strongly with ecosystem condition.

518

519 **Identification of management responses to collapse**

520

521 To illustrate how ecosystem collapse might relate to conservation management practice, we
522 here present a decision tree in the form of a flow chart (Figure 2). This is structured around a
523 logical sequence of questions that a conservation practitioner might usefully attempt to
524 answer about ecosystem collapse, in order to identify appropriate management responses.
525 The decision tree is structured into four stages, which respectively seek to: (A) identify
526 whether collapse is occurring, (B) diagnose the cause of collapse, (C) diagnose the cause of
527 a lack of recovery, and (D) identify potential consequences of collapse. These stages are
528 considered further below. To illustrate application of the decision tree, we also provide a set
529 of case studies drawn from terrestrial, freshwater and marine environments, and from a
530 range of different geographical regions (Table 2, Appendix 1). These were contributed by
531 individual authors of this publication, who collectively comprise a multi-disciplinary research
532 team with experience of working in freshwater, marine and terrestrial ecosystems. The
533 selection of case studies was therefore based on first-hand field experience, but inevitably
534 reflects the geographic biases and research interests of our research team. The examples
535 do not therefore provide a representative sample of ecosystem collapse, but they are
536 provided here for illustrative purposes, specifically to demonstrate how collapse analysis
537 using a decision tree can be used to inform choices regarding conservation actions.

538

539 *Identification of collapse.*

540 According to our proposed definition, identification of collapse depends on detection of
541 abrupt change, which represents a significant shift from a baseline state that both exceeds
542 natural variation (Figure 3) and is persistent. Application of these criteria ideally requires
543 access to long-term monitoring or palaeoecological data describing ecosystem dynamics.
544 Availability of such data varied between case studies. For example, in the New Forest
545 National Park, UK, palaeoecological data are available for the entire Holocene period,
546 indicating that the current collapse of beech forests is unprecedented in their entire history in
547 the region, which spans more than 8,000 years (Grant and Edwards, 2006; Grant et al.
548 2009; 2014). High-resolution palaeoecological data are similarly available for some of the
549 other case studies, such as the forests of southern Chile (e.g. Heusser et al., 2006) and
550 Lake Naivasha in Kenya. In the latter case, analysis of ostracod assemblages and stable-
551 isotopes indicated that a number of major ecosystem shifts have occurred over the past
552 1650 years, resulting from hydrological dynamics and associated changes in salinity and
553 wetland variation (Van der Meeren et al., 2019). In the absence of such evidence, other case
554 studies had to rely on available monitoring data over shorter timescales, such as repeated
555 vegetation monitoring in the example of Dorset heaths, UK (Diaz et al., 2013).

556

557 A key issue is whether a transition between the different successional stages of a community
558 might constitute an example of ecosystem collapse, as illustrated by the case studies of
559 Dorset heaths, the New Forest, and grasslands in the Pyrenees, Spain and Wessex, UK. At
560 first glance, successional transitions would seem to form part of the natural variation
561 occurring within an ecosystem. However, ecosystems can often be maintained indefinitely in
562 a successional state by chronic disturbance (Fukami and Nakajima, 2011). For example,
563 disturbances such as fire, herbivory or vegetation cutting can prevent the successional
564 transition from grassland or shrubland to forest in these case study examples. Given that the
565 biota and ecological processes of grassland, shrublands and forests can be very different,
566 the persistence of these successional states might be considered as a form of ecosystem
567 collapse, even though transitions between successional states form part of the natural
568 dynamics. Conversely, succession could in some cases be considered as a cause of
569 collapse. For example, alpine grasslands in the Pyrenees are threatened by succession to
570 forest owing to a reduction in herbivory. Given that these grasslands were maintained by
571 herbivory over long timescales, their successional development into forest after removal of
572 the herbivores would constitute collapse, according to our definition.

573

574 *Cause of collapse.*

575 In the decision-tree, we identified four mechanisms that could cause ecosystem collapse,
576 namely: (A) an abrupt change in anthropogenic pressures or underlying drivers, (B) an
577 interaction between different pressures, (C) an abrupt change in the state of the ecosystem
578 with a small or smooth change in pressures, (D) a positive feedback among intrinsic factors,
579 occurring when a pressure reaches a threshold value. All of the case study examples of
580 collapse were attributable to one or more of these causes. Virtually all cases (89%) were
581 associated with multiple causes, indicating that these causes were not mutually exclusive,
582 and typically do not act in isolation. Cause (A) was identified in all case study examples,
583 whereas causes (B), (C) and (D) were identified in 83%, 11% and 44% of cases
584 respectively.

