Operationalising the concept of ecosystem collapse for conservation practice

Authors and Affiliations:

Adrian C. Newton[1*], Robert Britton[1], Kimberley Davies[1], Anita Diaz[1], Daniel J. Franklin[1], Roger Herbert[1], Ross A. Hill[1], Kathy Hodder[1], Georgia Jones[1], Amanda H. Korstjens[1], Annesia Lamb[1], Jack Olley[1], Adrian C. Pinder[1], Catherine Gutmann Roberts[1,2], Rick Stafford[1].

[1]Centre for Ecology, Environment and Sustainability, Faculty of Science and Technology, Bournemouth University, BH12 5BB, UK.

Email: anewton@bournemouth.ac.uk;

[2]Current address: School of Geography, Earth & Environmental Science, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK

*Corresponding author

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Abstract

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

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

Introduction

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).

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

Identification of appropriate conservation management interventions to reduce the risk of ecosystem collapse requires an understanding of how and why it occurs, and what the potential consequences of it might be. Development of this understanding has been limited to date, reflecting a lack of consensus regarding the scientific foundations on which the RLE is based. Specifically, Boitani et al. (2015) highlighted a number of problems with the concept of ecosystem collapse presented by Keith et al. (2013), as the definition of an ecosystem might vary dependent on scale or ecological context, and according to the specific features under consideration. Further, Boitani et al. (2015) noted that the collapse of an ecosystem is not equivalent to the extinction of a species; while the latter has a clear theoretical endpoint, the endpoints for an ecosystem can be far more ambiguous. An ecosystem undergoing degradation might exhibit a range of different endpoints, and there may be no consensus on which are desirable or undesirable (Boitani et al., 2015). Progress in developing an understanding of the mechanisms responsible for ecosystem collapse has also been limited to date. Various elements of dynamical systems theory have dominated the literature on ecosystem collapse and on related phenomena such as tipping points, critical transitions, resilience, regime shifts and alternative stable states (Andersen et al., 2009; Bland et al., 2017a, 2018; Keith et al., 2013, 2015; Scheffer, 2009). While there has been substantial theoretical development in this area, not all of these ideas are accessible in a form that can be readily used by conservation practitioners. In addition, theoretical predictions relating to ecosystem collapse have not always been supported by empirical evidence (Hillebrand et al., 2020; Newton, 2021). Consequently there is a need to understand under which situations different theoretical ideas are likely to apply, and therefore which mechanisms are likely to be responsible for causing the collapse, so that appropriate management responses can be identified.

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

Defining ecosystem collapse

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

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

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)

A transformation of identity, a loss of defining features, and a replacement by a different ecosystem type. 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.	Bland et al. (2017a)
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.	Bland et al. (2018)
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.). 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.	Keith et al. (2013)
An abrupt and undesirable change in ecosystem state.	Lindenmayer *et al*. (2016)
Major changes in ecosystem conditions [that] are either irreversible or very time- and energy-consuming to reverse.	Lindenmayer and Sato (2018)

Ecosystem collapse can be considered as the result of environmental degradation, which IPBES (2018) defines as *"the persistent decline or loss in biodiversity and ecosystem functions and services that cannot fully recover unaided within decadal timescales"*. This describes a state that is persistent, because ecological recovery has been impeded or impaired. We suggest that this provides a basis for developing a working definition of an ecosystem that has collapsed, although 'land' should be extended to include 'water', so that marine and freshwater ecosystems are incorporated. Further, following Lindenmayer et al. (2016) we propose that the term 'ecosystem collapse' should be limited to those ecosystems that have been degraded rapidly, and that have undergone abrupt change. This is consistent with standard dictionary definitions of the word "collapse", which generally refer to a relatively sudden or abrupt event. Given that biodiversity, ecosystem function and services do not necessarily covary (Hansson et al., 2005), a collapsed ecosystem could therefore be defined as follows:

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

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

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

We note that some previous definitions of ecosystem collapse (Table 1) refer to the amount of ecosystem change that has occurred relative to a baseline value (Bergstrom et al., 2021) or to the “natural range of spatial and temporal variability” (Bland et al., 2017a). We accept that comparison of ecosystem characteristics with some form of reference value will likely be essential to establish whether or not collapse has occurred, an issue that we explore further below. However, we have omitted direct reference to these approaches in our proposed definition, as the results obtained are likely to be highly context specific. This is a point made forcefully by Boitani et al. (2015) in their critique of the definition offered by Keith et al. (2013) (Table 1). While noting that it is difficult to quantify the natural range of temporal variability of an ecosystem, Boitani et al. (2015) indicate that collapse will often need to be defined separately for each ecosystem considered, using a variety of different attributes and threshold values. This is because ecosystems are dynamic systems that change in time and space; both the structure and composition of ecosystems can change rapidly, together with the ecosystem processes with which they are associated. Ecosystem properties can sometimes change substantially with small variations in the biotic component, while in other situations, the converse may be true (Boitani et al., 2015). The fact that ecosystem collapse is context-specific limits the scope for developing standardised protocols that could be used to compare ecosystems at large spatial scales, as proposed by the RLE (Boitani et al., 2015). However, this does not prevent the concept of ecosystem collapse from being usefully applied at the local scale, so long as local context is taken into account.

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

As a consequence of such contrasting views, Boitani et al. (2015) suggest that there is no means by which ecosystems can be consistently defined for conservation management. However, Post et al. (2007) provide valuable guidance for operationalising the ecosystem concept, by highlighting the overriding importance of understanding ecosystem boundaries, which may be either structural or functional and either well-defined or diffuse. Specifically, the boundaries of an ecosystem in time and space need to relate to the ecological features or processes being studied, which may show little correspondence with physical boundaries. Here we follow Bland et al. (2017a) in supporting the use of the proxies for ecosystems that are widely used in conservation assessments, such as ecological communities, habitats, biotopes, and vegetation types. As these can usually be mapped, they can be readily used as a basis of developing conservation management plans. However, it should be remembered that such "tangible" boundaries do not always coincide with the ecological processes of interest, highlighting the need to use them with care (Post et al., 2007).

Causes of ecosystem collapse

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

To date, there has been no systematic assessment of the association between different threats and the risk of ecosystem collapse; this clearly merits further research. On the face of it, those threats associated with ecosystem conversion, as identified by Salafsky et al. (2008), would be more likely to cause ecosystem collapse than those associated with degradation or indirect damage to an ecosystem. However, this difference could simply reflect the different timescales involved; while ecosystem conversion could be very abrupt, continuous degradation over a longer period could result in a similar outcome. Newton (2021) reviewed empirical evidence of ecosystem collapse in relation to available theory, and reached the following conclusions regarding its potential causes:

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

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

The relative frequency of these different mechanisms of ecosystem collapse is currently unknown, as it has not been investigated systematically. However, much of the recent literature relating to transitions between ecosystem states has focused on application of different elements of dynamical systems theory, particularly bifurcation theory, catastrophe theory and theories of alternative stable states (Petraitis, 2013; Scheffer, 2009). Some authors have explicitly linked ecosystem collapse to these theoretical ideas (e.g. Keith et al., 2015; Lindenmayer et al., 2016). Although different states of ecosystems can be widely observed in nature, it is not always clear whether these correspond to the alternative stable states postulated by theory (Newton, 2021; Petraitis, 2013). In fact, this suggestion has been challenged in a variety of different ecosystem types, for example in coral reefs (Dudgeon et al., 2010), freshwater ecosystems (Capon et al., 2015) and savannas (Lloyd and Veenendaal, 2016), the very same ecosystems that are most often cited in support of the theory (Scheffer, 2009). This is partly because key assumptions of the theory have often not been met in field situations (e.g. Bruno et al., 2009; Möllmann and Diekmann, 2012; Capon et al., 2015; Newton and Cantarello, 2015). For example, transitions between ecosystem states are often associated with a change in environmental conditions, which is not consistent with theory relating to alternative stable states (Petraitis and Dudgeon, 2004; Dudgeon et al., 2010). Furthermore, according to theory, such transitions are driven by feedbacks among intrinsic ecological processes rather than by extrinsic factors acting in isolation. These theoretical ideas are therefore not relevant to situations where ecosystem collapse has been entirely caused by extrinsic factors, such as those examples involving complete and direct ecosystem conversion (Newton, 2021). As indicated earlier, this currently comprises the principal form of ecosystem collapse.