585

586 As indicated on the decision tree, identification of causal mechanism can help guide the
587 choice of conservation management interventions. For example, if interactions between
588 different pressures were identified (i.e. cause B), then management actions might usefully
589 focus on breaking these interactions. Similarly, if ecosystem change is driven by intrinsic
590 feedbacks, as posited by dynamical systems theory, then management should focus on
591 breaking the feedback loops. This has been identified as a critical issue explicitly in relation
592 to the management of coral reefs (Dudgeon et al., 2010), such as the Seychelles example

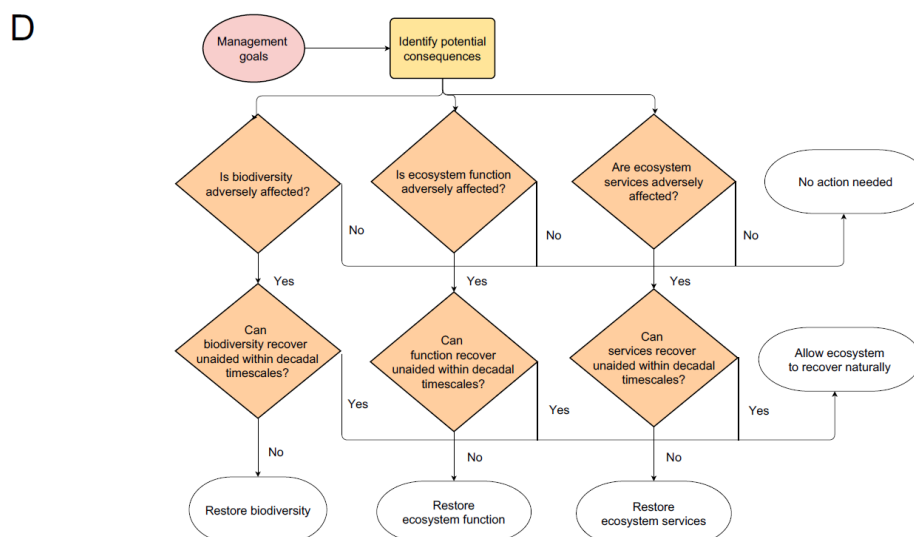
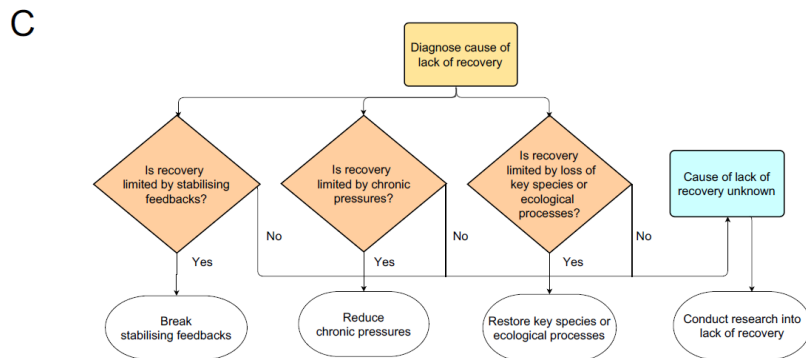
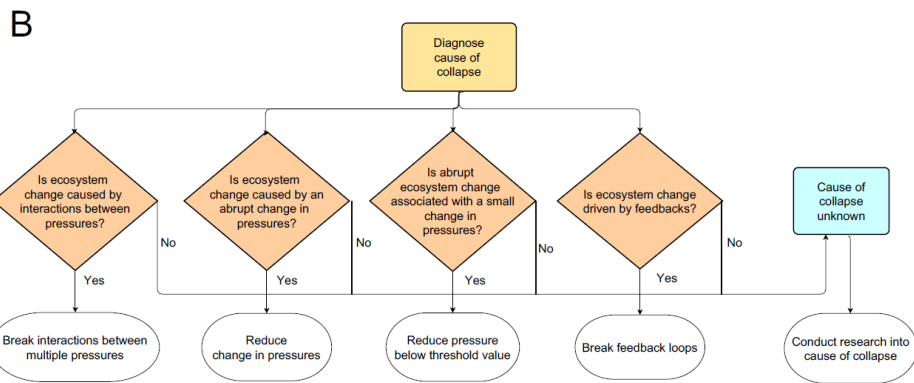
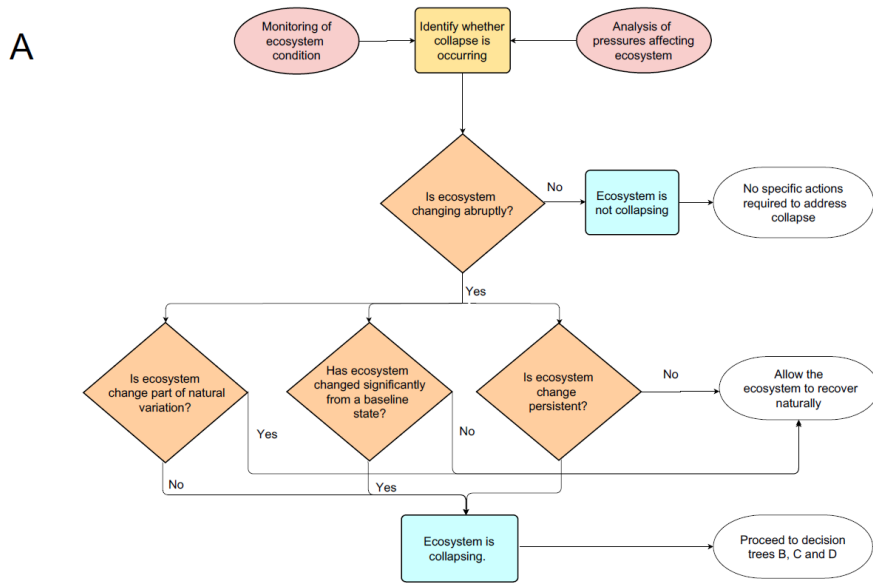
593 presented here, but is equally relevant to other ecosystem types. If collapse is driven by
594 intrinsic feedbacks, then management actions might need to focus on processes occurring
595 within the ecosystem itself, rather than solely seeking to change external conditions
596 (Dudgeon et al., 2010; Van Nes et al., 2016). This might be achieved by approaches such as
597 biomanipulation, for example by undertaking selective fish translocations to shift the fish
598 community away from dominance by zooplanktivorous species, as in the case of Barton
599 Broad, UK considered here. Further examples of such approaches in our case studies
600 include the reintroduction of large mammal herbivores on Dorset heaths, the removal of
601 macroalgal mats in Holes, Bay, UK, and the reintroduction of seed dispersal vectors in
602 Round Island, Mauritius.

603

604 However, given that an abrupt change in anthropogenic pressures (i.e. cause A) was also
605 implicated in all of the case studies considered here, management actions will also need to
606 reduce these pressures. Approaches suggested for the case studies presented here include
607 the control of fire, livestock and spread of invasive species in the case of Valdivian forests,
608 Chile; control of fire, livestock and fuelwood harvesting in the Mixteca Alta in Mexico;
609 reduction of pollution and coastal development in Derewan, Indonesia; reduction of fishing
610 pressure in Firth of Clyde, Scotland; reduction of deer browsing in Monks Wood, England;
611 and reduction of pollution, fishing, and spread of invasive species in the River Cauvery,
612 India.

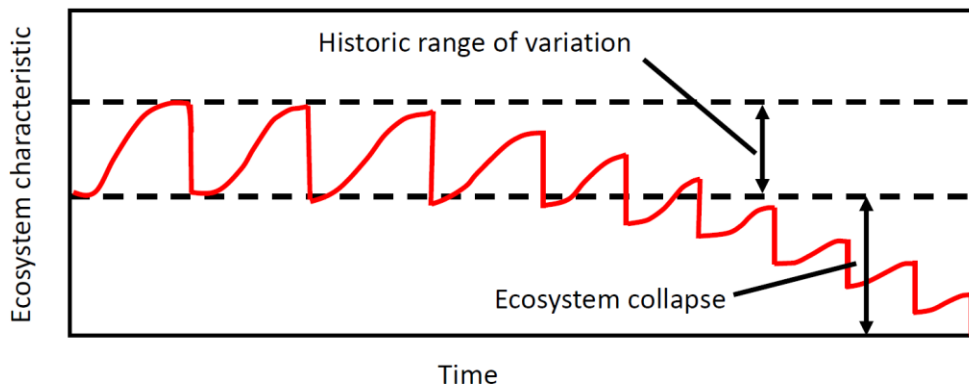
613

614 Figure 2. Decision tree for analysis of ecosystem collapse in relation to identification of
615 appropriate management responses. The decision tree is divided into four sections (A-D),
616 which are interconnected, as indicated on section A.



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Figure 3. Schematic illustration of how analysis of the historic range of variation may be used to identify the occurrence of ecosystem collapse. Adapted from McDowell et al. (2018).



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Lack of recovery.

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In the decision-tree, we identified three causal mechanisms that could account for a lack of recovery in ecosystems that have collapsed, namely: (1) the presence of ongoing chronic pressures, (2) the presence of stabilising feedbacks, or (3) the loss of key species, ecological processes or features. All of the case study examples of collapse were attributable to one or more of these causes. A majority of cases (72%) were associated with multiple causes, indicating that these causes were not mutually exclusive, and often do not act in isolation. Cause (1) was identified in all case study examples, whereas causes (2) and (3) were identified in 33% and 67% of cases respectively.