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

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

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

Ecosystem collapse can also usefully be considered in terms of the impact of threatening processes on interactions among species, and specifically the structure and dynamics of ecological networks. Based on a literature review, Bascompte and Stouffer (2009) found that ecological networks are relatively robust to the loss of the most specialised species, but are more vulnerable to the loss of more generalised species; and that network collapse can be non-linear, as secondary extinctions cascade through the network. In other words, once highly connected species begin to be removed from a network, a threshold is exceeded, after which the network collapses much more rapidly. This therefore provides a mechanism for an abrupt collapse of an ecosystem. However, not all studies have obtained this result; for example in their study of pollination networks, Memmott et al. (2004) observed a linear decline in plant species diversity with simulated species loss. Further analyses have shown that the structure of ecological networks, such as connectance or nestedness, can also influence their tolerance of species loss (Dunne et al., 2002; Memmott et al., 2004). The position of a species in a network, for example as a network hub, also influences the risk of collapse (Olesen et al., 2007). However, it should be noted that most previous research in this area has focused on the use of models; very few field-based empirical studies have documented the disassembly of ecological networks (Rodriguez-Cabal et al., 2013). The relevance of model-based analyses to real-world situations is therefore somewhat uncertain. Nonetheless, cascading secondary extinctions provide an example of how intrinsic ecological processes can contribute to ecosystem collapse.

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

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

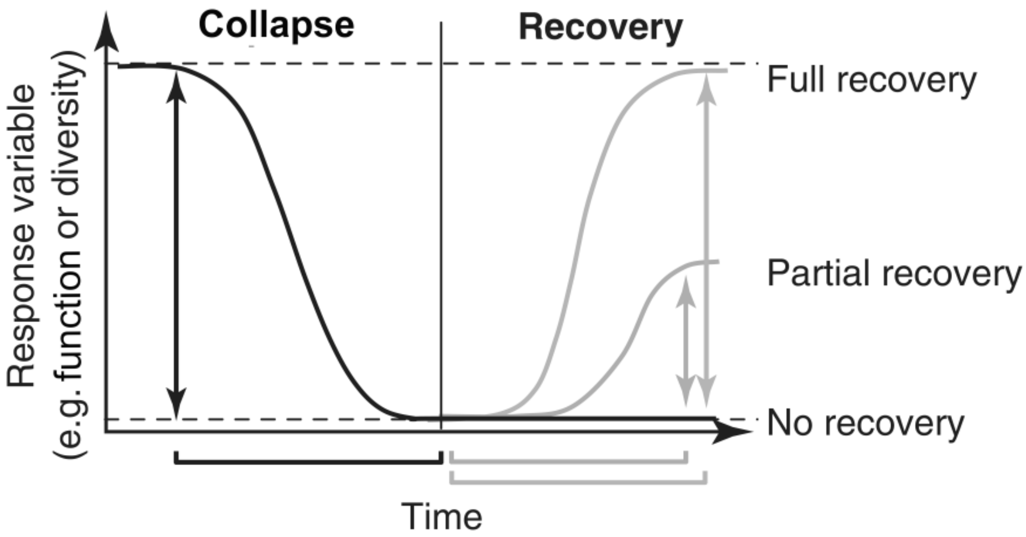


Figure 1. Simple schematic for illustrating the relationship between ecosystem collapse and recovery. Full recovery within a limited timescale could be considered part of the natural