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As in the case of collapse, identification of causal mechanisms can help guide the choice of conservation management interventions designed to support ecosystem recovery. For example, if recovery is being limited by ongoing chronic disturbances (i.e. cause 1), then conservation actions might usefully focus on reducing these pressures, which could enable the ecosystem to recover naturally. Similarly, if lack of recovery is attributable to the presence of stabilising feedbacks (i.e. cause 2), which maintain an ecosystem in a degraded state, then actions should be directed to breaking these feedback loops. Conversely, if recovery is limited by loss of species, ecological processes or features (i.e. cause 3), then management should seek to replace these, for example through ecological restoration or species reintroduction activities.

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The case studies provide examples of each of these different forms of intervention. For example, actions to reduce chronic disturbance (i.e. cause 1) were proposed in all case

646 studies, including phosphate stripping of sewage outflows in the case of Barton Broad, UK;
647 reduction of herbivore densities in the New Forest and Round Island, Mauritius; reduction of
648 pollution inputs in Poole Harbour, and the Humber and Tyne estuaries, UK; and prevention
649 of hunting and land cover change in Leuser, Indonesia. Stabilising feedbacks that prevent
650 ecosystem recovery (i.e. cause 2) have previously been reported in a number of different
651 ecosystem types, notably shallow lakes, seagrass beds and coral reefs (Suding, 2011).
652 Overcoming these feedbacks can be very challenging (van der Heide et al., 2007), as
653 recognised in some of the case studies considered here. However, potential actions aimed
654 to address this causal factor include active restoration of seagrasses in the UK and
655 Indonesia at a scale sufficient to reduce turbidity of the water (Green et al., 2021; van der
656 Heide et al., 2007); biomanipulation and sediment removal in Barton Broad; reintroduction of
657 large mammal herbivores in Dorset heathland; and removal of Crown of Thorns starfish
658 (*Acanthaster planci*) and increased protection of shark populations to enable coral reef
659 recovery at St. Anne in the Seychelles. Many case studies proposed reintroduction of
660 species or ecological features and processes to address these forms of biodiversity loss (i.e.
661 cause 3), which can potentially be achieved through ecological restoration approaches.
662 Examples include reintroduction of extirpated species in Wessex chalk grasslands, UK;
663 creation of artificial reefs in the Seychelles; planting of native tree species in Mauritius, UK,
664 Mexico and Chile; introduction of fish ladders or bypass channels on the River Don, UK and
665 the River Cauvery, India; and creation of habitat corridors in the Leuser Ecosystem,
666 Sumatra.

667
668 Table 2. Summary of case studies of ecosystem collapse, based on expert judgement of the
669 authorship team and supporting scientific literature. Causal mechanisms of collapse: (A) an
670 abrupt change in anthropogenic pressures or underlying drivers, (B) an interaction between
671 different pressures, (C) an abrupt change in the state of the ecosystem with a small or
672 smooth change in pressures, (D) a positive feedback among intrinsic factors, occurring when
673 a pressure reaches a threshold value. Causal mechanisms for lack of recovery: (1) the
674 presence of ongoing chronic pressures, (2) the presence of stabilising feedbacks, (3) the
675 loss of key species, ecological processes or features. For further details of the case studies,
676 see Appendix 1.

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Name, location	Ecosystem type	Principal threats or threatening processes	Causal mechanism of collapse (A-E, see caption)	Causal mechanism for lack of recovery (1-3, see caption)
Alpine pastures, Pyrenees mountains, Spain	Alpine pasture grassland	Vegetation succession Local nitrification Climate change Overgrazing resulting in soil erosion	A, B, D	1, 2, 3
Barton Broad, River Ant catchment, Norfolk, England	Temperate lake with connection to a river	Anthropogenic eutrophication (sewage effluent and agriculture)	A, B, D	1, 2, 3
Coastal range, Valdivian ecoregion, Chile	South temperate rain forest	Land cover change Logging Fire Invasive species	A, B	1, 3
Derewan, Kalimantan Indonesia	Tropical coastal marine, seagrass beds	Herbivory	A, B, D	1, 3
Dorset Heaths, Dorset, England	Temperate shrubland	Vegetation succession Nutrient addition through agricultural fertilisation and aerial deposition. Urbanisation Climate change	A, B, D	1, 2, 3
Firth of Clyde Scotland	Temperate subtidal habitats	Overfishing	A, B	1, 2
Holes Bay, Poole, England	Temperate coastal marine	Nutrient addition from agriculture and human waste Growth of macroalgal biomass Changes in redox reactions in sediment (oxygen decline, hydrogen sulfide increase)	A, B	1
Lake Naivasha basin, Kenya	Tropical lake and its basin	Invasive alien species Land use change Human development and associated land clearance River fragmentation	A, B	1
Leuser Ecosystem, Sumatra, Indonesia	Tropical rain forest	Land cover change (agricultural expansion) Road development Mining Hunting	A	1, 3

Mixteca Alta, Oaxaca, Mexico	Tropical dry forest	Land cover change Fire Fuelwood harvesting Herbivory	A	1
Monks Wood National Nature Reserve, England	North temperate forest	Combination of disease and fungal pathogen infection Herbivory Climate change	A, B, D	1
New Forest National Park, England	North temperate forest	Climate change Fungal pathogen attack Herbivory	A, B, C	1
River Cauvery, India	Sub-tropical monsoonal river	Alien invasive species Anthropogenic alteration (hydropower dams) Overfishing Pollution Over abstraction of potable water Deforestation	A, B	1, 3
River Don, South Yorkshire, England	Temperate river	Industrial pollution Mining effluents Land contamination Sewage effluent Habitat loss Habitat fragmentation	A, B	1, 3
Round Island, Mauritius	Tropical forest, palm savanna	Grazing by introduced goats and rabbits Invasive introduced plants	A, B, D	1, 3
Humber and Tyne estuaries	Temperate coastal marine, seagrass beds	Land/river/coastal pollution Disease Physical disturbance	A, D	1, 2, 3
St. Anne Marine Park, Seychelles	Tropical coral reef	Climate change/coral bleaching Crown of thorns starfish outbreaks Loss of top predators owing to overfishing	A, B, C, D	1, 2, 3
Wessex chalklands, England	Temperate grassland	Land cover change Eutrophication Climate change Succession	A, B	1, 3

683

684

685 *Potential consequences.*

686 In the decision-tree, we identified three potential consequences of ecosystem collapse that
687 might justify a management response: an adverse impact on (i) biodiversity, (ii) on
688 ecosystem function or on (iii) the provision of ecosystem services. In fact, collapse will
689 inevitably affect all three of these ecosystem attributes to some degree, as they are
690 inextricably linked (Cardinale et al., 2012; Hooper et al., 2005). The extent to which actions
691 are undertaken to address these potential consequences will depend on the specific
692 management goals. Traditionally, conservation management has focused primarily on
693 biodiversity conservation, but recently, ecosystem services and functions have increasingly

694 become incorporated within management goals. This relates to a major recent debate, which
695 is still ongoing, regarding what the objectives of conservation management should actually
696 be. Approaches referred to as the “new conservation” promote poverty alleviation and
697 economic development over traditional approaches to biodiversity conservation, such as
698 management of endangered species and designation of protected areas (Soulé, 2013;
699 Kareiva and Marvier, 2012; Tallis et al., 2014; Sandbrook et al., 2019). Consequently, some
700 major conservation organisations have shifted their management goals towards meeting the
701 needs of people rather than solely those of wildlife (Doak et al., 2014).

702

703 Identification of appropriate management actions will vary depending on the choice of goals,
704 as illustrated in our decision tree. The relationships between different measures of
705 biodiversity (including both composition and structural attributes) and both ecosystem
706 services and functions are complex and uncertain (Balvanera et al., 2014; Cardinale et al.,
707 2012). Consequently, management actions aiming to achieve improved biodiversity will not
708 necessarily deliver improvements in ecosystem functions or services (Cortina et al., 2006).
709 The converse can also be true. For example, if the management goal is to increase carbon
710 storage of a degraded forest, this might be achieved more rapidly by planting fast-growing
711 exotic tree species than relatively slow-growing native species, even though the latter are of
712 higher biodiversity value (Newton, 2021). In some cases, such as provision of fresh water,
713 the relationships between biodiversity and ecosystem service provision can even be
714 negative (Harrison et al., 2014). As a result, there are often trade-offs between biodiversity,
715 ecosystem functions and the provision of different services (Cordingley et al., 2015a,b;
716 McShane et al., 2011).

717

718 In our case studies, management actions were primarily aimed at the goal of strengthening
719 biodiversity conservation, in every example. However, some included actions aimed at
720 improving provision of ecosystem services and associated ecosystem functions, such as
721 support for traditional farming practices and increased use of livestock in alpine grasslands,
722 Spain and the Dorset heaths, England; improved hydrological management in Lake
723 Naivasha, Kenya and River Cauvery, India; and improved water treatment in the River Don
724 and the Humber and Tyne estuaries, England.