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

Assessing the risk of ecosystem collapse

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

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

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

Conservation practitioners might also value early-warning indicators of collapse, to help detect it at an early stage. Much of the research in this area has focused on the use of ecosystem models that represent dynamical systems theory. According to theory, there are three features of such models that might provide advance warning of a transition between system states (Hastings and Wysham, 2010): (i) an increase in variance around the mean population size or some other measure, (ii) an increase in skew, or (iii) critical slowing down, which is a decreasing rate of recovery from small perturbations. There have been relatively few field-based tests of such indicators. The limited evidence available suggests that often they are not effective in field situations (Dakos et al. 2015), as illustrated by cases from drylands (Bestelmeyer et al., 2013) and marine ecosystems (Lindegren et al., 2012). Clements and Ozgul (2018) suggest that such failures may often be attributed to the inherent complexity and low signal-to-noise ratios of ecosystems. Consequently, in their review Spears et al. (2017) conclude that confidence in early-warning indicators is currently too low to support their wide-scale practical application. Nevertheless, there are examples where indicators have been successfully tested (e.g. Wang et al., 2012), and this remains a very active research area that could make a significant contribution to practical conservation management in the future (Scheffer et al., 2009, 2015).

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

Identification of management responses to collapse

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

Identification of collapse.

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

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

Cause of collapse.

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

As indicated on the decision tree, identification of causal mechanism can help guide the choice of conservation management interventions. For example, if interactions between different pressures were identified (i.e. cause B), then management actions might usefully focus on breaking these interactions. Similarly, if ecosystem change is driven by intrinsic feedbacks, as posited by dynamical systems theory, then management should focus on breaking the feedback loops. This has been identified as a critical issue explicitly in relation to the management of coral reefs (Dudgeon et al., 2010), such as the Seychelles example presented here, but is equally relevant to other ecosystem types. If collapse is driven by intrinsic feedbacks, then management actions might need to focus on processes occurring within the ecosystem itself, rather than solely seeking to change external conditions (Dudgeon et al., 2010; Van Nes et al., 2016). This might be achieved by approaches such as biomanipulation, for example by undertaking selective fish translocations to shift the fish community away from dominance by zooplanktivorous species, as in the case of Barton Broad, UK considered here. Further examples of such approaches in our case studies include the reintroduction of large mammal herbivores on Dorset heaths, the removal of macroalgal mats in Holes, Bay, UK, and the reintroduction of seed dispersal vectors in Round Island, Mauritius.