725

726 **Discussion**

727

728 Here we have attempted to operationalise ecosystem collapse for conservation practice by
729 providing an operational definition of collapse, examining its potential causes, and evaluating
730 approaches for assessing the risk of collapse. In addition we provide a framework to identify

731 whether collapse is taking place and to inform the selection of appropriate management
732 responses, presented as a decision tree. We also explore the role of indicators for the early
733 detection of collapse and for monitoring the effectiveness of management responses. Our
734 approach is based on the following key beliefs. First, ecosystem collapse represents a
735 significant challenge to conservation practice, as abrupt changes in ecosystem structure,
736 function and composition can occur with relatively small changes in environmental
737 conditions. The consequences of these changes can be profound and far-reaching, in terms
738 of impacts on both biodiversity and human society. Second, the risks of ecosystem collapse
739 are increasing as multiple forms of environmental change, including climate change,
740 continue to intensify owing to human activity. Third, the selection of management responses
741 should be based on an understanding of the causal mechanisms responsible for abrupt
742 change in the ecosystem concerned.

743

744 Given that ecosystem collapse can be considered as an abrupt form of environmental
745 degradation, to some extent management responses will be the same as those that
746 constitute effective conservation action in a range of other contexts. A number of different
747 approaches have recently been developed aiming to increase the effectiveness of
748 conservation practice (Schwartz et al., 2017), including systematic conservation planning
749 approaches for prioritising locations for action (Margules and Pressey, 2000); evidence-
750 based approaches for informing management choices (Sutherland et al., 2004); adaptive
751 management approaches (Salafsky et al., 2002; Redford et al., 2018); and structured
752 decision-making to help choose between different management options (Gregory et al.,
753 2012). While ecosystem collapse is not explicitly considered by these approaches, they
754 could each be readily adapted to incorporate it. For example, in the generalised model of a
755 conservation project presented by Salafsky et al. (2002), an area or population is defined as
756 a conservation target, which is affected by different threats; conservation actions are then
757 taken to counter these threats. A conventional threat assessment therefore offers a useful
758 starting point for any conservation manager concerned about the risks of ecosystem
759 collapse. Such an assessment would need to be extended, if the causal mechanisms of
760 ecosystem collapse are to be identified. This would need to include identification of any
761 abrupt changes and thresholds in these threats, as well as interactions between them. This
762 would require monitoring to be conducted to provide evidence of threat dynamics; the
763 importance of undertaking such monitoring has been emphasized in development of
764 adaptive management approaches (Salafsky et al., 2002; Redford et al., 2018).

765

766 The decision tree presented here can be viewed as a contribution to the growing
767 assemblage of decision support tools designed to support implementation of the

768 conservation approaches listed above (Schwartz et al., 2017). While a range of different
769 types of tool have been developed, including multi-criteria assessment, adaptive optimisation
770 and Bayesian updating (Schwartz et al., 2017), none of these have explicitly been applied to
771 ecosystem collapse. A number of decision trees have been developed that address other
772 conservation management problems, such as using evidence in assessing a potential
773 conservation action (Salafsky et al., 2019), and for considering climate change adaptation in
774 biodiversity conservation planning (Oliver et al., 2012). In common with the current example,
775 these illustrate the value of decision trees for setting out potential choices and options in a
776 clear and logical way, thereby helping to structure the decision-making process.

777

778 Other types of decision support tool have been developed that explicitly relate to ecosystem
779 collapse. For example, Bergstrom et al. (2021) suggest using the “3As Pathway” to address
780 collapse risk, which is described as a “simple, top-level mnemonic” to support decision-
781 making. This tool combines elements of adaptive management prior to collapse
782 (‘Awareness’ and ‘Anticipation’) with ‘Action’ choices to avoid, reduce or mitigate the impact
783 of collapse. However, the “3As” tool does not consider specific management actions and
784 does not relate management options to different causes of collapse, as illustrated here.
785 Lindenmayer et al. (2016) describe a set of eleven principles to guide management of
786 forests to reduce the risk of ecosystem collapse. These highlight the need to define what
787 constitutes collapse for a given ecosystem, relative to reference conditions; the need to
788 consider multiple pressures and possible interactions between them; and the importance of
789 conducting long-term monitoring. All of these elements are also included in the framework
790 presented here. However Lindenmayer et al. (2016) also suggest that ecosystem
791 management should have well-defined “trigger points” for action, namely thresholds that
792 instigate a change in management, for example if a particular proportion of an area is
793 burned.

794

795 Assessment of ecosystem collapse using the decision tree presented here requires
796 information on whether the observed ecosystem change forms part of natural variation, and
797 whether it represents a significant departure from a baseline state. Ideally, evidence from
798 palaeoecological or long-term monitoring investigations would be available to determine
799 whether or not these conditions are met (Barnosky et al., 2017; Bennion et al., 2010). An
800 illustration of how this can be achieved in practice is provided by Bergstrom et al. (2021),
801 who used evidence obtained from a systematic literature review supported by expert
802 judgement to identify whether collapse has occurred. However no explicit guidance is given
803 in that study, nor in the RLE (Bland et al. 2017a), regarding the use of quantitative
804 approaches to detect ecosystem collapse using these forms of evidence. A number of other

805 investigations have sought to develop such quantitative approaches, involving analysis of
806 time-series data and pressure-state relationships to identify non-linearities and thresholds.
807 These can be supported by use of statistical techniques such as breakpoint analysis and
808 measures of variance, autocorrelation, similarity and recovery time (Andersen et al., 2009,
809 Bennion et al., 2010; Bestelmeyer et al., 2011; Carpenter et al., 2011; Coulson and Joyce,
810 2006; Ratajczak et al., 2018; Samhouri et al., 2017). As illustration, Watson et al. (2018)
811 used these approaches to develop a step-wise process for detecting abrupt change in a
812 coastal ecosystem, namely: (1) explore the potential for non-linear relationships in the time
813 series data, (2) determine appropriate pressure-state relationships, and (3) identify any
814 pressure-state thresholds and the location (inflection point) and strength of the thresholds.
815 Zhang et al. (2015) employed a similar process to examine collapse of ecosystem services
816 in the Lower Yangtze River Basin of China. Other quantitative methods of detecting abrupt
817 change in ecosystems in response to environmental change include modelling approaches
818 for simulating the distribution and niche limits of species (Trisos et al., 2020) and statistical
819 modelling of ecosystem vulnerability (Li et al., 2018).

820

821 Analysis of long-term data, and pressure-state relationships in particular, will also be of value
822 in diagnosing the causes of collapse (Ratajczak et al., 2018). A key issue in this context is
823 determining whether or not the ecosystem change is driven by feedbacks. Currently, much
824 of the research on abrupt ecosystem change focuses on various elements of dynamical
825 systems theory, which emphasizes the role of feedbacks as a driver of ecosystem change
826 (Scheffer et al., 2001; Scheffer and Carpenter, 2003; Scheffer, 2009; Folke et al., 2004).
827 However, the applicability of these theoretical ideas to field situations has been the subject
828 of some debate (Capon et al., 2015; Dudgeon et al., 2010; Lloyd and Veenendaal, 2016;
829 Newton, 2021; Schröder et al., 2005). For example, Hillebrand et al. (2020) surveyed 36
830 meta-analyses assessing more than 4,600 global change impacts on natural communities,
831 but found little evidence of threshold responses. Consequently, these authors concluded that
832 human-induced changes in ecosystems are typically characterized by gradual shifts as
833 pressures increase, implying little role for feedbacks. However, these results could be
834 attributable to limitations in available data, rather than to an absence of feedback
835 mechanisms.

836

837 The case studies presented here, where potential feedbacks were identified in 44% of
838 examples, are consistent with suggestions that feedback loops are widespread in nature
839 (Scheffer, 2009; Folke et al., 2004). However, it is often difficult to demonstrate that
840 feedback mechanisms – even where they can be identified – are actually responsible for
841 driving ecosystem change. For example in coral reefs, van de Leemput et al. (2016)

842 identified 19 different feedback mechanisms in the literature, relating to five different
843 ecological processes. However, these authors noted that these feedbacks have rarely been
844 quantified; there is a lack of empirical information on how these feedbacks vary in space or
845 time; and their role in causing ecosystem transitions has often not been confirmed. These
846 authors also emphasise that simply identifying a positive feedback mechanism does not by
847 itself prove that this could cause ecosystem change, because the feedback may be too weak
848 or intermittent to shift an ecosystem from one state to another (van de Leemput et al., 2016).
849 Maxwell et al. (2017) reach similar conclusions for seagrass ecosystems. This implies a
850 need for caution both when inferring the role of feedbacks, and when using this inference as
851 a basis for selecting an appropriate conservation management response. Identification of the
852 relative influence of feedbacks compared to other causes of ecosystem collapse might best
853 be achieved using an integrated approach that combines long-term monitoring,
854 experimentation, conceptual models, simulation and synthesis (Bowman et al., 2015).

855
856 Our results support suggestions that indicators of ecosystem collapse can potentially be
857 developed through analysis of empirical data and detailed knowledge of a study area
858 (Boettiger and Hastings, 2013; Burthe et al., 2016; Lindenmayer and Sato, 2018) (see
859 Appendix 1). These could potentially be used both for providing early warnings and for
860 monitoring the effectiveness of management interventions, as part of an adaptive
861 management process (Salafsky et al., 2002). Given that lack of recovery is one of the
862 characteristics of collapse, management responses could also usefully focus on supporting
863 the process of ecosystem recovery. The science and practice of ecological restoration,
864 which aims to facilitate such recovery, are now well established. Practical guidance to
865 implementing ecological restoration is now widely available (e.g. Clewell and Aronson,
866 2013), and is supported by international principles and standards (Gann et al., 2019), as well
867 as international networks of practitioners. A growing body of literature is also available
868 regarding the effectiveness of ecological restoration actions (e.g. Crouzeilles et al., 2016;
869 Meli et al., 2017; Rey Benayas et al., 2009; Huang et al., 2019), which could potentially be
870 strengthened using adaptive management approaches (Redford et al., 2018).