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

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

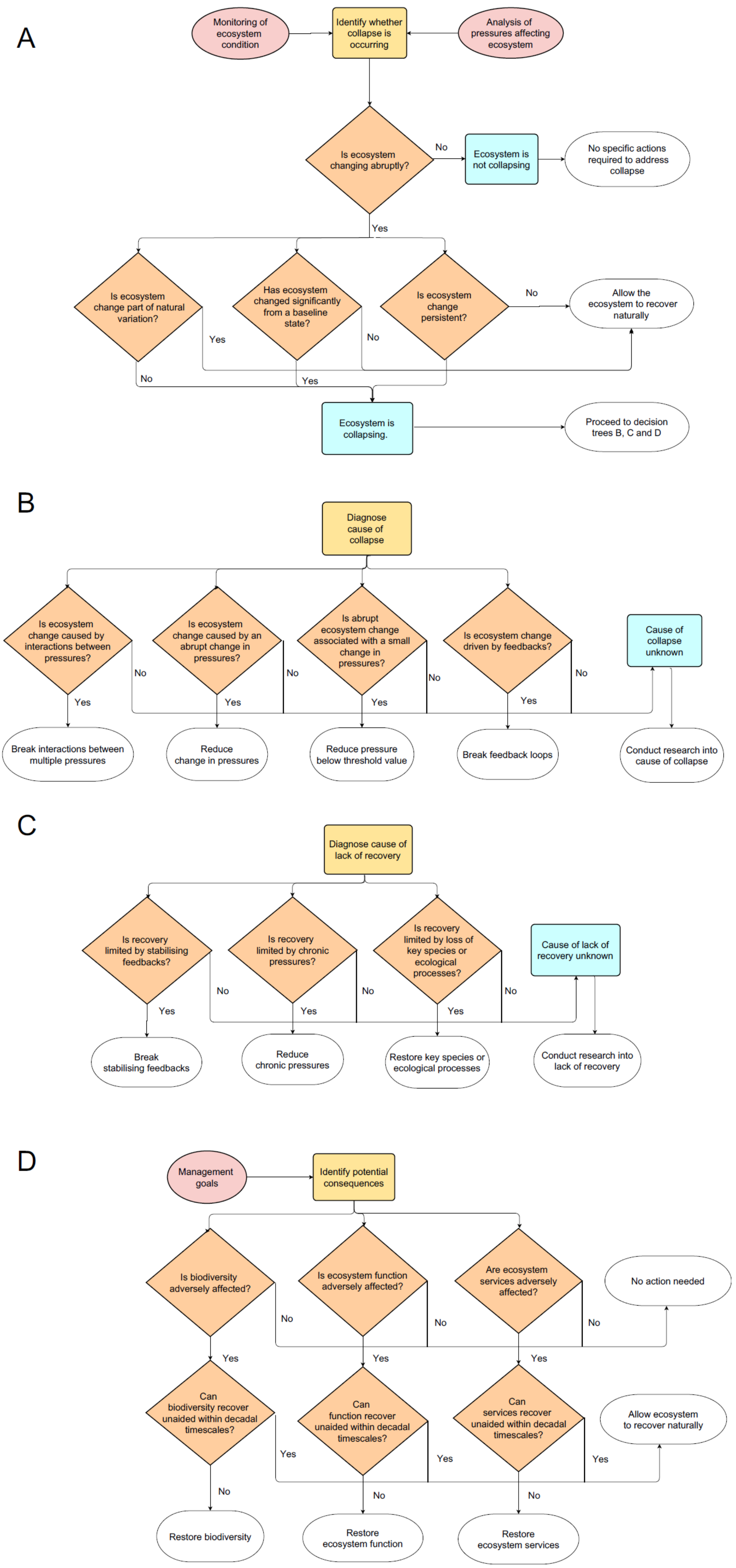
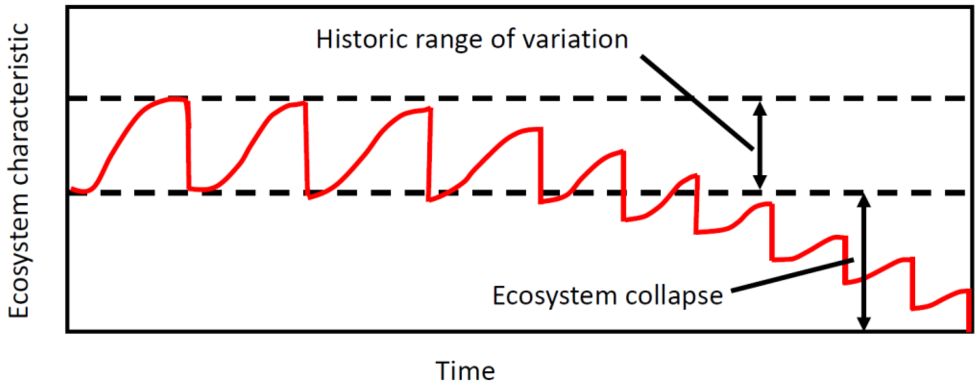