871
872 Despite the increasing availability of management guidance (e.g. see Appendix 2), the scale
873 and magnitude of ecosystem collapse can present immense challenges for conservation
874 practice, especially when driven by climate change. It is clear that ecosystem decline may
875 occur abruptly and with little prior warning. If monitoring indicates that collapse is occurring,
876 what should be done? While conservation practice has long been seen as a crisis discipline,
877 the scale and magnitude of the crises represented by ecosystem collapse can be
878 unprecedented, as in the case of mass bleaching events on coral reefs (Hughes et al. 2018).

879 Conservationists are beginning to consider how best to address this type of crisis situation.
880 For example, Derocher et al. (2013) explore some proactive management options for
881 conservation of polar bears, which are facing catastrophic declines in habitat owing to the
882 loss of Arctic sea ice. In this example, preplanning, consultation, and the need to coordinate
883 management responses were identified as key priorities, together with advance
884 consideration of the costs, logistical difficulties and likelihood of success of different
885 management options. This suggests that scenario planning approaches (Peterson et al.,
886 2003) might have particular value for conservation managers faced with the possibility of
887 ecosystem collapse.

888

889 Nevertheless, it is important to note that despite indications to the contrary (Bland et al.,
890 2017a; Lindenmayer et al., 2016), the consequences of ecosystem collapse may not always
891 be negative. There may be situations where managers decide not to take action, or even to
892 actively encourage collapse. This is best illustrated by the case of “novel ecosystems”,
893 namely those with assemblages of species or other characteristics that human activities
894 have created, either intentionally or inadvertently (Barnosky et al., 2017). These include
895 croplands, pasturelands, timber plantations, and land modified by human-caused erosion
896 and sedimentation, together with the novel assemblages of species that can form in
897 response to climate change (Barnosky et al., 2017; Keith et al., 2009).

898

899 Whether or not novel ecosystems represent acceptable conservation management goals
900 has proved highly controversial, particularly in the context of ecological restoration.
901 Traditionally, restoration has often focused on restoring historical assemblages of species.
902 Recognising that this is increasingly becoming untenable in a world affected by climate
903 change, a focus on creating and managing novel ecosystems has been proposed instead
904 (Hobbs et al., 2006; 2009; 2014; Higgs et al., 2018a,b). In response, concepts of novel
905 ecosystems have been accused of being ill-defined, based on faulty assumptions, and
906 driven by a “managerial mindset” that will lead to undesirable environmental outcomes, such
907 as a “domesticated Earth” (Aronson et al., 2014; Murcia et al., 2014). On the basis of the
908 definition presented here, rapid transformation into a novel ecosystem represents a form of
909 ecosystem collapse. Advocates of novel ecosystems are therefore suggesting acceptance of
910 such collapse among conservation goals. Whether or not this is deemed acceptable will
911 depend upon the specific management goals for the ecosystem in question, and the relative
912 value accorded to different management outcomes, such as conservation of native species
913 *versus* recovery of ecosystem function or provision of ecosystem services (Barnosky et al.,
914 2017). It is clear that novel ecosystems can sometimes be of significant value for biodiversity
915 conservation, such as urban gardens and grasslands with non-native species (Kennedy et

916 al., 2018). They can also make a positive contribution to conservation at the landscape scale
917 (Hobbs et al., 2014). A more nuanced approach to ecosystem collapse might therefore be
918 required in conservation assessment, policy and management, to balance its potential
919 benefits against the negative outcomes of biodiversity loss.

920

921 **References**

922

923

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1338 Appendix 1. Table of case studies of collapse.

1339 These examples were contributed by the authorship team, based on their own experience
1340 and supported by the scientific literature. All of the examples relate to the local scale at
1341 which conservation management decisions are typically made (i.e. 10-1000 ha) rather than
1342 the entire range of each ecosystem type. The management actions that are listed primarily
1343 represent suggestions for future interventions, based on the expert judgement of the
1344 authorship team. However, in some cases, these actions are recommended in the
1345 supporting literature, or have already been implemented.

1346 Appendix 2. Some potential management responses to the risk of ecosystem collapse
1347 (based on Newton, 2021).