A
Monitoring of ecosystem condition
Identify whether collapse is occurring
Analysis of pressures affecting ecosystem
Is ecosystem changing abruptly?
No
Ecosystem is not collapsing
No specific actions required to address collapse
Yes
Is ecosystem change part of natural variation?
Has ecosystem changed significantly from a baseline state?
Is ecosystem change persistent?
No
Allow the ecosystem to recover naturally
Yes
No
No
Yes
Ecosystem is collapsing.
Proceed to decision trees B, C and D
B
Diagnose cause of collapse
Is ecosystem change caused by interactions between pressures?
Is ecosystem change caused by an abrupt change in pressures?
Is abrupt ecosystem change associated with a small change in pressures?
Is ecosystem change driven by feedbacks?
Cause of collapse unknown
No
No
No
No
Yes
Yes
Yes
Yes
Break interactions between multiple pressures
Reduce change in pressures
Reduce pressure below threshold value
Break feedback loops
Conduct research into cause of collapse
C
Diagnose cause of lack of recovery
Is recovery limited by stabilising feedbacks?
Is recovery limited by chronic pressures?
Is recovery limited by loss of key species or ecological processes?
Cause of lack of recovery unknown
No
No
No
Yes
Yes
Yes
Break stabilising feedbacks
Reduce chronic pressures
Restore key species or ecological processes
Conduct research into lack of recovery
D
Management goals
Identify potential consequences
Is biodiversity adversely affected?
Is ecosystem function adversely affected?
Are ecosystem services adversely affected?
No action needed
No
No
No
Yes
Yes
Yes
Can biodiversity recover unaided within decadal timescales?
Can function recover unaided within decadal timescales?
Can services recover unaided within decadal timescales?
Allow ecosystem to recover naturally
Yes
Yes
Yes
No
No
No
Restore biodiversity
Restore ecosystem function
Restore ecosystem services

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).



Lack of recovery.

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.

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.

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

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

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, Valdividian 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

Potential consequences.

In the decision-tree, we identified three potential consequences of ecosystem collapse that might justify a management response: an adverse impact on (i) biodiversity, (ii) on ecosystem function or on (iii) the provision of ecosystem services. In fact, collapse will inevitably affect all three of these ecosystem attributes to some degree, as they are inextricably linked (Cardinale et al., 2012; Hooper et al., 2005). The extent to which actions are undertaken to address these potential consequences will depend on the specific management goals. Traditionally, conservation management has focused primarily on biodiversity conservation, but recently, ecosystem services and functions have increasingly become incorporated within management goals. This relates to a major recent debate, which is still ongoing, regarding what the objectives of conservation management should actually be. Approaches referred to as the “new conservation” promote poverty alleviation and economic development over traditional approaches to biodiversity conservation, such as management of endangered species and designation of protected areas (Soulé, 2013; Kareiva and Marvier, 2012; Tallis et al., 2014; Sandbrook et al., 2019). Consequently, some major conservation organisations have shifted their management goals towards meeting the needs of people rather than solely those of wildlife (Doak et al., 2014).

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

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

Discussion

Here we have attempted to operationalise ecosystem collapse for conservation practice by providing an operational definition of collapse, examining its potential causes, and evaluating approaches for assessing the risk of collapse. In addition we provide a framework to identify whether collapse is taking place and to inform the selection of appropriate management responses, presented as a decision tree. We also explore the role of indicators for the early detection of collapse and for monitoring the effectiveness of management responses. Our approach is based on the following key beliefs. First, ecosystem collapse represents a significant challenge to conservation practice, as abrupt changes in ecosystem structure, function and composition can occur with relatively small changes in environmental conditions. The consequences of these changes can be profound and far-reaching, in terms of impacts on both biodiversity and human society. Second, the risks of ecosystem collapse are increasing as multiple forms of environmental change, including climate change, continue to intensify owing to human activity. Third, the selection of management responses should be based on an understanding of the causal mechanisms responsible for abrupt change in the ecosystem concerned.

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

The decision tree presented here can be viewed as a contribution to the growing assemblage of decision support tools designed to support implementation of the conservation approaches listed above (Schwartz et al., 2017). While a range of different types of tool have been developed, including multi-criteria assessment, adaptive optimisation and Bayesian updating (Schwartz et al., 2017), none of these have explicitly been applied to ecosystem collapse. A number of decision trees have been developed that address other conservation management problems, such as using evidence in assessing a potential conservation action (Salafsky et al., 2019), and for considering climate change adaptation in biodiversity conservation planning (Oliver et al., 2012). In common with the current example, these illustrate the value of decision trees for setting out potential choices and options in a clear and logical way, thereby helping to structure the decision-making process.

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

Assessment of ecosystem collapse using the decision tree presented here requires information on whether the observed ecosystem change forms part of natural variation, and whether it represents a significant departure from a baseline state. Ideally, evidence from palaeoecological or long-term monitoring investigations would be available to determine whether or not these conditions are met (Barnosky et al., 2017; Bennion et al., 2010). An illustration of how this can be achieved in practice is provided by Bergstrom et al. (2021), who used evidence obtained from a systematic literature review supported by expert judgement to identify whether collapse has occurred. However no explicit guidance is given in that study, nor in the RLE (Bland et al. 2017a), regarding the use of quantitative approaches to detect ecosystem collapse using these forms of evidence. A number of other investigations have sought to develop such quantitative approaches, involving analysis of time-series data and pressure-state relationships to identify non-linearities and thresholds. These can be supported by use of statistical techniques such as breakpoint analysis and measures of variance, autocorrelation, similarity and recovery time (Andersen et al., 2009, Bennion et al., 2010; Bestelmeyer et al., 2011; Carpenter et al., 2011; Coulson and Joyce, 2006; Ratajczak et al., 2018; Samhouri et al., 2017). As illustration, Watson et al. (2018) used these approaches to develop a step-wise process for detecting abrupt change in a coastal ecosystem, namely: (1) explore the potential for non-linear relationships in the time series data, (2) determine appropriate pressure-state relationships, and (3) identify any pressure-state thresholds and the location (inflection point) and strength of the thresholds. Zhang et al. (2015) employed a similar process to examine collapse of ecosystem services in the Lower Yangtze River Basin of China. Other quantitative methods of detecting abrupt change in ecosystems in response to environmental change include modelling approaches for simulating the distribution and niche limits of species (Trisos et al., 2020) and statistical modelling of ecosystem vulnerability (Li et al., 2018).

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

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

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

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

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

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

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

Whether or not novel ecosystems represent acceptable conservation management goals has proved highly controversial, particularly in the context of ecological restoration. Traditionally, restoration has often focused on restoring historical assemblages of species. Recognising that this is increasingly becoming untenable in a world affected by climate change, a focus on creating and managing novel ecosystems has been proposed instead (Hobbs et al., 2006; 2009; 2014; Higgs et al., 2018a,b). In response, concepts of novel ecosystems have been accused of being ill-defined, based on faulty assumptions, and driven by a “managerial mindset” that will lead to undesirable environmental outcomes, such as a “domesticated Earth” (Aronson et al., 2014; Murcia et al., 2014). On the basis of the definition presented here, rapid transformation into a novel ecosystem represents a form of ecosystem collapse. Advocates of novel ecosystems are therefore suggesting acceptance of such collapse among conservation goals. Whether or not this is deemed acceptable will depend upon the specific management goals for the ecosystem in question, and the relative value accorded to different management outcomes, such as conservation of native species *versus* recovery of ecosystem function or provision of ecosystem services (Barnosky et al., 2017). It is clear that novel ecosystems can sometimes be of significant value for biodiversity conservation, such as urban gardens and grasslands with non-native species (Kennedy et al., 2018). They can also make a positive contribution to conservation at the landscape scale (Hobbs et al., 2014). A more nuanced approach to ecosystem collapse might therefore be required in conservation assessment, policy and management, to balance its potential benefits against the negative outcomes of biodiversity loss.

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Appendix 1. Table of case studies of collapse.

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

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